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Assessment of Data Collection Techniques and White-nose Syndrome Effects on Bat Communities of South Carolina

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ASSESSMENT OF DATA COLLECTION TECHNIQUES AND WHITE-NOSE
SYNDROME EFFECTS ON BAT COMMUNITIES OF SOUTH CAROLINA

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Katherine Dennie Teets
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ABSTRACT

White-nose syndrome (WNS), an infectious disease that has caused massive declines in bat populations since its discovery in 2006, may be indirectly affecting bat community structure. As WNS-susceptible species populations decline, WNS-resistant species may be taking over foraging niches formerly occupied by WNS-susceptible species. We hypothesized that bat communities located in WNS-positive areas in South Carolina have experienced niche partitioning relaxation.

First, because some pre-WNS acoustic data were collected using different methods than those primarily used today, we examined if sampling method affected detection probabilities and our interpretation of habitat use of bats. We collected data using passive and active techniques in July 2017 at the Savannah River Site in South Carolina. We used occupancy modeling to determine if data collection method influenced detection probability of bats. We found that method had a significant effect on detection probabilities of all species and that passively sampling throughout the night yielded the highest detection probability. To further examine if data collection method influenced habitat use conclusions, we used occupancy modeling to analyze data collected passively in July to August 2016 and July 2017 and compared our results to a historical study in which active acoustic sampling was used at the same sites in 2001. We found that some parameters had the same effect between studies for some species, while other parameters had a different effect between studies. We concluded that data collected using different methods was not comparable.

Second, revisiting a WNS-positive site where passive acoustic sampling was conducted historically, we examined the extent to which spatial and temporal niche partitioning occurred pre- and post-WNS. Specifically, we collected data using acoustic detectors from May to August 2004 and 2005 ("pre-WNS") and from May to August 2016 and May to June 2017 ("post-WNS") in the Andrew Pickens District (APD) of the Sumter National Forest in northwestern South Carolina. To examine changes in the spatial niche partitioning of the bat community, we used multi-season occupancy modeling and examined colonization and extinction probabilities. To examine temporal niche partitioning, we examined bat activity throughout the night using temporal overlap analysis. We found that the WNS-resistant species had higher colonization rates than WNS-susceptible species and changed their nightly activity so that it was more evenly distributed throughout the night post-WNS. Myotis, a WNS-susceptible genus, stopped using areas in hardwood habitat and changed when they were active at night post-WNS. Tricolored bats, a WNS-susceptible species, exhibited changes in the areas they were using, though this did not seem to be contingent on the presence of other species, and did not change when they were active at night post-WNS. These results provide evidence that WNS destabilized the spatial and temporal niche partitioning exhibited by bats pre-WNS in South Carolina and further evidence that WNS is both directly and indirectly affecting the bat communities in North America.

DEDICATION

I would like to dedicate my thesis to my family; Mom, Dad, Jessie, and Michael. I would

not be who I am today if it weren't for you all and I hope I make you proud. You are the

light of my life.

ACKNOWLEDGEMENTS

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CHAPTER ONE

COMPARISON OF PASSIVE AND ACTIVE ACOUSTIC SAMPLING AND
OCCUPANCY OF A BAT COMMUNITY IN SOUTH-CENTRAL SOUTH
CAROLINA

Techniques for monitoring bats have changed rapidly over the past 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 & Ward,
1967; Fleming et al., 1972; Kunz, 1973; Bell, 1980; Barclay, 1991; Kuenzi et al., 1999).
As acoustic sampling technologies were developed and improved upon, 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 become more heavily relied on in bat monitoring studies over
the past two decades because compared to mist netting and harp trapping, acoustic
sampling is (1) less invasive, (2) less time consuming, (3) can be used to sample a wide
variety of habitats, (4) can be used to estimate changes in species richness over time if
surveys are repeated, and (5) typically has fewer potential biases (O'Farrell, 1997;
Kuenzi & Morrison, 1998; Barclay, 1999; O'Farrell et al., 1999; Murray et al., 1999,
Barlow et al., 2015). However, acoustic sampling has limitations as it can only produce
estimates of activity, not abundance, and individuals cannot be identified from call data
(Hayes, 1997; 2000). Additionally, some species, such as the eastern red bat (*Lasiurus
borealis*) and the Seminole bat (*L. seminolus*), have very similar call structures, making
calls from these species difficult to differentiate from one another (Fenton, 1983; S. Loeb,
United States Forest Service, personal communication).

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There are two broad categories of acoustic sampling methodology in use today. Active sampling refers to 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 0200 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 & 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 in a longer call sequence, 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 one direction (Britzke, 2002). This can result in lower quality calls that have fewer pulses than actively collected data (Britzke, 2002; Milne et al., 2004). However, passive sampling can be less labor intensive, allowing for sampling across large spatial scales and throughout the night. Passive sampling is also 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 it remains unclear the extent to which data collected by different sampling methods can be compared.

The main concern in attempting to compare passive and active acoustic monitoring data is that passive and active acoustic techniques can yield different detection probabilities, that is, the probability 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 the same methodology (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, there has not been a comparative study conducted within the southern Coastal Plain, which has a different bat community than those of the previously mentioned studies.

The objectives of this study were to simultaneously compare passive and active acoustic sampling designs within a bat community in the Coastal Plain of South Carolina and to determine how sampling method (either active or passive) and environmental conditions influenced detection probabilities of species groups. In addition, we used occupancy modeling to examine habitat use by bats and compared our study's results to a previous study (Ford et al., 2006) that collected data actively at the same sites in 2001 to further evaluate the potential differences between passive (our study) and active (Ford et al., 2006) sampling methods. In doing so, we will provide information on the comparability between data collected using different methods, which will help researchers when they conduct comparative studies in other bat communities.

Methods

Study Site

We conducted our study on the Savannah River Site (SRS) which is situated in south-central South Carolina in Aiken, Allendale, and Barnwell counties. 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 (*Picolides borealis*). Other habitat types at SRS include bottomland hardwood forests (14.8%), upland hardwood (3.4%), and mixed pine-hardwood (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). To date, *Pseudogymnoascus destructans*, the fungus that causes white-nose syndrome (WNS), has not been detected on bats or known to impact bats at SRS (S. Loeb, United States Forest Service, personal communication). Ford et al. (2006) conducted an active acoustic survey at SRS in 2001. They selected 217 points that were at the center of Forest Inventory and Analysis (FIA) plots, which were systematically located across SRS on a 1 km x 1 km grid. An additional 213 points were placed both selectively (i.e., bridge crossings, Carolina bays, and lakes) and randomly in community types that were under-represented in the FIA database (e.g., bottomland hardwood stands and the lower stream reaches) (Ford et al., 2006). From these 430 points, we used stratified random sampling based on habitat type to select 140 points to sample in summer 2016 and 2017 that were allocated in proportion

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to habitat coverage on SRS. We sampled 110 points in June and July 2016 and 50 points in July 2017. All points sampled in 2016 and 2017 were sampled passively. Points sampled in 2017 were sampled actively during one of the nights that data were collected passively. Points sampled for this study were located from 0 to 340 m from the edge of a habitat stand (average = 65 m).

Acoustic Data Collection

For our first objective of comparing active and passive sampling, we used Anabat Express bat detectors (Titley Scientific, Brendale, Australia) to record bat calls. We collected data in five habitat types: upland pine, upland hardwood, mixed pine-hardwood, Carolina Bay, and bottomland. Habitat categorizations were based on data from Ford et al. (2006). We verified the habitat type when the point was sampled, and if the habitat type in 2016 or 2017 differed from that recorded by Ford et al. (2006), it was recorded to reflect the current habitat type. When passively sampling, we deployed detectors for between two and four consecutive nights. Detectors were set to record from sunset to sunrise and were attached to the top of 3.7 m painter's poles that were held upright using a PVC pipe that was connected to a U-pole. The same points were actively sampled during the passive sampling period following Ford et al. (2006), where active surveys were completed by sweeping the Anabat detector back and forth to scan for bat activity for 20 minutes from shortly after dusk to about 0100 hours. As Anabat Express detectors do not have built-in speakers, we used an Anabat SD2 Bat Detector (Titley Scientific, Brendale, Australia) to follow a bat's flight when they flew past. We avoided sampling during periods of high winds or moderate to heavy precipitation (Ford et al., 2005).

To address our second objective of estimating bat occupancy, we passively sampled 140 points in summer 2016 and 2017 across SRS from the 430 points sampled by Ford et al. (2006), including the 50 points included in the active versus passive survey. Sites were surveyed between two and four nights using Anabat Express bat detectors (Titley Scientific, Brendale, Australia) set atop of 3.7 m painter's poles.

For both objectives, calls were downloaded from SD cards and converted from ZCA files to Analook files using AnalookW (version 4.1z). We used two custom filters to separate passes ($\geq$ 1 pulse) from noise and to separate low quality calls ($<$ 5 pulses) from high quality calls ($\geq$ 5 pulses) (Loeb & O'Keefe, 2006). We used Kaleidoscope Pro (version 4.1.0a) to automatically identify calls collected passively to species and manually vetted and corrected mis-identified calls. Calls that were collected actively were manually identified. Nine species of bats have been previously documented to occur at SRS (Menzel et al., 2002; Ford et al., 2006). These species include two WNS-impacted species, the tricolored bat (*Perimyotis subflavus*) (Langwig et al., 2012), and the southeastern myotis (*Myotis austroriparius*) (USFWS, 2018), and seven non-impacted species (USFWS, 2018), the big brown bat (*Eptesicus fuscus*), the evening bat (*Nycticeius humeralis*), the hoary bat (*Lasiurus cinereus*), the eastern red bat, the Seminole bat, Rafinesque's big-eared bat (*Corynorhinus rafinesquii*), and the Brazilian free-tailed bat (*Tadarida brasiliensis*). We grouped species calls into five groups based on similar echolocation call structure. We grouped big brown bats and hoary bats into the "low frequency bat" category; eastern red bats and Seminole bats into the "red bat" category; and evening bats, tricolored bats, and southeastern myotis into their own

respective groups. Despite infrequent records of Brazilian free-tailed bats occurring at SRS (Menzel et al., 2002), we did not record any. We did not record Rafinesque's big-eared bats, most likely due to their low intensity calls (Clement & Castleberry, 2011).

Site Data Collection

We recorded basal area, habitat type, and amount of clutter at each point sampled. Basal area was measured using a JIM-GEM Cruz-All tool (Forestry Suppliers, Jackson, Mississippi) 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 & 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) from the University of Utah's Meso-West website (http://mesowest.utah.edu/cgi-bin/droman/mesomap.cgi?state=SC&rawsflag=3) for the closest weather station to SRS. We calculated the straight line distance from sample points to closest water source (m), closest road (m), and closest Carolina Bay (m) in ArcGIS 10.5 (ESRI, Redlands, California).

Statistical Analyses

For our first objective, we compared actively and passively collected data by first performing Kruskal-Wallis tests (Kruskal & Wallis, 1952) to determine if there was a

significant difference ($P \leq 0.05$) in the average number of calls collected per 20 minutes per species group among sampling methodologies (20-minute active, 20-minute passive, and all night passive). Calls were averaged per sampling night per 20 minute sampling period. We then used the package *unmarked* in program R (Fiske et al., 2011; R Development Core Team, 2010) to fit single-season site-occupancy models to examine factors that may influence the detection probability (*p*) of bat species (MacKenzie et al., 2006). We developed 10 *a priori* models using existing literature (Table 1.1), where we hypothesized that clutter amount (low, medium, high), precipitation, minimum nightly temperature, data collection method (20-minute active, 20-minute passive, and 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 & O'Keefe, 2006), precipitation (Kunz, 1973), and basal area (Ford et al., 2006) increased, bat species detections would decrease, and that bat species detections 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: $P < 0.5$, 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 ($QAIC_C$). If $\hat{c}$ was ≤ 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_C; Burnham & Anderson, 2002).

We ranked models based on either AIC_C or $QAIC_C$ and Akaike weights (w_i) (Burnham & Anderson, 2002) using the package *AICcmodavg* in R (Mazerolle, 2017). We considered models with Akaike weights that were ≤ 2 ΔAIC_C or $QAIC_C$ to have strong support (Burnham & 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 ΔAIC_C or $QAIC_C$ confidence set if the same covariates were

repeated within the confidence set (Burnham & 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.

For our second objective, we developed nine *a priori* models to investigate the relationship between habitat and landscape variables and bat occupancy (Ψ) using data that were collected passively throughout the night during summer 2016 and 2017 (Table 1.2). It is important to note the terms "site occupancy" and "occurrence" should be interpreted as "use" when applied to bat research (MacKenzie, 2005). Foraging bats are unlikely to constantly occupy a site due to their volant behavior, and therefore, the closure assumption of occupancy models is relaxed in bat research studies (MacKenzie, 2005). We used the package *unmarked* in program R (Fiske et al., 2011; R Development Core Team, 2010) to first fit detection probability models using the same covariates we used when comparing data collection methods (see above), but we excluded "method". After addressing detection, we fit occupancy probability models. We hypothesized that increasing structural complexity would have a negative impact on bat occupancy, and predicted that as basal area and clutter increased, bat occupancy would decrease (Ford et al., 2006; Loeb & O'Keefe, 2006). We hypothesized that habitat type would have an impact on bat occupancy, where we predicted that bats would be more likely to use upland pine, bottomland forest, and Carolina Bay habitats than mixed and upland hardwood habitats (Menzel et al., 2002; Menzel et al., 2005*a*). We also hypothesized that landscape variables would impact bat occupancy, whereas distance to closest Carolina

Bay ("Bay") and distance to closest water source ("Water") increased, we predicted bat occupancy would decrease, and as distance to closest road ("Road") increased, bat occupancy would increase (Ford et al., 2006; Loeb & O'Keefe, 2006). We included two additive models in our model set to examine the relationship between clutter and basal area ("Structure"), as well as clutter, basal area, and distance to closest water source ("Structure + Water"). We also fit a global model and null model. We standardized distance to closest water source, distance to closest Carolina Bay, distance to closest road, and basal area to a mean of zero and standard deviation of 1 before running the models, but back-transformed values to their original units when discussing model predictions. We tested our 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: $P < 0.5$, Pearson's chi-square: $P < 0.05$), therefore, all covariates were kept in all models. Goodness-of-fit tests, model selection procedures, model averaging (where appropriate), and calculation of back-transformed parameter estimates, standard errors, and 95% confidence intervals were the same as in models of active vs. passive sampling (see above).

Results

Active vs. Passive Techniques

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. The average number of call files collected per 20 minutes was significantly different ($P < 0.05$) among the different data collection methods for each species group. We collected the highest average number of call files per 20 minutes using passive sampling throughout the night compared to active sampling and passive sampling for 20 minutes, with each species group following this pattern (Table 1.3).

We found that the data were overdispersed for some species groups, and not for others, and that models containing "method" generally performed better at predicting detection probabilities across species groups. The goodness-of-fit tests for evening bats and southeastern myotis global detection models indicated that the data for each species were overdispersed. Therefore, we used $QAIC_C$ to rank detection probability models for those species. There was good fit for the global detection models for low frequency bats, red bats, and tricolored bats, therefore, we used AIC_C to rank detection probability models for those species. The global model did not converge for tricolored bats, so we did not include it in subsequent analyses. The method model was the top ranked model for low frequency bats, evening bats, southeastern myotis, and tricolored bats (Table 1.4). Detection probabilities for low frequency bats, evening bats, southeastern myotis, and tricolored bats were highest when collecting data passively throughout the night, followed by active sampling, followed by passive sampling for 20 minutes (Figure 1.1; Table 1.5). 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 1.5). Red bat detection probability increased by 10% for every 1 °C increase in minimum nightly temperature (Figure 1.2A), increased by 10% for every 120 m^2/ha increase in basal area (Figure 1.2B), was highest when collecting data passively all night, followed by actively sampling (Figure 1.2C), and highest in low clutter, followed by high and medium clutter (Figure 1.2D).

Occupancy Probability at SRS

During summer 2016 and 2017, we collected 8,377 call files from 140 passive survey points. We collected 2,587 low frequency bat call files, 1,956 red bat call files, 1,448 evening bat calls files, 269 southeastern myotis call files, 1,890 tricolored bat call files, and 227 unidentifiable call files.

We found that data for all of our species groups were overdispersed and we used $QAIC_C$ to rank species occupancy models (Tables 1.6 & 1.7). The ĉ for detection and occupancy parameters for evening bats were of special note, each higher than 4. This indicated that there was high uncertainty in our model rankings, and this caveat should be taken into account when examining these results (Burnham & Anderson, 2002). To rank our detection and occupancy models for evening bats, we set ĉ to 4, the highest estimate acceptable in *AICcmodavg* (Mazerolle, 2017); because of high uncertainty, we model-averaged occupancy parameters.

The null model was the top-ranked detection model for low frequency bats and southeastern myotis, therefore, no detection variables were used in these species' occupancy models (Table 1.6). The clutter model was the top-ranked model for red bats, evening bats, and tricolored bats and we used this detection parameter in these species' occupancy models (Table 1.6).

Multiple occupancy models fell within the 2 ΔQAIC$_C$ confidence set for all species (Table 1.7). When model averaging and examining parameter estimates, we included models that fell after the null model but were still within each species' candidate set (i.e., < 2 ΔAIC$_C$ or QAIC$_C$). If the null model and other models had similar AIC$_C$ or QAIC$_C$ weights, this suggested that each model had an equal chance of explaining what influenced each species' occupancy probability (Table 1.7). We model-averaged parameters included in the candidate sets for low frequency bats and southeastern myotis and found that low clutter was the only covariate that had a statistically significant effect on their occupancy (Table 1.8). Low frequency bats and southeastern myotis were more likely to use low clutter areas than medium or high clutter areas (Table 1.8). We found that red bat occupancy was negatively affected by basal area and distance to closest water source (Table 1.8). Red bat occupancy probability decreased by 10% for every 220 m increase in distance to closest water source and for every 782 m^2/ha increase in basal area (Figure 1.4). Evening bat occupancy was negatively affected by distance to closest water source, where occupancy probability decreased by 10% for every 230 m increase in distance to closest water source (Figure 1.5). We found that tricolored bat occupancy was negatively affected by basal area and distance to closest water source (Table 1.8).

Tricolored bat occupancy probability decreased by 10% for every 739 m^2/ha increase in basal area and for every 230 m increase in distance to closest water source (Figure 1.6).

Discussion

As we predicted, passively sampling throughout the night performed better in recording bat calls than sampling actively or passively for 20 minutes. Collecting data passively throughout the night yielded the highest estimated detection probabilities for each species, followed by active sampling. Coleman et al. (2014) found similar results in a different bat community in New York, where they collected more call files using passive sampling throughout the night and found that passively collected data yielded higher detection probabilities than actively collected data. However, unlike Milne et al. (2004) and Johnson et al. (2002), we did not find a difference between the number of different species detected between active and passive techniques. In contrast to these previous studies, we were able to use the same type of detector when collecting data both actively and passively, which we did simultaneously. This gave us data that were easily comparable and our study suggests that researchers should use passive sampling throughout the night to collect more call files and to have a better chance of their data yielding the highest detection probabilities.

Using passive sampling throughout the night in combination with accounting for detection probability produced different estimates of bat species presence or occupancy from previous studies. At the same survey locations 15 years prior, Ford et al. (2006) collected data actively and did not account for detection probability to examine presence

of bats at SRS. While some habitat relationships were similar (Table 1.9), we found that some parameters had different impacts on bat species presence or occupancy between studies. Distance to closest water source did not have an effect on red bats and evening bats in the Ford et al. (2006) study, however, we found a negative effect of distance to closest water source on these species. This negative effect of distance to closest water source is unsurprising because water sources are considered to be important to bats as they serve as a source for drinking water and as habitat for prey (Cross, 1988; Ford et al., 2006; Salvarina, 2016). Ford et al. (2006) found that basal area had a positive effect on hoary bat presence while basal area did not have a significant effect on low frequency bats in our study. We hypothesize these different results may be due to how the different studies dealt with hoary bats and big brown bats; in our study, we grouped hoary bats and big brown bats together while Ford et al., (2006) did not group hoary bats and big brown bats and analyzed these species' presence separately. Unlike Ford et al. (2006), we visually estimated clutter amount at each point sampled and found that low clutter was the only covariate to have a significant positive effect on low frequency bats. Despite both studies including structural complexity as a covariate that was measured in different ways, we both found that increasing structural complexity had a negative effect on big brown bats/ low frequency bats. We anticipated that increasing clutter would have a negative impact on low frequency bats, since these bats are considered to be clutter-intolerant according to their morphology and call structure (Brigham et al., 1997; Patriquin et al., 2003; Menzel et al., 2005*a*).

In addition to sampling and analysis methodology, the differences seen between Ford et al. (2006) and this study could have occurred for a number of reasons which need to be recognized when other researchers compare studies as we have done. First, the differences between studies could have been an artifact of including different variables in the analysis; Ford et al. (2006) included overstory canopy cover, insect abundance, barometric pressure, humidity, cloud cover, moon illumination, wind speed, landscape heterogeneity (i.e., number of distinct stands or compartments), landscape setting, and landscape condition as parameters in their *a priori* models. We did not include these parameters but did examine clutter amount in our study. Therefore, because some parameters were included in both studies and others were not, we opened up the possibility of generating different results. Despite these differences, for the most part, the parameters included in both studies were included in the top models for both studies, allowing us to still compare the results of these studies. Second, differences in these two studies could also be a result of bats changing their behavior or alterations in habitat (e.g., clear cutting a pine stand would change the amount of clutter; natural disturbances such as blow downs; successional changes in habitat) from the time Ford et al. (2006) collected their data and when we collected ours. We attempted to account for this change in habitat by updating the habitat type when visiting points in 2016 and 2017, when necessary. Third, we assumed the 190 points we sampled in 2016 and 2017 were representative of the 430 points sampled by Ford et al. (2006). Despite these caveats that likely complicated the comparison of these datasets we believe the major habitat use

differences observed are likely primarily driven by the different sampling and analytical methodologies used between studies.

Our comparison of active and passive data collection techniques demonstrates the pitfalls of comparing datasets collected using different methodology to gain insight on bat habitat use. As eastern 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. Overall, we found that different data collection methods yielded different detection probabilities and, as a result, comparison of historical active datasets with current passive datasets could lead to different insights into habitat selection by similar bat communities. We suggest that actively collected data are not comparable to passively collected data, and researchers should account for this within their study designs. We recommend that long-term bat monitoring programs include the use of passive sampling throughout the night so that researchers have consistently collected data sets that can provide more information on the bat community structure than actively collected data can provide.

Tables

Table 1.1. *A priori* model variables for detection probability (*p*) of bats at Savannah River Site. A null model was included in the analysis. All listed variables were included when comparing passive and active data collection methods (Objective 1). However, when examining variables that would influence bat detection during summer 2016 and 2017, "Method" was not included (Objective 2).

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 et al., 2006 Loeb & 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 (°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 et al., 2014
5	Basal Area (m²/ha)	Basal area will have an effect on bat *p*.	Continuous	As basal area increases, bat *p* decreases.	Ford et al., 2006
6	Temperature + Precipitation	Weather variables have an additive effect on bat *p*.	Continuous (°C & 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) & continuous (m^2/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 minutes in all clutter amounts.
9	Clutter + Precipitation + Temperature + Method + Basal Area + (Method * Clutter)	Global model	Continuous (mm; °C; m^2/ha) & categorical (low, medium, high; active, passive 20 min, passive all night)	

Table 1.2. *A priori* model variables for occupancy probability (Ψ) for bats in Savannah River Site during summer 2016 and 2017. A null model was included in the analysis.

Model #	Variable	Hypothesis	Covariates	Predicted Effects	Literature Cited
1	Clutter	Clutter has an effect on bat Ψ	Low, medium, high	As clutter amount increases, bat Ψ will decrease.	Ford et al., 2006 Loeb & O'Keefe, 2006
2	Habitat	Habitat has an impact on bat Ψ	Hardwood, pine, bottomland, Carolina bay, mixed	Bats will be less likely to use upland hardwood and mixed habitat more likely to use bottomland, upland pine, and Carolina bay.	Menzel et al., 2002; Menzel et al., 2005*a*
3	Water (m)	Distance to closest water source has an effect on bat Ψ	Continuous	As the distance to the closest water source increases, bat Ψ will decrease.	Ford et al., 2006
4	Bay (m)	Distance to closest Carolina Bay has an effect on bat Ψ	Continuous	As distance to closest Carolina Bay increases, bat Ψ will decrease.	Ford et al., 2006
5	Basal Area (m^2/ha)	Basal area has in impact on bat Ψ	Continuous	As basal area increases, bat Ψ will decrease.	Ford et al., 2006

6	Structure	Clutter and basal area have an additive effect on bat Ψ	Continuous (m^2/ha) & categorical (low, medium, high)	As clutter amount and basal area increases, bat Ψ will decrease.	Ford et al., 2006
7	Structure + Water	Structure (clutter and basal area) and distance to closest water source have an additive effect on bat Ψ	Continuous (m^2/ha & m) & categorical (low, medium, high)	As clutter amount, basal area, and distance to closest water source increases, bat Ψ will decrease.	Ford et al., 2006
8	Clutter + Habitat + Water + Bay + Basal Area	Global model	Continuous (m; m; m^2/ha) & categorical (low, medium, high; upland hardwood, upland pine, bottomland, Carolina Bay, mixed)		

Table 1.3. Average number of calls collected per 20 minutes using each method (active, passive throughout night, passive for 20 minutes) for each species group in Savannah River Site during summer 2017.

Species	Active	Passive (all night)	Passive (20 min)
Low Frequency bats	0.02	1.55	0.01
Red bats	0.03	0.94	0.01
Evening bats	0.02	0.50	0.01
Southeastern myotis	0.01	0.19	0
Tricolored	0.03	0.79	0

Table 1.4. Top-ranked models (ΔAIC$_C$ or ΔQAIC$_C \leq 2$) for passive vs. active detection probability (p) for bats at Savannah River Site. Data for low frequency bats, red bats, and tricolored bats were not overdispersed and AIC$_C$ was used to rank these species' models. Data for evening bats and southeastern myotis 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$_C$	ΔAIC$_C$ or ΔQAIC$_C$	w_i
Low frequency bats	Method	4	-71	150	0	0.79
Red bats	Global	13	-51	138	0	0.55
Evening bat	Method	5	-21	53	0	0.50
Southeastern Myotis	Method	5	-43	97	0	0.88
Tricolored bat	Method	4	-63	136	0	0.50

Table 1.5. 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, evening bats, and southeastern myotis at Savannah River Site when comparing passive and active acoustic sampling methods. Parameter estimates for tricolored bats are model-averaged.

Parameter	Estimate	SE	Upper 95% CI	Lower 95% CI
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 bats				
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
Evening bat				
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
Southeastern myotis				
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
Tricolored bat				
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

Table 1.6. Top-ranked models (ΔQAIC$_C \leq$ 2) for detection probability (p) for bats at Savannah River Site during summer 2016 and 2017. Data for all species groups were overdispersed and QAIC$_C$ was used to rank these species' models.

Species Group	Model Name	K	Q-LogLik	QAIC$_C$	ΔQAIC$_C$	w_i
Low frequency bats	Null	3	-112.13	230.43	0	0.28
	Precipitation	4	-111.28	230.86	0.43	0.23
	Basal area	4	-111.95	232.20	1.78	0.12
	Temperature	4	-111.97	232.24	1.81	0.11
	Clutter	5	-110.92	232.29	1.86	0.11
Red bats	Clutter	5	-47.33	150.11	0	0.49
	Clutter + Basal area	6	-47.00	106.63	1.52	0.23
Evening bats	Clutter	5	-35.07	80.60	0	0.42
Southeastern myotis	Null	3	-99.38	204.93	0	0.33
	Clutter	5	-97.93	206.31	1.38	0.16
	Basal area	4	-99.02	206.33	1.40	0.16
Tricolored bats	Clutter	5	-96.16	202.76	0	0.44
	Clutter + Basal area	6	-95.28	203.20	0.44	0.36

Table 1.7. Top-ranked models for occupancy probability (Ψ) for bats at Savannah River Site with data that was not overdispersed (AIC_C) and overdispersed ($QAIC_C$) during summer 2016 and 2017. Almost all species groups had overdispersed data and $QAIC_C$ was used to rank these species' models. Southeastern myotis did not have overdispersed data and AIC_C was used to rank their models.

Species Group	Model Name	K	LogLik or Q-LogLik	AIC_C or $QAIC_c$	ΔAIC_C or $\Delta QAIC_c$	w_i
Low frequency bats	Ψ(Structure), p(.)	6	-109.80	232.23	0	0.26
	Ψ(Clutter), p(.)	5	-110.90	232.26	0.03	0.26
	Ψ(Clutter + Basal area + Water), p(.)	7	-109.35	233.56	1.32	0.13
	Ψ(.), p(.)	3	-113.85	233.88	1.65	0.11
Red bats	Ψ(.), p(Clutter)	5	-45.66	101.78	0	0.30
	Ψ(Water), p(Clutter)	6	-45.07	102.77	0.99	0.18
	Ψ(Basal area), p(Clutter)	6	-45.33	103.30	1.52	0.14
Evening bats	Ψ(.), p(.)	5	-35.07	80.60	0	0.35
	Ψ(Water), p(.)	6	-34.61	81.85	1.26	0.19
	Ψ(Basal area), p(.)	6	-34.87	82.38	1.79	0.14
Southeastern myotis	Ψ(Clutter), p(.)	4	-104.47	217.24	0	0.30
	Ψ(Clutter + Basal area), p(.)	5	-104.10	218.65	1.40	0.15
	Ψ(.), p(.)	2	-107.33	218.74	1.50	0.14
	Ψ(Bay), p(.)	3	-106.45	219.08	1.84	0.12
Tricolored bats	Ψ(Basal area), p(Clutter)	6	-113.23	239.10	0	0.22
	Ψ(.), p(Clutter)	5	-114.40	239.26	0.16	0.21
	Ψ(Water), p(Clutter)	6	-113.39	239.41	0.31	0.19
	Ψ(Road), p(Clutter)	6	-114.09	240.81	1.71	0.09

Table 1.8. Parameter estimates, standard errors (SE), and 95% confidence intervals (CI) of parameters in the top models for occupancy (Ψ) models for red bats, evening bats, and tricolored bats at Savannah River Site during the summer of 2016 and 2017. Model-averaged parameter estimates, standard errors (SE), and 95% confidence intervals (CI) of parameters within the top models for occupancy (Ψ) models of low frequency bats and southeastern myotis.

Parameter	Estimate	SE	Upper 95% CI	Lower 95% CI
Low Frequency bats				
Intercept	-0.77	0.51	0.23	-1.78
Medium clutter	0.72	0.58	1.85	-0.41
Low clutter	1.29	0.53	2.34	0.24
Basal area	-0.29	0.22	0.14	-0.72
Water	-0.19	0.22	0.23	-0.62
Red bats				
Intercept	0.14	0.25	0.39	-0.11
Basal area	-0.20	0.20	-0.001	-0.40
Water	-0.38	0.22	-0.12	-0.56
Evening bats				
Intercept	0.16	0.23	0.39	-0.07
Basal area	-0.16	0.19	0.03	-0.35
Water	-0.35	0.22	-0.13	-0.57
Southeastern myotis				
Intercept	-1.68	0.61	-0.49	-2.87
Medium clutter	0.56	0.70	1.93	-0.81
Low clutter	1.32	0.62	2.54	0.10
Basal area	-0.19	0.23	0.27	-0.66
Bay	-0.30	0.24	0.16	-0.77
Tricolored bats				
Intercept	0.54	0.29	0.83	0.25
Basal area	-0.29	0.22	-0.07	-0.51
Water	-0.30	0.22	-0.08	-0.52
Road	-0.10	0.22	0.12	-0.32

Table 1.9. Comparison of parameters that were included in Ford et al., 2006 and this study. Parameters that had a significant effect have parentheses surrounding the sign. A negative sign refers to a negative effect of the parameter and a positive sign refers to a positive effect. A zero (0) indicates the parameter did not have an impact in the corresponding study. See Ford et al. (2006) for full descriptions of models and variables.

Species Groups	Parameter	Effect of parameters (Ford/current study)
Hoary bats & Big brown bats (Ford et al., 2006) / low frequency bats (this study)	Distance to water source	(–) hoary bats / – low frequency bats
	Distance to road	(–) hoary bats / 0 low frequency bats
	Basal area	(+) hoary bats, (–) big brown bats / – low frequency bats
Red bats	Distance to water source	0/(–)
	Basal area	(–)/(–)
Evening bats	Distance to closest water source	0/(–)
	Basal area	(–)/0
Southeastern myotis	Distance to Carolina Bay	(–)/–
	Basal area	0/–
Tricolored bats	Distance to water source	(–)/(–)
	Basal area	(–)/(–)

Figures
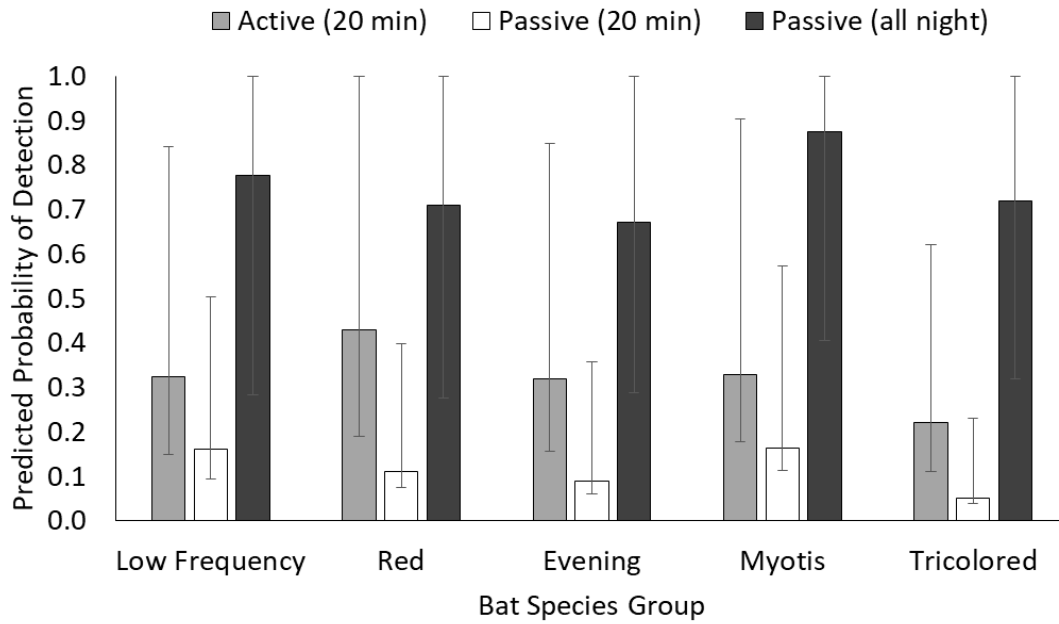
Figure 1.1. Predicted probability of detection (*p*) for each species group for each data collection method when comparing passive and active sampling techniques at Savannah River Site. The error bars represent the 95% confidence interval.
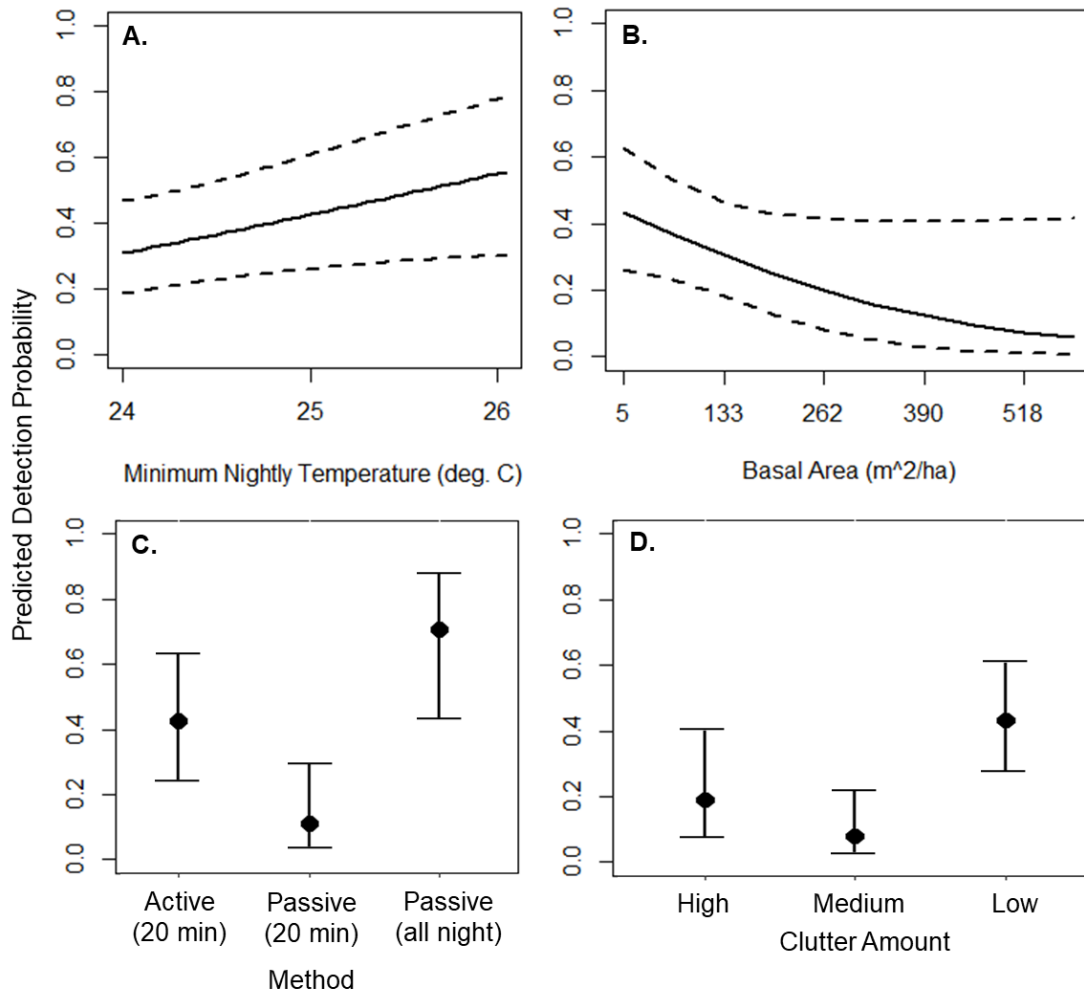
Figure 1.2. Influence of (A) minimum nightly temperature (°C), (B) basal area (m²/ha), (C) method, and (D) clutter amount on probability of detection (*p*) of red bats during July 2017 at Savannah River Site. Covariates are from the top-ranked detection model. The dotted lines and vertical lines represent 95% confidence intervals.
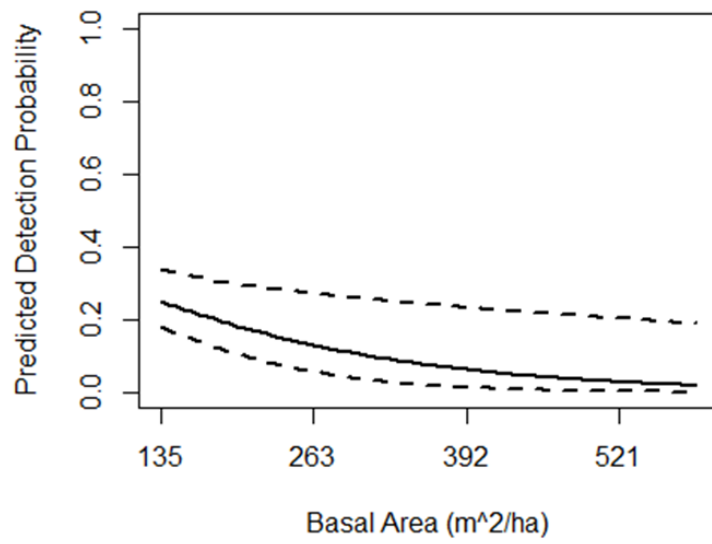
Figure 1.3. Influence of basal area (m^2/ha) on probability of detection (p) of tricolored bats during July 2017 at Savannah River Site. The covariate is the only significant covariate from the top-ranked detection model. The dotted lines represent the 95% confidence interval.
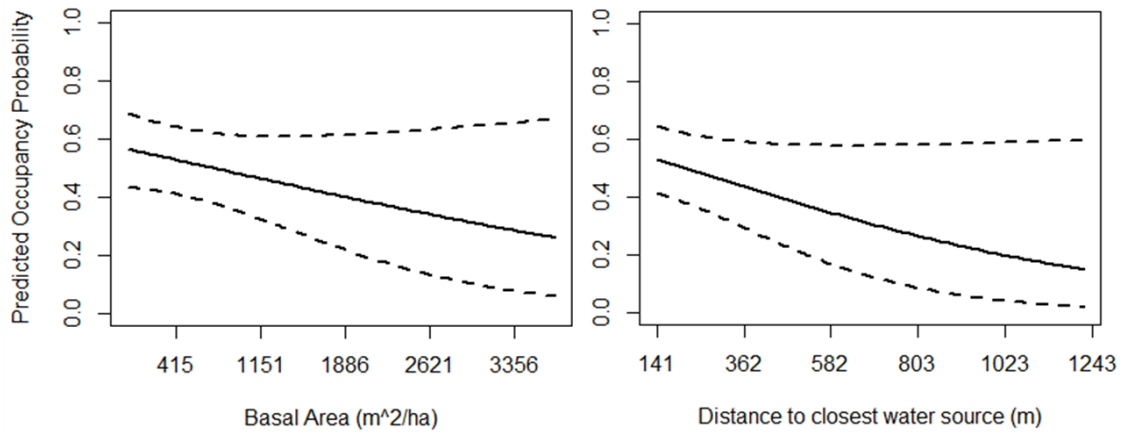
Figure 1.4. The effect of basal area and distance to closest water source on red bat occupancy (Ψ) during summer 2016 and 2017 at Savannah River Site. The covariates are the only significant covariates within the top-ranked occupancy model. The dotted lines represent the 95% confidence interval.
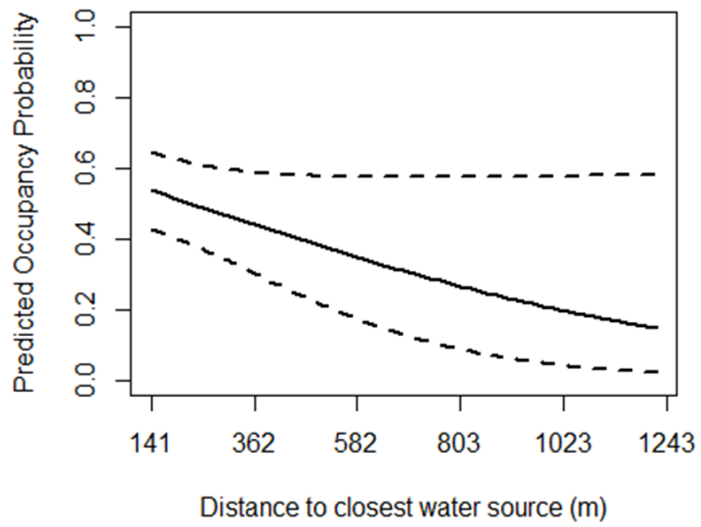
Figure 1.5. The effect of distance to closest water source on evening bat occupancy (Ψ) during summer 2016 and 2017 at Savannah River Site. The covariate is the only significant covariate within the top-ranked occupancy model. The dotted lines represent the 95% confidence interval.
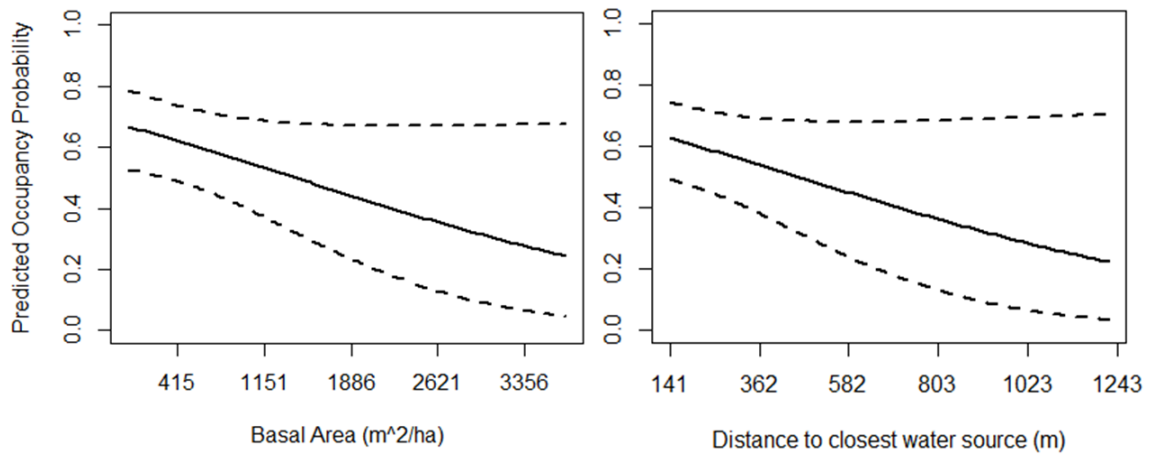
Figure 1.6. The effect of basal area and distance to closest water source on tricolored bat occupancy (Ψ) during summer 2016 and 2017 at Savannah River Site. The covariates are the only significant covariates within the top-ranked occupancy model. The dotted lines represent the 95% confidence interval.

CHAPTER TWO
BEHAVIORAL CHANGES OF BATS FOLLOWING THE ARRIVAL OF WHITE-
NOSE SYNDROME IN NORTHWESTERN SOUTH CAROLINA

The structure of ecological communities can be influenced by biotic and abiotic factors (Smith, 1966). Niche partitioning is the process in which competing species divide resources so that they may coexist (Schoener, 1974), and tends to occur in assemblages where species are diverse and highly structured by competition (Begon et al., 1996). For mammalian communities, niche partitioning has been observed among individuals within the same genus (western chipmunks *Eutamias amoenus* and *E. townsendii*; Trombulak, 1985 and spiny mice *Acomys cahirinus* and *A. russatus*; Jones et al., 2001) as well as among genera (large herbivores in Africa; Valeix et al., 2007, and ungulates in the Rocky Mountains; Stewart et al., 2002). In particular, bats often exist in highly diverse communities in which niche partitioning has been observed in several systems globally (Aldridge & Rautenbach, 1987; Adams & Thibault, 2006; Razgour et al., 2011). Sympatric bat species can exhibit niche partitioning through morphology (Brigham et al., 1989), prey selection (Barclay, 1988), habitat use (Arlettaz, 1999; Arlettaz et al., 2000; Nicholls & Racey, 2006) use of different areas within an ecosystem (Arlettaz et al., 2000; Patterson et al., 2003; Nicholls & Racey, 2006; Razgour et al., 2011), and time of activity (Kunz, 1973; Reith, 1980; Kronfeld-Schor & Dayan, 2003; Adams & Thibault, 2006). Niche partitioning can be destabilized by a number of things, such as loss of a certain species, which can occur when an emerging infectious disease is introduced into a system (Dobson & Hudson, 1986; Lips et al., 2006).

Bat communities in the eastern United States have come under threat of an emerging infectious disease called white-nose syndrome (WNS), which has killed more than 6 million bats since it was first detected in 2006 (Blehart et al., 2008; USFWS, 2018). All symptomatic species hibernate in caves or mines, with declines of cavernicolous bat species ranging from 30 to 99% annually (Frick et al., 2010). The little brown bat (*Myotis lucifugus*), the federally threatened northern long-eared bat (*M. septentrionalis*), the federally endangered Indiana bat (*M. sodalis*), and the tricolored bat (*Perimyotis subflavus*) are the four most susceptible species (Langwig et al., 2012; USFWS, 2018). One cave-hibernating bat species, the big brown bat (*Eptesicus fuscus*), may be resistant to WNS due to significantly greater mean body fat content during hibernation (Frank et al., 2014). While the fungus that causes WNS (*Pseudogynmoascus destructans*) has been detected on some tree-dwelling species such as the eastern red bat (*Lasiurus borealis*) and silver-haired bat (*Lasionycteris noctivagans*), the disease has not been confirmed in these species (Bernard et al., 2015). These tree-dwelling species use winter roosts with unstable temperatures, are often more exposed to the elements, and tend to arouse from torpor and become active to forage or to move to other roosts in winter (Whitaker, 1967; Padgett & Rose, 1991; Saugey et al., 1998; Boyles & Robbins, 2006; Boyles et al., 2003, Boyles et al., 2005; Hein et al., 2005; Mormann & Robbins, 2007).

Because tree-dwelling and cave-dwelling species are differentially impacted by WNS, remnant tree-dwelling and cave-hibernating bats may be utilizing available niches differently after WNS detection. Jachowski et al. (2014) found that spatial and temporal

niche partitioning was relaxed post-WNS with the rapid decline of the once abundant little brown bat. They proposed that non-impacted bat species (e.g., hoary bat, *L. cinereus*, red bat) were able to forage in areas and at times formerly dominated by the little brown bat, because the little brown bat was no longer as abundant as it once was, and therefore no longer able to outcompete hoary bats and red bats for foraging niches. Thalken et al. (2018) found that non-impacted species at Mammoth Cave National Park also experienced an ecological release after the onset of WNS and resulting decline of impacted species. Changes in niche partitioning, like those seen by Jachowski et al. (2014) and Thalken et al. (2018) are important for researchers to take into account, as data collected pre-WNS may no longer be relevant to a system's community structure and species-specific habitat associations post-WNS. Further, because these data are often used as the basis for bat habitat management decisions (e.g., Menzel et al., 2005*a*; 2005*b*; Loeb & O'Keefe, 2006; Brooks, 2008; Castro-Arellano et al., 2009), it is important to ensure the data used are accurate and specific to the system and species of interest. Additionally, such pre- vs. post-disease comparative studies provide a broader ecological understanding of how bats are responding to WNS at a community-level. However, to date, such pre- vs. post-WNS comparisons of bat activity outside of caves have been restricted to portions of Tennessee (Thalken et al. 2018) and New York (Jachowski et al. 2014), with no investigations into the response of bat communities in South Carolina.

In this study, we investigated the foraging activity of a bat community in northwestern South Carolina that was previously studied by Loeb & O'Keefe (2006) prior to the arrival of WNS in 2012 (SCDNR, 2016). We focused on examining niche

partitioning between low frequency bats (WNS-resistant), red bats (WNS-resistant), evening bats (WNS-resistant), Myotis (WNS-susceptible), and tricolored bats (WNS-susceptible) because we predicted that niche partitioning between these species would change pre- to post-WNS (Table 2.1). Our objectives were to: (1) examine colonization and extinction probabilities of bats between pre- and post-WNS periods, and (2) examine the temporal foraging niches of bats and compare partitioning of these niches by bats pre- and post-WNS. We hypothesized that post-WNS, there would be a relaxation of niche partitioning among WNS-resistant and WNS-susceptible species, as the WNS-susceptible species have suffered population declines due to WNS. Specifically, because of similar call structure and habitat use patterns (Table 2.1), we predicted that red bats and evening bats (*Nycticeius humeralis*) (WNS-resistant species) would move into areas previously used by Myotis and tricolored bats (WNS-susceptible), and be active at times of night in which Myotis and tricolored bats were once more active. At the same time, we predicted that Myotis and tricolored bats would change where and when they were active, as remnant WNS-susceptible species will use areas in which it is easiest to forage while keeping competition with WNS-resistant species low. Lastly, because of different call structure and habitat associations compared to WNS-vulnerable species (Table 2.1), we predicted that low frequency bats would not change their spatial and temporal foraging niches post-WNS. Our results further test how WNS could be indirectly effecting bat communities and provides land managers in the southeastern U.S. with important information regarding both where and when remnant bats are most likely to forage following WNS.

Methods

Study Site

Our study area was the Andrew Pickens District (APD) of the Sumter National Forest is in northwestern South Carolina in Oconee county. Topography ranges from gentle slopes and hills in the Piedmont to steep slopes in the Mountains and elevation ranges from 218 to 995 m. APD consists of 34,220 ha with privately owned land interspersed throughout. Forest types include pine (37%), mixed pine and upland hardwood (36%), and hardwood (27%). The Chattooga River borders the western side of APD and the Chauga River bisects APD and drains throughout most of the area (Loeb & O'Keefe, 2006; Stottlemyer et al., 2009). WNS was confirmed in neighboring Pickens county in 2012-13 and in Oconee county in 2013-2014 (SCDNR, 2016). We selected stands that were representative of the different habitat types and structures present in APD (Loeb & O'Keefe, 2006). We used the Forest Service Continuous Inventory of Stand Condition database to select pine, hardwood, and mixed pine-hardwood stands. Stands that contained sampling points ranged in size from 2 to 105 ha and sampling points were at least 50 m from the edge of the stand.

Acoustic Data Collection

We monitored acoustic activity within our study area during 2004 and 2005 (i.e. pre-WNS), and then again in 2016 and 2017 (i.e., post-WNS). In summer 2004 and 2005, we passively surveyed bats using Anabat II bat detectors (Titley Scientific, Brendale, Australia) that were connected to programmable zero-crossings analysis interface modules (Anabat CF Storage ZCAIM; Loeb & O'Keefe, 2006). In May to August 2004,

we sampled 89 points, and in May to August 2005, we sampled 98 points, with 78 points being sampled both years. We sampled 80 of the 89 points from 2004 for one night, and in 2005, we sampled points for one to three nights. During June to August 2016 and June and July 2017, we collected acoustic data at 105 of the 109 points sampled in 2004 and 2005. We used Anabat Express bat detectors (Titley Scientific, Brendale, Australia) to record bat calls for ≥ 2 consecutive nights. Detectors were set to record from sunset to sunrise and were attached to the top of 3.7 m painter's poles that were held upright using a PVC pipe connected to a U-pole.

We used two custom filters to separate bat passes (≥ 1 pulse) from noise, and to separate low quality passes (< 5 pulses) from high quality passes (≥ 5 pulses) from the resulting acoustic data (Loeb & O'Keefe, 2006). We used Kaleidoscope Pro (version 3.1.8) to identify calls to species and then manually vetted and corrected mis-identified calls. Ten species of bats have been documented to occur at APD (Loeb & O'Keefe, 2006). These are four WNS-susceptible species (the tricolored bat, the small-footed bat [*Myotis leibii*], the little brown bat, and the northern long-eared bat; Langwig et al., 2012; USFWS, 2018), as well as six WNS-resistant species (the evening bat, the big brown bat, the hoary bat, the eastern red bat, the silver haired bat, and Rafinesque's big-eared bat [*Corynorhinus rafinesquii*]; USFWS, 2018). We grouped species calls into five groups based on similar call structure. Big brown bats, hoary bats, and silver haired bats were grouped into the "low frequency bats" category, the small-footed bat, the little brown bat, and the northern long-eared bat were grouped into the "Myotis" category, and eastern red bats, evening bats, and tricolored bats were categorized into their own groups,

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respectively. Rafinesque's big-eared bats were not detected, likely due to their low intensity calls (Clement & Castleberry, 2011).

Site Data Collection

In 2004 and 2005, we obtained habitat type (pine, hardwood, or mixed pine-hardwood) data from the Forest Service Continuous Inventory of Stand Condition database. In 2005, we visually estimated the amount of clutter above and immediately surrounding each sampling point. In revisiting points in 2016 and 2017, we similarly categorized habitat type and amount of clutter at each point sampled. Amount of clutter was visually categorized as low, medium, or high based on understory conditions in all directions up to 5 m from the detector in 2004 and 2005, and up to 3 m away from the detector in 2016 and 2016. 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. If clutter amount changed in revisiting sites in 2016 or 2017, the change was noted and included in the detection probability models (clutter amount changed pre- to post-WNS at 69 points). However, due to our inability to account for changes in clutter amount when examining occupancy probabilities in our multi-season occupancy analysis, clutter amount was kept as the category assigned in 2004 or 2005. Minimum nightly temperature (°C) and total nightly precipitation (mm) were downloaded from the Western Regional Climate Center's Remote Automatic Weather Station (RAWS) located in APD (https://wrcc.dri.edu/cgi-bin/rawMAIN.pl?laSANP).

Straight line distance from sample points to closest stream (m) and closest road (m) were calculated in ArcGIS 10.5 (ESRI, Redlands, California).

Hypothesized changes in niche partitioning

We developed *a priori* predictions on which species were more likely to exhibit relaxed niche partitioning post-WNS by examining call structure, foraging habitat, foraging strategy, and known prey items of each species (Table 2.1). We used an index to determine where competition was high among the different species. We based this point system on the amount of acoustic and foraging behavior (habitat, time of day, and diet) similarity each WNS-resistant species had with WNS-susceptible species (i.e., Myotis and tricolored bats). For example, if red bats and Myotis had similar call structures, red bats were awarded a point for this category. Following this protocol, we determined that red bats and evening bats had an index score of 4 with Myotis and tricolored bats, while low frequency bats had an index score of 1 with Myotis and tricolored bats (Table 2.1). Therefore, we predicted that Myotis and tricolored bats would more likely experience relaxed niche partitioning with red bats and evening bats, while there would not be relaxation in niche partitioning between low frequency bats and Myotis and tricolored bats, since these species did not have a lot of overlap in call structure, foraging habitat, foraging times, or known prey items.

Statistical Analyses

We used multi-season single-species occupancy models to examine factors that may influence the probability of occurrence and detection of each bat species in APD (MacKenzie et al., 2006; Fiske et al., 2011). It is important to note the terms "site

occupancy" and "occurrence" should be interpreted as "use" when applied to bat research (MacKenzie, 2005). Foraging bats do not constantly occupy a site and therefore, the closure assumption of occupancy models is relaxed in bat research studies (MacKenzie, 2005). We used data that were collected in summer 2004 and 2005 ("pre-WNS data") as our first primary sampling period, and considered data that were collected in summer 2016 and 2017 ("post-WNS data") as our second primary sampling period to estimate the dynamic occupancy of bats in APD, which consisted of occupancy (Ψ), site colonization rates (γ), site extinction rates (ε), and detection probability (p) (MacKenzie et al., 2006; Fiske et al., 2011). Colonization (γ) and extinction (ε) govern changes in occupancy between successive primary sampling periods. The colonization parameter denotes the probability of an unoccupied site in sampling period t becoming an occupied site in sampling period $t + 1$. Conversely, the extinction parameter denotes the probability that an occupied site in sampling period t becomes unoccupied in sampling period $t + 1$. We combined 2004 and 2005 data where necessary to create two sampling occasions for our first primary sampling period (i.e., we considered the one night of data collected in 2004 as our first secondary sampling occasion and the first night sampled in 2005 as our second secondary sampling occasion). As this likely violated the assumption that sites were closed to changes in occupancy between sampling occasions, the following results should be considered with this caveat in mind (MacKenzie & Bailey, 2004; MacKenzie et al., 2006).

We used a two-step process in our occupancy analysis. In our first step, we examined factors we thought would influence detection of bats to account for imperfect

detection. We developed seven *a priori* models using existing literature (Table 2.2). We hypothesized that clutter amount (low, medium, high), precipitation, minimum nightly temperature, and Julian day would have an effect on our ability to detect bat species. Specifically, we predicted that as clutter (Sleep & Brigham, 2003) and precipitation (Yates & Muzika, 2006) increased, bat species detectability would decrease. We also predicted that bat species detectability would increase with temperature (Yates & Muzika, 2006; Starbuck et al., 2015) and Julian day (Starbuck et al., 2015). Prior to model fitting, we standardized precipitation, temperature, and Julian day 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* detection and occupancy models were correlated (Pearson's product-moment correlation coefficient > 0.5, ANOVA: $P < 0.5$, Pearson's chi-square: $P < 0.05$), therefore, all covariates were retained.

We incorporated the covariates included in the most supported detection probability model into our second step of fitting occupancy, colonization, and extinction models for each species (MacKenzie et al., 2006). We compared a set of six *a priori* models that examined environmental variables that we hypothesized might affect occupancy (Ψ) (Table 2.3). We hypothesized that clutter amount, habitat type, distance to closest stream, and distance to closest road would impact bat occupancy in APD. Specifically, we predicted that as clutter amount (Loeb & O'Keefe, 2006; Yates &

Muzika, 2006) and distance to closest stream (Cross, 1988; Racey, 1998; Ford et al., 2006) increased, bat occupancy probabilities would decrease for all species. We also predicted that as distance to closest road increased, all bat species' occupancy would increase (Starbuck et al., 2015). We predicted low frequency bats would most likely use pine habitat (Perry et al., 2007), red bats would most likely use hardwood habitat (Hutchinson & Lacki, 2000; Perry et al., 2007), evening bats and Myotis would more likely use mixed habitat (Perry et al., 2007), and tricolored bats would most likely use hardwood and mixed habitat types (Perry et al., 2007).

We compared three *a priori* models to determine if clutter amount, habitat type, or neither of these parameters affected colonization (γ) and extinction (ε) probabilities of our species of interest. Because the first primary sampling period took place prior to WNS being detected at APD and the second primary sampling period took place after WNS was detected, we assumed the structure of our data captured pre- and post-WNS colonization and extinction rates. We predicted that generally, Myotis and tricolored bat (WNS-susceptible) colonization probabilities would be lower and extinction probabilities would be higher than low frequency bats, red bats, and evening bats (WNS-resistant). We predicted that colonization probabilities and extinction probabilities of low frequency bats, red bats, and evening bats would be impacted by clutter amount because they would forage more often in lower clutter sites post-WNS since there would be fewer Myotis and tricolored bats in those areas. We predicted that colonization and extinction probabilities of Myotis and tricolored bats would not be affected by clutter amount or habitat type, because they would already be in areas where they would most likely forage and would

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not move out of those areas. Similar to detection probability modeling described above, prior to model fitting we standardized continuous covariates and checked for correlations among predictor variables. None of the variables included in our *a priori* models were correlated (Pearson's product-moment correlation coefficient > 0.5, ANOVA: $P < 0.5$, Pearson's chi-square: $P < 0.05$), therefore, all covariates were kept in all models. We calculated parameter estimates for occupancy, colonization, and extinction probabilities for each bat species. Lastly, we compared colonization and extinction rates among the species group by examining predicted colonization and extinction probabilities and 95% confidence intervals of each species.

We used the package *unmarked* in program R to fit our multi-season single-species occupancy models (Fiske et al., 2011; R Development Core Team, 2010). We compared models using AIC scores and AIC weights (w_i), and considered models within 2 ΔAIC to be top-ranked models, with the model with the lowest ΔAIC value to be the most parsimonious model (Burnham & Anderson, 2002). To address model uncertainty (i.e., multiple models fell within 2 ΔAIC and included the same covariates), we model-averaged parameter estimates, standard errors and calculated 95% confidence intervals based on all models in our 2 ΔAIC confidence set (Burnham & Anderson, 2002). If multiple models were highly competitive and did not repeat the same covariates, we examined parameter estimates of covariates included in the top models to determine what covariates had a statistically significant effect on detection and occupancy. We considered covariates to have a statistically significant effect on bat detection or occupancy if the confidence interval of the covariate did not cross zero.

To examine temporal niche partitioning, we first used two-tailed t-tests to determine if there was a significant difference between the number of calls per night collected from all points sampled pre- and post-WNS. Then, to examine activity of low frequency bats, red bats, evening bats, Myotis, and tricolored bats throughout the night during pre- and post-WNS sampling periods, we used the non-parametric kernel density estimation procedure as described by Ridout & Linkie (2009) and Wang et al. (2015). Using the *overlap* package in program R (R Development Core Team, 2010; Meredith & Ridout, 2018), we converted the time stamp associated with each call file to radians and used kernel density estimation to generate a probability density distribution of each species' activity throughout the night during both sampling periods. We then calculated the overlap term (Δ), a value that ranges from 0 (complete activity shift) to 1 (no activity shift), to quantify the amount of temporal overlap that occurred between sampling periods. Ridout & Linkie (2009) recommended using Δ_1 for small sample sizes ($n < 50$) and Δ_4 for larger sample sizes ($n \geq 50$). Therefore, we estimated Δ_4 and calculated 95% confidence intervals for estimates from 1000 bootstrap samples. To determine if a significant shift had occurred, we examined the 95% bootstrapped confidence intervals; if estimates did not overlap, they were considered to be significantly different (Ridout & Linkie, 2009).

First, we compared species' nightly activity pre- and post-WNS (e.g., red bat activity in pre-WNS vs. red bat activity post-WNS) to determine if each species changed when and how much they changed their activity at night. We predicted that low frequency bats would exhibit a small change in their activity pre- to post-WNS and that

red bats and evening bats would exhibit larger shifts in activity throughout the night than the WNS-susceptible species. Second, we compared species activity between pairs of species we hypothesized would exhibit more or less overlap of temporal foraging niches WNS (Table 2.1). We hypothesized that red bats and evening bats would change their activity at night to take advantage of times when WNS-susceptible species were once more active and become more active during the times of night in which low frequency bats are active, thus, we predicted that the level of temporal overlap would increase between red bats and all other species and evening bats and all other species. We hypothesized that Myotis and tricolored bats would change their activity to avoid each other, thus, we predicted that the level of overlap would decrease between Myotis and tricolored bats. We also hypothesized that there would not be much competition between low frequency bats and WNS-susceptible bats (Table 2.1), thus, we predicted that the level of overlap between WNS-susceptible species and low frequency bats would decrease.

Results

Occupancy modeling at APD

From the 109 points sampled during summer 2004 and 2005 and the 105 points during summer 2016 and 2017, we were able to include 86 points in our occupancy modeling. Points were not included if they had missing habitat covariate data or if they were not sampled during both primary sampling periods. All species were recorded during both primary sampling periods (Table 2.4).

We found that the most parsimonious models with covariates that influenced bat detection probabilities were species-specific. The global model was the top model for low frequency bats (Table 2.5) and we found that Julian day, minimum nightly temperature, and clutter amount affected detection probabilities (Table 2.6). Low frequency bat detection probability increased by 10% every 37.5 days and for every 5 °C increase in minimum nightly temperature (Figure 2.1). Additionally, we were 25% more likely to detect a low frequency bat low clutter than medium clutter and 40% more likely in low clutter than high clutter (Figure 2.1). For red bats, we observed strong support for the clutter model and the global model (Table 2.5). From model-averaging, we found that low clutter was the only significant covariate for red bat detection probability (Table 2.6). Red bat detection probability was 15% lower in medium clutter than low clutter and 12% lower in high clutter than low clutter (Figure 2.2A). The clutter model was the top-ranked model for evening bats (Table 2.5). As we predicted, as clutter increased, the probability of detecting evening bats decreased (Table 2.6). Detection probability of evening bats was 25% lower in medium clutter than low clutter and 35% lower in high clutter than low clutter (Figure 2.2B). We observed support for the Julian day model, the precipitation model, the temperature model, and the clutter model for Myotis bats (Table 2.4). From examining the parameter estimates of each covariate in these models, we found that low clutter was the only covariate that had a statistically significant effect on Myotis detection (Table 2.6). Myotis detection probability was 20% lower in medium clutter than in low clutter and 21% lower in high clutter than in low clutter (Figure 2.2C). The Julian day model was the top-ranked model for tricolored bats (Table 2.5). As we predicted, Julian

day had a significant positive affect on tricolored bats (Table 2.6). Tricolored bat detection probability increased by 10% every 20 days (Figure 2.2D).

We found that the most parsimonious models with covariates that influenced bat occupancy were also species-specific. Multiple models fell within 2 ΔAIC for low frequency bats; this included the null model, the stream model, the road model and the clutter model (Table 2.7). From examining the parameter estimates for these covariates, we found that only distance to closest road had a significant effect on low frequency bat occupancy probability (Table 2.8). Low frequency bat occupancy probability decreased by 10% for every 281 m increase in distance to closest road (Figure 2.3A). The global model was the top model for red bat occupancy (Table 2.7). From examining the parameter estimates, we found that habitat type, clutter amount, distance to closest road, and distance to stream impacted red bat occupancy probabilities (Table 2.8). Red bat occupancy probability was 35% higher in hardwood than pine habitat, 11% lower in pine than mixed habitat, and 23% lower in mixed than hardwood habitat. Red bat occupancy was 35% higher in medium clutter than low clutter and 2% higher in high clutter than low clutter. Red bat occupancy also decreased by 10% for every 131 m increase in distance to closest road; and was lowest when 8 m from a stream but increased toward one at 123 m (Figure 2.4). Multiple models fell within 2 ΔAIC for evening bats; these included the null model, the global model, the road model, and the stream model (Table 2.7). When we attempted to examine the parameter estimates for the global model, we found that it did not converge and we eliminated it from our model set. After doing so, we found support for the null model, the road model, and the stream model. From examining parameter

estimates of the covariates included in these models, we found that distance to closest road was the only covariate that had a significant effect on evening bat occupancy probability (Table 2.8). Evening bat occupancy decreased by 10% for every 263 m increase in distance to closest road (Figure 2.3B). We found support for multiple models for Myotis occupancy; these models included the null model, the road model, the habitat model, and the stream model (Table 2.7). Myotis occupancy was significantly affected by habitat type and distance to closest road (Table 2.8). Myotis occupancy probability was 29% higher in hardwood than pine habitat, 30% lower in pine than mixed habitat, and 10% higher in mixed than hardwood habitat, and decreased by 10% for every 197 m increase in distance to closest road (Figure 2.5). The null model, road model, and the stream model were highly competitive for tricolored bat occupancy (Table 2.7) and we found that distance to closest road had a significant impact on tricolored occupancy (Table 2.8). Tricolored bat occupancy probability was predicted to decrease by 10% for every 133 m increase in distance to closest road (Figure 2.3C).

Some of our predictions were supported by the results for colonization and extinction probabilities, which were species-specific. Low frequency bats exhibited the highest colonization probabilities, followed by red bats, then, unlike what we predicted, tricolored bats had the third highest colonization probabilities. Evening bats had the second lowest colonization probabilities and Myotis colonization probabilities fell between evening bats and tricolored bats (Table 2.9). The colonization probability of low frequency bats was affected by habitat type, where they were most likely to move into areas in mixed habitat, followed by pine, and least likely to move into areas in hardwood

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habitat (Table 2.9). We found that Myotis colonization probabilities were affected by clutter amount, where Myotis were most likely to move into areas of high clutter, followed by medium clutter, and were least likely to move into areas of low clutter post-WNS (Table 2.9). We did not find any support for clutter amount or habitat type when examining colonization probabilities of red bats, evening bats, and tricolored (Table 2.9). As with our predictions for colonization probabilities, some of our predictions regarding what species had higher extinction probabilities were supported by our results. As we predicted, Myotis exhibited the highest extinction probabilities, however, unlike our predictions, evening bats exhibited the second-highest extinction probabilities. Red bats had the third highest extinction rates, followed by tricolored bats, and low frequency bats exhibited the lowest extinction rates (Table 2.10). Myotis extinction probabilities were affected by habitat type, where Myotis were most likely to stop using points in hardwood habitat, followed by mixed habitat, and were least likely to stop using points in pine habitat (Table 2.10). Evening bat extinction probabilities were affected by clutter amount, where these bats were most likely to move out of medium clutter, followed by low clutter, and were least likely to move out of high clutter areas (Table 2.10). Red bat extinction probabilities were affected by habitat type, where red bats were most likely to stop using points in mixed habitat, followed by pine, and were least likely to stop using points in hardwood habitat (Table 2.10). Low frequency bat and tricolored bat extinction probabilities were not affected by clutter amount or habitat type (Table 2.10).

Temporal Niche Partitioning

A total of 1,555 call files were collected from the 109 points sampled during summer 2004 and 2005. Of those call files, 195 were low frequency bat call files, 372 were red bat call files, 77 evening bat call files, 255 Myotis call files, 573 tricolored bat call files, and 83 were unidentified. During summer 2016 and 2017, we collected 2,684 bat call files from the 105 points sampled. We collected 1,286 low frequency bat call files, 669 red bat call files, 253 evening bat call files, 225 Myotis bat call files, 130 tricolored bat call files, and 121 were unidentified. We found a significant difference between the number of files collected per night pre- and post-WNS for low frequency bats, with significantly more calls collected post-WNS (Table 2.11). There was no significant difference in the number of calls collected pre- and post-WNS for all other species (Table 2.11).

While all species changed when they were active at night, some of our predictions regarding the amount of change in activity for bat species from pre- to post-WNS were supported by our results (Figure 2.6). Unlike our predictions, low frequency bats shifted their activity the most pre- to post-WNS, with activity becoming more evenly distributed throughout the night. Additionally, the amount of shift low frequency bats exhibited was significantly different from the amount of shift exhibited by all other species. Red bats exhibited the second-greatest amount of change in activity pre- to post-WNS, with activity becoming more evenly distributed throughout the night post-WNS. Myotis shifted their activity the most out of the WNS-susceptible species and third-most overall, becoming less active at the beginning of the night and more active at the end of the night post-WNS. Additionally, the amount of change exhibited by Myotis and red bats was

significantly different from tricolored bats. Tricolored bats changed their activity the least amount, followed by evening bats.

Some of our predictions regarding the change in level of overlap between species pre- and post-WNS were supported by our results (Table 2.12). Following our predictions, the level of overlap between low frequency bats and red bats and evening bats increased, however, unlike our predictions, the level of overlap between low frequency bats and WNS-susceptible species also increased (Table 2.12). In particular, the level of overlap between low frequency bats and tricolored bats was significantly different from pre- to post-WNS (Table 2.12). As we predicted, the level of overlap increased between red bats and WNS-resistant species increased, but unlike our predictions, the level of overlap between red bats and WNS-susceptible species also increased, with the level of overlap between red bats and Myotis and red bats and tricolored bats being significantly different from pre- to post-WNS (Table 2.12). Following our predictions, the level of overlap decreased between evening bats and Myotis (Table 2.12). As we predicted, the level of overlap significantly decreased between Myotis and tricolored bats (Table 2.12).

Discussion

Our data suggest that in forests of South Carolina, tree-dwelling and cave-hibernating bat species are utilizing available niches differently following the arrival of WNS. Similar to previous studies in other portions of the U.S. (Jachowski et al., 2014;

Thalken et al., 2018), as WNS-susceptible species became less abundant on the landscape, WNS-resistant species moved into the areas and times in which WNS-susceptible species were once more active. Specifically, low frequency bats, red bats, and evening bats, the WNS-resistant species, moved into previously unused areas and changed when they were active at night. Myotis, which are susceptible to WNS, moved out of previously used areas and changed when they were active at night, potentially so that they would not have to compete with evening bats. At the same time, tricolored bats, our other WNS-susceptible species, moved into previously unused areas, left previously used areas, and did not change when they were active at night. This suggests that WNS destabilized the spatial and temporal niche partitioning exhibited by each species in APD.

Our research suggests that spatial niche partitioning between bats at APD has changed pre- to post-WNS. Specifically, we saw that Myotis stopped using hardwood habitat, which may have allowed low frequency bats to start using hardwood habitat. While we did not predict to see such a movement in the areas they used between Myotis and low frequency bats, we did hypothesize that there would be relaxed niche partitioning exhibited by WNS-susceptible species. As Myotis altered which habitat they used for foraging, the spatial niche partitioning between them and low frequency bats relaxed. Evening bats, red bats, and tricolored bats also changed the areas they used, though these movements did not seem to be directly related to other species' movements. As was seen by Jachowski et al. (2016) and suggested by Thalken et al. (2018), WNS-susceptible species altered their habitat use and as a result, WNS-resistant species were able to alter their habitat use as well.

Our results also suggest that bats altered temporal activity pre- to post-WNS at APD. Contrary to our predictions, low frequency bats exhibited the most amount of shift in activity pre- to post-WNS. Though we hypothesized that low frequency bats would not compete with other species, they seem to still be taking advantage of times of night when WNS-susceptible species used to be active. Additionally, we considered red bats to be the most adaptable of the species included in this study. Because they are adaptable, our findings support our prediction that they were likely able to become active during times when WNS-susceptible species were once more active. By contrast, we did not consider Myotis bats to be as adaptable as red bats, as their calls do not fluctuate between pulses and they rely on gleaning to capture prey items (Faure et al., 1993). Despite this, Myotis activity shifted towards the end of the night, which may have happened because they may be experiencing some increased competition from WNS-resistant bats, especially evening bats. As we predicted, evening bats were able to shift their activity to times of night so that they could take advantage of times of night when Myotis bats were no longer as active as they were pre-WNS. Contrary to our predictions, tricolored bats shifted their activity the least amount. Tricolored bats were the smallest-bodied bat of the species included in this study, had the highest call frequency, and preyed soft-bodied prey items, therefore, they may have been able to continue to be active during the same times of night pre- and post-WNS, since competition between them and other species was considered to be low.

As bats changed when they were active at night, they in turn altered temporal niche partitioning, though the degree to which these alterations occurred varied between

species. As we predicted, the level of overlap between WNS-resistant species increased and the level of overlap between Myotis and tricolored bats decreased pre- to post-WNS. We predicted the level of overlap between WNS-susceptible species would decrease for two reasons; (1) both species were less abundant on the landscape due to WNS, and (2) both species had high frequency calls and if they foraged in the same areas during the same times, they may have experienced jamming of their calls. Echolocation jamming occurs when sympatric species emit echolocation calls in the same area and equates to interference for each species (Bates et al., 2008; Takahashi et al., 2014). Therefore, Myotis and tricolored bats would try to avoid each other so that they would avoid jamming each other's call. Contrary to our predictions, we saw a decrease in the level of overlap between evening bats and Myotis and an increase in the level of overlap between low frequency bats and Myotis and low frequency bats and tricolored bats. Additionally, the level of overlap between low frequency bats and tricolored bat was significantly different pre- to post-WNS. The level of overlap between evening bats and Myotis bats might have decreased for two reasons: (1) there were fewer Myotis on the landscape post-WNS and (2) Myotis were not be able to compete with evening bats. These bats had similar prey items, call frequencies that included 40 kHz, and foraged along edges (Barbour & Davis, 1969; LaVal et al., 1977; Caire et al., 1979; Fenton et al., 1983; Whitaker & Clem, 1992; Feldhamer et al., 1995; Lacki et al., 2007). Despite our prediction that low frequency bats would not compete with WNS-susceptible species, we found evidence that low frequency bats changed when they foraged post-WNS and seem to be taking advantage of fewer WNS-susceptible species on the landscape.

Overall, our findings lend additional support for the results of other studies conducted in different bat communities while also building upon these previous studies in a number of ways. As we found evidence of destabilized niche partitioning post-WNS in South Carolina, Jachowski et al. (2014) found relaxed niche partitioning in New York after the little brown bat population succumbed to WNS and Thalken et al. (2018) found that species that were not impacted by WNS were exploiting niche space formerly used by WNS-susceptible species in Kentucky. Therefore, we can infer that niche partitioning in widespread communities has been affected by WNS, both directly and indirectly. Our study also differed from these previous studies; unlike Jachowski et al. (2014), we did not have one dominant species in our bat community, and, therefore, we could compare multiple species instead of one. Thalken et al. (2018) collected data using mist nets instead of acoustic detectors. These two methods have their own advantages: for example, captures from mist nets allow researchers to identify bats by sex, age, and species in the case of Myotis (Keunzi & Morrison, 1998) while acoustic detectors generally yield higher species richness values (Murray et al., 1999). Despite these differences, data collected by both techniques were still able to capture the effect WNS has had on niche partitioning in two different bat communities. We would suggest using acoustic detectors to collect community data, however, as acoustic detectors can be deployed in areas otherwise difficult to sample using mist nets (Murray et al., 1999) and mist nets can be avoided by some species (Kunz & Kurta, 1988).

Our findings also have implications to the conservation of bat species due to some species' threatened status and on how managers will conserve them through habitat

management. As WNS continues to impact bats in North America, it is important to collect data that provides an up-to-date representation of the bat communities affected by this disease. It is particularly important to collect recent data on little brown bats and tricolored bats, as both of these species are under review by the U.S. Fish and Wildlife Service for listing under the Endangered Species Act. Recent data on northern long-eared bats are also necessary to collect, as this species is federally listed (USFWS, 2016; 2018). As part of their listed status or potential listed status, additional information on these species, including habitat requirements, current range, summer population estimates, and species-specific population data pre- and post-exposure to WNS, is necessary in order to warrant their status (USFWS, 2016; 2017). As such, this study provides an up-to-date representation of post-WNS habitat requirements for tricolored bats and Myotis species, as well as other species, in APD. Additionally, changes in niche partitioning among bats impact the habitat management decisions land managers will need to make to conserve these species. As habitat use by bats changes post-WNS, land managers may no longer be able to rely on research conducted pre-WNS. For example, we found evidence that Myotis are more likely to use high clutter areas from pre- to post-WNS. As such, if land managers decide to focus on conserving habitat for Myotis, using our results, they could decide to alter their land management so that there would be more high clutter areas available for remnant Myotis to forage in. Similarly, changes in temporal niche partitioning can also clue us in to how well remnant bats will be able to survive in the coming years. We found evidence that Myotis are now active at the end night and they may be expending more energy than they should to catch prey during this time of night

(Kunz, 1973; Eckert, 1982; Racey & Swift, 1985). The habitats Myotis forage in, therefore, may become more important for land managers to maintain and create when attempting to conserve these WNS-susceptible species.

As WNS continues to spread across the U.S., it is important to continue investigating the direct and indirect effects the disease has had on remnant bat community structure. When continuing this research, we suggest that studies are conducted for longer periods of time (e.g., more than 4 years; Jachowski et al., 2014) so that researchers can determine if changes in niche partitioning have any long-term or cascading effects on bats. Acquiring such knowledge will provide an accurate baseline and in turn improve land management decisions for WNS-impacted communities. Additionally, we suggest that researchers conduct additional studies in different bat communities so that we can determine if relaxed niche partitioning affects demographic increases of WNS-resistant species and the ability of remnant WNS-susceptible species to persist. Other systems are also under threat from emerging infectious diseases, such as chytridiomycosis in amphibian communities (Lips et al., 2006), sylvatic plague in grassland ecosystems (Antolin et al., 2002), and snake fungal disease in North America (Lorch et al., 2016). As such, we suggest research be conducted within these communities as well to determine the direct and indirect effects of emerging infectious diseases.

Tables

Table 2.1. *A priori* prediction index regarding level of overlap between bat species in Andrew Pickens District. Prediction index scores were based on amount of overlap in call structure, foraging habitat, foraging times, and known prey items with Myotis and tricolored bats. If species overlapped in one of these categories, they earned one point; if they did not overlap, they earned a zero for that category.

Species	Characteristic call frequency	Foraging habitat	Foraging times	Known prey items	Prediction index score
Low frequency bats (WNS-resistant)	20-30 kHz (Brigham et al., 1989; Thomas et al., 1987; Crampton & Barclay, 1998)	Generalist; clutter-intolerant (Furlonger et al., 1987; Geggie & Fenton, 1985; Brigham et al., 1997; Menzel et al., 2005*a*)	Forage throughout the night with most activity within second hour after sunset (Kunz, 1973)	"Beetle specialist"; katydids, flies, hymenopterans (Black, 1974)	1
Red bats (WNS-resistant)	35-40 kHz, fluctuates (Brigham et al., 1989)	High above treetops/ canopy; clutter-adapted (LaVal et al., 1977)	Forage in early evening, (Harvey et al., 2011)	Moths, beetles, flies, mayflies, grasshoppers (Carter et al., 2004; Clare et al., 2009)	4
Evening bats (WNS-resistant)	35-40 kHz (Menzel et al., 2003)	Along edges; clutter-adapted (Lacki et al., 2007)	First hours of night (Lowery, 1974)	Beetles, moths, flies, leafhoppers (Whitaker & Clem, 1992; Feldhamer et al., 1995)	4
Myotis (WNS-susceptible)	40 kHz (Fenton & Bell, 1979; 1981; Thomas et al., 1987; Crampton &	Along edges, underneath canopy; clutter-adapted	First hours of the night (dusk to 2400) then again from 0100 to	Moths, wasps, mosquitoes, craneflies (Barbour & Davis, 1969)	Tricol-ored: 4

	Barclay, 1998)	(LaVal et al., 1977; Caire et al., 1979; Fenton et al., 1983)	0500 (Anthony & Kunz, 1977)		
Tricolored bats (WNS-susceptible)	40-50 kHz (MacDonald et al., 1994)	Generally do not use cluttered habitats, though they are clutter-adapted; waterways and forest edges (LaVal et al., 1977)	Early in evening (Davis & Schmidly, 1997)	Moths, flies, beetles, ants (Barbour & Davis, 1969; Fujita & Kunz 1984)	Myotis: 4

Table 2.2. *A priori* model variables for detection probability (*p*) of bats in Andrew Pickens District in summer 2016 & 2017. A null model was included in the analysis.

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.	Sleep & Brigham, 2003
2	Julian day	Julian day has an effect on bat *p*.	Continuous	As Julian day increases, bat *p* increases.	Starbuck et al., 2015
3	Precipitation (mm)	Precipitation has an effect on bat *p*.	Continuous	As amount of precipitation increases, bat *p* decreases.	Yates & Muzika, 2006
4	Minimum nightly temperature (°C)	Temperature has an effect on bat *p*.	Continuous	As temperature increases, bat *p* increases.	Yates & Muzika, 2006; Starbuck et al., 2015
5	Minimum nightly temperature + Precipitation	Weather variables have an additive effect on bat *p*.	Continuous (°C & mm)	Temperature will have a positive effect on bat *p* as it increases, but precipitation will have a negative effect on bat	

			p as it increases.
6	Clutter + Julian day + Precipitation + Temperature	Global model	Categorical (low, medium, high) & continuous (date; mm; °C)

Table 2.3. *A priori* model variables for occupancy probability (Ψ) of bats in Andrew Pickens District in summer 2016 & 2017. A null model was included in the analysis.

Model #	Variable	Hypothesis	Covariates	Predicted Effects	Literature Cited
1	Clutter	Clutter will have an effect on bat Ψ.	Low, medium, high	As clutter amount increases, bat Ψ will decrease.	Yates & Muzika, 2006
2	Habitat type	Habitat type will have an effect on bat Ψ.	Pine, hardwood, mixed	Low frequency bats more likely to use pine habitat, red bats more likely to use hardwood habitat, evening bats and Myotis more likely to use mixed habitat. Tricolored bats more likely to use mixed and hardwood habitat.	Low frequency bats, evening bats, Myotis, tricolored bats: Perry et al., 2007 Red bats: Hutchinson & Lacki, 2000; Perry et al., 2007
3	Stream (m)	Distance to closest stream source will have an	Continuous	As distance to closest water source increases,	Cross, 1988; Racey, 1998; Ford et al., 2006

		effect on bat Ψ.		bat Ψ will decrease.	
4	Road (m)	Distance to closest road will have an effect on bat Ψ.	Continuous	As distance to closest road increases, bat Ψ will increase.	Starbuck et al., 2015
5	Clutter + Habitat type + Water + Road	Global occupancy model	Categorical (low, medium, high; pine, hardwood, mixed) & continuous (m^2/ha; m)		

Table 2.4. Number of points species groups colonized (i.e., started using) and became extinct (i.e., stopped using) pre- to post-WNS at Andrew Pickens District.

Species group	# points species colonized pre- to post-WNS	# points where species became extinct pre- to post-WNS
Low frequency bats	24	19
Red bats	19	27
Evening bats	15	24
Myotis	19	30
Tricolored bats	13	36

Table 2.5. Top-ranked models for detection probability (*p*) for species groups in Andrew Pickens District pre- and post-WNS. Only top-ranked models ($\Delta AIC \leq 2$) are included.

Species Group	Model Name	K	AIC	ΔAIC	w$_i$
Low frequency bats	Clutter + Julian day + Precipitation + Minimum nightly temperature	9	396.06	0	0.73
Red bats	Clutter	6	388.74	0	0.52
	Clutter + Julian day + Precipitation + Minimum nightly temperature	9	389.55	0.82	0.32
Evening bats	Clutter	6	324.44	0	0.84
Myotis	Julian day	5	358.89	0	0.27
	Null	4	359.00	0.10	0.25
	Precipitation	5	360.22	1.32	0.14
	Clutter	6	360.39	1.49	0.13
	Minimum nightly temperature	5	360.43	1.54	0.12
Tricolored bats	Julian day	5	321.62	0	0.79

Table 2.6. Parameter estimates, standard errors (SE), and 95% confidence intervals (CI) of parameters within the top models for detection (*p*) models (< 2 ΔAIC) of low frequency bats, evening bats, Myotis, and tricolored bats in Andrew Pickens District. Model-averaged parameter estimates, standard errors (SE) and 95% confidence intervals (CI) for the two top models for red bats.

Parameter	Estimate	SE	Upper 95% CI	Lower 95% CI
Low frequency bats				
Intercept	-1.08	0.30	-0.78	-1.39
Low clutter	2.17	0.56	2.73	1.61
Medium clutter	0.59	0.40	1.00	0.19
Precipitation	-0.16	0.18	0.02	-0.33
Minimum nightly temperature	0.23	0.20	0.44	0.03
Julian day	0.31	0.21	0.53	0.10
Red bats				
Intercept	-0.40	0.33	0.25	-1.05
Low clutter	1.09	0.48	2.04	0.15
Medium clutter	-0.19	0.43	0.66	-1.04
Precipitation	0.09	0.17	0.42	-0.24
Minimum nightly temperature	0.22	0.19	0.60	-0.15
Julian day	0.17	0.19	0.55	-0.21
Evening bats				
Intercept (high clutter)	-1.62	0.39	-1.24	-2.01
Low clutter	1.67	0.48	2.15	1.18
Medium clutter	0.52	0.46	0.98	0.06
Myotis				
Intercept	-0.03	0.57	0.54	-0.60
Low clutter	0.66	0.60	1.26	0.06
Medium clutter	-0.10	0.53	0.43	-0.63
Precipitation	0.19	0.26	0.45	-0.07
Minimum nightly temperature	0.06	0.22	0.28	-0.16
Julian day	0.26	0.29	0.55	-0.03
Tricolored bats				
Intercept	-0.41	0.17	-0.24	-0.58
Julian day	0.57	0.18	0.75	0.39

Table 2.7. Top-ranked models for occupancy probability (Ψ) for species groups in Andrew Pickens District pre- and post-WNS. Only top-ranked models (ΔAIC ≤ 2) are included.

Species Group	Model Name	K	AIC	ΔAIC	w_i
Low frequency bats	Null	11	395.24	0	0.35
	Stream	12	396.40	1.16	0.19
	Road	12	396.47	1.23	0.19
	Clutter	13	397.12	1.88	0.14
Red bats	Clutter + Road + Habitat + Stream	17	378.98	0	0.97
Evening bats	Null	8	323.49	0	0.41
	Road	9	325.20	1.71	0.18
	Stream	9	325.34	1.84	0.16
Myotis	Null	9	361.65	0	0.36
	Road	10	362.58	0.93	0.23
	Habitat	11	363.25	1.60	0.16
	Stream	10	363.40	1.75	0.15
Tricolored bats	Null	5	321.62	0	0.32
	Road	6	321.64	0.02	0.32
	Stream	6	322.23	0.61	0.24

Table 2.8. Parameter estimates, standard errors (SE), and 95% confidence intervals (CI) of parameters in the top models for occupancy (Ψ) models for bats in Andrew Pickens District.

Parameter	Estimate	SE	Upper 95% CI	Lower 95% CI
Low frequency bats				
Intercept	0.04	0.87	0.84	-0.91
Road	-0.37	0.33	-0.04	-0.70
Stream	0.24	0.33	0.57	-0.09
Low clutter	-0.73	0.99	0.26	-1.72
Medium clutter	0.52	1.09	1.61	-0.57
Red bats				
Intercept	16.02	11.79	27.81	4.23
Road	-17.30	12.51	-4.79	-29.81
Stream	11.96	8.53	20.49	3.43
Mixed habitat	-15.66	12.09	-3.57	-27.75
Pine habitat	-23.31	15.88	-7.43	-39.19
Low clutter	4.02	3.27	7.29	0.75
Medium clutter	40.09	28.36	68.45	11.73
Evening bats				
Intercept	-0.57	1.90	1.33	-2.47
Road	-3.50	3.09	-0.41	-6.59
Stream	0.37	0.80	1.17	-0.43
Low clutter	-0.92	2.63	1.71	-3.55
Medium clutter	16.24	26.19	42.43	-9.95
Myotis				
Intercept	0.61	0.64	1.25	-0.04
Road	-0.35	0.32	-0.03	-0.67
Stream	0.11	0.30	0.41	-0.19
Mixed habitat	0.44	1.26	1.70	-0.82
Pine habitat	-0.90	0.74	-0.17	-1.64
Tricolored bats				
Intercept	1.44	0.46	1.90	0.99
Road	-0.40	0.35	-0.05	-0.75
Stream	0.44	0.56	1.00	-0.12

Table 2.9. Parameter estimates, standard errors, and 95% confidence intervals (CI) for colonization (γ) probabilities of bats in Andrew Pickens District. Low frequency bats and Myotis colonization probabilities were affected environmental covariates (i.e., habitat type or clutter amount). Red bats, evening bats, and tricolored bats colonization probabilities were not affected by either clutter amount or habitat type.

Species	Estimate	Standard Error	Upper 95% CI	Lower 95% CI
Low frequency bats				
Hardwood habitat	0.61	0.56	1.17	0.04
Pine habitat	1.22	0.72	1.94	0.50
Mixed habitat	19.57	315.18	334.76	-295.61
Red bats	9.31	31.7	41.01	-22.39
Evening bats	6.91	17.8	24.71	-10.89
Myotis				
Low clutter	-1.25	0.80	-0.45	-2.05
Medium clutter	-0.54	0.66	0.11	-1.20
High clutter	0.73	1.24	1.97	-0.52
Tricolored bats	9.04	29.00	38.04	-19.96

Table 2.10. Parameter estimates, standard errors, and 95% confidence intervals (CI) for extinction (ε) probabilities of bats in Andrew Pickens District. Red bats, evening bats, and Myotis extinction probabilities were affected environmental covariates (i.e., clutter amount or habitat type). Low frequency bats and tricolored bats extinction probabilities were not affected by either clutter amount or habitat type.

Species	Estimate	Standard Error	Upper 95% CI	Lower 95% CI
Low frequency bats	0.24	0.40	0.64	-0.17
Red bats				
Hardwood habitat	0.48	0.69	1.17	-0.21
Pine habitat	0.29	0.82	1.11	-0.53
Mixed habitat	2.20	1.25	3.45	0.96
Evening bats				
Low clutter	1.18	1.01	2.18	0.17
Medium clutter	3.26	1.31	4.57	1.95
High clutter	-0.76	0.87	0.11	-1.63
Myotis				
Hardwood habitat	8.76	24.2	32.96	-15.44
Pine habitat	-6.66	24.2	17.54	-30.86
Mixed habitat	-6.26	24.3	18.04	-30.56
Tricolored bats	2.27	0.56	2.83	1.71

Table 2.11. Average number of call files collected pre- and post-WNS and two-tailed t-test results from comparing number of call files collected per night for species in Andrew Pickens District in pre- and post-WNS. Number of call files collected per night are statistically different if $P \leq 0.05$.

Species group	Average # call files pre-WNS	Average # call files post-WNS	Test statistic	SE	Df	P
Low frequency bats	2.67	17.26	-2.19	0.16	72	0.03
Red bats	5.10	8.03	-0.87	0.13	72	0.38
Evening bats	1.05	2.86	-1.89	0.02	72	0.06
Myotis	3.49	3.04	0.23	0.02	72	0.82
Tricolored bats	7.85	1.73	1.55	0.09	72	0.13

Table 2.12. Temporal overlap between bats in Andrew Pickens District. An asterisk (*) by the species names indicates the level of overlap was significantly different between pre- and post-WNS.

| Species comparison	Pre-WNS Δ_4	Pre-WNS CI (lower, upper)	Post-WNS Δ_4	Post-WNS CI (lower, upper)	Pre-Post difference
Low frequency bats – red bats	0.81	0.74, 0.86	0.83	0.77, 0.85	-0.02
Low frequency bats – evening bats	0.67	0.58, 0.79	0.81	0.75, 0.87	-0.14
Red bats – evening bats	0.77	0.70, 0.86	0.88	0.82, 0.94	-0.11
Tricolored bats – Myotis*	0.92	0.87, 0.95	0.78	0.71, 0.85	0.14
Low frequency bats – Myotis	0.62	0.52, 0.67	0.76	0.66, 0.77	-0.14
Low frequency bats – tricolored bats*	0.63	0.55, 0.69	0.89	0.83, 0.91	-0.26
Red bats – Myotis*	0.63	0.54, 0.68	0.83	0.76, 0.88	-0.10
Red bats – tricolored bats*	0.64	0.54, 0.65	0.81	0.73, 0.86	-0.17
Evening bats – Myotis	0.77	0.64, 0.85	0.75	0.65, 0.80	0.02
Evening bats – tricolored bats	0.76	0.63, 0.85	0.81	0.70, 0.87	-0.05

Figures
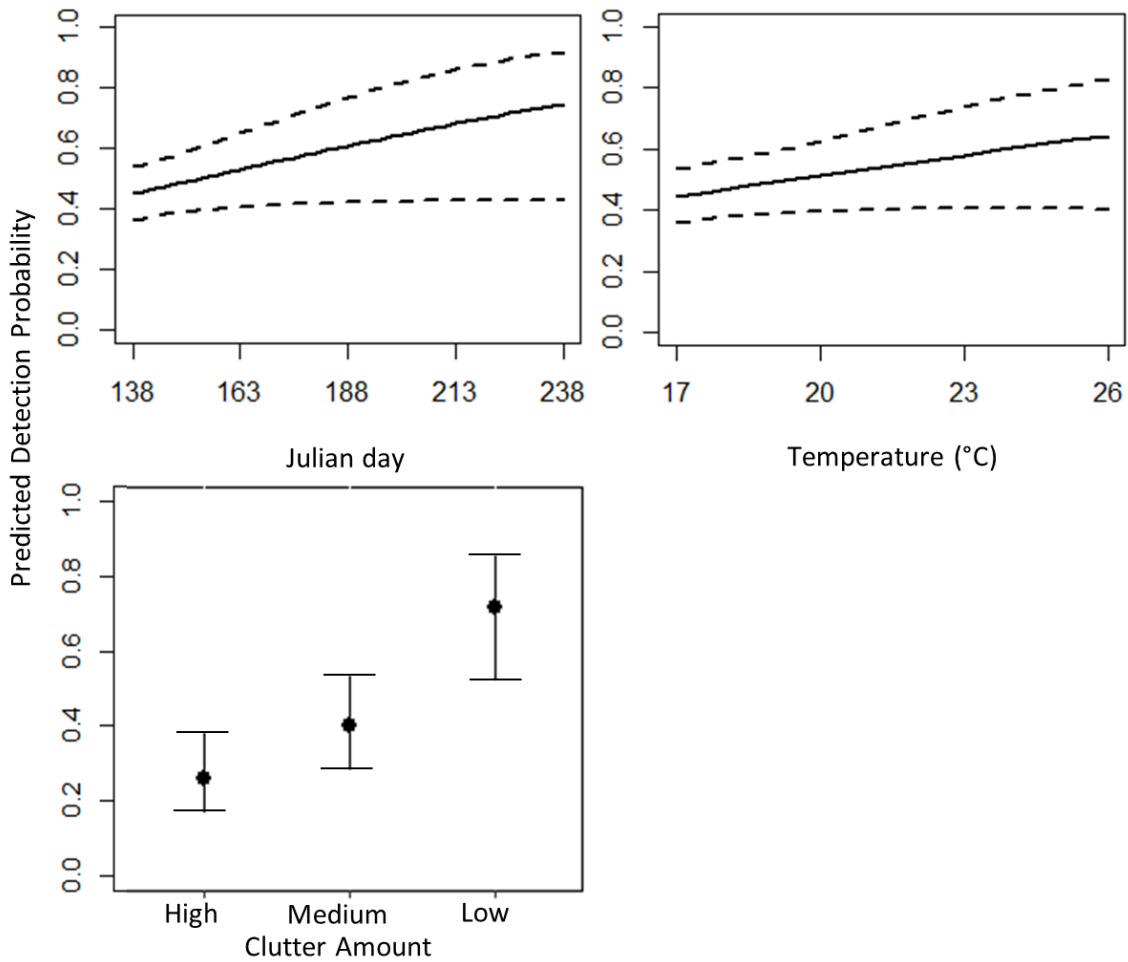
Figure 2.1. Influence of Julian day, minimum nightly temperature, and clutter amount on detection probabilities (p) of low frequency bats in Andrew Pickens District. The dotted lines (Julian day and temperature) and vertical black lines (clutter amount) represent the 95% confidence interval.
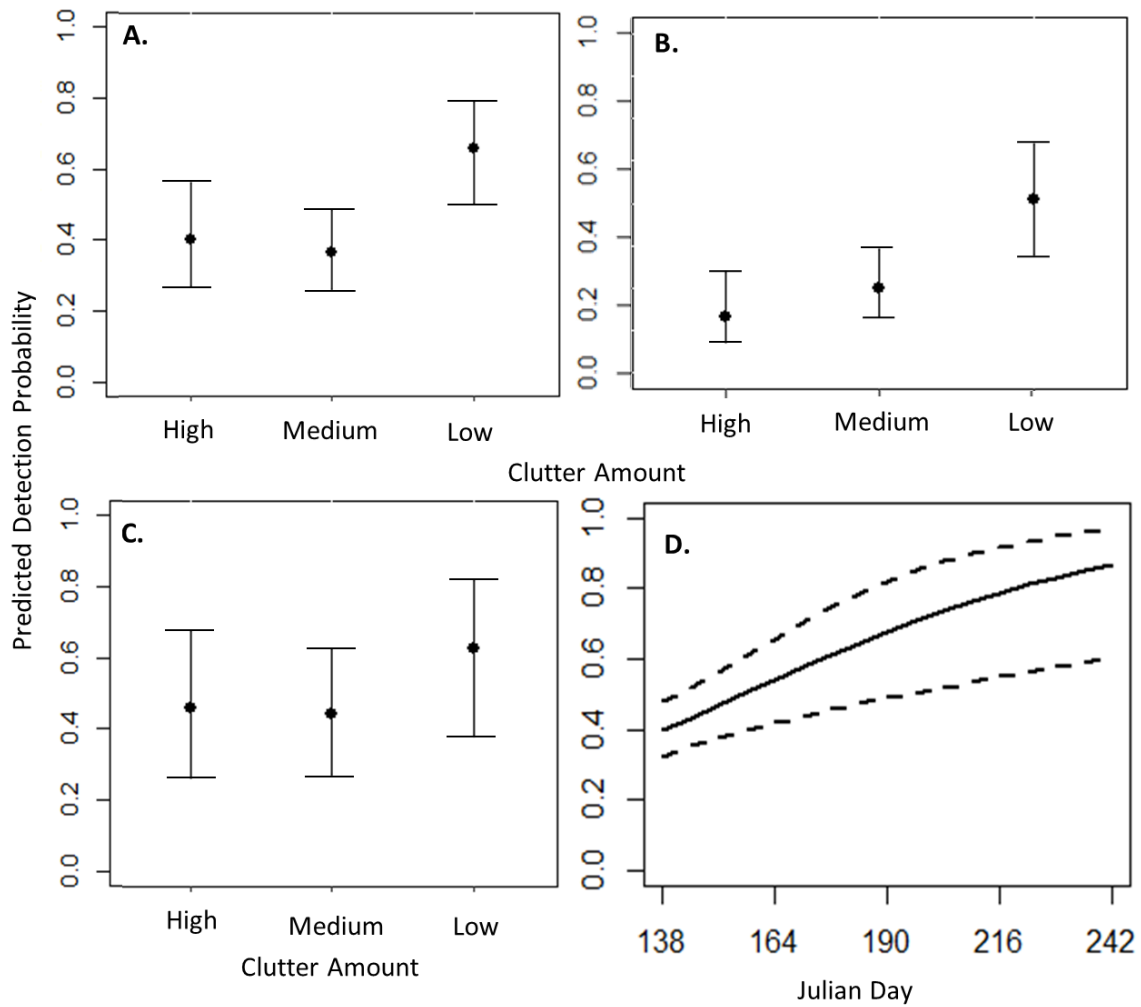
Figure 2.2. Influence of clutter on (A) red bat, (B) evening bat, and (C) Myotis detection probabilities (*p*) and (D) Julian day on tricolored bats detection probabilities in Andrew Pickens District. The horizontal black lines (A, B, & C) and dotted lines (D) represent the 95% confidence interval.
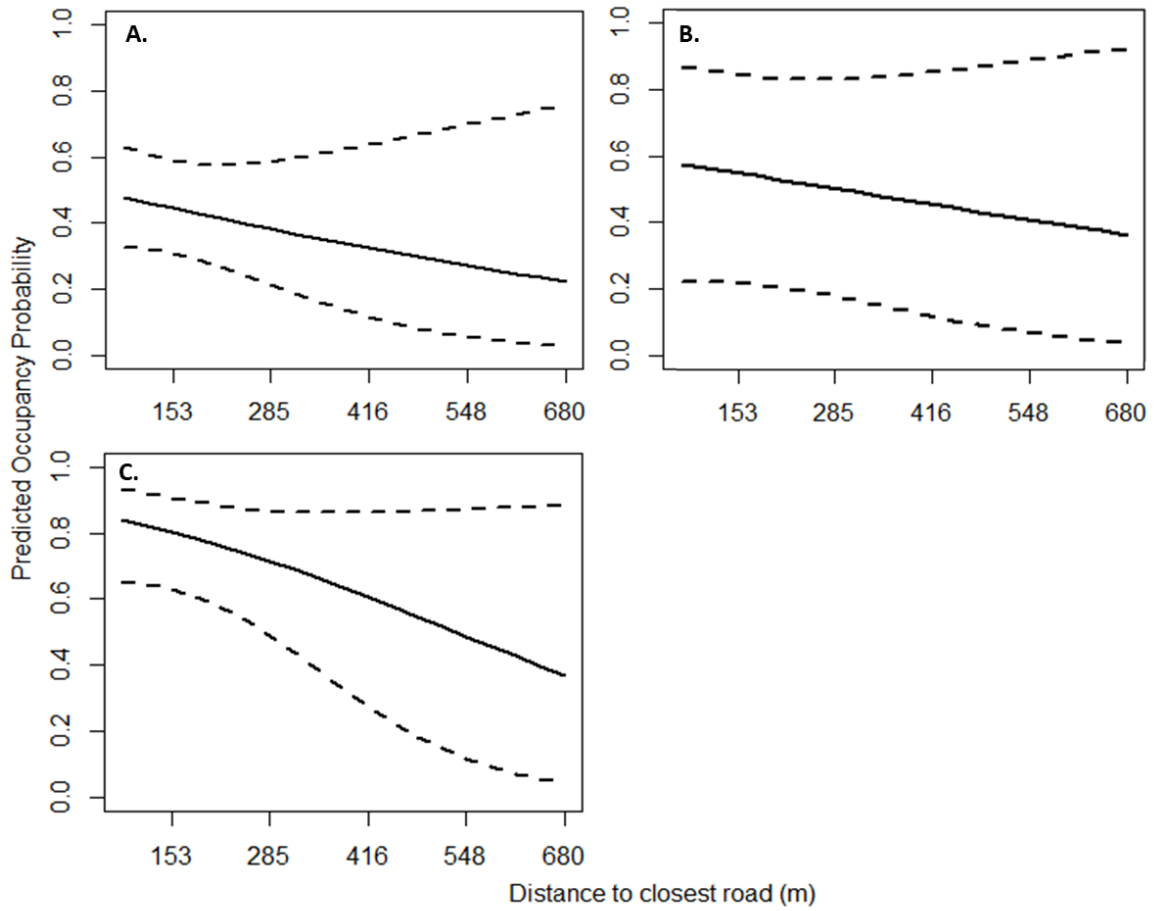
Figure 2.3. Predicted occupancy (Ψ) probability of (A) low frequency bats, (B) evening bats, and (C) tricolored bats as distance to closest road increases. The solid line represents the predicted occupancy probability estimate and the dotted lines represent the 95% confidence intervals.
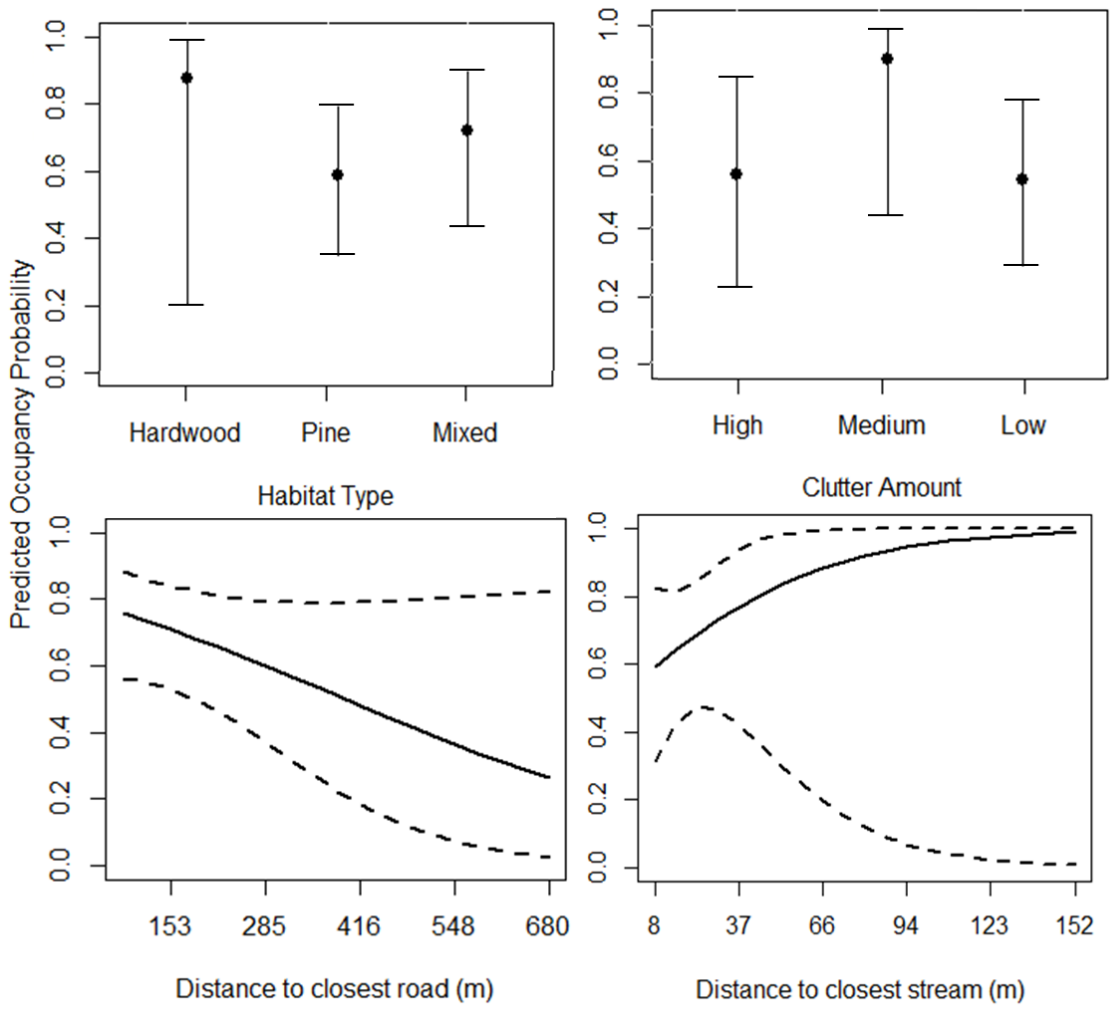
Figure 2.4. Predicted occupancy (Ψ) probability of red bats in each habitat, clutter amount, and as distance to closest road and distance to closest stream increases in Andrew Pickens District. The points (habitat type and clutter amount) and solid line (distance to closest road and closest stream) represent the predicted occupancy probability estimate and the error bars (habitat type and clutter amount) and dotted lines (distance to closest road and closest stream) represent the 95% confidence intervals.
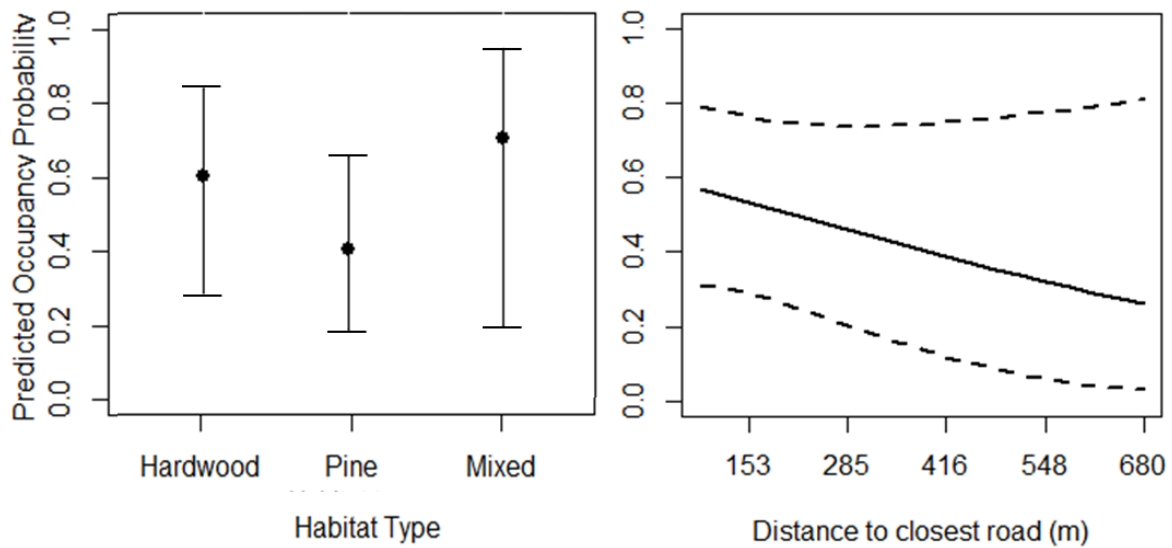
Figure 2.5. Predicted occupancy (Ψ) probability of Myotis in different habitat types and as distance to closest road increases. The point (habitat type) solid line (distance to closest road) represents the predicted occupancy probability estimate and the vertical lines (habitat type) and dotted lines (distance to closest road) represent the 95% confidence intervals.
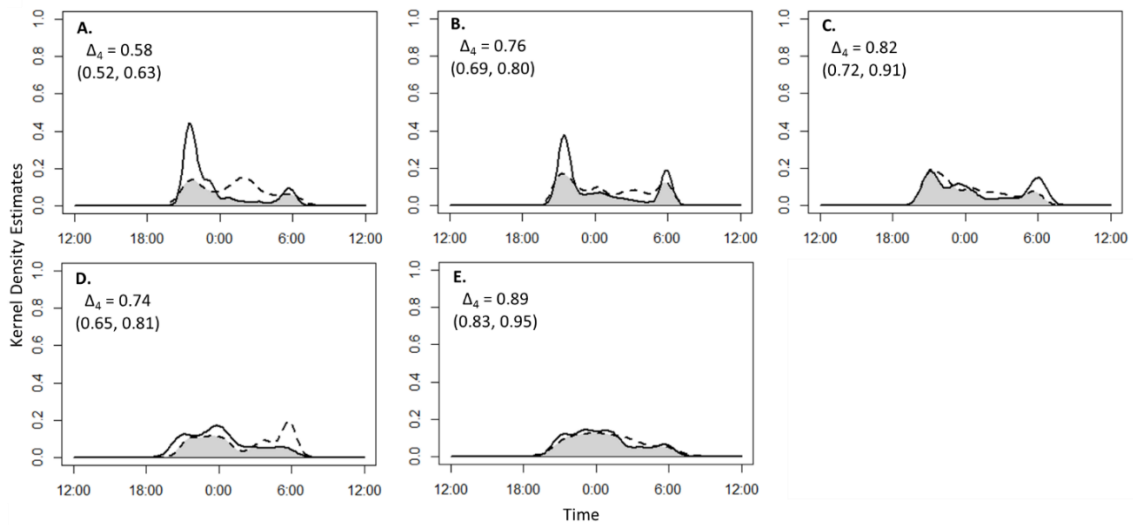
Figure 2.6. Kernel density estimates of (A) low frequency bats, (B) red bats, (C) evening bats, (D) Myotis, and (E) tricolored bats pre- (solid black lines) and post-WNS (dotted black lines) in Andrew Pickens District. The shaded gray areas represent the amount of overlap in activity between pre- and post-WNS. Temporal shifts of species pre- to post-WNS are represented by Δ_4, with $\Delta_4 = 1$ representing no temporal shifts pre- to post-WNS and $\Delta_4 = 0$ representing complete temporal shift. Midnight is represented by 0:00 and noon is represented by 12:00.

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