

## Detection probability of bats using active versus passive monitoring

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As technology has evolved, bat researchers have relied more heavily on using acoustic techniques to collect data on bat communities. Acoustic data can be collected actively, where the researcher is present at the sampling point and follows the bat with the detector, or passively, where the researcher is not present and the detector is set out by itself. Active sampling can yield longer, clearer calls, and is only conducted during part of the night (usually from sunset to about 02:00 hours) for short bouts (20 minutes). By contrast, passive sampling can yield lower quality calls, but procedures are easily repeatable and data can be used to measure temporal variation in activity throughout the night and detect individuals and species that are missed during active sampling. Researchers are increasingly attempting to monitor and compare bat communities over time, including sites where both active and passive sampling have occurred. However, these two techniques can yield different detection probabilities and the extent to which data collected using these two techniques can be compared is unclear. Thus, in July 2017 we simultaneously collected acoustic data actively and passively to compare detection probabilities of bats at the Savannah River Site, South Carolina, USA. Using Anabat Express detectors, we detected five species or species groups (*Eptesicus fuscus*/*Lasiurus cinereus*, *L. borealis*/*L. seminolus*, *Perimyotis subflavus*, *Myotis austroriparius*, and *Nycticeius humeralis*) using each method. Using single season occupancy modeling, we found that method (passive vs. active sampling) had a significant effect on detection probabilities of all species, and that passively sampling throughout the night yielded the highest detection probability for all species. As a result, if differences in detection probability are not taken into account, comparison of historical active datasets with current passive datasets could lead to different insights into habitat use by similar bat communities. Based on our findings, we recommend that researchers use passive sampling throughout the night when studying and monitoring bat communities.

*Key words:* acoustics, active sampling, clutter, passive sampling, occupancy probability

### INTRODUCTION

Techniques for monitoring bats have changed rapidly over the past few decades as technology has evolved. In early bat studies, capture methods such as mist netting and harp trapping were heavily relied upon to collect basic community data (Baker and Ward, 1967; Fleming *et al.*, 1972; Kunz, 1973; Bell, 1980; Barclay, 1991; Kuenzi *et al.*, 1999). As acoustic sampling technologies were developed and improved, biologists began to study bats in locations that were otherwise difficult to sample using capture methods (e.g., Hayes, 1997; Wickramasinghe *et al.*, 2003; Williams *et al.*, 2006; Brooks, 2008). Acoustic techniques have been used more heavily in bat monitoring studies over the past two decades because compared to mist netting and harp trapping, acoustic sampling is (1) less invasive (no direct capture or handling of bats required), (2) less time consuming,

(3) can be used to sample a wide variety of habitats, and (4) can be used to estimate changes in species richness over time if surveys are repeated (O'Farrell, 1997; Kuenzi and Morrison, 1998; Barclay, 1999; O'Farrell *et al.*, 1999; Murray *et al.*, 1999; Barlow *et al.*, 2015). However, because individuals cannot be identified from call data, acoustic surveys can only produce estimates of activity and not true abundance (Hayes, 1997, 2000). Additionally, some species such as several *Myotis* spp. have very similar call structures that makes differentiating among them difficult (Loeb *et al.*, 2015).

There are two broad categories of acoustic sampling methods in use today, passive and active sampling (O'Farrell, 1998). Active sampling occurs when a surveyor is present at the survey point and actively changes the direction of the microphone to follow the flight path of a passing bat (Menzel *et al.*, 2002). Active sampling typically occurs from sunset

to 02:00 hours with each survey period lasting 20–30 minutes (Johnson *et al.*, 2002; Menzel *et al.*, 2003; Francl *et al.*, 2004; Milne *et al.*, 2004; Brooks and Ford, 2005; Coleman *et al.*, 2014). Because the researcher follows the flight of a passing bat, active sampling can result in higher quality calls and a longer call sequence than other methods, which can make identification of the call easier (Britzke, 2002; Milne *et al.*, 2004). By contrast, passive sampling uses automatic or remote recording techniques, where the surveyor is not present at the time of recording and the detector's microphone is fixed in space (one height, direction and orientation — Britzke, 2002). This can result in lower quality calls that have fewer pulses than actively collected recordings (Britzke, 2002; Milne *et al.*, 2004). However, passive sampling is less labor intensive and more cost efficient (Coleman *et al.*, 2014), allowing sampling of multiple sites simultaneously across large spatial scales and throughout the night. Passive sampling can be sustained for multiple nights, is easily repeatable and can be used to measure temporal variation in activity within and across nights (Hayes, 1997; Murray *et al.*, 1999; Razgour *et al.*, 2011; Coleman *et al.*, 2014). Due to these benefits, biologists are increasingly shifting toward passive sampling instead of active sampling, but the extent to which data collected by different sampling methods can be compared remains unclear.

There is an urgent need to evaluate trends in bat populations due to widespread declines in bat species from disease, habitat loss, and wind energy development (Arnett *et al.*, 2008; Jones *et al.*, 2009; USFWS, 2018) and associated changes in bat communities (Jachowski *et al.*, 2014; Teets, 2018; Thalke *et al.*, 2018). However, if trend analyses rely on both passive and active datasets, it is important to determine whether the methods are comparable. Passive and active acoustic techniques can yield different probabilities that a species is detected during a survey period given that the site is occupied (MacKenzie *et al.*, 2006; Coleman *et al.*, 2014). For example, when using active sampling techniques the researcher may miss peaks of activity throughout the night, which can lead to lower detection probabilities (Hayes, 2000). While some studies have attempted to test and compare passive and active acoustic methods, to our knowledge, these studies either did not collect passive and active data using identical methods (e.g., Johnson *et al.*, 2002; Milne *et al.*, 2004) or did not collect all of their passive and active data simultaneously (e.g., Coleman *et al.*, 2014). Further, no such comparative study has been

conducted in the southern U.S. Coastal Plain, which has a different bat community than those of the previous studies.

The objective of this study was to simultaneously compare passive and active acoustic sampling designs in a bat community in the Coastal Plain of South Carolina, USA. Specifically, we determined how sampling method (either passive or active) and environmental conditions influenced detection probabilities of species groups. In doing so, we generated information on the comparability of data collected using different methods, which will help researchers when they conduct comparative or long-term studies in other bat communities.

## MATERIALS AND METHODS

### *Study Site and Sampling*

We conducted our study on the Savannah River Site (SRS) which is situated in Aiken, Allendale, and Barnwell counties of south-central South Carolina, USA. SRS is located in the upper Coastal Plain physiographic region and is a United States Department of Energy nuclear weapons production and maintenance facility and National Environmental Research Park (Menzel *et al.*, 2003). SRS encompasses 80,267 ha of land dominated by upland pine forests (62%) that are actively managed through pine harvest and prescribed fire for red-cockaded woodpeckers (*Picoides borealis*). Other habitat types at SRS include bottomland hardwood forests (14.8%), upland hardwood forests (3.4%), and mixed pine-hardwood forests (5.2%). Carolina bays, a unique wetland ecosystem, are also interspersed throughout SRS, as well as man-made structures such as utility right-of-ways and production facilities (14.6% — Ford *et al.*, 2006). We selected sampling points by revisiting a random subsample ( $n = 50$ ) of sites sampled previously by Ford *et al.* (2006): upland pine ( $n = 18$ ), upland hardwood ( $n = 2$ ), mixed pine-hardwood ( $n = 6$ ), Carolina bay ( $n = 8$ ), and bottomland hardwood ( $n = 16$ ) in July 2017. All points sampled were located from 0 to 192 m (mean = 48 m) from the edge of a habitat.

We used Anabat Express bat detectors (Titley Scientific, Brendale, Australia) to record bat calls in the five habitat types. When sampling passively, we placed detectors at the top of 3.7-m poles and set them to record from sunset to sunrise for two to four consecutive nights. During the passive sampling period, the same points were actively sampled using a second detector. When conducting active sampling, we followed the methods of Ford *et al.* (2006) and swept the Anabat detector back and forth to scan for bat activity for 20 minutes from shortly after dusk to about 01:00 hours. As Anabat Express detectors do not have built-in speakers, we used an Anabat SD2 Bat Detector (Titley Scientific, Brendale, Australia) to follow the path of a bat when it flew past. We avoided sampling during periods of high winds or moderate to heavy precipitation (Ford *et al.*, 2005).

Calls were downloaded from SD cards using AnalookW (version 4.1z). We used two custom filters to separate passes ( $\geq$  one pulse) from noise and to separate low-quality calls ( $<$  five pulses) from high-quality calls ( $\geq$  five pulses) (Loeb

and O’Keefe, 2006). We used Kaleidoscope Pro (version 4.1.0a) to identify calls collected passively to species and manually vetted and corrected misidentified calls. Actively collected calls were manually identified. Nine species of bats have been previously documented to occur at SRS (Menzel *et al.*, 2003; Ford *et al.*, 2006): *Perimyotis subflavus*, *Myotis austroriparius*, *Eptesicus fuscus*, *Nycticeius humeralis*, *Lasiurus cinereus*, *L. borealis*, *L. seminolus*, *Corynorhinus rafinesquii*, and *Tadarida brasiliensis*. We grouped species calls into five groups based on similar echolocation call structure. *Eptesicus fuscus* and *L. cinereus* were grouped as ‘low frequency bats’; *L. borealis* and *L. seminolus* were in the ‘red bats’ category; and *N. humeralis*, *P. subflavus*, and *M. austroriparius* were in their own respective groups. *Tadarida brasiliensis* was occasionally detected acoustically at SRS (Menzel *et al.*, 2003) but, we did not record any of this species. We also did not record *C. rafinesquii*, most likely due to its low-intensity calls (Clement and Castleberry, 2011).

### Site Data Collection

We recorded basal area of trees and amount of vegetative clutter at each point sampled. Basal area was measured using a JIM-GEM Cruz-All tool (Forestry Suppliers, Jackson, Mississippi, USA) for trees up to 10 m from each survey point (BCF, 2016). We visually categorized the amount of clutter as low, medium, or high based on understory conditions in all directions up to 3 m from the detector (Loeb and O’Keefe, 2006). Areas with little or no structural obstructions (e.g., branches) were considered to be low clutter, while areas with enough structural obstructions that would make it difficult for a bat to fly through were considered to be high clutter. Any amount of structural obstructions that fell between low and high clutter was considered to be medium clutter. We downloaded minimum nightly temperature (°C) and total nightly precipitation (mm) for the closest weather station to SRS (<http://mesowest.utah.edu/cgi-bin/droman/mesomap.cgi?state=SC&drawflag=3>).

### Statistical Analyses

Treating each of the three sampling methods as a sampling occasion, we used the package ‘unmarked’ in program R (R Development Core Team, 2010; Fiske *et al.*, 2011) to fit single-season site-occupancy models to examine factors that might influence the detection probability ( $p$ ) of bat species (MacKenzie *et al.*, 2006). We developed 10 a priori models using existing literature (Table 1), where we hypothesized that clutter amount (low, medium, high), precipitation, minimum nightly temperature, data collection method (20-minute active, 20-minute passive, or all-night passive), and basal area would have an effect on our ability to detect bat species. Specifically, we predicted that as clutter (Ford *et al.*, 2006; Loeb and O’Keefe, 2006), precipitation (Kunz, 1973), and basal area (Ford *et al.*, 2006) increased, bat species detectability would decrease, and that bat species detectability would increase with temperature (Kunz, 1973). We also predicted that we would be more likely to detect bats when sampling passively throughout the night, and less likely to detect bats when sampling actively or passively for 20 minutes (Coleman *et al.*, 2014). We included an interaction model, method \* clutter, to test the hypothesis that certain methods would perform better in different clutter amounts. We predicted that we would be less likely to detect bats using passive sampling in medium and high clutter than

when using active sampling. We also included a global and null model in our model set. Prior to model fitting, we standardized precipitation, temperature, and basal area to a mean of zero and standard deviation of 1. We checked the variables within our a priori models for correlation by calculating Pearson’s correlation coefficients for continuous variables and ANOVAs for categorical and continuous variables. We used Pearson’s chi-square tests to examine the independence of categorical variables. None of the variables included in our a priori models were correlated (Pearson’s product-moment correlation coefficient  $< 0.5$ , ANOVA:  $P < 0.05$ , Pearson’s chi-square:  $P < 0.05$ ), therefore, all covariates were kept in all models.

Before conducting model selection, we assessed goodness-of-fit of the global model for each species. Using methods described by MacKenzie and Bailey (2004), we determined the value of the overdispersion factor ( $\hat{c}$ ) using 1000 bootstrap simulations. If  $\hat{c}$  was  $> 1$ , we considered our data to be overdispersed and used the resulting  $\hat{c}$  to calculate the quasi-likelihood Akaike’s Information Criterion adjusted for overdispersion and small sample sizes (QAIC<sub>C</sub>). If  $\hat{c}$  was  $\leq 1$ , we assumed our data were not overdispersed and used  $\hat{c} = 1$  to calculate the Akaike’s Information Criterion adjusted for small sample sizes (AIC<sub>C</sub> — Burnham and Anderson, 2002).

We ranked models based on either AIC<sub>C</sub> or QAIC<sub>C</sub> and Akaike weights ( $w_i$ ) (Burnham and Anderson, 2002) using the package ‘AICcmodavg’ in R (Mazerolle, 2017). We considered models that were  $\leq 2 \Delta\text{AIC}_C$  or  $\leq 2 \Delta\text{QAIC}_C$  units from the top model to have strong support (Burnham and Anderson, 2002; MacKenzie *et al.*, 2006). If there was only one top model, we back-transformed parameter estimates, standard errors, and 95% confidence intervals. To address model selection uncertainty, we calculated model-averaged parameter estimates, standard errors, and 95% confidence intervals based on all detection models in our  $2 \Delta\text{AIC}_C$  or  $2 \Delta\text{QAIC}_C$  confidence set (Burnham and Anderson, 2002). Covariates with confidence intervals that did not overlap zero were considered to significantly influence detection probabilities. Lastly, we calculated detection probability estimates of each species group for each data collection method.

## RESULTS

During July 2017, we collected 108 call files using active sampling, 18 call files using passive sampling during the same 20-minute time period active data were collected, and 1,463 call files using passive sampling throughout the night. We observed that each of our five species groups was detected at least once using each method.

We found that data were overdispersed for some species groups but not for others, and that models containing ‘method’ generally performed better at predicting detection probabilities across species groups (Table 2). The goodness-of-fit tests for *N. humeralis* and *M. austroriparius* global detection models indicated that data for each species were overdispersed. Therefore, we used QAIC<sub>C</sub> to rank detection probability models for those species. There was good fit for the global detection models

TABLE 1. A priori model variables for detection probability ( $p$ ) of bats at Savannah River Site, South Carolina, USA. A null model was included in the analysis. All listed variables were included when comparing passive and active data collection methods

Model #	Variable	Hypothesis	Covariates	Predicted effects	Literature cited
1	Clutter	Clutter has an effect on bat $p$	Low, medium, high	As clutter amount increases, bat $p$ decreases	Ford <i>et al.</i> (2006); Loeb and O'Keefe, (2006)
2	Precipitation (mm)	Precipitation has an effect on bat $p$	Continuous	As amount of precipitation increases, bat $p$ decreases	Kunz (1973)
3	Minimum nightly temperature ( $^{\circ}$ C)	Temperature has an effect on bat $p$	Continuous	As temperature increases, bat $p$ increases	Kunz (1973)
4	Method	Method of data collection has an effect on bat $p$	Passive all night, passive 20 min, active	More likely to detect bats passively all night, less likely to detect bats passively for 20 min and actively	Coleman <i>et al.</i> (2014)
5	Basal area ( $\text{m}^2/\text{ha}$ )	Basal area will have an effect on bat $p$	Continuous	As basal area increases, bat $p$ decreases	Ford <i>et al.</i> (2006)
6	Temperature + Precipitation	Weather variables have an additive effect on bat $p$	Continuous ( $^{\circ}$ C and mm)	Temperature will have a positive effect on bat $p$ as it increases, but precipitation has a negative effect on bat $p$ as it increases	
7	Clutter + Basal area	Clutter and basal area have an additive effect on bat $p$	Categorical (low, medium, high) and continuous ( $\text{m}^2/\text{ha}$ )	Clutter and basal area will have a negative impact on bat $p$ as both variables increase (low to medium to high clutter; increasing basal area)	
8	Method * Clutter	Certain methods will perform better in different clutter amounts	Categorical (passive 20 min, passive all night, and active; low, medium, high)	$p$ will be lower when using passive all night in medium and high clutter sites than using active sampling. $p$ will be low when using passive 20 min in all clutter amounts	
9	Clutter + Precipitation + Temperature + Method + Basal area + (Method * Clutter)	Global model	Continuous (mm; $^{\circ}$ C; $\text{m}^2/\text{ha}$ ) and categorical (low, medium, high; active, passive 20 min, passive all night)		

for low-frequency bats, red bats, and *P. subflavus*; therefore, we used  $\text{AIC}_C$  to rank detection probability models for those species. The global model did not converge for *P. subflavus*, so we did not include it in subsequent analyses. The method model was the top ranked model for low frequency bats, *N. humeralis*, *M. austroriparius*, and *P. subflavus* (Table 2). Detection probabilities for low-frequency bats, *N. humeralis*, *M. austroriparius*, and *P. subflavus* were highest when collecting data passively throughout the night, followed by active sampling, followed by passive sampling for 20 minutes (Fig. 1 and Table 3). The global model was the top-ranked

model for red bats, followed by the interaction model (method \* clutter). However, the interaction model did not converge and thus we proceeded with interpretation from the global model. Temperature, basal area, clutter amount, and method were the parameters within the top model for red bats with a 95% confidence interval that did not bound zero (Table 3). Red bat detection probability increased by 10% for every  $1^{\circ}$ C increase in minimum nightly temperature (Fig. 2A), increased by 10% for every 40  $\text{m}^2/\text{ha}$  decrease in basal area (Fig. 2B), was highest when collecting data passively all night, followed by actively sampling (Fig. 1), and highest

TABLE 2. Top-ranked models ( $\Delta AIC_C$  or  $\Delta QAIC_C \leq 2$ ) for passive vs. active detection probability ( $p$ ) for bats at Savannah River Site, South Carolina, USA, July 2017. Data for low-frequency bats, red bats, and *P. subflavus* were not overdispersed and  $AIC_C$  was used to rank these species' models. Data for *N. humeralis* and *M. austroriparius* bats were overdispersed and  $QAIC_C$  was used to rank their models

Species group	Model name	K	LogLik or Q-LogLik	$AIC_C$ or $QAIC_C$	$\Delta AIC_C$ or $\Delta QAIC_C$	$w_i$
Low-frequency bats	Method	4	-71	150	0	0.79
Red bat	Global	13	-51	138	0	0.55
	Method * Clutter	10	-56	139	0.65	0.40
<i>N. humeralis</i>	Method	5	-21	53	0	0.50
<i>M. austroriparius</i>	Method	5	-43	97	0	0.88
<i>P. subflavus</i>	Method	4	-63	136	0	0.87

in low clutter, followed by high and medium clutter (Fig. 2C).

## DISCUSSION

As we predicted, passively sampling throughout the night performed better in detecting bats than sampling actively or passively for 20 minutes. Collecting data passively throughout the night yielded detection probabilities that were consistently two to four times higher than active sampling across all bat species. Coleman *et al.* (2014) found similar 2–4 fold differences in bat detection probability between active and passive sampling in a different bat community in New York, collectively suggesting that passive sampling is a superior sampling method overall compared to active sampling. However, passive sampling for only 20 minutes consistently had lower estimated detection probabilities compared

to active sampling during the same 20 minutes interval, similar to Johnson *et al.* (2002). While we can think of no practical reason to run passive sampling for only 20 minutes, if time and equipment are limited for the researcher to survey a site, active sampling will improve probability of detection compared to similarly short (i.e., 20 minutes) periods of passive sampling.

Higher detection probabilities using full-night passive sampling compared to active or passive sampling for only 20 minutes are likely due to the greater time period available for bats to be detected during full-night recording. Bats often travel over long distances each night and visit various habitat types in a night (Lacki *et al.*, 2007) and thus, at least two nights of either mist-netting or acoustic surveys are necessary to maximize the number of species detected (Francl *et al.*, 2011). Further, activity of bats is not constant over the night (e.g., Jones

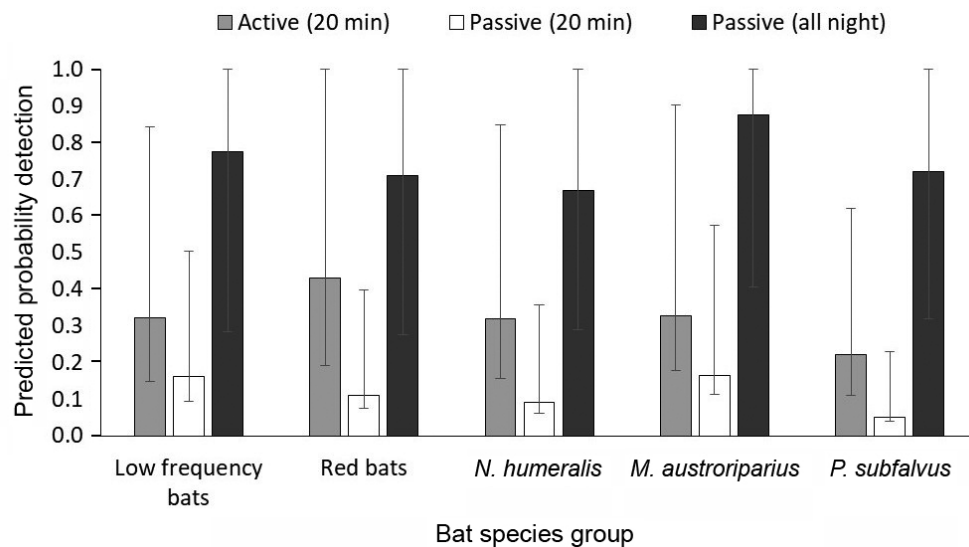


FIG. 1. Predicted probability of detection ( $p$ ) for each species group for each data collection method when comparing passive and active sampling techniques at Savannah River Site, South Carolina, USA, July 2017. The error bars represent the 95% confidence interval

TABLE 3. Parameter estimates, standard errors (SE), and 95% confidence intervals (CI) of parameters within the top models for detection ( $P$ ) models of low-frequency bats, red bats, *N. humeralis*, and *M. austroriparius* at Savannah River Site, South Carolina, USA, when comparing passive and active acoustic sampling methods

Parameter	Estimate	SE	95% CI	
			Upper	Lower
Low-frequency bats				
Intercept (Active)	-0.74	0.42	-0.32	-1.16
Passive (20 min)	-0.91	0.62	-0.29	-1.53
Passive (all night)	1.98	0.66	2.64	1.32
Red bat				
Intercept	-1.71	0.64	-1.08	-2.35
Low clutter	1.40	0.64	2.04	0.75
Medium clutter	-1.53	0.85	-0.68	-2.38
Precipitation	-0.07	0.29	0.22	-0.36
Temperature	0.85	0.33	1.18	0.51
Passive (20 min)	-2.03	0.77	-1.26	-2.80
Passive (all night)	1.08	0.54	1.61	0.54
Basal area	-0.36	0.33	-0.04	-0.69
<i>N. humeralis</i>				
Intercept (Active)	-0.76	0.45	-0.32	-1.21
Passive (20 min)	-1.49	0.72	-0.77	-2.21
Passive (all night)	1.46	0.59	2.05	0.87
<i>M. austroriparius</i>				
Intercept (Active)	-0.72	0.52	-0.20	-1.24
Passive (20 min)	-0.91	0.81	-1.20	-1.72
Passive (all night)	2.67	1.08	3.75	1.59
<i>P. subflavus</i>				
Intercept (Active)	-1.25	0.43	-0.82	-1.68
Passive (20 min)	-1.70	0.82	-0.88	-2.52
Passive (all night)	2.18	0.63	2.81	1.55

*et al.*, 1965; Adams and Fenton, 2017; Teets, 2018) and if surveys are not conducted during a particular species' peak activity period, it is less likely to be detected. Therefore, longer surveys will more likely record bats as they traverse the landscape and allow for varying activity patterns, resulting in higher detection probabilities. Maximizing detection probabilities is important for obtaining robust estimates of occupancy and minimizing the number of surveys that are needed to obtain those estimates (MacKenzie and Royle, 2005). For example, when detection probabilities are  $\geq 0.24$ , three nights are sufficient to obtain precise estimates of occupancy for eight species of bats in California (Weller, 2008). However, far greater effort would be necessary to obtain robust occupancy estimates for five other species with very low detection probabilities. Fortunately, technological advances in the amount of memory on memory cards used in bat detectors and use of solar panels to extend battery life now make it possible to leave detectors for multiple days, weeks or even months

— potentially allowing future researchers to gain insights on these species.

Despite the inclusion of environmental covariates that are known to influence bat detection probability in other studies (e.g., Yates and Muzika, 2006; Kaiser and O'Keefe, 2015; Starbuck *et al.*, 2015), sampling method alone was the most parsimonious predictor of variation in bat detection probability for all bat species except the red bats. Detection probability of *L. borealis* and *L. seminolus* increased with temperature but decreased with basal area, similar to red bats in Missouri (Starbuck, 2013). However, they were also more likely to be detected in low and high clutter habitats than in medium clutter habitats. Red bats use a wide variety of habitats and are considered to be clutter-adapted as well as open-space foragers (Menzel *et al.*, 2005; Morris *et al.*, 2010). The relationships between clutter and basal area and red bat detection probability suggests that these variables should be considered in other models of detection and occupancy as they can greatly influence the ability of detectors to pick up echolocation calls as well as the structure of the echolocation calls emitted (Britzke *et al.*, 2013).

Accounting for differences in detection probability among techniques is important in studies that utilize multiple acoustic sampling methods. With the multitude of threats facing North American bats, there is increasing need to track trends in bat populations (Loeb *et al.*, 2015). Further, remnant bat populations have been found to change their habitat selection patterns in response to community-level changes in bat occurrence (Jachowski *et al.*, 2014). Our findings suggest that failing to account for different probabilities of detection between methods could bias monitoring data and affect the resulting inferences of population trends or changes in habitat selection patterns. For example, 15 years prior to this study, Ford *et al.* (2006) collected acoustic data using active sampling at this site and did not account for detection probability when examining bat habitat use. We used passive sampling during 2016 and 2017 at a subset of the points Ford *et al.* (2006) established and observed several differences in bat species habitat use from their study (Teets, 2018). Because of differences in detection probability, it is difficult to tease apart whether these differences could be due to sampling method or actual changes in habitat associations by the species over time. Thus, we caution against attempts to compare historical active sampling datasets with more recent passive sampling datasets to gain insights in the response of bat communities to white-nose syndrome

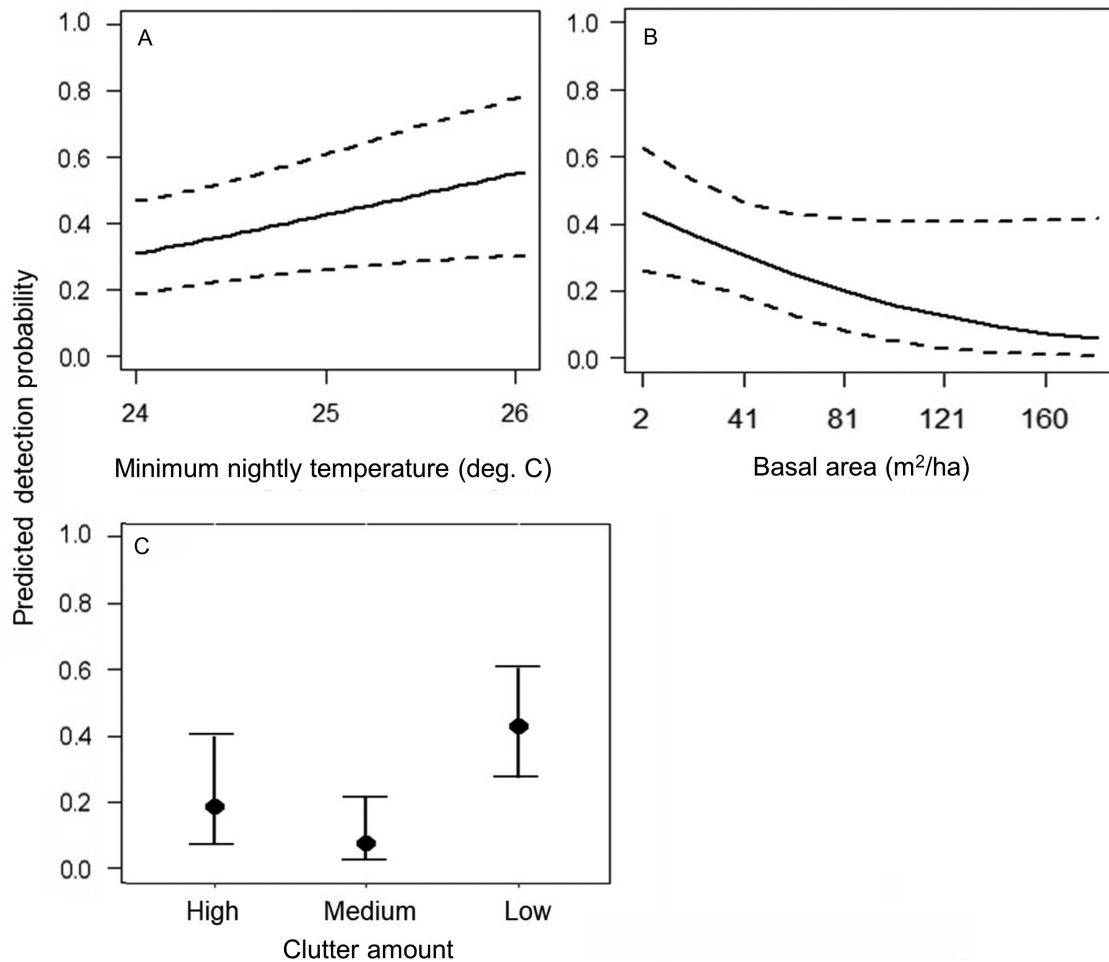


FIG. 2. Influence of (A) minimum nightly temperature ( $^{\circ}\text{C}$ ), (B) basal area ( $\text{m}^2/\text{ha}$ ), and (C) clutter amount on probability of detection ( $p$ ) of red bats during July 2017 at Savannah River Site, South Carolina, USA. Covariates are from the top-ranked detection model. The dotted lines and vertical lines represent 95% confidence intervals

(WNS) or other recent disturbances without trying to account for differences in detection probability, as contrasting results could simply be due to method rather than actual changes in bat communities.

Similar to Coleman *et al.* (2014), while detection probability varied among species, we still detected the same total number of species across methods. However, this could be due to the relatively large number of sites surveyed using each technique, and the resident community of bats at each site. Elsewhere, studies have observed a difference in the number of species detected between active and passive techniques (Johnson *et al.*, 2002; Milne *et al.*, 2004), suggesting care needs to be taken when trying to assume either active or passive sampling is sufficient for determining the number of species within an area. For example, while known to exist in our study area, neither *C. rafinesquii* nor *T. brasiliensis* were detected by either method, suggesting that alternative sampling methods might be needed

to monitor these species over time (Clement and Castleberry, 2011; Neece, 2017).

Our comparison of active and passive data collection techniques demonstrates the pitfalls of comparing datasets collected using different methods. As North American bat populations become increasingly vulnerable to threats including WNS, wind energy development, and habitat loss and degradation (Arnett *et al.*, 2008; Jones *et al.*, 2009; USFWS, 2018), monitoring these populations becomes increasingly important. To understand the structure of these bat communities, researchers need to have the most accurate information that is comparable over time. At a minimum, we encourage researchers to account for variation in species-specific detection probability between sampling methods. Because of the issues identified above, we recommend that long-term bat acoustic monitoring programs adopt the consistent use of passive sampling throughout the night.

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## LITERATURE CITED

- ADAMS, A. M., and M. B. FENTON. 2017. Identifying peaks in bat activity: a new application of SaTScan's space-time scan statistic. *Wildlife Research*, 44: 392–399.
- ARNETT, E. B., W. K. BROWN, W. P. ERICKSON, J. K. FIEDLER, B. L. HAMILTON, T. H. HENRY, A. JAIN, G. D. JOHNSON, J. KERNS, R. R. KOFORD, *et al.* 2008. Patterns of bat fatalities at wind energy facilities in North America. *Journal of Wildlife Management*, 72: 61–78.
- BAKER, R. J., and C. M. WARD. 1967. Distribution of bats in southeastern Arkansas. *Journal of Mammalogy*, 48: 130–132.
- BARCLAY, R. M. R. 1991. Population structure of temperate zone insectivorous bats in relation to foraging behavior and energy demand. *Journal of Animal Ecology*, 60: 165–178.
- 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.
- BARLOW, K. E., P. A. BRIGGS, K. A. HAYSOM, A. M. HUTSON, N. L. LECHIARA, P. A. RACEY, A. L. WALSH, and S. D. LANGTON. 2015. Citizen science reveals trends in bat populations: The National Bat Monitoring Programme in Great Britain. *Biological Conservation*, 182: 14–26.
- BCF [British Columbia Ministry of Forests, Lands, and Natural Resource Operations]. 2016. Choosing BAF. Accessed 22 May 2016 at [https://www.for.gov.bc.ca/hfp/silviculture/MPBI/documents/sampling\\_basal\\_area.pdf](https://www.for.gov.bc.ca/hfp/silviculture/MPBI/documents/sampling_basal_area.pdf).
- BELL, G. P. 1980. Habitat use and response to patches of prey by desert insectivorous bats. *Canadian Journal of Zoology*, 58: 1876–1883.
- BRITZKE, E. R. 2002. Designing monitoring programs using frequency-division bat detectors: active versus passive sampling. Pp. 79–83, *in* Bat echolocation research: tools, techniques, and analysis (R. M. BRIGHAM, E. K. V. KALKO, G. JONES, S. PARSONS, and H. J. G. A. LIMPENS, eds.). Bat Conservation International, Austin, 167 pp.
- BRITZKE, E. R., E. H. GILLAM, and K. L. MURRAY. 2013. Current state of understanding of ultrasonic detectors for the study of bat ecology. *Acta Theriologica*, 58:109–117.
- BROOKS, R. T. 2008. Habitat-associated and temporal patterns of bat activity in a diverse forest landscape of southern New England, USA. *Biodiversity Conservation*, 18: 529–545.
- BROOKS, R. T., and W. M. FORD. 2005. Bat activity in a forest landscape of central Massachusetts. *Northeastern Naturalist*, 12: 447–462.
- BURNHAM, K. P., and D. R. ANDERSON. 2002. Model selection and multi-model inference: a practical information-theoretic approach, 2nd edition. Springer, New York, USA, 488 pp.
- CLEMENT, M. J., and S. B. CASTLEBERRY. 2011. Comparison of survey methods for Rafinesque's big-eared bats. Pp. 147–157, *in* Conservation and management of eastern big-eared bats: a symposium (S. C. LOEB, M. J. LACKI, and D. A. MILLER, eds.). U.S. Forest Service Southern Research Station, Clemson, SC, USA, 157 pp.
- COLEMAN, L. S., W. M. FORD, C. A. DOBONY, and E. R. BRITZKE. 2014. A comparison of passive and active acoustic sampling for a bat community impacted by white-nose syndrome. *Journal of Fish and Wildlife Management*, 5: 217–226.
- FISKE, I. J., R. B. CHANDLER, and J. A. ROYLE. 2011. Unmarked: models for data from unmarked animals. Available at <http://CRAN.R-project.org/package=unmarked>.
- FLEMING, T. H., E. T. HOOPER, and D. E. WILSON. 1972. Three Central American bat communities: structure, reproductive cycles, and movement patterns. *Ecology*, 53: 555–569.
- FORD, W. M., M. A. MENZEL, J. L. RODRIGUE, J. M. MENZEL, and J. B. JOHNSON. 2005. Relating bat species presence to simple habitat measures in a central Appalachian forest. *Biological Conservation*, 126: 528–539.
- FORD, W. M., J. M. MENZEL, M. A. MENZEL, J. W. EDWARDS, and J. C. KILGO. 2006. Presence and absence of bats across habitat scales in the upper Coastal Plain in South Carolina. *Journal of Wildlife Management*, 70: 1200–1209.
- FRANCL, K. E., W. M. FORD, and S. B. CASTLEBERRY. 2004. Bat activity in central Appalachian wetlands. *Georgia Journal of Science*, 62: 87–94.
- FRANCL, K. E., R. C. BLAND, J. S. LUCAS, and V. BRACK, JR. 2011. Comparison of survey techniques for documenting summer bat communities in Pennsylvania and New Jersey. *Journal of the Pennsylvania Academy of Science*, 85: 52–56.
- HAYES, J. P. 1997. Temporal variation in activity of bats and the design of echolocation-monitoring studies. *Journal of Mammalogy*, 78: 514–524.
- HAYES, J. P. 2000. Assumptions and practical considerations in the design and interpretation of echolocation-monitoring studies. *Acta Chiropterologica*, 2: 225–236.
- JACHOWSKI, D. S., C. A. DOBONY, L. S. COLEMAN, W. M. FORD, E. R. BRITZKE, and J. L. RODRIGUE. 2014. Disease and community structure: white-nose syndrome alters spatial and temporal niche partitioning in sympatric bat species. *Diversity and Distributions*, 20: 1002–1015.
- JOHNSON, J. B., M. A. MENZEL, J. W. EDWARDS, and W. M. FORD. 2002. A comparison of two acoustical bat survey techniques. *Wildlife Society Bulletin*, 30: 931–936.
- JONES, C., W. M. HOWELL, R. D. CALDWELL, H. L. COOK, M. A. MURPHY, M. A. MOE, and G. T. MARTIN. 1965. Ecological distribution and activity periods of bats of the Mogollon Mountains area of New Mexico and adjacent Arizona. *Tulane Studies in Zoology*, 12: 93–100.
- JONES, G., D. S. JACOBS, T. H. KUNZ, M. R. WILLIG, and R. A. RACEY. 2009. Carpe noctem: the importance of bats as bioindicators. *Endangered Species Research*, 8: 93–115.
- KAISER, Z. D., 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.
- KUENZI, A. J., and M. L. MORRISON. 1998. Detection of bats by mist-nets and ultrasonic sensors. *Wildlife Society Bulletin*, 26: 301–311.
- KUENZI, A. J., G. T. DOWNARD, and M. L. MORRISON. 1999. Bat distribution and hibernacula use in west central Nevada. *The Great Basin Naturalist*, 59: 213–220.
- KUNZ, T. H. 1973. Resource utilization: temporal and spatial components of bat activity in Central Iowa. *Journal of Mammalogy*, 54: 14–32.
- LACKI, M. J., S. K. AMELON, and M. D. BAKER. 2007. Foraging ecology of bats in forests. Pp. 83–127, *in* Bats in forests:



- conservation and management (M. J. LACKI, J. P. HAYES, and A. KURTA, eds.). Johns Hopkins University Press, Baltimore, Maryland, 329 pp.
- LOEB, S. C., and J. O'KEEFE. 2006. Habitat use by forest bats in South Carolina in relation to local, stand, and landscape characteristics. *Journal of Wildlife Management*, 70: 1210–1218.
- LOEB, S. C., T. J. RODHOUSE, L. E. ELLISON, C. L. LAUSEN, J. D. REICHARD, K. M. IRVINE, T. E. INGERSOLL, J. T. H. COLEMAN, W. E. THOGMARTIN, J. R. SAUER, *et al.* 2015. A plan for the North American Bat Monitoring Program (NABat). A plan for the North American Bat Monitoring Program (NABat). General Technical Report SRS-208, U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC, 100 pp.
- MACKENZIE, D. I., and L. L. BAILEY. 2004. Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics*, 9: 300–318.
- MACKENZIE, D. I., and A. ROYLE. 2005. Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology*, 42: 1105–1114.
- MACKENZIE, D. I., J. D. NICHOLS, J. A. ROYLE, K. H. POLLOCK, L. L. BAILEY and J. E. HINES. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Academic Press, New York, USA, 648 pp.
- MAZEROLLE, M. J. 2017. Model selection and multimodel inference based on (Q)AIC(c). Available at <https://cran.r-project.org/web/packages/AICcmodavg/index.html>.
- MENZEL, M. A., T. C. CARTER, J. M. MENZEL, W. M. FORD, and B. R. CHAPMAN. 2002. Effects of group selection silviculture in bottomland hardwoods on the spatial activity patterns of bats. *Forest Ecology and Management*, 162: 209–218.
- MENZEL, M. A., J. M. MENZEL, J. C. KILGO, W. M. FORD, T. C. CARTER, and J. W. EDWARDS. 2003. Bats of the Savannah River Site and vicinity. USDA Forest Service, Southern Research Station, Asheville, NC. General Technical Report GTR-SRS-68, 69 pp.
- MENZEL, J. M., M. A. MENZEL, JR., J. C. KILGO, W. M. FORD, J. W. EDWARDS, and G. F. MCCracken. 2005. Effect of habitat and foraging height on bat activity in the coastal plain of South Carolina. *Journal of Wildlife Management*, 69: 235–245.
- MILNE, D. J., M. ARMSTRONG, A. FISHER, T. FLORES, and R. PAVEY. 2004. A comparison of three survey methods for collecting bat echolocation calls and species-accumulation rates from nightly Anabat recordings. *Wildlife Research*, 31: 57–63.
- MORRIS, A. D., D. A. MILLER, and M. C. KALCOUNIS-RUEPPELL. 2010. Use of forest edges by bats in a managed pine forest landscape. *Journal of Wildlife Management*, 74: 26–34.
- MURRAY, K. L., E. R. BRITZKE, B. M. HADLEY, and L. W. ROBINS. 1999. Surveying bat communities: a comparison between mist nets and the Anabat II bat detector system. *Acta Chiropterologica*, 1: 105–112.
- NEECE, B. D. 2017. North American Bat Monitoring Program (NABat) in South Carolina: acoustic detection and landscape occupancy of bats. Clemson University, Clemson, SC, 85 pp.
- O'FARRELL, M. J. 1997. Use of echolocation calls for the identification of free-flying bats. *Transactions of the Western Section of the Wildlife Society*, 33: 1–8.
- O'FARRELL, M. J. 1998. A passive monitoring system for Anabat II using a laptop computer. *Bat Research News*, 39: 147–150.
- O'FARRELL, M. J., C. CORBEN, W. L. GANNON, and B. W. MILLER. 1999. Confronting the dogma: a reply. *Journal of Mammalogy*, 80: 297–302.
- R DEVELOPMENT CORE TEAM. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <http://www.R-project.org>.
- RAZGOUR, O., C. KORINE, and D. SALTZ. 2011. Does interspecific competition drive patterns of habitat use in desert bat communities? *Oecologia*, 167: 493–502.
- STARBUCK, C. 2013. Bat occupancy of forests and managed savanna and woodland in the Missouri Ozark Region. M.Sci. Thesis, University of Missouri, Columbia, MO, USA, 82 pp.
- STARBUCK, C. A., S. K. AMELON, and F. R. THOMPSON, III. 2015. Relationships between bat occupancy and habitat and landscape structure along a savanna, woodland, forest gradient in the Missouri Ozarks. *Wildlife Society Bulletin*, 39: 20–30.
- TEETS, K. D. 2018. Assessment of data collection techniques and white-nose syndrome effects on bat communities of South Carolina. M.Sci. Thesis, Clemson University, Clemson, SC, USA, ix + 92 pp.
- THALKEN, M. M., M. J. LACKI, and J. S. JOHNSON. 2018. Shifts in assemblage of foraging bats at Mammoth Cave National Park following arrival of white-nose syndrome. *Northeastern Naturalist*, 25: 202–214.
- USFWS [UNITED STATES FISH AND WILDLIFE SERVICE]. 2018. White-nose syndrome: the devastating disease of hibernating bats in North America April 2018. Accessed 17 May 2018 at [https://www.whitenosesyndrome.org/sites/default/files/resource/white-nose\\_fact\\_sheet\\_4-2018\\_0.pdf](https://www.whitenosesyndrome.org/sites/default/files/resource/white-nose_fact_sheet_4-2018_0.pdf).
- WELLER, T. J. 2008. Using occupancy estimation to assess the effectiveness of a regional multiple-species conservation plan. *Biological Conservation*, 141: 2279–2289.
- WICKRAMASINGHE, L. P., S. HARRIS, G. JONES, and N. VAUGHAN. 2003. Bat activity and species richness on organic and conventional farms: impact of agricultural intensification. *Journal of Applied Ecology*, 40: 984–993.
- WILLIAMS, J. A., M. J. O'FARRELL, and B. R. RIDDLE. 2006. Habitat use by bats in a riparian corridor of the Mojave desert in Southern Nevada. *Journal of Mammalogy*, 87: 1145–1153.
- YATES, M. D., and R. M. MUZIKA. 2006. Effect of forest structure and fragmentation on site occupancy of bat species in Missouri Ozark forests. *Journal of Wildlife Management*, 70: 1238–1248.

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