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## Articles

# Implementing and Assessing the Efficacy of the North American Bat Monitoring Program

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## Abstract

Bats are under threat from habitat loss, energy development, and the disease white-nose syndrome; therefore, an efficient and effective means to monitor bat populations is needed. The North American Bat Monitoring Program (NABat) was initiated in 2015 to provide standardized, large-scale monitoring to benefit bat biologists, managers, and policy makers. Given the recency of this program, our first objective was to determine the efficacy of implementing NABat. Further, because the probability of detecting a bat varies among species and survey conditions, our second objective was to determine factors affecting detection probabilities of bats using NABat acoustic surveys. We conducted surveys across South Carolina from mid-May through July 2015 and 2016. To determine efficacy of NABat, we compared species detections with historical known distributions and predicted distributions based on environmental occupancy models. To determine factors that affected detection probability, we evaluated support for predictive detection models for each species or species grouping. In general, we found that predicted distributions closely matched known distributions. However, we detected some species in  $\leq 50\%$  of cells within their ranges and others outside their ranges, suggesting NABat may also reveal new information about species distributions. Most species had higher detection probabilities at stationary points than mobile transects, but the influence of interrupted surveys, environmental conditions (e.g., temperature, rainfall, and wind) and habitat conditions often varied among species. Overall, our results suggest NABat is an effective and efficient method for monitoring many bat species, but we suggest that future efforts account for species-specific biological and behavioral characteristics influencing detection probability.

Keywords: acoustic; bat; monitoring

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## Introduction

Bat populations in North America are currently under stress from a number of major threats (Loeb et al. 2015; Pauli et al. 2015). For example, white-nose syndrome (WNS) has caused severe declines in hibernating bat populations since 2007 in the northeastern United States

(Turner and Reeder 2009). The epidemic has continued to spread across the East and Midwest regions, and was recently discovered in the western state of Washington, suggesting future declines will occur at a continental scale (Lorch et al. 2016). Additionally, bat populations are being negatively affected by energy development (Kunz



et al. 2007; Arnett and Baerwald 2013), habitat alteration, and climate change (Jones et al. 2009; Rebelo et al. 2010).

To develop effective bat conservation strategies, managers require a robust and repeatable method of monitoring bat populations. Acoustic monitoring has become a common method of monitoring bat populations because of the ease of the equipment setup and low personnel requirement. Relative to more traditional methods such as mist-netting, acoustic monitoring requires no bat handling and thus is less invasive and requires less training. Detectors are also more cost-effective than mist-netting (Coleman et al. 2014). Therefore, it is relatively easy to conduct acoustic surveys of bats in a variety of habitat types (Murray et al. 1999; Britzke et al. 2013). As a result, several acoustic monitoring approaches have been developed, including passive stationary-point sampling (placing a microphone at a site and leaving it deployed without a person being present; Johnson et al. 2002) and mobile survey techniques (Loeb et al. 2015). Unfortunately, each of these approaches varies in its probability of detecting a species, thus limiting our ability to make comparisons among methods over time (Tonos et al. 2014; Whitby et al. 2014; Braun de Torrez et al. 2017).

The North American Bat Monitoring Program (NABat) was recently developed to provide standardized methods to monitor bat populations across the continent (Loeb et al. 2015). Surveys can be implemented from local to range-wide scales, and researchers can analyze their data to make inferences about local populations and develop suitable management strategies. Data can be submitted to a national database, and with NABat's standardized site selection and sampling methods, large-scale analyses of changes in bat relative abundance and distributions are possible (Loeb et al. 2015). The NABat guidelines were released in 2015, when we began our study. The guidelines suggest that each cell have one mobile transect and two to four stationary points and recommend sampling  $\geq 30$  cells within each state. Thus, our first objective was to determine the efficacy of NABat methods by implementing the suggested protocols within South Carolina and comparing species detection locations to their known distributions based on historical survey records and to their predicted distributions based on landscape occupancy models. Fourteen bat species are known to occur in South Carolina, 12 of which are considered species of greatest conservation need by the State Wildlife Action Plan (South Carolina Department of Natural Resources 2015), including the northern long-eared myotis *Myotis septentrionalis* (MYSE), which was recently listed as a threatened species under the U.S. Endangered Species Act (ESA 1973, as amended) due to declines from WNS (Federal Register 2015). White-nose syndrome is also severely affecting little brown bats *M. lucifugus* (MYLU) and tricolored bats *Perimyotis subflavus* (PESU) in South Carolina, and can infect eastern small footed bats *M. leibii* (MYLE) and big brown bats *Eptesicus fuscus* (EPFU; U.S. Fish and Wildlife Service 2014); however, the latter two species are not experiencing significant declines due to WNS (Langwig et al. 2012).

The probability of detecting bats with any acoustic survey method varies based on effort, timing, weather, and habitat conditions (Yates and Muzika 2006; Hein et al. 2009; Bender et al. 2015). Variation in detection probability can affect the level of sampling effort needed (i.e., high variation may require more sampling effort) to detect some species (Law et al. 2015). Also, a failure to detect a species when it is present (i.e., a false negative) can misinform management of critical habitat (MacKenzie 2005). Therefore, because detection probability should be accounted for in analyses of NABat acoustic data, our second objective was to determine which factors significantly affect detection probabilities for each species of bat in South Carolina. We expect results of this study to help improve implementation of NABat acoustic surveys by showing which factors affect detection probabilities, so they may be taken into account in future studies and monitoring efforts.

## Study Area

We collected data throughout South Carolina, which consists of five major physiographic regions in a gradient from northwest to southeast: Blue Ridge, Piedmont, Southeastern Plains, Middle Atlantic Coastal Plain, and Southern Coastal Plain (U.S. Environmental Protection Agency 2011). We also collected a small amount of data in bordering areas of Georgia and North Carolina. Land use in South Carolina includes various intensities of urban development, silviculture, agriculture, livestock, and undeveloped land. Land cover in the Blue Ridge is dominated by deciduous, evergreen, and mixed forests; the Piedmont by deciduous and evergreen forests and hay or pasture; the Southeastern Plains and Middle Atlantic Coastal Plains by woody wetlands, evergreen forests, shrub lands, and cultivated crops; and the Southern Coastal Plain by emergent herbaceous wetlands, woody wetlands, evergreen forests, and open water (Homer et al. 2015). The northwestern part of the state is mountainous with elevations up to 1,085 m. The Piedmont is characterized by high hills in the upper part of the region and rolling hills in the lower Piedmont. The Coastal Plains range from rolling hills in the north to low-lying wetlands near the coast.

## Methods

We utilized the NABat continent-wide grid of  $10 \times 10$  km cells to identify priority cells for acoustic surveys within South Carolina. The sampling design for NABat is the generalized random tessellation stratified algorithm, which assigns priority numbers to cells to maintain a spatially balanced, random sample (Loeb et al. 2015). We followed the NABat recommendations and selected the top 30 priority cells from the NABat master sample for South Carolina (U.S. Geological Survey 2019). We developed mobile transect routes 25–48 km in length that were primarily contained within the cells; passed through common habitat types of the area; did not come within 100 m of another transect section; required minimal stopping; passed through no stoplights; and

did not include roads with heavy traffic, gates to open and close, or sections where driving at 32 km/h was dangerous (Loeb et al. 2015). We utilized the National Transportation Dataset RoadSegment data (U.S. Geological Survey, National Geospatial Technical Operations Center 2014) to select roads for transect routes, and filtered it to only include secondary and tertiary road classes because these typically meet the transect criteria. We also examined the National Forest System Roads (U.S. Forest Service 2015a) because some of these road segments are not included in the National Transportation Dataset and were suitable for transects. We categorized habitat types within the cells using the National Land Cover Database (U.S. Geological Survey 2014) and made certain transects passed through or adjacent to common habitat types in each cell. Finally, we cross-checked the Geographic Information System data by examining roads in Google Maps and used Google Street View to make sure routes did not pass through stoplights. If cells were not suitable for mobile transects, we dropped them from the sample or surveyed them with stationary detectors only, and selected replacement cells sequentially from the generalized random tessellation stratified list until 30 transects could be developed.

We followed the NABat criteria for stationary sampling points and attempted to find sites that maximized the quality of recordings as well as the diversity of species detected. We sought 2–4 points/cell and ideally, one point in each quadrant of a cell, or in different habitats in cells that had heterogeneous habitat types. To select sites for stationary point surveys, we used the National Land Cover Database to examine habitat types within each cell and the U.S. Forest Service Basic Ownership database (U.S. Forest Service 2015b) to identify public lands. We also viewed aerial imagery from Google Maps to examine land cover and vegetation structure so the most appropriate survey locations could be determined based on two criteria. First, during summer, bat species in South Carolina commonly roost in trees or human structures and fly along edges to reach water and foraging areas (Menzel et al. 2003). Therefore, we typically sought out forest edges and water sources. Second, for long-term monitoring, access to the same sites is needed for many years. Therefore, we prioritized sites on public land. However, few cells contained public lands and we found it necessary to also secure permission to survey private lands.

For both mobile transect and stationary-point acoustic surveys, we used Anabat SD2 bat detectors with directional, stainless steel microphones (Tittley Scientific, Columbia, MO) and 2.5-m microphone cables. We used 10 detectors for stationary surveys and 4 for mobile surveys. Before each survey season, we calibrated detector sensitivities using the Anabat Equalizer (Tittley Scientific). We set the internal sensitivity to 30% and kept detectors, microphones, and cables together throughout the season to retain calibrations. Logistical constraints meant that we were not able to recalibrate detectors during the survey season. During 2015 we randomly assigned detectors to sites, but during 2016 we assigned

the detector from the previous year to each site to ensure consistency between years. For mobile surveys, we kept detectors in the cabin during operation to monitor its functionality throughout the surveys. The microphone was attached to the center of the roof near the front and was oriented straight up from the roof of the vehicle, with no housing or weatherproofing; the surface of the microphone was 18.5 cm above the vehicle's roof.

For stationary point surveys, we placed the microphone at one end of a 3.8-cm-diameter polyvinyl chloride (PVC) tube attached to the top of a 1.8-m camera tripod, with the opening of the PVC set so that the microphone was at a 45° angle. Detectors were set 3–5 m from clutter and oriented away from it. We took 360° panoramic photographs of the area surrounding each stationary point and recorded the microphone's bearing to ensure this remained constant between survey years.

We conducted surveys mid-May through July 2015 and 2016 as suggested by Loeb et al. (2015) to capture the summer resident population even though this time period may result in lower detections of migratory species such as hoary bats *Lasiurus cinereus* (LACI) and silver-haired bats *Lasionycteris noctivagans* (LANO). To efficiently use and distribute survey equipment and complete surveys within the sampling season, we grouped two to six neighboring cells into nine weekly survey areas. Parturition dates in temperate bats are related to temperature (Racey 1982). The NABat surveys should be completed before young become volant to obtain estimates of the adult population (Kunz 2003; Loeb et al. 2015); therefore, we began surveys in the southeastern-most cells and proceeded north and west through the state, with the final surveys occurring in the Blue Ridge region in the northwest.

We surveyed all stationary points for four consecutive nights from 15 min prior to sunset to 15 min after sunrise. We surveyed each mobile transect twice during this period, beginning 45 min after sunset, with the same start and end locations. The same points and transects were surveyed in both 2015 and 2016, where possible. If it rained or wind speed was >10 km/h during a mobile survey, we paused for up to 15 min to allow conditions to improve. If they did not, we ended the survey at that location and made another attempt to survey the entire transect later in the week.

## Data analysis

We removed acoustic files that contained no bat calls using a custom noise filter in AnaloookW version 4.2.7, and then manually removed files that contained fewer than three bat call pulses. For 2015 data, we classified the remaining files using EchoClass version 3.1 and Kaleidoscope Pro version 3.1.5, and then manually vetted all classifications based on reference calls of each species. We often observed misclassifications and low agreement between the two automated classifiers. Thus, for 2016 data, we did not use classification software and instead manually classified all high-quality calls. We used

reference calls that were recorded from identified captured bats that were light-tagged (Britzke et al. 2011), and used characteristics such as the minimum and characteristic frequencies, slope, and variation in minimum frequencies of pulses within the call files to identify calls. All vetting and identification of calls was done by the senior author (BDN) to ensure consistency with consultation with the second author (SCL) when calls were questionable. Some species have very similar call characteristics and cannot always be discriminated, so we grouped calls of EPFU and silver-haired bat as EPFULANO, and eastern red bat *Lasiurus borealis* (LABO) and Seminole bat *L. seminolus* (LASE) as LABOLASE. We had very few MYLE, MYLU, and MYSE detections and it is sometimes difficult to discriminate among their calls, so we combined their detection histories into one group (MYLELUSE) for more robust modeling of these species. We also included unknown *Myotis* calls from the Blue Ridge and Piedmont regions in this group because no other *Myotis* species occur in these regions. We did not include unknown *Myotis* calls from the other regions because those may have been calls of southeastern myotis *Myotis austroriparius* (MYAU), which has different habitat associations than the other three species.

We used two methods to evaluate the efficacy of NABat. If NABat acoustic surveys are a good approach to monitoring bat species in South Carolina, we expected to detect species in each cell within their known distributions. Thus, we compared our detections with previously known species ranges throughout the state (Menzel et al. 2003). However, if species distributions have shifted in South Carolina due to habitat changes and the presence of WNS, or if historical surveys were insufficient, distribution maps from 2003 may not be accurate. Thus, we also compared detections with predicted distribution maps that we developed with landscape occupancy models (Neece et al. 2018). For both 2003 known ranges and predicted distributions, we determined the percentage of the cells surveyed within each species' range in which it was detected. Detections of species outside of their 2003 known ranges provides new information for effective bat conservation and habitat management and is another measure of the efficacy of NABat; therefore, we also counted the number of cells outside of the 2003 known range in which each species was detected.

We used a Bayesian occupancy modeling approach to evaluate the relative importance of hypothesized environmental and survey factors on the detection probability for each species. We first created presence–nondetection tables for each species on each survey occasion within each cell. We treated one night at a stationary point as a survey occasion and one mobile transect survey as a separate survey occasion, even if they occurred on the same night. This allowed us to compare the effects of survey method on detection probabilities.

The type of acoustic survey—mobile transect or stationary point—is known to influence detection probability of bat species. Some studies comparing the two methods have found higher probabilities of detection at stationary points (Tonos et al. 2014; Whitby

**Table 1.** Predicted effects of covariates on the probability of detection for bat species or species groups using acoustic detectors across South Carolina during summer 2015 and 2016. Symbols indicate positive (+), negative (–), no (0), and unknown (?) effect. “Type” is mobile survey (0) or stationary point survey (1). “Duration” is the length of the survey period in minutes. “Clutter” is categorical with mobile transect (0) and low- (1), medium- (2), or high- (3) vegetation-clutter stationary point. “Date” is Julian day of the survey occasion. “Temp” (temperature), “RH” (relative humidity), and “Wind” (wind speed) are mean values during the survey period. “Rain” is categorical with either no rain (0) or rain (1) during the survey period.

Species <sup>a</sup>	Type	Duration	Clutter	Date	Temp	RH	Wind	Rain
CORA	+	+	–	0	+	?	–	–
LAIN	+	+	–	–	+	?	–	–
EPFULANO	+	+	–	0	+	?	–	–
LABOLASE	+	+	0	0	+	?	–	–
LACI	+	+	–	+	+	?	–	–
MYAU	+	+	0	–	+	?	–	–
MYLE	+	+	0	+	+	?	–	–
MYLU	+	+	0	+	+	?	–	–
MYSE	+	+	0	+	+	?	–	–
NYHU	+	+	0	0	+	?	–	–
PESU	+	+	0	0	+	?	–	–
TABR	+	+	–	0	+	?	–	–

<sup>a</sup> *Corynorhinus rafinesquii* (CORA), *Lasiurus intermedius* (LAIN), *Eptesicus fuscus* or *Lasionycteris noctivagans* (EPFULANO), *Lasiurus borealis* or *L. seminolus* (LABOLASE), *L. cinereus* (LACI), *Myotis austroriparius* (MYAU), *M. leibii* (MYLE), *M. lucifugus* (MYLU), *M. septentrionalis* (MYSE), *Nycticeius humeralis* (NYHU), *Perimyotis subflavus* (PESU), and *Tadarida brasiliensis* (TABR).

et al. 2014), and others have found higher probabilities of detection on mobile transects (Fisher-Phelps et al. 2017). The NABat stationary-point surveys last all night and mobile transect surveys are approximately 1 h, so we hypothesized that detection probabilities would be higher at stationary points compared with mobile transects for all species in our study (Table 1). We used two approaches to test this hypothesis. One approach utilized a categorical covariate designating either mobile transect or stationary point for each occasion. The second approach used the duration of each survey occasion in minutes. This variable was another comparison of the two methods but also considered variation within each survey method, particularly the differences in duration of mobile transects and stationary point surveys.

Vegetation clutter, such as dense forest and shrub stands, can also influence detection probabilities within and among bat species. Bats have evolved morphological and call structure adaptations to clutter (Menzel et al. 2005), so species abundances may vary by the amount of clutter, which could result in variation in probabilities of detection among species based on clutter amount. Additionally, sound transmission is affected by the amount of clutter, and the effects vary by echolocation call frequency (Patriquin et al. 2003). Therefore, even if the abundance of a species is not affected by vegetation clutter, the probability of detecting it could still vary by

clutter amount. Both open-adapted and clutter-adapted bat species occur in South Carolina, and the areas we surveyed varied in vegetation clutter amount. Thus, we hypothesized increasing vegetation clutter around stationary points would decrease detection probabilities for open-adapted species, but would not affect detection of clutter-adapted species (Yates and Muzika 2006; O’Keefe et al. 2013). To test this hypothesis, we created a categorical covariate based on the vegetation cover surrounding each detector as viewed in the 360° panoramic photos. Vegetation clutter varies along mobile transects, so we used those as the reference value (0). We considered points in the open or with very little forest nearby as low clutter (1), points with  $\geq 90\%$  forest within 10 m and filling the frame as high clutter (3) and points intermediate between low and high clutter as medium clutter (2).

Reproductive phenology can affect bat activity (Hayes 1997) and, therefore, survey date could affect detection probability. Our surveys were conducted within a few months and before young became volant, so we hypothesized that survey date would not affect detection probabilities of species distributed statewide. Conversely, we hypothesized that detection probability of species with limited distributions would be positively affected by survey date if areas surveyed later in the season were in their known range, and negatively affected by survey date if areas surveyed earlier in the season were in their known range.

Equipment malfunction and weather conditions could also influence detection probabilities. We hypothesized that an equipment malfunction (e.g., a stationary detector was knocked over, not functioning properly upon retrieval), or an incomplete mobile transect survey would result in lower probability of detection. Bat activity tends to increase with increasing temperature (O’Donnell 2000; Broders et al. 2006; Kitzes and Merenlender 2014; Wolbert et al. 2014); therefore, we hypothesized that the probability of detection for all species would increase as temperature increased. Relative humidity affects the attenuation of sound waves (Bass et al. 1990) and may both positively and negatively affect the detection of bats (Starbuck 2013). Thus, we tested whether it had an effect for any species in our surveys. Increasing wind speed decreases the probability of detection (O’Farrell et al. 1967; Rydell 1989), and the occurrence of rain can reduce bat activity (Loeb et al. 2015; Appel et al. 2017). Therefore, we also hypothesized that wind and rain would negatively affect detection probabilities of all species (Table 1). We obtained data from the nearest Meteorological Terminal Aviation Routine Weather Reports stations to each cell. We used the mean temperature, relative humidity, and wind speed over each survey period, and created a categorical covariate for whether or not it rained during the survey.

We used a Bayesian approach to fit detection models for each species independently while holding occupancy constant. We used noninformative priors and treated all terms as fixed. We used three independent Markov chains, each with 25,000 iterations after discarding the first 5,000 iterations as burn-in and retained every fourth

iteration for a total of 18,750 iterations/model. We fit models by calling JAGS version 4.1.0 (<http://mcmc-jags.sourceforge.net/>) with the package ‘rjags’ in Program R version 3.3.3 (<https://www.r-project.org/>).

Prior to analysis, we standardized all continuous covariates to have a mean of 0 and standard deviation of 1. We used Pearson’s correlation to test for correlations among covariates and considered those with a Pearson’s  $|r| > 0.7$  as correlated and did not include them in the same model. “Type,” “Duration,” and “Clutter” were correlated with one another, so we did not include them in the same models (Table S1, *Supplemental Material*).

We evaluated support of a null model and single-term models for each of the nine covariates (“Type,” “Duration,” “Clutter,” “Issue,” “Date,” “Temp,” “RH,” “Wind,” “Rain”). We expected survey method and factors negatively affecting acoustic detectors would strongly affect probabilities of detection, so we also tested a model with the best performing survey method covariate with “Issue” and “Rain.” We tested a global model composed of the best performing survey method covariate and the six other covariates. Finally, we tested all combinations of covariates from the three best performing single-term models.

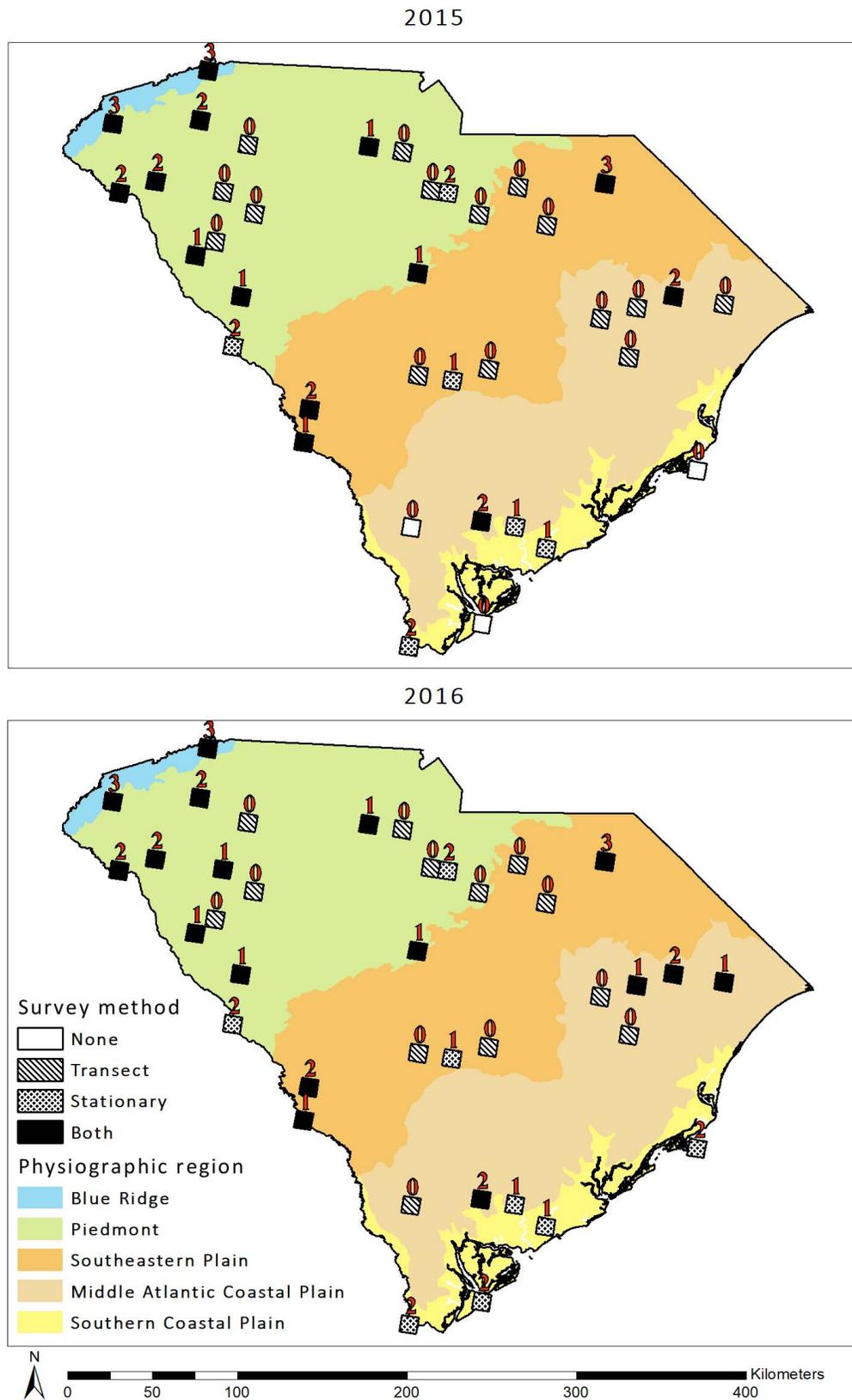
We monitored model convergence using the potential scale-reduction factor (i.e., the Brooks–Gelman–Rubin diagnostic) and assumed convergence when the  $R$ -hat of each parameter was  $< 1.1$ . To rank models, we calculated the Widely Applicable Information Criterion (WAIC) for each model using the package ‘loo’ version 1.1.0. For each species, we calculated  $\Delta$ WAIC from the top-ranked model and each model’s relative likelihood and weight. We calculated 95% credible intervals for covariate estimates and considered their effects significant if the intervals did not include zero. For the top-ranked model for each species, we evaluated model performance with  $k$ -fold cross-validation. We created five random partitions of the data, with 66% of each partition as a training data set and the remainder as a testing data set. We reviewed each training partition to be sure at least one cell from each of the five ecoregions was in each data set, and used the same partitions to evaluate models for each species. For each model, we used the package ‘ROCR’ version 1.0.7 to calculate area under the receiver-operating curve. Area-under-curve values range from 0 to 1, with 0.5 indicating no predictive power (i.e., random) and 1.0 indicating perfect predictive performance (Cumming 2000).

## Results

### Cell, survey point, and transect selection

In total, we surveyed 35 cells in 2015 and 38 cells in 2016 (Figure 1). In 2015 we surveyed 29 cells with mobile transects (15 with mobile transects only and 14 with both mobile transects and stationary points) and 30 cells with mobile transects in 2016 (13 with mobile transects only and 17 with both methods; Figure 1). We were unable to develop routes in nine of the top-priority NABat cells. Issues that prevented development of





**Figure 1.** North American Bat Monitoring Program acoustic survey methods used and number of stationary points surveyed within each cell in summer 2015 (top) and 2016 (bottom) and cell distributions throughout the physiographic regions of South Carolina (U.S. Environmental Protection Agency 2011).

**Table 2.** Number of North American Bat Monitoring Program (NABat) survey cells where we detected each bat species or species group during NABat surveys in South Carolina in summer 2015 and 2016. “% within range” and “% within prediction” represent the percentage of cells surveyed within each species’ 2003 known range, and predicted range (Neece et al. 2018), respectively, in which each species or species group was detected each year. “# outside range” columns indicate number of cells surveyed outside each species’ 2003 known range in which they were detected each year.

Species <sup>a</sup>	2015	2016	% within range 2015	% within range 2016	% within prediction 2015	% within prediction 2016	# outside range 2015	# outside range 2016
CORA	0	0	0.0	0.0	NA	NA	0	0
LAIN	3	7	37.5	63.6	50.0	100.0	0	0
EPFULANO	30	28	85.7	73.7	NA	NA	0	0
LABOLASE	35	38	100.0	100.0	NA	NA	0	0
LACI	6	8	100.0	50.0	23.5	21.1	4	7
MYAU	11	7	47.6	25.0	NA	NA	1	1
MYLE	1	0	20.0	0.0	NA	NA	0	0
MYLU	2	2	50.0	100.0	NA	NA	1	0
MYSE	2	1	25.0	0.0	NA	NA	1	1
NYHU	34	31	97.1	81.6	97.1	81.6	0	0
PESU	33	36	94.3	94.7	97.1	94.6	0	0
TABR	33	38	94.3	100.0	94.3	100.0	0	0
MYOTIS	3	4	NA	NA	NA	NA	NA	NA
MYLELUSE	3	4	40.0	40.0	100.0	100.0	1	2

NA = nonapplicable.

<sup>a</sup> *Corynorhinus rafinesquii* (CORA); *Lasiurus intermedius* (LAIN); *Eptesicus fuscus* or *Lasionycteris noctivagans* (EPFULANO); *Lasiurus borealis* or *L. seminolus* (LABOLASE); *L. cinereus* (LACI); *Myotis austroriparius* (MYAU); *M. leibii* (MYLE); *M. lucifugus* (MYLU); *M. septentrionalis* (MYSE); *Nycticeius humeralis* (NYHU); *Perimyotis subflavus* (PESU); *Tadarida brasiliensis* (TABR); *Myotis* spp. (MYOTIS); and *M. leibii*, *M. lucifugus*, or *M. septentrionalis* (MYLELUSE).

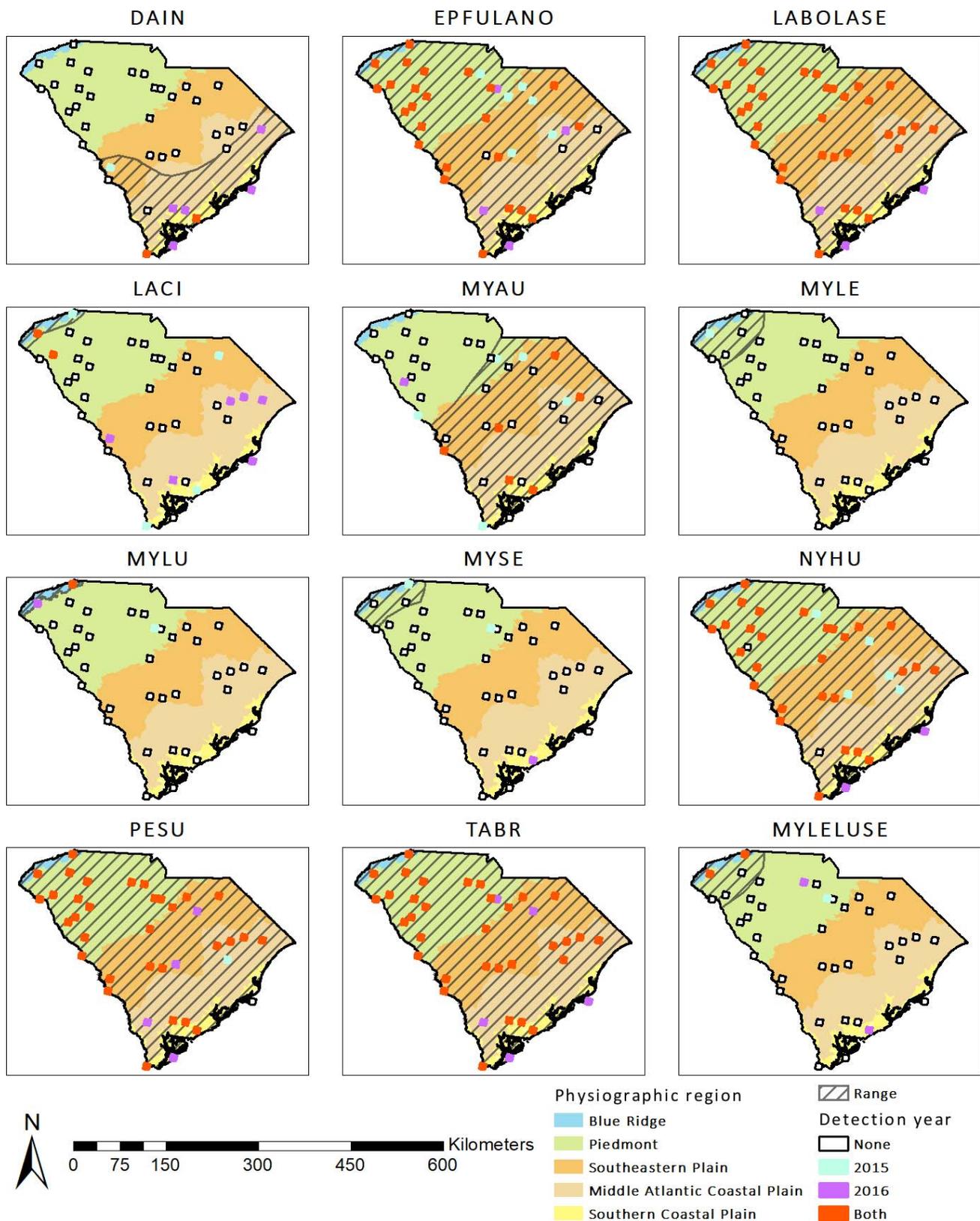
transect routes included cells that did not contain enough suitable roads, gates and stoplights restricting use of roads that were otherwise suitable, and road segments that were not connected within the cells and would require too much time driving outside the cells (e.g., in coastal cells where waterways limited road intersections). One transect had to be modified in 2016 due to a road closure on a section of the route. Transect lengths were 25.5–49.5 km (mean = 33.5 km). Mobile surveys were conducted on 65 occasions each season and ranged in duration from 1 to 99 min (mean = 62.4 min) not including time paused for weather or other issues.

We completed stationary point surveys in 20 cells in 2015, 6 of which were surveyed with stationary points only, and 25 cells in 2016, 8 of which were surveyed with stationary points only (Figure 1). In 2015, we surveyed eight cells with one stationary point, nine cells with two stationary points, and three cells with three stationary points. In 2016, we surveyed 10 cells with 1 stationary point, 11 cells with 2 stationary points, and 4 cells with 3 stationary points. We were able to establish stationary point surveys in all cells that were unsuitable for mobile transect surveys, with the exception of one cell that was primarily in the Atlantic Ocean and contained very little accessible land. We moved all three stationary-point survey locations within one cell to new locations in 2016 because of concerns with long-term access. Stationary point surveys were conducted on 147 occasions in 2015 and 200 occasions in 2016 and ranged in duration from 601 to 640 min/night (mean = 615.7 min).

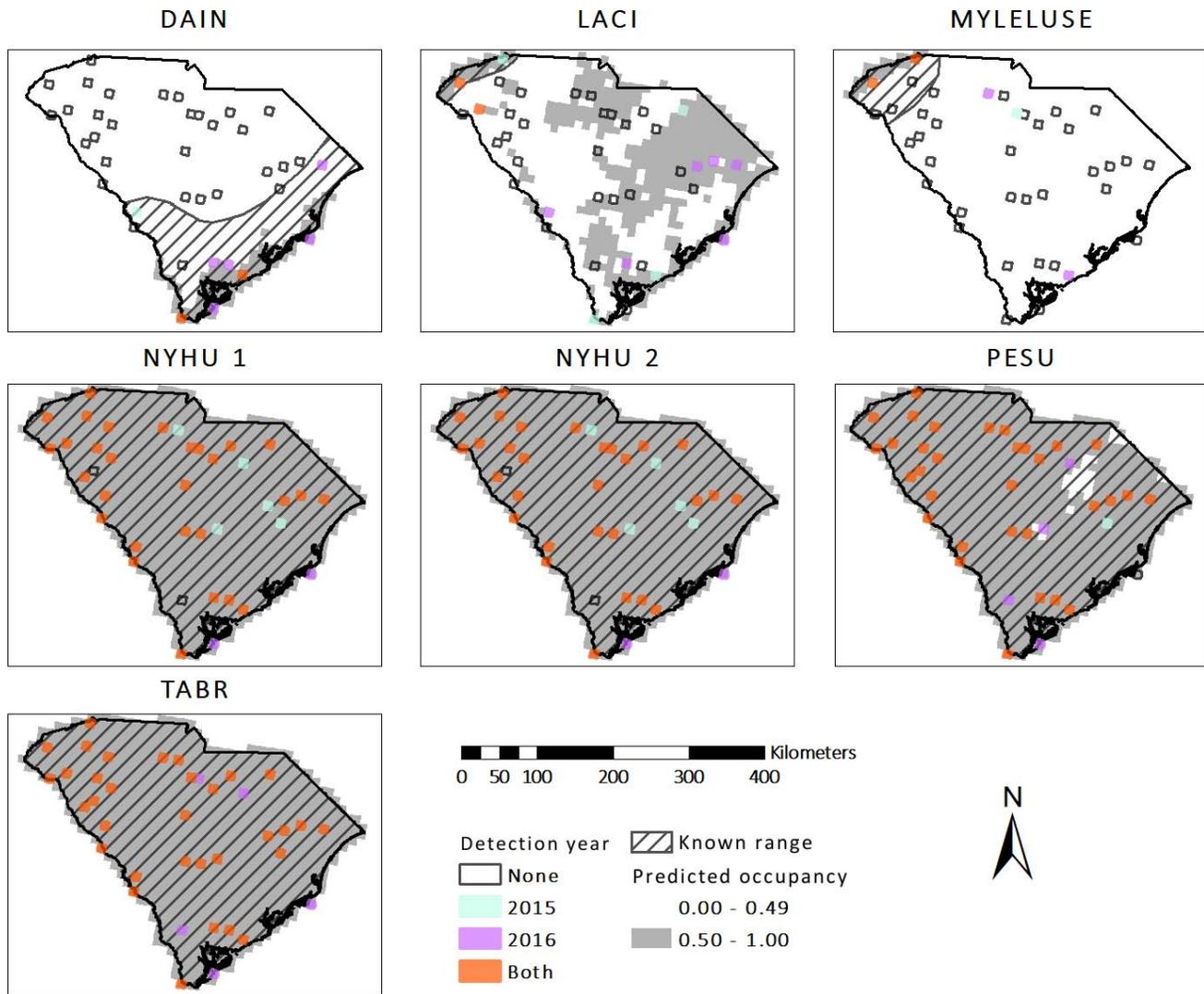
### Species distributions

We recorded 61,397 and 65,727 call files in 2015 and 2016, respectively; 21,972 call files from 2015 and 42,960 call files from 2016 passed our custom noise filter. After manually removing remaining noise files and poor quality and non-search-phase calls, 15,292 identifiable bat call files from 2015 remained. We manually classified 27,380 of the 2016 call files to species and labeled the rest as unknown species or as containing no bat calls.

Species distributions based on our detections varied in how well they matched 2003 known distributions and predicted distributions as well as by year (Table 2; Figures 2, 3). *Corynorhinus rafinesquii* (CORA) was the only species known to occur in the state that we never detected during our surveys. In 2015, we detected EPFULANO, LABOLASE, LACI, MYLU, evening bat *Nycticeius humeralis* (NYHU), PESU, and Mexican free-tailed bat *Tadarida brasiliensis* (TABR) in  $\geq 50\%$  of the cells surveyed in their 2003 known ranges, while we detected northern yellow bat *Lasiurus intermedius* (LAIN), MYAU, MYLE, and MYSE in  $< 50\%$  of the cells within their 2003 known ranges (Table 2; Figure 2). In 2016, we detected LAIN, EPFULANO, LABOLASE, LACI, MYLU, NYHU, PESU, and TABR in  $\geq 50\%$  of cells within their 2003 known ranges, while we detected MYAU, MYLE, and MYSE in  $< 50\%$  of the cells within their 2003 known ranges (Table 2; Figure 2). We were able to generate predicted range maps for six species from our occupancy models (Neece et al. 2018), and all species were detected in higher percentages of their predicted range than their 2003 known ranges, except PESU in



**Figure 2.** Summer ranges for all bat species or species groupings within South Carolina (Menzel et al. 2003), and their detection/ nondetection histories during North American Bat Monitoring Program acoustic surveys in summer 2015 and 2016. Species codes are as follows: *Lasiurus intermedius* (LAIN), *Eptesicus fuscus* or *Lasionycteris noctivagans* (EPFULANO), *Lasiurus borealis* or *L. seminolus* (LABOLASE), *L. cinereus* (LACI), *Myotis austroriparius* (MYAU), *M. leibii* (MYLE), *M. lucifugus* (MYLU), *M. septentrionalis* (MYSE), *Nycticeius humeralis* (NYHU), *Perimyotis subflavus* (PESU), *Tadarida brasiliensis* (TABR), and MYLE, MYLU, or MYSE (MYLELUSE).



**Figure 3.** Predicted distribution maps and detection histories in South Carolina for bat species based on nonnull top-ranked occupancy models (see Table 3). Gray shaded areas represent 10 × 10 km NABat cells where models predicted ≥50% probability of occupancy. See Table S3 (*Supplemental Material*) for covariate effects used to generate distribution maps. Species codes are as follows: *Lasiurus intermedius* (LAIN); *Lasiurus cinereus* (LACI); *Myotis leibii*, *M. lucifugus*, or *M. septentrionalis* (MYLELUSE); *Nycticeius humeralis* (NYHU); *Perimyotis subflavus* (PESU); and *Tadarida brasiliensis* (TABR).

2016 and LACI in both years (Table 2; Figure 3). All species except LACI were detected in ≥50% of the surveyed cells within their predicted distributions (Table 2). We also detected species outside of their 2003 known ranges. We detected LACI both years in a cell 28 km outside its known range, and in nine other cells, one year each, up to 353 km outside its known range (Table 2; Figure 2). We detected MYAU in 2015 in a cell 17 km outside its known range, and in 2016 in a cell 72 km outside its known range (Table 2; Figure 2). In 2015, we detected MYLU in a cell 128 km outside its known range (Table 2; Figure 2). We detected MYSE in 2015 in a cell 114 km outside its known range, and in 2016 in a cell 305 km outside its known range (Table 2; Figure 2).

**Detection probabilities**

The top-ranked detection models differed substantially among species, but predictive performance was >0.70 for all species except PESU (area under curve = 0.68; Table 3). Only one top model, “Clutter+Issue,” was shared by multiple species (LAIN, LABOLASE, and MYAU; Table 3). “Issue,” “Clutter,” and “Duration” were contained in top-ranked models for seven, five, and three species, respectively. We did not observe support for “Type” in top-ranked models for any species; however, for all species except NYHU we observed support for either “Clutter” or “Duration” (Table 3), which were highly correlated with “Type” (Table S1, *Supplemental Material*).

**Table 3.** Top detection probability models (total weights  $\geq 0.95$ ) for each bat species or species group detected during North American Bat Monitoring Program acoustic surveys in South Carolina during summer 2015 and 2016. Models are ordered from highest to lowest performance based on the Widely Applicable Information Criterion (WAIC). Model weights based on WAIC scores are shown. “AUC” is the area under the receiver operating curve and represents the predictive power of the model, with 0.5 indicating no predictive power and 1.0 indicating perfect predictive power.

Species <sup>a</sup>	Model <sup>b</sup>	WAIC	$\Delta$ WAIC	Relative likelihood	Weight	AUC
LAIN	Clutter+Issue	124.6	0.0	1.00	0.33	0.99
	Clutter+Issue+Temp	125.3	0.7	0.70	0.23	
	Clutter+Issue+Rain	125.8	1.2	0.55	0.18	
	Issue	126.1	1.5	0.47	0.15	
	Issue+Temp	127.9	3.3	0.19	0.06	
EPFULANO	Clutter+Issue+Date+Temp+RH+Wind+Rain	440.0	0.0	1.00	1.00	0.88
LABOLASE	Clutter+Issue	127.4	0.0	1.00	0.45	0.70
	Clutter+Issue+Wind	127.7	0.3	0.86	0.38	
	Clutter+Issue+Rain	129.7	2.3	0.32	0.14	
LACI	Duration+Temp	172.1	0.0	1.00	0.38	0.93
	Duration	173.3	1.2	0.55	0.21	
	Type	174.2	2.1	0.35	0.13	
	Duration+Temp+RH	175.0	2.9	0.23	0.09	
	Duration+RH	175.1	3.0	0.22	0.08	
	Clutter	175.9	3.8	0.15	0.06	
MYAU	Duration+Issue	214.7	0.0	1.00	0.45	0.90
	Duration+Issue+Temp	215.7	1.0	0.61	0.27	
	Duration+Issue+Rain	216.9	2.2	0.33	0.15	
	Issue+Temp	220.1	5.4	0.07	0.03	
	Issue	220.2	5.5	0.06	0.03	
	Duration+Temp	221.1	6.4	0.04	0.02	
MYLELUSE	Clutter+Issue	83.2	0.0	1.00	0.66	0.97
	Clutter+Issue+Rain	85.0	1.8	0.41	0.27	
	Clutter	88.7	5.5	0.06	0.04	
NYHU	Issue+Date+Wind	457.8	0.0	1.00	0.44	0.73
	Issue+Date	458.7	0.9	0.64	0.28	
	Issue+Wind	459.7	1.9	0.39	0.17	
	Issue	462.3	4.5	0.11	0.05	
	Date+Wind	463.9	6.1	0.05	0.02	
PESU	Duration+Date	472.4	0.0	1.00	0.51	0.68
	Duration+Date+Rain	473.5	1.1	0.58	0.29	
	Duration+Issue+Date+Temp+RH+Wind+Rain	477.4	5.0	0.08	0.04	
	Duration	477.5	5.1	0.08	0.04	
	Clutter	477.7	5.3	0.07	0.04	
	Type	478.6	6.2	0.05	0.02	
TABR	Clutter+RH+Issue	392.4	0.0	1.00	0.61	0.88
	Clutter+Issue	394.8	2.4	0.30	0.18	
	Clutter+Issue+Rain	395.8	3.4	0.18	0.11	
	Clutter+Issue+Date+Temp+RH+Wind+Rain	396.2	3.8	0.15	0.09	

Duration = the length of the survey period in minutes; Clutter = categorical with mobile transect (0) and low- (1), medium- (2), or high- (3) vegetation-clutter stationary point; Date = Julian day of the survey occasion; Issue = equipment malfunction; Temp (temperature), RH (relative humidity), Wind (wind speed) = mean values during the survey period; Rain = categorical with either no rain (0) or rain (1) during the survey period.

<sup>a</sup> *Lasiurus intermedius* (LAIN); *Eptesicus fuscus* or *Lasionycteris noctivagans* (EPFULANO); *Lasiurus borealis* or *L. seminolus* (LABOLASE); *L. cinereus* (LACI); *Myotis austroriparius* (MYAU); *Myotis leibii*, *M. lucifugus*, or *M. septentrionalis* (MYLELUSE); *Nycticeius humeralis* (NYHU); *Perimyotis subflavus* (PESU); and *Tadarida brasiliensis* (TABR).

<sup>b</sup> “Type” is mobile survey (0) or stationary point survey (1).

“Duration” was in the top-ranked models for three species (LACI, MYAU, and PESU; Table 3). As we predicted, the effects of “Duration” on detection probabilities were positive (Table 4). Over the range of survey duration (1–640 min), detection probability increased from 0.19% to 23% for LACI (which was never detected on mobile surveys), 7.9% to 44% for MYAU, and 60% to 85% for PESU (Figure 4). Additionally, as we predicted, these three species had higher probabilities of

detection at stationary points than on mobile transect surveys (Figure 4).

We observed support for an effect of “Clutter” on LAIN, EPFULANO, LABOLASE, MYLELUSE, and TABR (Table 3). As we predicted, LAIN, EPFULANO, LABOLASE, and TABR detection probabilities declined with increasing clutter (Figure 5; Table 4); and detection probabilities were significantly higher in at least one stationary-point clutter class than in mobile transects for LAIN, EPFULA-

**Table 4.** Estimated effects of coefficients from top-ranked detection models for each bat species or species group detected during North American Bat Monitoring Program acoustic surveys across South Carolina during summer 2015 and 2016.

Species <sup>a</sup>	Type	Duration	Clutter	Date	Issue	Temp	RH	Wind	Rain
LAIN	0	0	—*	0	+*	0	0	0	0
EPFULANO	0	0	—*	+*	—	+*	+	—	—
LABOLASE	0	0	—*	0	—*	0	0	0	0
LACI	0	+*	0	0	0	—*	0	0	0
MYAU	0	+*	0	0	—*	0	0	0	0
MYLELUSE	0	0	+*	0	—*	0	0	0	0
NYHU	0	0	0	—	—*	0	0	—	0
PESU	0	+*	0	+*	0	0	0	0	0
TABR	0	0	—*	0	—*	0	+*	0	0

+ = positive effect, — = negative effect; 0 = coefficient not retained in a top-ranked model; \* = the effect was statistically significant; Type = mobile survey (0) or stationary point survey (1); Duration = the length of the survey period in minutes; Clutter = categorical with mobile transect (0) and low- (1), medium- (2), or high- (3) vegetation-clutter stationary point; Date = Julian day of the survey occasion; Issue = equipment malfunction; Temp (temperature), RH (relative humidity), Wind (wind speed) = mean values during the survey period; Rain = is categorical with either no rain (0) or rain (1) during the survey period.

<sup>a</sup> *Lasiurus intermedius* (LAIN); *Eptesicus fuscus* or *Lasionycteris noctivagans* (EPFULANO); *Lasiurus borealis* or *L. seminolus* (LABOLASE); *L. cinereus* (LACI); *Myotis austroriparius* (MYAU); *Myotis leibii*, *M. lucifugus*, or *M. septentrionalis* (MYLELUSE); *Nycticeius humeralis* (NYHU); *Perimyotis subflavus* (PESU); and *Tadarida brasiliensis* (TABR).

NO, and MYLELUSE (Figure 5). Therefore, these results also supported our prediction that stationary points would yield higher probabilities of detection than mobile transects for these species. Contrary to what we predicted, detection probability was significantly greater at high-clutter points than along mobile transects or low-clutter points for the MYLELUSE group, and did not differ between mobile transects and stationary points for TABR (Figure 5).

We found support for an effect of “Date” for EPFULANO, NYHU, and PESU (Table 3). “Date” had a significant positive effect on detection probabilities of EPFULANO and PESU, contrary to what we predicted, and a negative but nonsignificant effect on detection probability of NYHU (Table 4; Table S2, *Supplemental Material*). Detection probability from the first day (Julian day 133) to the final day (Julian day 198) increased from 18% to 89% for EPFULANO and 70% to 87% for PESU. As we predicted, detection probabilities of LABOLASE, NYHU, and TABR were not significantly affected by “Date” (Table 4; Table S2, *Supplemental Material*). We observed support for an effect of “Issue” for seven (LAIN, EPFULANO, LABOLASE, MYAU, MYLELUSE, NYHU, and TABR) of the nine species (Table 3). Detection probabilities significantly declined with the occurrence of “Issue” for all species except LAIN, where the effect was significantly positive, and EPFULANO, where the effect was negative but nonsignificant (Table 4; Table S2, *Supplemental Material*).

Although we predicted detection probabilities of all species would be affected by weather covariates, we only found significant effects in three cases (Table 4). Over the range of temperatures (12–32C), detection probability of EPFULANO increased from 13% to 86%, and detection probability of LACI decreased from 16% to 1.8%. “Humidity” had a positive effect on detection probabilities of EPFULANO and TABR, but it was only statistically significant for the latter (Table 4; Table S2, *Supplemental Material*), where detection probability

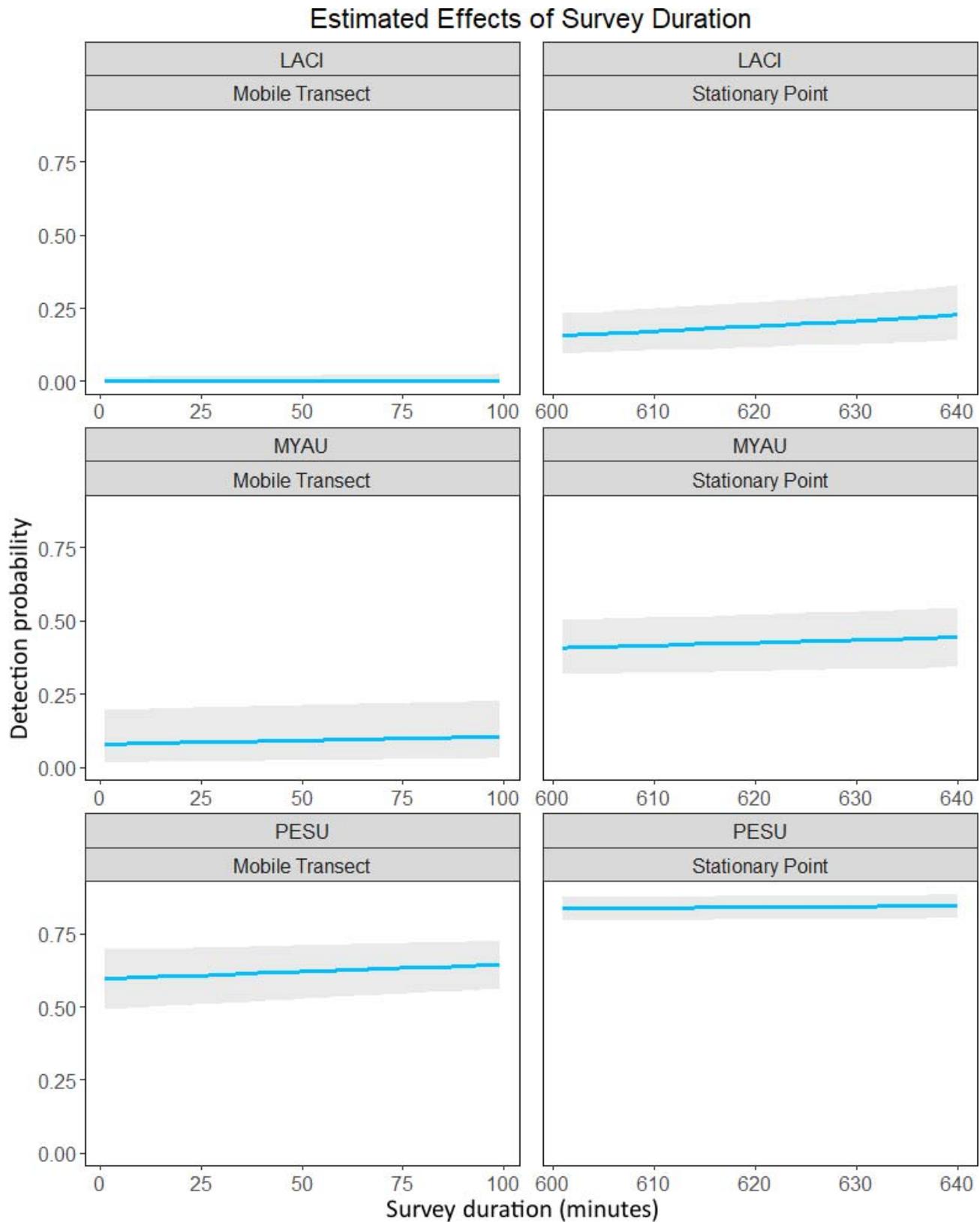
increased from 78% to 92% over the range of “Humidity” (43.5–100%). We hypothesized a negative effect of wind speed and rain on detection probability, but “Wind” was only retained in top-ranked models for EPFULANO and NYHU, and “Rain” was only retained in the top-ranked model for EPFULANO (Table 4). In all cases the effects were negative but nonsignificant (Table S2, *Supplemental Material*).

Based on the top-ranked detection models, we found great variability in the average detection probabilities among species. Mean estimated detection probabilities ranged from 0.04 to 0.98 (Table 5). All detection models we tested converged well, with no *R*-hat values exceeding 1.1.

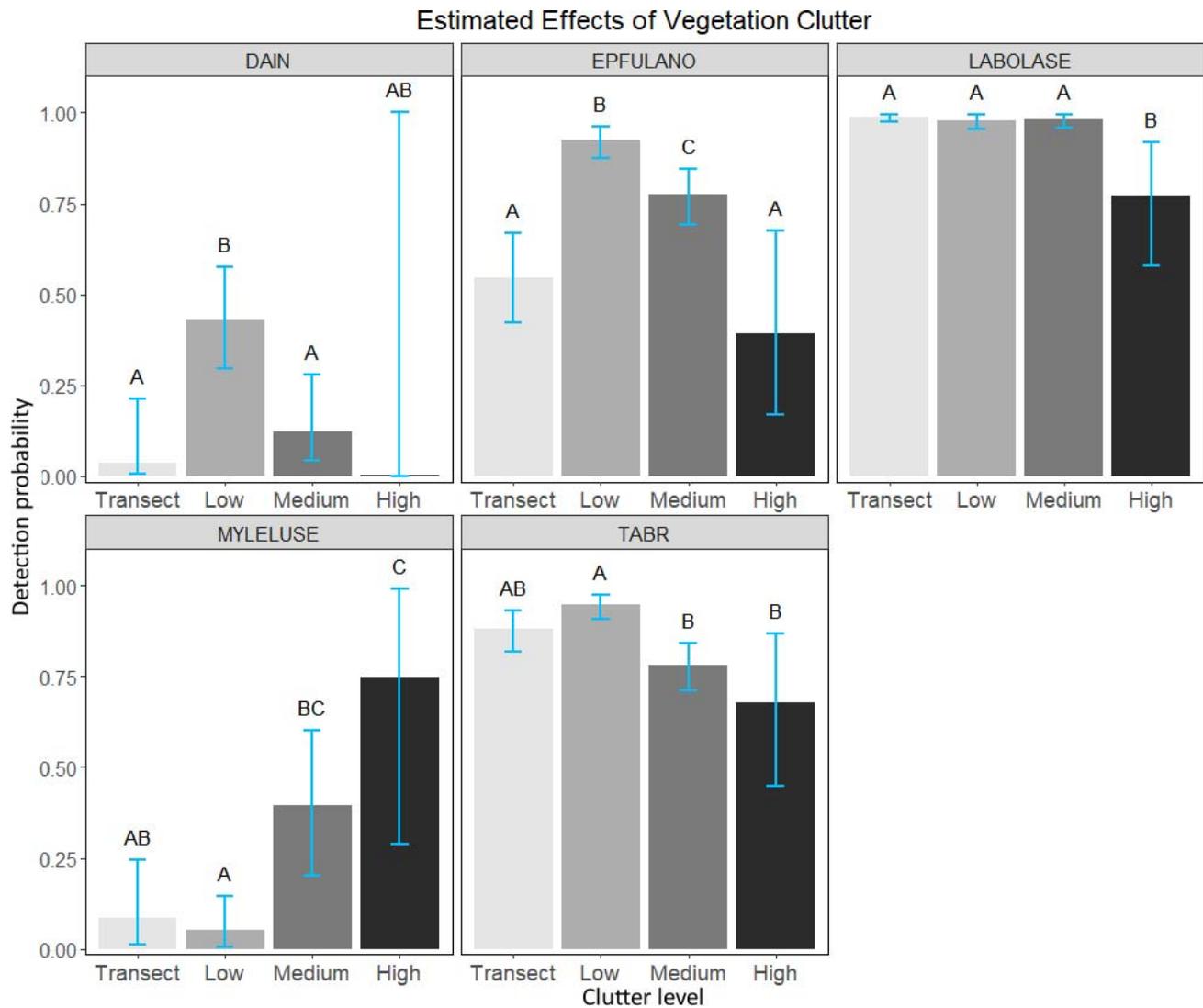
## Discussion

We demonstrated that state-wide implementation of NABat acoustic surveys is feasible if there is strong coordination and participation of volunteers and personnel from state and federal agencies. Further, we demonstrated that data collected from these surveys can provide valuable, large-scale information about species distributions and detection probabilities. We found that species detections appear to more closely match predicted distributions from our surveys than known range maps from 2003. We also found that it is important to control for variation in detection probabilities among species and survey occasions and that multiple factors should be considered when conducting NABat surveys.

With one lead coordinator, we were able to follow the NABat guidelines to establish our goal of 30 mobile transects and  $\geq 1$  stationary point survey within 25 cells. Public land managers and private landowners we contacted were willing to grant permission to conduct stationary surveys on their property, suggesting that NABat stationary-point surveys are feasible even in areas with few public lands. We established three stationary point surveys in each cell in northwestern South



**Figure 4.** Estimated effects of acoustic survey duration (minutes) on the probability of detection for bat species during North American Bat Monitoring Program acoustic surveys in summer 2015 and 2016 across South Carolina with *Duration* retained in their top-ranked model. Duration ranged from 1 to 99 min on mobile transect surveys, and 601 to 640 min on stationary point surveys. Gray shading indicates the 95% credible interval. Species codes are as follows: *Lasiurus cinereus* (LACI), *Myotis austroriparius* (MYAU), and *Perimyotis subflavus* (PESU).



**Figure 5.** Mean estimated detection probabilities at each vegetation clutter level for bat species or species groupings with “Clutter” retained in their top-ranked models from North American Bat Monitoring Program acoustic surveys conducted across South Carolina during summer 2015 and 2016. Transect is the reference value, and Low, Medium, and High are categorical levels of clutter at stationary points. Blue bars indicate 95% credible intervals. Within species, clutter levels that share a letter above their intervals are not significantly different from one another. Species codes are as follows: *Lasiurus intermedius* (LAIN); *Eptesicus fuscus* or *Lasionycteris noctivagans* (EPFULANO); *Lasiurus borealis* or *L. seminolus* (LABOLASE); *Myotis leibii*, *M. lucifugus*, or *M. septentrionalis* (MYLELUSE); and *Tadarida brasiliensis* (TABR).

Carolina, where public land is more common; but due to the lack of public lands within many cells, 40% of the cells that we surveyed had only one stationary point. If time and effort can be dedicated to identifying and contacting private landowners, it may be possible to establish two to four points within each cell where public land is not prevalent.

We determined NABat acoustic surveys were effective at monitoring all species except CORA, MYAU, MYLE, MYLU, and MYSE. However, our results are based on the assumption that identification of acoustic files were accurate although we were not able to quantify our error rate. Regardless of whether it is done manually or with the aid of an auto-identification program, bat acoustic identification is rarely 100% accurate because of a variety

of reasons including the quality of the reference library, the effects of habitat on call structure, and age, sex, and geographic variation in call structure (Russo and Voight 2016; Russo et al. 2018). Some auto-identification programs provide estimates of error, but false positives still occur (Clement et al. 2014; Rojas et al. 2019), which can be detected by manual vetting (Fritsch and Bruckner 2014). Thus, as with all studies based on bat acoustic data, results must be viewed with some caution and extra-range detections should be verified with mist-netting. For example, we detected MYSE in the Coastal Plains, which is far outside the known range of MYSE in South Carolina (Figure 2). However, mist-netting efforts approximately 93 km northeast and 72 km southwest from our detection in the Coastal Plain resulted in the

**Table 5.** Mean estimated detection probabilities (Mean  $P$ ) and 95% credible intervals (Lower CI and Upper CI) based on the top-ranked detection model for each bat species and species group detected during North American Bat Monitoring Program acoustic surveys across South Carolina during summer 2015 and 2016.

Species <sup>a</sup>	Mean $P$	Lower CI	Upper CI
LAIN	0.16	0.01	0.97
EPFULANO	0.77	0.17	0.99
LABOLASE	0.98	0.76	0.99
LACI	0.04	8E-6	0.39
MYAU	0.26	0.03	0.51
MYLELUSE	0.10	8E-4	0.77
NYHU	0.81	0.56	0.91
PESU	0.81	0.66	0.91
TABR	0.86	0.52	0.97

<sup>a</sup> *Lasiurus intermedius* (LAIN); *Eptesicus fuscus* or *Lasionycteris noctivagans* (EPFULANO); *Lasiurus borealis* or *L. seminolus* (LABOLASE); *L. cinereus* (LACI); *Myotis austroriparius* (MYAU); *Myotis leibii*, *M. lucifugus*, or *M. septentrionalis* (MYLELUSE); *Nycticeius humeralis* (NYHU); *Perimyotis subflavus* (PESU); and *Tadarida brasiliensis* (TABR).

capture of MYSE in 2016 and 2017, corroborating our extrarange acoustic detections (White et al. 2018).

Most species detections more closely matched predicted distributions than their 2003 known ranges. This suggests that the distribution of those species has either changed since 2003, or that we conducted more thorough surveys throughout the state than historical efforts. For LACI and MYLELUSE in particular, which were detected well outside their historical range, surveying more cells with either acoustics or mist-netting in extrarange detection areas may improve current range maps. This is particularly important because the four species we detected outside their 2003 known ranges, including three *Myotis* species, are all considered species of greatest conservation need within the state by the SCDNR (South Carolina Department of Natural Resources 2015).

Compared with species with statewide distributions, we detected species with more limited distributions, especially the *Myotis* species, in lower percentages of cells within their 2003 known ranges. We found higher detection probabilities of MYLELUSE in high-clutter habitats than low- and medium-clutter habitats. However, many of the sites we selected for stationary point surveys were along forest edges and in less cluttered areas to decrease distortion of bat echolocation calls and increase detection range, which may account for the small number of detections of MYLELUSE in their known ranges. Additionally, all *Myotis* species' 2003 known ranges in South Carolina except that of MYAU overlap the area impacted by WNS. White-nose syndrome has contributed to declines of MYLU and MYSE in South Carolina (Loeb et al. 2016), and may have led to low acoustic detections.

We observed great variability in the top-ranked detection model among species, but predictive performance of most models was very high. "Issue" was the most commonly retained covariate in top-ranked models among species, likely because it negatively impacts the

acoustic detector itself. This result emphasizes the importance of fully completing mobile transect surveys and taking measures to ensure stationary point detectors do not fall over (e.g., anchoring, staking, or attaching guy-lines to tripods or poles). The significant positive association of LAIN detection probability with survey issue seems counterintuitive but may have been due to an artifact of detectors at two stationary points where LAIN were detected having fallen over but still functioning and recording bat calls.

"Clutter" was another commonly supported predictive covariate, but the effects varied by species and appeared to be related to the clutter adaption of each species. LAIN, EPFULANO, and TABR are considered open-adapted species (Menzel et al. 2005; Loeb and O'Keefe 2006) and we accordingly found negative effects of increasing vegetation clutter for these species. *Myotis* species are considered clutter-adapted species (Patriquin and Barclay 2003; Starbuck 2013), and accordingly, we found the probability of detecting MYLELUSE was very high at high-clutter stationary points and low at low- and medium-clutter stationary points and along mobile transects. However, it must be noted that for modeling purposes it was necessary to combine all *Myotis* detections other than those of MYAU. Although this may have obscured some subtle differences in habitat use among MYLU, MYLE, and MYSE, the strong effect of "Clutter" on MYLELUSE suggests that combining species did not significantly affect our results. LABOLASE are considered open- or semi-clutter-adapted species (Menzel et al. 2005; Loeb and O'Keefe 2006; Starbuck et al. 2015), and we found detection probabilities did not significantly differ among mobile transect and stationary point surveys, except at high-clutter points where detection probability was significantly lower. Our results suggest researchers conducting NABat stationary-point surveys should consider selecting locations from a range of vegetation clutter amounts, not just open areas, to increase the probability of detecting *Myotis* and other clutter-adapted species.

"Duration" was retained in top-ranked models for LACI, MYAU, and PESU. Longer duration surveys may increase the chance of bats encountering detectors during a survey occasion. We never detected LACI on mobile surveys, unlike Whitby et al. (2014), which may be due to its migratory behavior (Cryan 2003). *Lasiurus cinereus* individuals may have been moving north at the beginning of our survey season and we may have detected transient individuals at stationary points, but not at mobile transects because stationary point surveys were conducted during twice as many nights and had longer durations than mobile transect surveys.

Although survey method (i.e., "Type") was not retained in the top model for any species, six out of nine bat species had significantly higher probabilities of detection at stationary points than on mobile transect surveys, similar to other studies (Tonos et al. 2014; Whitby et al. 2014; Braun de Torrez et al. 2017). In contrast, detections of bats in Texas are greater along mobile transects than at stationary points, possibly due to the abundance of TABR in their study area (Fisher-

Phelps et al. 2017). We similarly found that detection probabilities of TABR along mobile transects were high (Figure 5). We also found that detection probabilities of LABOLASE along mobile transects did not differ from those at medium- and low-clutter stationary points. Overall, our results suggest that stationary points may be more effective than mobile transects for detecting some species, but mobile transects may still be suitable in cases where it is not possible or feasible to conduct stationary point surveys, even for species with low probabilities of detection on mobile transects. Positive effects of increasing survey duration suggest higher probabilities of detection could be achieved with longer mobile transects or multiple passes within one night, but further research is needed.

In general, it appears that NABat survey guidelines appropriately control for reproductive phenology, seasonal activity patterns, and weather effects in South Carolina. We hypothesized “Date” would be a significant factor for detection of species with limited distributions, but we found only significant positive effects for EPFULANO and PESU, both of which had statewide distributions. This may have been due to increasing levels of activity as the summer progressed, or perhaps higher abundance in cells sampled later in the season (MacKenzie 2005). *Perimyotis subflavus* are positively associated with forest cover (Farrow and Broders 2011). Even though PESU are experiencing significant declines in northwestern South Carolina (S. Loeb, unpublished data), which we sampled later in the season, these cells were dominated by forests; whereas, those sampled earlier in the season were dominated by agriculture and forested wetlands. Higher forest cover may have resulted in higher probabilities of detection later in the season. Although most LACI in South Carolina are migratory, we did not find an effect of “Date” on their probability of detection. We detected them primarily early in the season, perhaps before they had migrated north, or late in the season when we might have been detecting resident individuals in the mountainous regions. Weather covariates rarely had a significant effect on bat detection probabilities in this study. However, it is possible that our use of weather station data did not capture variation in wind speed, temperature, and relative humidity at the site level. Therefore, we encourage researchers to investigate the potential impacts of fine-scale weather conditions on NABat survey results.

We found very high mean estimated probabilities of detection for EPFULANO, LABOLASE, NYHU, PESU, and TABR. These species are known to occur throughout our study region and only PESU is affected by WNS. We found low probabilities of detection for other species, and we never detected CORA even though they are known to occur in the state (e.g., Lucas et al. 2015; Loeb 2017). *Corynorhinus rafinesquii* are less likely to be detected with acoustic surveys than other methods because of their relatively quiet echolocation calls (Clement and Castleberry 2011; although, see Comer et al. 2014). Even though we combined MYLE, MYLU, and MYSE into one group, the mean estimated detection probability remained very low (0.10). These species have

relatively high-frequency, short-duration echolocation pulses, which attenuate more rapidly than lower frequency calls and often resemble feeding buzzes of other species, so some of their calls may have been dismissed during classification. Also, MYLU and MYSE populations have declined in South Carolina because of WNS, and mist-netting efforts have captured fewer MYLU and MYSE than in the past (Loeb et al. 2016). Thus, lower rates of positive identification in combination with relatively low abundance may be driving low probabilities of detection. Our mean estimated detection probability for MYAU was also relatively low. *Myotis austroriparius* have specific habitat requirements, preferring low-lying forested wetlands and roosts in large tree cavities in bottomland hardwood forests (Gooding and Langford 2004; Carver and Ashley 2008; Bender et al. 2015). The NABat priority survey cells are randomly distributed, so rare habitats can be missed, decreasing the probability of detection. We found the lowest mean estimated probability of detection (0.04) for LACI, which have a small known summer distribution in South Carolina and exhibit migratory behavior (Cryan 2003). Additionally, LACI are high-flying bats (Kalcounis et al. 1999) and often do not echolocate during flight (Gorresen et al. 2017; Corcoran and Weller 2018), which would further reduce their probability of detection.

Overall, it appears that NABat acoustic survey methods were suitable for monitoring most species in South Carolina, but not appropriate for others (e.g., CORA). Further, we found that survey method affects the probability of detecting many species, and that mobile transect surveys may be more effective for some species than for others. We had no or very low acoustic detections of CORA, LAIN, and *Myotis* species, so in addition to NABat acoustic surveys, it may be necessary to conduct hibernacula or summer roost surveys, mist-netting, and possibly active acoustic surveys for monitoring these species. We also found that biological and behavioral differences among species can influence whether survey variables affect their probabilities of detection as well as whether the effects are positive or negative. To effectively utilize the results of acoustic surveys when determining management actions, mapping species distributions, and evaluating bat activity and habitat use, we suggest that researchers record survey variables and determine how they may affect the probability of detecting bat species.

## Management Implications

The results of our study demonstrate that NABat surveys are a feasible means of conducting state-wide monitoring of bats but also demonstrate some of the pitfalls of this type of monitoring. For example, there are higher detection probabilities at stationary points than mobile transects for most species, so we suggest dedicating time toward establishing at least two stationary point surveys in each of the top-priority cells. Stationary points should be in a variety of habitats within each cell, even in areas with vegetation clutter, because we found that detection of clutter-adapted *Myotis*

species was significantly higher in more cluttered areas. We also recommend taking detailed, accurate measures of survey-level variables, particularly whether a survey issue occurred (i.e., detector malfunction or incomplete mobile transect) and the vegetation clutter around stationary points, to account for variation in detection probabilities. We realize government agencies and nongovernmental organizations may not have qualified personnel or financial resources to manually classify tens of thousands of echolocation calls to species each year, and it may therefore be necessary to rely on automated classification software. If automated software is used, we recommend vetting calls or estimating false-positive rates (Banner et al. 2018). When extrarange acoustic detections occur, we recommend conducting further studies in these areas (e.g., mist-netting) to verify the acoustic detections and to learn more about populations in these areas.

### Supplemental Material

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**Table S1.** Results of Pearson's correlation test for each detection covariate we tested. Data are for bat acoustic calls collected during summers 2015 and 2016 across South Carolina using the North American Bat Monitoring Program (NABat) protocols. We considered an absolute  $r$ -value  $>0.7$  (black background with white text) as an indication of significant correlation and did not include those covariates in the same models.

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**Table S2.** Estimated  $\beta$  for intercepts and covariates in top-ranked detection models for each bat species or species group detected during acoustic surveys using the North American Bat Monitoring Program (NABat) protocol during summer 2015 and 2016 across South Carolina, their 95% credible intervals (Lower and Upper CI), and their convergence values ( $R$ -hat). Species codes are as follows: *Lasiurus intermedius* (LAIN); *Eptesicus fuscus* or *Lasionycteris noctivagans* (EPFULANO); *Lasiurus borealis* or *L. seminolus* (LABOLASE); *L. cinereus* (LACI); *Myotis austroriparius* (MYAU); *Myotis leibii*, *M. lucifugus*, or *M. septentrionalis* (MYLELUSE); *Nycticeius humeralis* (NYHU); *Perimyotis subflavus* (PESU); and *Tadarida brasiliensis* (TABR).

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**Table S3.** Estimated  $\beta$  for intercepts and covariates in top-ranked occupancy models for each bat species or species group detected during acoustic surveys using the North American Bat Monitoring Program (NABat) protocol during summer 2015 and 2016 across South Carolina, their 95% credible intervals (Lower and Upper CI), and their convergence values ( $R$ -hat). These models

were used to generate predicted distributions of bat across South Carolina (Figure 3). Species codes are as follows: *Lasiurus intermedius* (LAIN); *Eptesicus fuscus* or *Lasionycteris noctivagans* (EPFULANO); *Lasiurus borealis* or *L. seminolus* (LABOLASE); *L. cinereus* (LACI); *Myotis austroriparius* (MYAU); *Myotis leibii*, *M. lucifugus*, or *M. septentrionalis* (MYLELUSE); *Nycticeius humeralis* (NYHU); *Perimyotis subflavus* (PESU); and *Tadarida brasiliensis* (TABR).

Found at DOI: <https://doi.org/10.3996/092018-JFWM-087.S3> (19 KB DOCX).

**Reference S1.** Clement MJ, Castleberry SB. 2011. Comparison of survey methods for Rafinesque's big-eared bats. Pages 147–157 in Loeb SC, Lacki MJ, Miller DA, editors. Conservation and management of eastern big-eared bats: a symposium. U.S. Forest Service Southern Research Station General Technical Report SRS-145, Asheville, North Carolina.

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**Reference S2.** Kunz TH. 2003. Censusing bats: challenges, solutions, and sampling biases. Pages 9–19 in O'Shea TJ, Bogan MA, editors. Monitoring trends in bat populations of the United States and territories: problems and prospects. U.S. Geological Survey, Biological Resources Division, Information and Technology Report, USGS/BRD/ITR-2003-003.

Found at DOI: <https://doi.org/10.3996/092018-JFWM-087.S5> (9.54 MB PDF); also available at <https://pubs.usgs.gov/itr/2003/0003/report.pdf>.

**Reference S3.** Loeb SC, Rodhouse TJ, Ellison LE, Lausen CL, Reichard JD, Irvine KM, Ingersoll TE, Coleman JT, Thogmartin WE, Sauer JR, Francis CM, Bayless ML, Stanley TR, Johnson DH. 2015. A plan for the North American bat monitoring program (NABat). U.S. Department of Agriculture Forest Service, Southern Research Station Report No. SRS-208, Asheville, North Carolina.

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**Reference S4.** South Carolina Department of Natural Resources. 2015. South Carolina bat conservation plan. South Carolina Department of Natural Resources, Columbia.

Found at DOI: <https://doi.org/10.3996/092018-JFWM-087.S7> (7.13 MB PDF); also available at <http://www.dnr.sc.gov/wildlife/bats/batconsplan.html>.

**Reference S5.** Starbuck C. 2013. Bat occupancy of forests and managed savanna and woodland in the Missouri Ozark region. Master's thesis. University of Missouri - Columbia.

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**Reference S6.** U.S. Fish and Wildlife Service. 2014.

White-nose syndrome: the devastating disease of hibernating bats in North America.

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