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False-positive occupancy models produce less-biased occupancy estimates for a rare and elusive bat species

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Confirming presence and distribution of a species is necessary for effective conservation. However, obtaining robust occupancy estimates and confidently identifying factors important to occupancy may be difficult for rare and elusive species. Further, in surveys to assess presence, false-positive detections bias results; however, false-positive occupancy models can resolve this bias and, thus, better support conservation. We assessed the performance of false-positive versus standard occupancy models and important factors predicting presence for a low-density bat population in the southern Appalachian Mountains. From May to August 2013–2015, we surveyed 35 sites for northern long-eared bats (*Myotis septentrionalis*) using both mist-net and acoustic methods. We compared AIC_c values for 13 standard occupancy models and 13 corresponding false-positive occupancy models. In our model comparison, false-positive models received more support, while none of the standard occupancy models were plausible. False-positive occupancy models produced a wider range of probability of occupancy estimates (0.004–0.998) and lower mean occupancy estimate (0.62) than standard models (0.482–0.970, mean = 0.86). Weighted parameter estimates for important predictors in two plausible false-positive occupancy models indicated the probability of occupancy for northern long-eared bats was higher at less-rugged, lower-elevation sites. In contrast, there was more ambiguity regarding the most plausible standard occupancy models and important predictors of occupancy from standard models. Due to low capture rates and the uncertainty of acoustic identifications, we recommend coupling a certain method with uncertain methods when surveying rare and elusive bat species. Applying false-positive occupancy models to our data yielded less-biased site-specific occupancy estimates and informative predictors, and, hence, more reliable predictions to inform conservation management plans.

Key words: acoustic surveys, bats, capture surveys, *Myotis septentrionalis*, occupancy modeling

It is crucial to resource managers to be able to accurately and efficiently monitor animal populations, but it can be difficult to confirm presence for rare and elusive species (McDonald 2004). While mark–recapture methods are ideal for estimating abundance, this approach may be impractical for rare species due to low recapture rates, as well as time and cost constraints. Cryptic species may go undetected even when present (MacKenzie et al. 2004) and the probability of detection will vary depending on the survey method used (e.g., Bailey et al. 2013). For example, when surveying for the red fox (*Vulpes vulpes*), Vine et al. (2009) concluded that the efficacy of four different methods varied seasonally; these authors advised the appropriate method should be selected with consideration for time of year and species' biology. Likewise, detection probability varies with the method used to survey rare species, such as the northern flying squirrel (*Glaucomys sabrinus*—Diggins et al. 2016).

Surveying for bats, which tend to be cryptic (Weller 2007) and increasingly uncommon (O'Shea et al. 2016), presents particular challenges. In eastern North America, *Myotis* bats are small (4–14 g—Reid 2006), typically brown or gray, and use high-frequency echolocation calls (around 40 kHz) that attenuate rapidly (Jones 1999). During the summer, eastern *Myotis* mainly roost in relatively small colonies (typically 10–80 individuals), often hidden in cavities or crevices of dead trees (Barclay and Kurta 2007). Adding to the challenge of detecting these elusive bats, *Myotis* populations are in steep decline in eastern North America, primarily due to disease, habitat loss, and other anthropogenic factors (O'Shea et al. 2016). For example, the fungal disease white-nose syndrome (WNS) has decimated *Myotis* bat populations. Data from over 400 winter hibernacula documented local extinctions for four *Myotis* species, with local extinctions for northern long-eared bats (*Myotis septentrionalis*) at 69% of 468 caves surveyed (Frick et al. 2015). In the study described herein, we examined summer occupancy rates for the northern long-eared bat, now designated as federally threatened due to declines from WNS (U.S. Fish and Wildlife Service 2016).

There are two primary methods used to survey for *Myotis* bats in summer: mist-net surveys and acoustic surveys. While each has limitations, combining methods alleviates some known issues (Robbins et al. 2008). Biologists conduct mist-net surveys in suitable habitat and count on the certain identification of a captured bat to assess site-specific presence or probable absence of eastern *Myotis* (U.S. Fish and Wildlife Service 2017). However, capture surveys may be less effective for documenting presence for species that exist in dispersed, low-density populations. For example, Murray et al. (1999) documented *Myotis* presence during 43% of mist-net surveys and 91% of acoustic surveys in the midwestern United States, suggesting low detection probabilities during mist-net surveys. Acoustic surveys, which are noninvasive, require less labor per site than mist netting, and allow sampling of sites that are impractical for capture surveys (e.g., open areas), are also recommended for detecting rare and cryptic *Myotis* bats (U.S. Fish and Wildlife Service 2017). Using acoustic detectors, we can record the unique echolocation calls of bats, some of which are specific to the genus or species level; yet, we lack the identification certainty associated with mist-net captures (Barclay 1999; Britzke et al. 2013; Russo et al. 2018). For example, for three eastern *Myotis*—*M. sodalis*, *M. lucifugus*, and *M. septentrionalis*—there is significant overlap in the characteristic frequency and duration of their echolocation calls (e.g., Broders et al. 2004; Szewczak and Harris 2013). Automated identification software programs allow consistent, unbiased measurements of call parameters and decrease analysis time, but misidentifications still occur (Lemen et al. 2015; Russo and Voigt 2016). Supplementing mist-netting methods with acoustic methods could enhance the sensitivity of presence surveys, but due to limitations in the accuracy of identification, acoustic surveys should not simply replace mist-net captures (O'Farrell and Gannon 1999; Robbins et al. 2008; Romeling et al. 2012).

Along with survey methods with high detection probabilities, it is important to use appropriate analytical tools that account for the difficulty of detecting rare and elusive species. Sampling species to estimate detection and occupancy probabilities yields informative survey data (e.g., identifying factors affecting detection and presence), while also accommodating for multiple sampling methods and protocols (MacKenzie et al. 2004; Bailey et al. 2013). Multiple studies have applied occupancy models to estimate probability of detection and probability of presence for bats (Yates and Muzika 2006; Gorresen et al. 2008; Weller 2008; Hein et al. 2009; Kaiser and O'Keefe 2015). Such models generate occupancy estimates that include a probability of detection parameter, which accounts for false negatives (i.e., not detecting a species when it is present—MacKenzie et al. 2017). Standard occupancy models incorporate site-history data (number of surveys and detections) and probability of detection parameters for calculating probability of occupancy. However, standard models assume that all methods have complete certainty, e.g., detection from a captured bat in the hand is equal to that of a recorded echolocation call, and do not account for misidentifications that lead to false-positive detections. Although accounting for false negatives can lessen biases, using a method prone to false positives (e.g., acoustic recordings of bats—Kaiser and O'Keefe 2015) without accounting for uncertainties might yield biased occupancy estimates (Miller et al. 2011).

A new approach has emerged that accounts for false positives in occupancy models; this approach allows us to combine mist-net and acoustic survey results, accounting for the uncertainty in acoustic identification. Building on an idea first presented by Royle and Link (2006), Miller et al. (2011) devised a method to improve occupancy estimates when some positive detections are actually false positives. Unlike standard models, false-positive occupancy models include a parameter that accounts for the probability of incorrectly detecting the species at an unoccupied site. Miller et al. (2013) applied false-positive occupancy methods to a multi-season wolf study where radiocollared gray wolves (*Canis lupus*) were considered certain detections and hunter surveys with potential for misidentifications were considered uncertain detections. Clement et al. (2014) used false-positive occupancy models in a single-season study on little brown bats (*M. lucifugus*) in Oregon; here, mist-net captures were certain detections, while acoustic surveys yielded uncertain detections. Clement et al. (2014) recommended the use of false-positive models over standard models for bat surveys, as these models provide more robust occupancy estimates. Early efforts to apply this method have demonstrated that we can generate more accurate occupancy estimates by treating certain and uncertain detections differently in the modeling process. However, the single-season study conducted by Clement et al. (2014) was with a relatively healthy population of little brown bats in Washington and Oregon that had not been impacted by WNS.

We assessed the performance of false-positive occupancy models with a low-density *Myotis* population in the southern Appalachian Mountains. Evidence of WNS was discovered in this region during winter 2008–2009 (Samoray 2011; Ford et al. 2012; Powers et al. 2015). Subsequently, winter captures of northern long-eared bats decreased by 52% in northeastern Tennessee (Bernard and McCracken 2017) and summer captures declined by 41% in West Virginia (Ford et al. 2012). We used mist-net and acoustic survey data collected in 2013–2015 to compare the efficacy of standard and false-positive occupancy models for predicting northern long-eared bat presence across a seven-county area. Our main objective was to assess which models (standard or false positive) produced the most plausible northern long-eared bat occupancy estimates. We also aimed to determine, based on our plausible models, what parameters were important for detecting and predicting occupancy by northern long-eared bats.

Materials and Methods

Study area.—Our study was conducted in the northern districts of the Cherokee National Forest (NCNF) in northeastern Tennessee. The 140,350 ha of the NCNF is encompassed within the southern Appalachian Mountains and ranges from 457 to 1,487 m a.s.l. in elevation. The major forest type was chestnut oak (*Quercus montana*), with oak-yellow pine (*Pinus* subgenus *Diploxylon*) and poplar (*Liriodendron*)-oak as secondary forest types (Southeast Gap Analysis Project 2010). From May to August 2013–2015, monthly mean temperatures ranged from 16°C to 23°C and monthly mean rainfall accumulation ranged from 81 to 263 mm (monthly mean 129 mm); June and July 2013 were the rainiest months, with mean accumulations of 205 and 263 mm, respectively, across multiple weather stations (see "Environmental data"—National Ocean and Atmospheric Administration 2016a, 2016b).

Site selection.—We selected survey sites that were on gravel roads and under a closed forest canopy. We used tools in ArcMap (v10.3.1—Esri 2015) to select roads ≤ 100 m from perennial water (stream or pond, based on demonstrated success for O'Keefe and Loeb 2017), using a road layer from the U.S. Forest Service (excluding sections that were U.S. or state routes, paved, or private roads; A. Bailey, U.S. Forest Service, Cleveland, Tennessee, pers. comm.) and a water layer from the National Hydrography Dataset (U.S. Geological Survey Hydrography 2013). For locations that met the initial criteria, we assessed roads in the field for accessibility, safety, and to affirm that all sites were comparable in forest structure, with closed-canopy corridors. We assessed 100 locations, and after identifying 51 suitable sites, we divided the NCNF into four sections and used a random number generator to select 9–11 sites to survey within each of the sections. For our occupancy analyses, we used 35 sites (Fig. 1) that met the minimum criteria for number of surveys (i.e., both mist-net and acoustic surveys in at least two of the three summers). Although it is possible to create occupancy models using data for sites where only one survey method was used, for our analysis all sites were surveyed with two methods.

Mist-net surveys.—We used mist nets to survey 35 sites (Fig. 1) from May to August 2013–2015, with each site netted a minimum of two nights during the 3 years (total of 74 survey nights). Following the standard Indiana bat (*Myotis sodalis*) survey protocol (U.S. Fish and Wildlife Service 2017), we netted each site for 5 h (21:00–02:00 EDT) per night, using two to five single- or double-high mist nets (2–12 m widths; Avinet, Inc., Dryden, New York) set across roads, trails, or along pond edges. In the event of hazardous weather resulting in partial

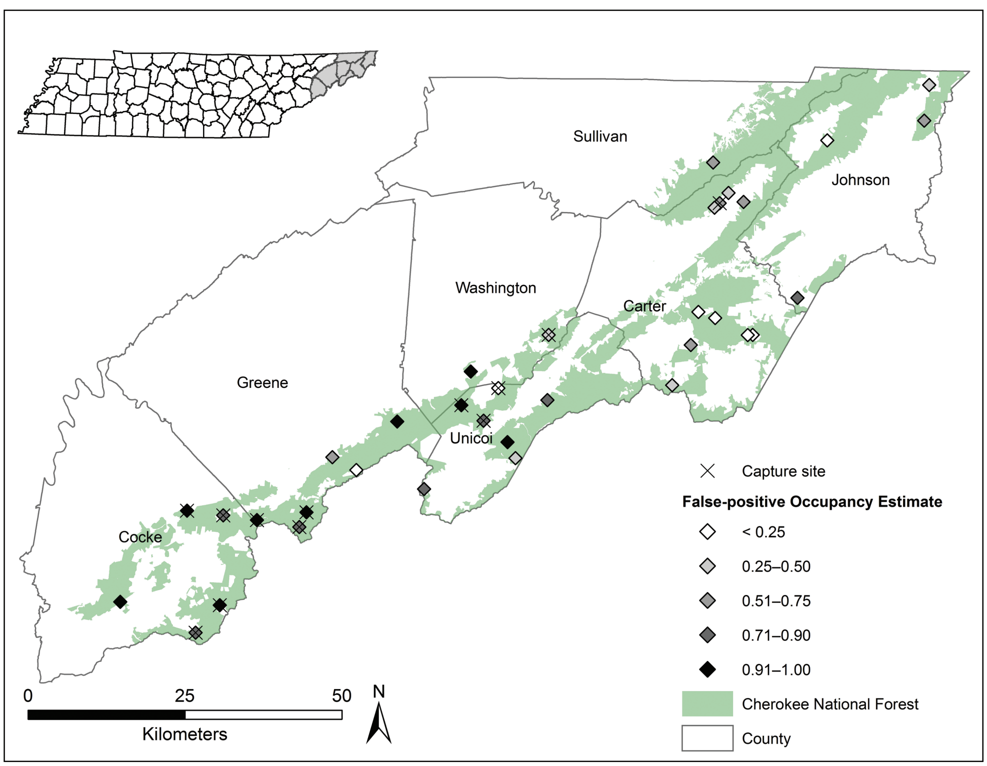

Fig. 1.—Site-specific false-positive occupancy estimates shown for northern long-eared bats (*Myotis septentrionalis*) using capture and acoustic data collected at 35 sites during surveys in the northern districts of the Cherokee National Forest, Tennessee, May to August 2013–2015. Survey sites are indicated by diamonds, color-coded by conditional probability of occupancy estimates. A black X indicates a site where northern long-eared bats were captured in mist nets.

surveys (< 5 h), we returned to conduct a full survey and did not include data from incomplete surveys in occupancy models. We checked mist nets for bat captures at 8-min intervals and used key features (e.g., presence of keeled calcar, fur color) and measurements (e.g., forearm, tragus, and foot length) to confirm species identification (Reid 2006). Prior to release, we secured a unique aluminum band (2.9 mm; Porzana, Ltd, East Sussex, United Kingdom) to the forearm of each northern long-eared bat. We required only a single mist-net capture of a northern long-eared bat at a site to consider the species present for that night. Field studies were conducted under federal (ID: TE206872) and state (TN ID: 3148) permits following Institutional Animal Care and Use Committee (IRBNet package ID: 531861-4) regulations and the American Society of Mammalogists' guidelines (Sikes et al. 2016).

Acoustic surveys.—We used acoustic detectors to survey the same 35 sites from May to August 2013–2015, surveying each site over at least 2 years for a minimum of five nights total (2–9 nights per survey). Detectors were ≤ 50 m from a mist net (never between nets) and, generally, at least one night of an acoustic survey coincided with a mist-net survey. Data were recorded automatically between 20:00 and 08:00 Eastern Daylight Time (EDT) onto compact flash cards using Titley Anabat SD2s (henceforth, "Anabat"; Titley Scientific, Columbia, Missouri). A 10-m waterproof cable connected the Anabat device to a weatherproofed microphone (all hi-type microphones; one was replaced in the third summer with new stainless steel model) housed inside a 31.75-mm polyvinyl chloride (PVC) tube with a 40° axis angle (Titley Scientific, Columbia, Missouri) and mounted atop a 2-m tall PVC post. We set the microphone ≥ 1 m from the nearest vegetation, directed at a 30° angle across the road corridor. Prior to the start of each field season, Titley Scientific quality checked microphones; we then used an ultrasonic device (Dazer International, London, United Kingdom) to standardize sensitivity settings at ~6.5 for each microphone and its associated Anabat acoustic detector (Larson and Hayes 2000).

Environmental data.—We gathered data on nightly temperature, wind, and precipitation from two weather stations located in the NCNF and monitored by the U.S. Forest Service, with data access through National Oceanic Atmospheric Administration's National Weather Service Weather Forecast Office (National Ocean and Atmospheric Administration 2016a, 2016b). The Nolichucky station (ID: PGVT1; elevation: 701 m—National Ocean and Atmospheric Administration 2016a) was in Greene County, while the Watauga weather station (ID: UNIT1; elevation: 878 m—National Ocean and Atmospheric Administration 2016b) was in Unicoi County. We assigned data from the nearest functional weather station to each survey site and night.

We used ArcMap (v10.3.1—Esri 2015) to measure multiscale characteristics associated with each survey site, assuming land cover was static across the 3 years of our study. Using digital elevation models (DEMs; 10 m resolution, 7.5 min) sourced from Tennessee Geographic Information Council (2016), we extracted the elevation (m) for each survey site. To determine site terrain ruggedness, we calculated Topographic Position Index (TPI; using a 10-cell DEM grid—Weiss 2001); values range from 0 to 1, with 1 being the most rugged. The TPI uses classifications (e.g., low, medium, high) based on the natural breaks in the output data. Based on these natural breaks, we used the following index for ruggedness: sites with TPI < 0.3 were least rugged, sites with TPI > 0.6 were most rugged, and values between 0.3 and 0.6 were moderately rugged. We downloaded and filtered forest layers from the Southeast Gap Analysis Project (30 m resolution—Southeast Gap Analysis Project 2010) and combined three forest classes (Deciduous Forest, Evergreen Forest, and Mixed Forest) from the 29 broad land cover classes in our study region; we then calculated the proportion of combined forest within a 2-km buffer around each site (based on typical northern long-eared bat home range size—Henderson et al. 2008). We also calculated the area of developed land (km^2; filtered from Southeast Gap Analysis Project 2010) in a 4-km buffer around each site; we used 4 km because this was the minimum buffer size at which there were noticeable differences among our largely forested sites. We calculated distance (km) to nearest permanent large stream or river (U.S. Geological Survey Hydrography 2013) for each site.

Stationary acoustic analysis.—For acoustic analyses, we used automated identification software, Bat Call Identification (BCID; v2.7c—Bat Call Identification 2016), to identify bat echolocation calls to species from BCID's default Tennessee list of 13 species. BCID's default setting is to discard files that have noise or no bat pulses, where a pulse is defined as an individual sound wave that is a part of the larger bat echolocation call sequence; files that pass the filter are identifiable sequences of search phase calls. For species identification, we required call sequences with a five-pulse minimum within 15 s, an 80% species confidence level (at least four pulses identified as one species), and minimum discriminant probability of 0.35. If the minimum discriminant probability was not met, BCID marked the file as unknown. BCID presents a maximum likelihood estimate (MLE) of the probability of presence for each species on each survey night; this estimate is the probability of presence given the number of files recorded during the survey and the suite of potential species considered (Allen 2015). We concluded northern long-eared bats were detected at a site on a particular night when $P < 0.05$ for the likelihood ratio test. While the calculation of the MLE within BCID has some limitations (Allen 2015), this method is currently recommended for presence determinations for federally endangered Indiana bats during acoustic surveys (U.S. Fish and Wildlife Service 2017).

Occupancy modeling.—We selected covariates for probability of detection and occupancy (ψ or psi) models based on hypotheses developed using published literature. The probability of detection at an occupied site using a certain method (mist netting) is represented by parameter $r11$ (Miller et al. 2011). Two probability of detection estimates with an uncertain method (acoustics) are included with false-positive occupancy models: $p11$ represents the detection probability using an uncertain method (acoustics) at an occupied site and $p10$ is the false-positive detection probability at an unoccupied site (Miller et al. 2011). The temporal probability of detection covariates included the following weather measurements:

minimum nightly temperature (°C), maximum wind gust (m/s), and precipitation (1/0, coded as 1 when the nearest weather station recorded ≥ 1 h of rain during survey night; 20:00–08:00 EDT). We chose temperature as a covariate rather than sampling date because mean nightly temperature was the better predictor of detection probability for *Myotis* bats in Indiana (Kaiser and O'Keefe 2015). In the current study, we found minimum nightly temperature and day of year were correlated ($|r| = 0.4$, $P < 0.001$), with temperatures increasing as the summer progressed. We surveyed sites with similar structure and vegetation, and thus, assumed detection probabilities were similar across space. Occupancy covariates included elevation (m), terrain ruggedness (TPI), proportion of forest in a 2-km buffer, area of developed land (km^2) in a 4-km buffer, and distance to large stream or river (km; Table 1). We tested for covariate correlation using Spearman's rank correlation tests (R v3.3.2—R Core Team 2015) and found $|r|$ ranged from 0.07 to 0.45; we did not include the most highly correlated variables ($|r| > 0.4$, $P < 0.05$) in the same models. We normalized all occupancy covariates using the normalize function in program Presence (v.11.5—Hines 2016) which calculates a new covariate value using a linearly transformed *Z*-score.

We created a binary detection history for northern long-eared bats for each method (capture or acoustics), site, and survey night. For false-positive occupancy models, mist-net captures were coded as "certain" detections, whereas acoustic detections were coded as "uncertain" detections (Clement et al. 2014). Subsequently, we used the information-theoretic approach (Burnham and Anderson 2002) to develop and test hypotheses regarding factors that could affect detection and occupancy probabilities for northern long-eared bats.

For detection models, we compared five models with one or two weather variables per model using program Presence; we tested all single-variable detection models, a precipitation + wind model, and a null model. As per MacKenzie et al. (2017), we fit all detection models using a global occupancy model (elev + tpi + strm). We considered detection models to be plausible only if they had substantial support ($\Delta AIC_c \leq 2.0$); we included important detection parameters from the plausible models in the occupancy models described below.

Next, we fit 26 occupancy models using program Presence; these models included probability of detection (weather) and occupancy (landscape). Given our limited sample size, we did not assess extinction-colonization rates. Instead, we combined the three seasons and tested single-season occupancy models. We compared Akaike's Information Criterion (AIC_c; corrected for small sample sizes) values for 13 standard models and 13 corresponding false-positive models. We tested models with all possible combinations of one to three covariates, excluding correlations; both standard and false-positive candidate sets included a null model.

To identify the plausible set of occupancy models, we required models to have substantial support ($\Delta AIC_c \leq 2.0$); models with an Akaike weight (w_i) within 10% of the top model's weight were in the confidence set (Arnold 2010). To identify important factors predicting presence, we model-averaged estimates for parameters in plausible models across the confidence set of models (Burnham and Anderson 2002). A parameter was considered important if the 85% confidence interval (*CI*) values of the parameter estimate did not cross 0; using this threshold is more appropriate for the information-theoretic approach, as it reduces the risk of excluding legitimate parameters (as demonstrated in Arnold 2010). We present means ± 1 *SE* where appropriate.

Results

Survey efforts were similar across years; however, mist-net and acoustic detections of northern long-eared bats decreased annually (Table 2). We did not observe the same rate of decline with the two methods. The greatest difference in detections between the methods was in 2015, when northern long-eared bats were detected 28% of the time with acoustic surveys, but only 4% with mist-net captures.

Northern long-eared bats were only 7% of all captures and mist-net detections decreased by 89% over the course of the 3-year study (Table 2). We captured 19 northern long-eared bats at 12 sites; 10 individuals were captured during the first year, while only one individual was captured in the final year (Table 2). We captured an additional 266 bats, including 149 big brown bats (*Eptesicus fuscus*), 94 eastern red bats (*Lasiurus borealis*), four tri-colored bats (*Perimyotis subflavus*), four silver-haired bats (*Lasionycteris noctivagans*), one seminole bat (*Lasiurus seminolus*), and one Rafinesque's big-eared bat (*Corynorhinus rafinesquii*). We captured two other *Myotis* species: nine eastern small-footed bats (*M. leibii*) and four gray bats (*M. grisescens*). We recaptured individual big brown bats

Table 1.—Occupancy covariate means, *SD*s, minimum, and maximum values for 35 sites surveyed for northern long-eared bats (*Myotis septentrionalis*) using mist-net and acoustic sampling methods in the northern districts of the Cherokee National Forest, Tennessee, May to August 2013–2015. We tested false-positive occupancy models and standard occupancy models with the following occupancy covariates: elevation (elev), terrain ruggedness (tpi), proportion of forest in a 2-km buffer around site (for), area of development (km^2) in a 4-km buffer around site (dev), and distance (km) to nearest large stream or river (strm).

Variable	Description	Mean	*SD*	Minimum	Maximum
elev	Elevation (m)	748	185	460	1057
tpi	Terrain ruggedness (Topographic Position Index)	0.43	0.08	0.29	0.64
for	Proportion of forest in a 2-km buffer around site	0.87	0.11	0.49	0.98
dev	Area of development (km^2) in a 4-km buffer around site	263	821	0	4870
strm	Distance (km) to nearest large stream or river	3.52	2.05	0.61	9.23

Table 2.—Number of sites sampled and detection data for northern long-eared bats (*Myotis septentrionalis*) by year for mist-net and acoustic sampling surveys in the northern districts of the Cherokee National Forest, Tennessee, May to August 2013–2015. Each of the 35 sites was surveyed at least two nights with mist-net methods and at least five nights with acoustic methods during the entire 3-year survey period. Calls were identified using Bat Call Identification software (v2.7c).

Year	Sites surveyed	Mist-net method				Acoustic detector method			
		Survey nights[a]	Survey detections[b]	Detection proportion[c]	Individuals captured	Survey nights[d]	Survey detections[e]	Detection proportion[c]	Call files
2013	28	28	10	0.36	10	108	49	0.45	286
2014	23	23	6	0.26	8	102	31	0.30	104
2015	23	23	1	0.04	1	96	27	0.28	57
Total	35	74	17		19	306	107		447

[a] One mist-net survey night is 5 h.
[b] Defined as ≥ 1 capture per survey.
[c] Proportion of surveys in which bat was detected.
[d] One acoustic survey is 12 h, pre-dusk to post-dawn.
[e] Defined as $P \leq 0.05$ for maximum likelihood estimate for species detection.

during our surveys, but never recaptured northern long-eared bats or other species.

During acoustic surveys, we recorded 6,566 identifiable call sequences of 12 species (19,823 files were classified as unknown); 447 of the identifiable call sequences were identified as northern long-eared bats. When determining presence at a site we excluded 12 of the 447 files BCID identified as northern long-eared bat files because they were recorded on survey nights that did not meet our MLE standards ($P < 0.05$). While we did not apply the same MLE method to identify other bat species, BCID results showed the following species present: big brown bats, eastern red bats, tri-colored bats, silver-haired bats, Rafinesque's big-eared bats, gray bats, little brown bats, Indiana bats, evening bats (*Nycticeius humeralis*), and hoary bats (*Lasiurus cinereus*).

Seven percent of identifiable acoustic call sequences were northern long-eared bats; acoustic detections decreased by 38% during our survey period (Table 2). Declines in acoustic detections were not as drastic as for capture detections; overall, we detected northern long-eared bats more often with acoustic surveys (Table 2). Of the 107 acoustic survey nights, 35% contained at least one northern long-eared bat sequence. When they were detected at a site, we detected northern long-eared bats during four nights, on average. During the 3-year period, five sites did not have northern long-eared bat detections and eight sites had only one detection night (sites surveyed 6–11 nights each). For the remaining 22 sites, northern long-eared bats were detected on 2–11 nights (sites surveyed 5–17 nights each).

Of the five probability of detection models we tested, only the rain model was supported (ΔAIC_c for next closest model = 4.74). Detection rates for northern long-eared bats were higher on nights without significant rainfall (parameter estimate = −1.02 ± 0.37). Therefore, we included rain as a detection covariate in all occupancy models described hereafter.

False-positive occupancy models received more support than standard models (lower AIC_c scores and higher weights; Table 3). AIC_c values were large for standard models ($\Delta AIC > 35$) and, thus, none were plausible. Two false-positive models were plausible ($\Delta AIC_c \leq 2$) and four false-positive models were in the confidence set (w_i within 10% of the top model's weight; Table 3).

We model-averaged estimates for the three parameters in the plausible false-positive occupancy models (elev, tpi, and strm), using parameter estimates from the four models in the confidence set in our calculations (Table 4). Weighted parameter estimates indicated that the probability of occupancy for northern long-eared bats was higher at less-rugged, lower-elevation sites. Probability of occupancy for northern long-eared bats was higher at lower elevations; bats were more likely to be present at sites < 800 m a.s.l. in elevation (Fig. 2A). Probability of occupancy was below 0.5 when the site was moderately to highly rugged (TPI > 0.4; Fig. 2B). Distance to large stream or river was an uninformative parameter as indicated by *CI*s crossing 0 (Table 4).

False-positive occupancy models produced a wider range of occupancy estimates that were generally lower than estimates for standard models. For one plausible false-positive model, FP ψ(elev + tpi) *r11*(rain) *p11*(rain) *p10*(rain), site-specific occupancy estimates ranged from 0.004 to 0.998 (Fig. 1), while estimates from the corresponding standard model, Std ψ(elev + tpi) *p*(rain), ranged from 0.482 to 0.970 (Supplementary Data SD1). Across all sites, the mean occupancy estimate was lower for the false-positive model (mean_{FP} = 0.615) than for the standard model (mean_{Std} = 0.859; Supplementary Data SD1).

The probability of detecting northern long-eared bats when they were present was similar for certain (mist net) and uncertain (acoustics) methods, although there was a low but not trivial probability of false-positive detection during acoustic surveys. For one plausible false-positive model, FP ψ(elev + tpi) *r11*(rain) *p11*(rain) *p10*(rain), the probability of detecting northern long-eared bats at an occupied site with mist-net methods (*r11*) ranged from 0.372 to 0.566 (mean = 0.479 ± 0.006; Supplementary Data SD1). The probability of detecting a bat using uncertain acoustic methods given the site was occupied (*p11*) ranged from 0.244 to 0.600 (mean = 0.437 ± 0.076; Supplementary Data SD1). The probability of a false-positive detection (*p10*) of northern long-eared bats with the acoustic method ranged from 0.067 to 0.332 (mean = 0.204 ± 0.091; Supplementary Data SD1).

Discussion

False-positive occupancy models account for the probability of not detecting a species when it is present (false negative) and misidentifications (false positive). We demonstrated that false-positive occupancy models produce a broad range of occupancy estimates when compared to standard occupancy models for the rare and cryptic northern long-eared bat, which appeared to decline in abundance during our 3-year study. Our results indicated that federally threatened northern long-eared bats were more likely to occupy less-rugged, lower-elevation sites in northeastern Tennessee. Due to the uncertainty of acoustic identifications and bats' ability to avoid capture, we recommend combining acoustic and capture methods when conducting bat surveys, and using false-positive occupancy models to predict occupancy across survey areas, when possible.

Compared to false-positive occupancy models, standard occupancy models produce a narrower range of estimates and, when tested in simulation where occupancy is known, false-positive occupancy models yield more accurate estimates (Miller et al. 2013; Clement et al. 2014). The results of our comparison of standard and false-positive occupancy estimates were similar to those of Clement et al. (2014) and Miller et al. (2013). While our site occupancy estimates for standard models ranged from 0.482 to 0.970, false-positive occupancy models yielded a wider range of estimates, from 0.004 to 0.998 (Supplementary Data SD1). In addition, there was more model uncertainty with standard occupancy models; two false-positive occupancy models were within 2 AIC_c of the top model (i.e., plausible) while five standard models were plausible when considering only the set of standard models (Table 3). Clement et al. (2014) obtained similar results for little brown bats in the Pacific Northwest; site occupancy estimates from standard occupancy models were always 1.0, while estimates from false-positive occupancy models ranged from 0.02 to 1.00. Likewise, in a study of gray wolves in Montana, site-specific occupancy estimates from standard models ranged from ~0.45 to 1.0, while the range of estimates from false-positive occupancy models was almost double, < 0.1–0.8 (Miller et al. 2013). While a narrower range of estimates would seem to be more precise, these similar results across multiple studies suggest false-positive occupancy models actually provide more accurate estimates of species occupancy. A simulation study with known occupancy provides additional support. When true occupancy is known (simulated), standard models overestimate occupancy by nearly 80%, while models that account for detection certainty accurately estimate occupancy (Miller et al. 2011). Comparing false-positive and standard occupancy models for three frog species, Miller et al. (2011) found false-positive models were

Table 3.—Multi-method occupancy models using detection data for northern long-eared bats (*Myotis septentrionalis*) collected during mist-net and acoustic surveys at 35 sites in the northern districts of the Cherokee National Forest, Tennessee, May to August 2013–2015. We tested false-positive (FP) models and standard (Std) models with the following occupancy (ψ) covariates: elevation (elev), terrain ruggedness (tpi), proportion of forest in a 2-km buffer around site (for), area of development (km^2) in a 4-km buffer around site (dev), and distance (km) to nearest large stream or river (strm). Rain, the only important factor in detection models, was used as a probability of detection covariate (*p*, *r11*, *p11*, *p10*) in all occupancy models. Null models lacked occupancy covariates. The difference in the value of Akaike's Information Criterion between the focal model and the top-ranked model (**Δ**AIC_c), model weights (w_i), and number of model parameters (*K*) are presented.

Model	ΔAIC_c	w_i	*K*
FP ψ(elev + tpi) *r11*(rain) *p11*(rain) *p10*(rain)[a,b]	0	0.509	13
FP ψ(elev + tpi + strm) *r11*(rain) *p11*(rain) *p10*(rain)[a,b]	1.88	0.199	14
FP ψ(tpi + for) *r11*(rain) *p11*(rain) *p10*(rain)[b]	2.70	0.132	13
FP ψ(tpi + for + strm) *r11*(rain) *p11*(rain) *p10*(rain)[b]	4.02	0.068	14
FP ψ(tpi) *r11*(rain) *p11*(rain) *p10*(rain)	5.39	0.034	12
FP ψ(tpi + dev) *r11*(rain) *p11*(rain) *p10*(rain)	6.02	0.025	13
FP ψ(for) *r11*(rain) *p11*(rain) *p10*(rain)	7.09	0.015	12
FP ψ(elev + strm) *r11*(rain) *p11*(rain) *p10*(rain)	8.37	0.008	13
FP ψ(elev) *r11*(rain) *p11*(rain) *p10*(rain)	9.31	0.005	12
FP ψ(strm) *r11*(rain) *p11*(rain) *p10*(rain)	11.17	0.002	12
FP ψ(dev + strm) *r11*(rain) *p11*(rain) *p10*(rain)	12.03	0.001	13
FP ψ(null) *r11*(rain) *p11*(rain) *p10*(rain)	12.30	0.001	11
FP ψ(dev) *r11*(rain) *p11*(rain) *p10*(rain)	12.64	0.001	12
Std ψ(dev) *p*(rain)	35.05	< 0.001	7
Std ψ(tpi + dev) *p*(rain)	35.78	< 0.001	8
Std ψ(null) *p*(rain)	36.30	< 0.001	6
Std ψ(elev) *p*(rain)	36.74	< 0.001	7
Std ψ(dev + strm) *p*(rain)	37.01	< 0.001	8
Std ψ(tpi) *p*(rain)	37.22	< 0.001	7
Std ψ(for) *p*(rain)	37.54	< 0.001	7
Std ψ(elev + tpi) *p*(rain)	37.80	< 0.001	8
Std ψ(strm) *p*(rain)	38.14	< 0.001	7
Std ψ(elev + strm) *p*(rain)	38.30	< 0.001	8
Std ψ(tpi + for) *p*(rain)	38.65	< 0.001	8
Std ψ(elev + tpi + strm) *p*(rain)	39.65	< 0.001	9
Std ψ(tpi + for + strm) *p*(rain)	40.64	< 0.001	9

[a]Plausible set.

[b]Confidence set.

Table 4.—Model-averaged estimates, *SE*s, and 85% confidence levels for parameters in the two plausible false-positive models for capture and acoustic data collected at 35 sites during surveys for northern long-eared bats (*Myotis septentrionalis*) in the northern districts of the Cherokee National Forest, Tennessee, May to August 2013–2015. Parameter estimates were averaged across four models in confidence set. Distance to large stream or river was not important, as 85% *CI*s crossed 0. Estimates presented are for normalized covariate values. Parameter names defined in Table 1.

Parameter	Estimate	*SE*	85% confidence level	
			Lower	Upper
Intercept	0.59	± 0.32	−0.27	1.44
tpi	−1.95	± 0.94	−3.36	−0.53
elev	−1.45	± 0.88	−2.76	−0.13
strm	0.12	± 0.26	−0.64	0.88

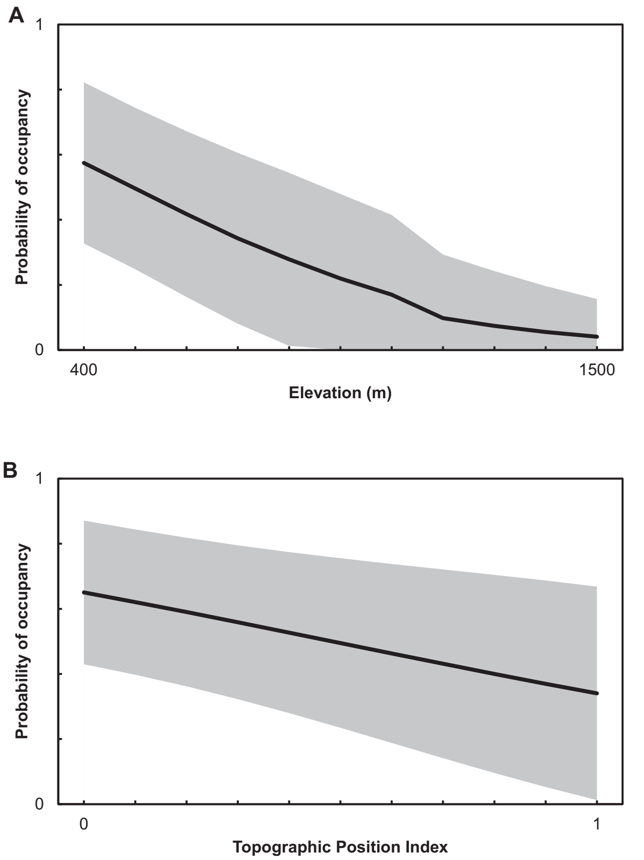

Fig. 2.—Important predictors of northern long-eared bat (*Myotis septentrionalis*) occupancy. Elevation (A) and terrain ruggedness (Topographic Position Index; B) are shown as non-normalized values in relation to conditional probability of occupancy estimates for the highest ranked model (where values closer to 1 indicate a higher probability of occupancy). Data are from acoustic and capture surveys for northern long-eared bats at 35 sites in northern districts of the Cherokee National Forest, Tennessee; surveys were conducted May to August 2013–2015. Shaded areas display 95% *CI*s for occupancy estimates.

generally more plausible than standard models and produced lower (more realistic) occupancy estimates; in some cases, standard site-specific occupancy estimates were double the values predicted by false-positive models.

Although we selected our sites to optimize our ability to capture northern long-eared bats, the covariates in our occupancy models varied widely across sites (Table 1). The false-positive occupancy models showed that the probability of northern long-eared bat occupancy was higher at less-rugged, lower-elevation sites. In contrast, standard occupancy models predicted that elevation and terrain ruggedness were uninformative parameters for predicting probability of northern long-eared bat presence. If we had relied on predictions from standard occupancy models, we would have concluded that development was the main driving factor affecting occupancy, as this parameter was in three of the top five standard models. Further, the standard models indicated a high probability of occupancy at most sites; only four of the 35 sites surveyed had site-specific occupancy estimates below 0.75 (mean = 0.859), of which the lowest was 0.482. False-positive occupancy estimates should be more accurate, which will enable managers to focus future surveys and management efforts on the most probable areas for northern long-eared bat occupancy (i.e., low-elevation sites in our study area).

Predictions of the false-positive model fit with prior knowledge on the importance of elevation and terrain to bats. The higher probability of northern long-eared bats at lower elevations is likely attributable to warmer temperatures being more suitable for reproductive females (Grindal et al. 1999; Cryan et al. 2000) and to greater prey availability (Grindal and Brigham 1999; Erickson and Adams 2003). In a nearby region of southern Appalachia, northern long-eared bats roost at relatively low elevations (mean elevation = 473 ± 78 m) even though available habitat ranges in elevation from low to quite high (250 to 2,025 m—Rojas et al. 2017). In the southern Appalachian Mountains, large colonies of northern long-eared bats may use large trees as roosts (Rojas et al. 2017). The size of a tree can limit cavity volume and the size of available bark patches, and, thus, may impact the size of a bat maternity colony (Barclay and Kurta 2007). Soils are more favorable for the development of large trees in areas of low terrain ruggedness (Carmean 1975), which could explain the significance of this factor.

We recommend coupling capture and acoustic methods when surveying rare and elusive bat species; combining a certain and uncertain method is an optimal survey approach when the probability of detection is relatively high (> 0.6) for the uncertain method (Clement 2016). With acoustic surveys we were able to survey more nights and had more detections than with mist-net surveys. Using only acoustic methods has disadvantages, such as long analysis times and inconsistencies in identification when calls are identified manually (Barclay 1999; Russo et al. 2018). We used conservative, automated filtering methods for acoustic identifications and the results of our comparison of standard and false-positive occupancy model performance suggest we should have less confidence in our acoustic identifications compared with our capture results. However, this does not mean these uncertain acoustic data lack value. In fact, as noted above, incorporating uncertain detections into occupancy models can improve model performance (Miller et al. 2011; Banner et al. 2018). When surveying for bats, we agree with Robbins et al. (2008), Clement et al. (2014), and Ford et al. (2016) that a multi-method approach will produce more useful data on occupancy and habitat preferences. However, we note that when occupancy is low, uncertain detection probability is low, and the probability of false-positive detections is high, it may be advisable to focus resources on certain survey methods instead (Clement 2016). Further, heterogeneity in detection probabilities across space and time can still lead to bias in false-positive occupancy models. Selecting appropriate survey methods or modifying existing methods might help to reduce this bias (Clement 2016).

Limitations.—Accounting for false-positive detections requires additional parameters in occupancy models and, hence, a larger sample size and more effort in the field. The effort will pay off, however, with less-biased and more accurate estimates.

Because we combined seasons and used a single-season model approach, we were unable to test for year-to-year changes in detection and occupancy estimates. Further, estimates from our single-season models may be biased by the ongoing extinction of northern long-eared bats in our study area. For multi-season studies, we recommend running multi-season models and estimating extinction and colonization rates. Such models allow assessment of the impact of abiotic or biotic factors that may affect population size and provide valuable data on population dynamics. To facilitate parameterizing multi-season models, we recommend increasing sample sizes (e.g., more sites even at the expense of fewer surveys at each site). A simulation study can be used to identify the sample size required for desired levels of accuracy (Clement et al. 2014; Clement 2016). Clement (2016) addresses the trade-offs of adding additional parameters to account for false-positive detections; we recommend reviewing the scenarios presented in that study prior to implementing an occupancy study.

Management implications.—By accounting for imperfect detections, occupancy models can improve the accuracy of species monitoring programs. We observed capture and acoustic declines for northern long-eared bat detections, presumably due to WNS, and had few certain detections. Miller et al. (2011) emphasized that false-positive occupancy models were an improvement on standard occupancy models when species occupancy was low, certain detections were few, and when sites were surveyed a large number of times. While not accounting for false negatives may lead to an underestimation of occurrence, not accounting for false positives may lead to overestimation of occurrence (Miller et al. 2013); these biased estimates may result in poor management decisions when sites with true high occupancy are more likely to be overlooked. To avoid depleting limited resources on sites with low probability of occupancy, managers should use the results of false-positive occupancy modeling to target sites with high probability of occupancy for continued monitoring and conservation efforts.

Future directions.—Although false-positive occupancy estimates require more effort in the field, there are multiple ways to achieve our recommendations. With the standardized procedures of the North American Bat Monitoring Program, acoustic surveys can be supplemented with paired mist-net surveys within a defined survey unit (Clement et al. 2014; Loeb et al. 2015). If researchers reduce time spent on analyses of call identification by using automated identification software rather than manual identification and use false-positive occupancy models to account for potential misidentifications, then they should be able to increase acoustic survey efforts (Banner et al. 2018).

Data collected by citizen scientists can also be incorporated into occupancy analyses with the reassurance that it is possible to account for uncertain identification (Miller et al. 2013). A recent extension of false-positive occupancy models includes a calibration design that is useful for citizen science studies as it allows for testing observation error rates by use of reference sites where true occupancy is known (Chambert et al. 2015). For rare and elusive species such as the northern long-eared bat, we recommend testing presence data collected from novel survey methods (e.g., scent-tracking dogs, thermal imaging of potential roosts, and guano analysis) in false-positive models. Ultimately, the application of false-positive occupancy models should yield less-biased site-specific occupancy estimates and, hence, better predictions of suitable habitat for bats and other species of conservation concern.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Site characteristics, probability of occupancy, and probability of detection for multi-method occupancy models using detection data for northern long-eared bats (*Myotis septentrionalis*) collected during mist-net and acoustic surveys at 35 sites in the northern districts of the Cherokee National Forest, Tennessee, May to August 2013–2015. We tested standard (Std) models and false-positive (FP) models with the following occupancy (ψ) covariates: elevation (elev, m), terrain ruggedness (tpi, Topographic Position Index), proportion of forest in a 2-km buffer around site (for), area of development (km^2) in a 4-km buffer around site (dev), and distance (km) to nearest large stream or river (strm). We present conditional occupancy estimates and 95% *CI*s for standard and FP occupancy models. We define *r11* as detection probability at an occupied site using mist-net surveys, *p11* as detection probability using acoustic surveys at an occupied site, and *p10* as FP detection probability using acoustic surveys at an unoccupied site. Rain (≥ 1 h of precipitation during survey night; 20:00–08:00 EDT) was used as a probability of detection covariate for *r11*, *p11*, and *p10* in FP occupancy models and we present mean survey night detection probabilities for each of these parameters. Summarizing data across all sites, we also present means, *SD*s, and minimum (Min) and maximum (Max) values for each column.

Literature Cited

Allen, R. 2015. Bat call identification manual. 2nd ed. Online manual. Bat Call Identification, Inc., Kansas City, Missouri.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Bailey, L. L., D. I. MacKenzie, and J. D. Nichols. 2013. Advances and applications of occupancy models. Methods in Ecology and Evolution 5:1269–1279.

Banner, K. M., K. M. Irvine, T. J. Rodhouse, W. J. Wright, R. M. Rodriquez, and A. R. Litt. 2018. Improving geographically extensive acoustic survey designs for modeling species occurrence with imperfect detection and misidentification. Ecology and Evolution 8:6144–6156.

Barclay, R. M. R. 1999. Bats are not birds: a cautionary note on using echolocation calls to identify bats: a comment. Journal of Mammalogy 80:290–296.

Barclay, R. M. R., and A. Kurta. 2007. Ecology and behavior of bats roosting in tree cavities and under bark. Pp. 17–60 in Bats in forests (M. J. Lacki, J. P. Hayes, and A. Kurta, eds.). The Johns Hopkins University Press, Baltimore, Maryland.

Bat Call Identification. 2016. Bat call identification software. Kansas City, Missouri. www.batcallid.com/allsoftware.html. Accessed 1 June 2016.

Bernard, R. F., and G. F. McCracken. 2017. Winter behavior of bats and the progression of white-nose syndrome in the southeastern United States. Ecology and Evolution 7:1487–1496.

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.

Broders, H. G., C. S. Findlay, and L. Zheng. 2004. Effects of clutter on echolocation call structure of *Myotis septentrionalis* and *M. lucifugus*. Journal of Mammalogy 85:273–281.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference. 2nd ed. Springer, New York.

Carmean, W. H. 1975. Forest site quality evaluation in the United States. Pp. 209–269 in Advances in agronomy (N. C. Brady, ed.). Elsevier Academic Press, Cambridge, Massachusetts.

Chambert, T., J. D. Nichols, and D. A. W. Miller. 2015. Modeling false positive detections in species occurrence data under different study designs. Ecology 96:332–339.

Clement, M. J. 2016. Designing occupancy studies when false-positive detections occur. Methods in Ecology and Evolution 7:1538–1547.

Clement, M. J., T. J. Rodhouse, P. C. Ormsbee, J. M. Szewczak, and J. D. Nichols. 2014. Accounting for false-positive acoustic detections of bats using occupancy models. Journal of Applied Ecology 51:1460–1467.

Cryan, P. M., M. A. Bogan, and J. S. Altenbach. 2000. Effect of elevation on distribution of female bats in the Black Hills, South Dakota. Journal of Mammalogy 81:719–725.

Diggins, C. A., L. M. Gilley, and C. K. W. Society. 2016. Comparison of survey techniques on detection of northern flying squirrels. Wildlife Society Bulletin 40:654–662.

Erickson, J. L., and M. J. Adams. 2003. A comparison of bat activity at low and high elevations in the Black Hills of western Washington. Northwest Science 77:126–130.

Esri. 2015. ArcMap software. Ver. 10.3.1. Environmental System Research Institute, Redlands, California.

Ford, W. M., J. L. Rodrigue, and J. B. Johnson. 2016. Deriving habitat models for northern long-eared bats from historical detection data: a case study using the Fernow Experimental Forest. Journal of Fish and Wildlife Management 7:86–98.

Ford, W. M., 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.

Frick, W. F., S. J. Puechmaille, and J. R. Hoyt. 2015. Disease alters macroecological patterns of North American bats. Global Ecology and Biogeography 24:741–749.

Gorresen, P. M., A. C. Miles, C. M. Todd, F. J. Bonaccorso, and T. J. Weller. 2008. Assessing bat detectability and occupancy with multiple automated echolocation detectors. Journal of Mammalogy 89:11–17.

Grindal, S. D., and R. M. Brigham. 1999. Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. Ecoscience 6:25–34.

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

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

Henderson, L. E., L. J. Farrow, and H. G. Broders. 2008. Intra-specific effects of forest loss on the distribution of the forest-dependent northern long-eared bat (*Myotis septentrionalis*). Biological Conservation 141:1819–1828.

Hines, J. E. 2016. Presence software. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland. www.mbr-pwrc.usgs.gov/software/presence.html. Accessed 1 October 2016.

Jones, G. 1999. Scaling of echolocation call parameters in bats. Journal of Experimental Biology 202:3359–3367.

Kaiser, Z. D. E., and J. M. O'Keefe. 2015. Factors affecting acoustic detection and site occupancy of Indiana bats near a known maternity colony. Journal of Mammalogy 96:344–360.

Larson, D. J., and J. P. Hayes. 2000. Variability in sensitivity of Anabat II bat detectors and a method of calibration. Acta Chiropterologica 2:209–213.

Lemen, C., P. W. Freeman, J. A. White, and B. R. Andersen. 2015. The problem of low agreement among automated identification programs for acoustical surveys of bats. Western North American Naturalist 75:218–225.

Loeb, S. C., et al. 2015. A plan for the North American Bat monitoring program (NABat). U.S. Forest Service, General Technical Report SRS-208:1–100.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2017. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier Academic Press, Cambridge, Massachusetts.

MacKenzie, D. I., J. A. Royle, J. A. Brown, and J. D. Nichols. 2004. Occupancy estimation and modeling for rare and elusive populations. Pp. 149–172 in Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters (W. L. Thompson, ed.). Island Press, Washington, D.C.

McDonald, L. L. 2004. Sampling rare populations. Pp. 11–42 in Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters (W. L. Thompson, ed.). Island Press, Washington, D.C.

Miller, D. A. W., J. D. Nichols, B. T. McClintock, E. H. Campbell Grant, L. L. Bailey, and L. A. Weir. 2011. Improving occupancy estimation when two types of observational error occur: non-detection and species misidentification. Ecology 92:1422–1428.

Miller, D. A. W., et al. 2013. Determining occurrence dynamics when false positives occur: estimating the range dynamics of wolves from public survey data. PLoS One 8:1–9.

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

National Ocean and Atmospheric Administration. 2016a. Nolichuky RAWS site information. National Weather Service Weather Forecast Office, Morristown, Tennessee. www.srh.noaa.gov/mrx/?n=nolichucky. Accessed 4 February 2016.

National Ocean and Atmospheric Administration. 2016b. Watauga RAWS site information. National Weather Service Weather Forecast Office, Morristown, Tennessee. www.srh.noaa.gov/mrx/?n=watauga. Accessed 4 February 2016.

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

O'Keefe, J. M., and S. C. Loeb. 2017. Indiana bats roost in ephemeral, fire-dependent pine snags in southern Appalachian Mountains, USA. Forest Ecology and Management 391:264–274.

O'Shea, T. J., P. M. Cryan, D. T. S. Hayman, R. K. Plowright, and D. G. Streicker. 2016. Multiple mortality events in bats: a global review. Mammal Review 46:1–16.

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

R Core Team. 2015. R: a language and environment for statistical. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org/. Accessed 15 October 2016.

Reid, F. A. 2006. Mammals of North American North of Mexico. Houghton Mifflin Company, New York.

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.

Rojas, V. G., J. M. O'Keefe, and S. C. Loeb. 2017. Baseline capture rates and roosting habits of *Myotis septentrionalis* (northern long-eared bat) prior to white-nose syndrome detection in the southern Appalachians. Southeastern Naturalist 16:140–148.

Romeling, S., C. R. Allen, and L. W. Robbins. 2012. Acoustically detecting Indiana bats: how long does it take. Bat Research News 53:51–58.

Royle, J. A., and W. A. Link. 2006. Generalized site occupancy models allowing for false positive and false negative errors. Ecology 87:835–841.

Russo, D., L. Ancillotto, and G. Jones. 2018. Bats are still not birds in the digital era: echolocation call variation and why it matters for bat species identification. Canadian Journal of Zoology 96:63–78.

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

Samoray, S. 2011. White-nose syndrome monitoring and bat population survey of hibernacula in Tennessee. The Tennessee Chapter of the Nature Conservancy. www.tnbwg.org/2011%20Tennessee%20Hibernaculum%20Survey%20Report_FINAL.pdf/. Accessed 21 February 2018.

Sikes, R. S., and The Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Southeast Gap Analysis Project. 2010. National gap analysis program. www.basic.ncsu.edu/segap/. Accessed 15 April 2013.

Szewczak, J. M., and L. S. Harris. 2013. A field test of two acoustic classification systems to discriminate Indiana bats. Presented at the Northeast Bat Working Group, Albany, New York. www.nebwg.org/AnnualMeetings/2013/2013presentations/SzewczakTestforIBATs.pdf/. Accessed 1 September 2015.

Tennessee Geographic Information Council. 2016. Tennessee GIS clearinghouse: an official source of Tennessee GIS data. www.tngis.org/. Accessed 12 August 2016.

USFWS. 2016. Endangered and threatened wildlife and plants; Determination that designation of critical habitat is not prudent for the northern long-eared bat. Federal Register 81(50 CFR 17):24707–24717. www.federalregister.gov/a/2016-09673. Accessed 27 April 2016.

U.S. Fish and Wildlife Service. 2017. Range-wide Indiana bat summer survey guidelines. www.fws.gov/midwest/endangered/mammals/inba/surveys/pdf/2017INBASummerSurveyGuidelines9May2017.pdf. Accessed 15 May 2017.

U.S. Geological Survey Hydrography. 2013. National Hydrography Dataset (NHD). www.nhd.usgs.gov/data.html. Accessed 15 April 2013.

Vine, S. J., et al. 2009. Comparison of methods to detect rare and cryptic species: a case study using the red fox (*Vulpes vulpes*). Wildlife Research 36:436–446.

Weiss, A. 2001. Topographic position and landform analysis. Poster presentation, Esri User Conference, San Diego, California. http://www.jennessent.com/downloads/tpi-poster-tnc_18x22.pdf. Accessed 15 August 2017.

Weller, T. J. 2007. Assessing population status of bats in forests: challenges and opportunities. Pp. 263–292 in Bats in forests (M. J. Lacki, J. P. Hayes, and A. Kurta, eds.). The Johns Hopkins University Press, Baltimore, Maryland.

Weller, T. J. 2008. Using occupancy estimation to assess the effectiveness of a regional multiple-species conservation plan: bats in the Pacific Northwest. Biological Conservation 141:2279–2289.

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

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