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Distribution and Habitat Association of the Northern Long-eared Bat

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DISTRIBUTION AND HABITAT ASSOCIATION OF THE NORTHERN LONG-EARED BAT

by

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DISTRIBUTION AND HABITAT ASSOCIATION OF THE NORTHERN LONG-EARED BAT

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Because of white-nose syndrome, the northern long-eared bat (*Myotis septentrionalis*) is experiencing rapid population declines across the majority of its range. This decline has prompted increased regulatory protection and thus an increased need for effective habitat management strategies. Insight into the species habitat associations, however, is a prior necessity to ensure management practices are biologically relevant. Understanding these relationships requires a holistic approach that addresses the multiple ways in which the species is interacting with its environment. The objective of my thesis was to address these relationships following a multi-scale approach that assessed the factors associated with roost tree selection, distribution, and habitat use. I conducted a quantitative meta-analysis of all northern long-eared bat roost-selection studies, thus enabling inference across the range of the species. Secondly, I sought to understand the factors associated with the northern long-eared distribution in Nebraska by conducting a multiscale occupancy study with four acoustic survey stations nested within 101 10 km x 10 km grids distributed across Nebraska. Lastly, to assess factors associated with multi-scale occupancy at finer spatial scales, I combined presence/absence results from 5 intensively sampled study sites in Nebraska with on-the-ground habitat measurements. Results from the meta-analysis indicate selected roost trees had a greater amount of bark remaining on the bole, a larger diameter at breast height, a lower decay class, and were

taller. Results from the statewide occupancy study provide evidence for relationships between large-scale occupancy (ψ) and forest clumpiness, proximity to potential hibernacula, and summer temperature. Within occupied grids, evidence supported a positive relationship between small-scale occupancy (θ) and forest area within 125 m. Results failed to provide evidence of habitat factors associated with ψ at the 5 study sites likely due to high presence of the species. Evidence, however, did support a positive relationship between canopy closure and θ. Reported occupancy estimates between the two studies results serve as a pre-white-nose syndrome baseline, as I collected all data prior to the detection of white-nose syndrome in Nebraska.

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CHAPTER 1: AN INTRODUCTION TO THE DISTRIBUTION AND HABITAT ASSOCIATION OF THE NORTHERN LONG-EARED BAT

Introduction

Bats have existed for approximately 52 million years, and their taxonomic order, Chiroptera, contains >1200 species, second only in number to Rodentia (Simmons et al. 2008, Altringham 2011). They exhibit diverse dietary habits ranging from species that feed on insects and other arthropods to those that feed on fruit, nectar, fish, and blood (Kunz et al. 2011). This variety of life strategies results in billions of dollars in ecosystem services to humans in form of pest control, pollination, and seed dispersion (Boyles et al. 2011, Kunz et al. 2011). The reliability of these services is increasingly jeopardized as bat populations decline globally as a result of habitat fragmentation (Estrada-Villegas et al. 2010), deaths caused by wind energy (Frick 2017), global climate change (Sherwin et al. 2013), culling initiatives (Florens 2015), and of particular importance to North American hibernating bats, human-transported emerging diseases (Burton 2008, Frick et al. 2010). Despite the combination of economic value and precipitous decline, bats remain a relatively understudied taxonomic group with many unanswered questions and gaps in knowledge that impede evidence-based conservation (Fenton 2003, Hayes 2003, Miller et al. 2003).

A regional-scale driver of population decline in North American hibernating bats is the fungal-caused disease white-nose syndrome (Fenton 2012). Once infected by the fungal pathogen, *Pseudogymnoascus destructans*, some species exhibit a ~95% mortality rate (Frick et al. 2010, Minnis and Lindner 2013). This resulted in an estimated 5.5 million bats dying as result of the disease between its first discovery in 2007 and 2012

(U.S. Fish and Wildlife Service 2012). Of the 10 North American species identified with symptoms of the disease (Kansas Department of Wildlife, Parks, and Tourism 2018), 5 are present in Nebraska: the big brown bat (*Eptesicus fuscus*), the little brown bat (*Myotis lucifugus*), the tricolored bat (*Perimyotis subflavus*), the long-legged bat (*M. volans*), and the northern long-eared bat (*M. septentrionalis*) (Czaplewski et al. 1979).

Of the species in Nebraska, the northern long-eared bat is particularly susceptible to the effects of the disease. A study by Frick and colleagues (2015) concluded that of the 6 most affected species, the northern long-eared bat had the highest probability of extinction. By comparing data on known hibernacula pre- and post-infection, the northern long-eared bat experienced a 69% local extinction rate (Frick et al. 2015). Although the species is far ranging, as of the summer of 2018, >98% of United State counties within the range of the northern long-eared bat are within 150 miles of an infected county (U.S. Fish and Wildlife Service 2018). Due to the population declines caused by white-nose syndrome and the disease unabated spread, the northern long-eared bat was listed as threatened under the U.S. Endangered Species act in the spring of 2015 (Fish and Wildlife Service 2016).

The northern long-eared bat belongs in the order Chiroptera, suborder Microchiroptera, family Vespertilionidae, and genus *Myotis* (Findley 1972, Caceres and Barclay 2000). Its distribution includes the eastern United States from the Atlantic coast to eastern Montana, northwest into British Columbia, and south into central Louisiana and the Carolinas (Barbour and Davis 1969, van Zyll de Jong 1979, Caceres and Barclay 2000, U.S. Fish and Wildlife Service 2018). Indicative of its namesake, the northern long-eared bat has relatively long ears when compared to its eastern congeners (Caceres and Barclay 2000). Typical of other long-eared bats, the northern long-eared bat exhibits a gleaning foraging strategy (i.e. capturing non-airborne prey from a substrate such as foliage) (Faure et al. 1993), but will also capture prey mid-flight through aerial hawking (Fenton and Bogdanowicz 2002). Generally considered an interior-forest species, observers describe the northern long-eared bat foraging between the understory and the canopy (Nagorsen et al. 1993) within the forest's interior rather than in clearings or over water (LaVal et al. 1977, Brack, Jr. and Whitaker Jr. 2001, Carroll et al. 2002, Patriquin and Barclay 2003).

As a “forest specialist”, the northern long-eared bat may be more vulnerable to habitat conversion and more likely to experience population declines (Jung et al. 1999, Clavel et al. 2011). Research of post-white-nose syndrome population trends support this possibility and suggest threats other than white-nose syndrome are also contributing to declines in northern long-eared bat abundance (Ingersoll et al. 2016). If this true, then effective habitat management strategies are required in conjunction with white-nose syndrome mitigation efforts. However, in order to manage and a conserve a species, an understanding of its habitat requirements is a critical requirement (Morrison et al. 2006).

Understanding habitat associations of bats requires a holistic approach, as selection occurs across multiple spatial and ecological scales (Miller et al. 2003). For example, individual roost trees are important to survival and reproduction as they provide shelter and satisfy temperature requirements for females during the summer maternity season (Cryan et al. 2001, Boyles 2007). Ensuring availability and recruitment of these suitable roost trees and predicting the potential effects of disturbance, however, requires an understanding of the characteristics bats select for when choosing a roost (Kunz and

Lumsden 2005). Roost trees must also be within commuting distance of suitable foraging habitat that may differ from their roosting habitat (Hutchinson and Lacki 1999, Rainho and Palmeirim 2011). Additionally, as bats disperse from their winter hibernacula to these summer maternity roosting grounds they may travel >300 km occupying areas potentially restricted geographically by climatic conditions and habitat connectivity (Griffin 1940, Barnhart and Gillam 2014).

The purpose of this study was to assess factors associated with habitat use or selection of the northern long-eared bat. Rather than conducting a labor-intensive roost selection study that would only allow inference within the study area (Miller et al. 2003), I instead chose to synthesize existing studies on northern long-eared bat roost selection thru a quantitative meta-analysis. This enabled insight into associated roost tree characteristics across the species range. To describe factors associated with the species distribution in Nebraska, I acoustically surveyed 101 10 km x 10 km grids and conducted multi-scale occupancy modeling to model the likelihood of occupancy across the state. Then, at 5 locations within the Nebraska distribution of the species, I conducted further acoustic surveys and combined presence/non-detection results with on-the-ground habitat measurements to assess finer-scale forest structure variables associated with occupancy and detection probability. Conclusions gleaned from these studies can contribute to a cross-scale understanding of the factors associated with northern long-eared bat habitat use. Additionally, I conducted all field studies prior to the detection of white-nose syndrome in Nebraska. Estimates of occupancy derived from these studies provide a potential baseline of pre-white-nose syndrome occupancy in Nebraska.

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CHAPTER 2: A QUANTITATIVE META-ANALYSIS OF NORTHERN LONG-EARED BAT ROOSTING BEHAVIOR

Introduction

Rapid declines in North American bat populations have prompted protection and management of winter hibernacula and known summer roost trees (Fish and Wildlife Service 2016). These roost trees are important to survival and reproduction because they provide shelter and satisfy temperature requirements for females during the maternity season (Cryan et al. 2001, Boyles 2007). Managing for these roost trees requires an understanding of the characteristics bats select for when choosing a roost. However, roost studies conducted at single locations only enable inference within a single study area and managers should use caution when extrapolating beyond the bounds of a study's inferential space (Miller et al. 2003).

Across all tree-roosting species in temperate North America and relative to surrounding trees within a stand, bats generally select for trees that are taller, greater in diameter, decayed, and with greater solar exposure (Miller et al. 2003). However, there is a great deal of variation in conclusions between studies even where a single species is concerned. For example, Johnson (2009) concluded northern long-eared bats (*Myotis septentrionalis*) selected trees in larger canopy gaps while Badin (2014) concluded the opposite. This lack of consistency is likely due to a combination of small sample size, restricted length and scope, local effects, and unstandardized study designs (Miller et al. 2003). In an attempt to overcome some of these issues, others have conducted several meta-analyses to examine roost selection of bats (Lacki and Baker 2003, Kalcounis-Rueppell et al. 2005, Lacki et al. 2009, Fabianek et al. 2015).

Quantitative meta-analyses that combined multiple species have concluded that bats generally select roost trees that are taller, larger, with high solar exposure, and in stands with greater availability of snags (Kalcounis-Rueppell et al. 2005). Additionally, Fabianek et al. (2015) describes an inverse correlation between mean summer temperature and the relative difference in diameter at breast height in cavity roosting bats. All of these previous quantitative meta-analyses, however, have resorted to combining studies of multiple species together into a single analysis due to a lack of previously published literature. Fabianek et al. (2015) attempted to account for species-specific differences when modeling effects on diameter selection but ultimately lumped together all *Myotis* species into a single group for analysis due to a lack of studies for many species within the genera.

Studies that have compared roost selection between *Myotis* species, however, have found significant differences in roosting behavior and selection. For example, Indiana Myotis (*Myotis sodalis*) roosted almost solely under exfoliating bark slabs with high amounts of solar exposure while northern long-eared bats, in the same study, selected for a variety of trees, both live and dead, and roosted within cavities of trees under a closed canopy (Carter and Feldhamer 2005). Lacki et al. (2009) echoed these differences between the two species in a comparative analysis of previously published literature. They hypothesized that differences in roost selection may serve as a mechanism for reducing competition among congenerics (Lacki et al. 2009). If two species are selecting different roost characteristics, then a meta-analysis that combines the two species into a single analysis could hypothetically conclude that no selection was occurring due to the two effects canceling each other. Miller et al. (2003) initially raised this concern when they critically reviewed habitat and roosting studies and recommended against lumping species.

Almost twenty years of comparative roost studies have now yielded sufficient published reports to conduct single species meta-analyses to overcome the shortcomings of multi-species analyses. Additionally, a range-wide metanalysis allows for the assessment of relationships between regional variables, such as climatic conditions, and roost selection, something not possible with single-location studies. The objectives of this meta-analysis were as follows: 1) assess evidence of roost tree selection by the northern long-eared bat for variables reported in at least 5 studies, 2) perform a multi-model meta-regression analysis of covariates potentially related to roost tree diameter selection, 3) perform a meta-analysis of roosting behavior measurements such as distance traveled to first roost tree from the capture site, and 4) place findings in context with current federal regulations.

Methods

SELECTION OF STUDIES

To summarize roost selection and roosting related behavior, I obtained all previously reported theses, dissertations, published articles, and agency reports that assessed northern long-eared bat roosting behavior through telemetry or direct observation. I applied the same Boolean search term to both Web of Science and Google Scholar. I extracted abstracts using Data Miner (Data Miner 2017) and then manually assessed for applicability. I also checked previous meta-analyses and reviews (Lacki and Baker 2003, Miller et al. 2003, Kalcounis-Rueppell et al. 2005, Lacki et al. 2009, Fabianek et al. 2015) against my results to assess effectiveness of my search terms.

Reviewing obtained articles, revealed three additional sources that did not appear in my search results.

LOCATION EXTRACTION AND ANALYSIS

I estimated a single point location for each study from descriptions or from reported coordinates. For studies which contained more than one study site but reported combined results (n = 3), I calculated the geographic center of the study sites through averaging coordinates and obtaining the approximate center. The furthest distance between two averaged study sites was 283 km and all were within the same USFS ecoregion. For studies that reported only a physical description (i.e. Shawnee National Forest), the approximate center of that description was selected as the study point. To visualize the concentration of studies, I applied a kernel density estimator to the study points using the R package "ks" (Duong 2017) and a plug-in bandwidth selector (Wand and Jones 1994). I visualized the 75%, 50%, and 25% isopleths in ArcMap (ESRI 2011). I also summarized study points by the USFS ecoregion (Bailey 1997) in which they occurred to understand historic survey effort.

DATA EXTRACTION AND STANDARDIZATION

Many studies reported results from multiple separate study populations such as the roosting characteristics of males as well as females. I treated each study population as a separate study unit following the procedure of previous studies (Kalcounis-Rueppell et al. 2005, Fabianek et al. 2015). I extracted all reported means of roost characteristics and their corresponding standard error, standard deviation, and sample size. I also extracted the values of behavioral characteristics including the distance from the capture site to the first roost, the distance between subsequent roosts, and the number of days per roost. I converted all characteristics pertaining to density, size, or distance to the same scale to enable comparison (i.e. stems/ha). I converted standard error of the mean to standard deviation by multiplying the standard error by the square root of sample size.

BEHAVIORAL CHARACTERISTICS

I generated intercept only random-effects models for each of the following behavioral characteristics: the distance from the first roost to the capture site, the distance between subsequent roosts, and the number of days spent in a roost before switching. I chose these metrics because researchers regularly reported the estimates and because they are the most applicable to management of the species. I conducted the analysis using the Metafor package (Viechtbauer 2010) in R (2017) using raw means as the effect sizes. I used the restricted maximum-likelihood approach to estimate heterogeneity between studies (Viechtbauer 2005).

RANDOM EFFECTS MODELING

For roost tree characteristics with ≥5 separate studies that utilized a roost vs. available (experimental/control) study design, I calculated Hedges' *g* Standardized Mean Difference (SMD) to compare effect sizes (Hedges 1981). Hedges' *g* is calculated by subtracting the mean of the roost tree and the mean of the random tree or stand and taking into account sample size. For example, a positive *g* estimate for diameter at breast height (DBH) indicates that the mean DBH of the roost trees was larger than available trees within that study.

I then applied an intercept-only random-effects model to data from characteristics that at least five unique studies examined. I examined the following roost characteristics: percent bark cover (%), basal area of the surrounding stand (m^2/ha), canopy cover (%), diameter at breast height (cm), decay class, distance to the nearest tree (m), roost tree height (m), mean diameter of the surrounding trees (cm), slope (%), snag density (snags/ha), and stand density (stems/ha).

META-REGRESSION

I applied a multi-model meta-regression approach to determine which moderators explained the most variation in the standardized mean difference of roost tree diameter. Tree diameter was selected because this was the most reported variable ($k = 29$) and was most applicable to management and regulation. Additionally, Fabianek (2015) modeled this variable for all North American tree-roosting species and allowed me to make qualitative comparison.

I collected moderators from a variety of sources. I extracted latitude from the reported study site locations. I calculated the ratio of roost trees that were softwood from the reported roost tree species in each study. Ideally, I would have calculated this ratio from the available trees in the stand but the vast majority of studies only reported the species of roost trees and not available trees. I calculated the mean day of the year for a study by averaging the reported start day and the end day of a study within a season. If studies encompassed multiple seasons, I took the mean of the seasons. Most studies did not provide precise start or end dates and simply provided months so I chose to estimate days. For example, if a study stated it ran from May through August, I used the days May 1 to August 31. If a study stated it ran from mid-May to August, I used the days May 15 to August 31. I extracted sex of the study population (Male, Female, or Mixed) and the mean DBH of the available trees. I created a binary covariate to access the scale at which the primary researchers selected available trees. I divided studies based upon whether or not the available tree could be greater than or equal to 250 meters from the roost tree. This separated the "random walk" studies from studies that randomly selected coordinates within a study area to select available trees.

I calculated the average maximum temperature of the summer maternity season (June – August) by downloading Worldclim 1.4 (Hijmans et al. 2005) monthly average maximum temperatures for the study sites using package raster (Hijmans 2017) in R at 5 minute spatial resolution. I calculated the averages for this dataset using observations from ~1960 – 1990. I then averaged June thru August's values. Because I was interested in testing whether roosting habits responded to long-term climatic influences or short-term weather events, I also calculated average maximum temperatures for a study during the actual study period. I calculated study period temperatures by gathering historic observations from NOAA GHCND stations near my study sites using package rnoaa (Chamberlain 2016) in R. I combined the five closest stations to each study site using an inverse distance weighting approach where the nearest sites received the greatest weight when I averaged the temperatures. The mean distance of weather stations to the study sites were 29.81km ± 4.11 SE. The mean distance of the closest and furthest weather stations to their respective study sites were 12.84km ± 2.86 SE and 42.3 km ± 6.24 SE respectively.

I compared fifteen meta-regression models to explain the heterogeneity in the standardized mean difference of tree diameter using the *metafor* package in R (Viechtbauer 2010). The models chosen for multi-model inference corresponded to discrete testable hypotheses. I removed five datasets from two studies that did not report roost-tree species, as I required this information to calculate the softwood ratio variable.

This provided a balanced number of data points for all models (k = 24). I ranked candidate models using Akaike's Incormation Criterion for small samples (AICc). I then calculated ΔAICc values and Akaike's weights to assess candidate models explanatory ability relative to the top model. I considered models receiving a ΔAICc ≤ 2 equivalent. I calculated Psuedo-R^2 to assess the amount of heterogeneity explained by the model.

Results

Twenty-eight studies reported either roosting characteristics in a roost vs. available study design and/or behavioral findings on northern long-eared bat roosting ecology (Figure 2.1). Of those 28 studies, 15 yielded both suitable roost characteristic and behavioral findings, 8 yielded only behavioral data, and 5 provided only data on roost characteristics. These studies provided 43 separate datasets. For the purpose of this paper, I defined a dataset as findings from independent study populations. For example, if a study summarized findings for males and females separately then that paper would contribute two datasets to the analysis. Of the 43 datasets, I found 22 in published articles, 18 in unpublished dissertations and theses, two in governmental reports, and one in research symposium. The majority of my datasets described the roosting behavior of females (60%, n = 26). This was followed by males (28%, n = 12), combined findings of both sexes (9%, n = 4), and one study did not specify the sex of the individuals (Timpone et al. 2010).

STUDY SITE LOCATIONS

Included studies ranged from the northern edge of the species distribution in the Northwest Territories southeast to western North Carolina (Figure 2.2). Kernel density analysis revealed that 50 % of the studies were located within the Ohio River valley and it's convergence with the Mississippi River (Figure 2.2). The dominate ecoregion within the range of the northern long-eared bat is the Subartic Division with 32% of its range being encompassed within this division. However, only 7% of the studies (n = 2) were located within this ecoregion (Table 2.2). The Hot Continental ecoregion was the ecoregion with the greatest number of studies (n = 9; 32%) yet only represented 16% of the species range. The subtropical division, the Subartic Mountains, and the subtropical mountains contained no studies that satisfied my criteria for inclusion.

BEHAVIORAL CHARACTERISTICS

I located twenty studies that reported means and standard error/standard deviation for at least one of the three behavioral characteristics. These twenty studies yielded twenty-two unique data sets. I found on average an individual northern long-eared bat's first roost was 521 ± 173 meters (SE = 88.3, k = 13) from its capture location (Figure 2.3). The average number of days spent at a roost before switching to another roost was 2.17 ± 0.48 days (SE = 0.24, k = 10) (Figure 2.4). Northern long-eared bats moved an average of 327 ± 123 meters (SE = 62.6, k = 11) between consecutive roosts (Figure 2.5).

ROOST-TREE CHARACTERISTICS

I found significant standardized mean differences (SMDs) across 20 studies and 43 unique datasets for four of the eleven roost-tree characteristics (Table 2.3; Figure 2.6). When compared to available trees, selected roost trees had a greater amount of bark remaining on the bole (k = 14, SMD = 0.48 ± 0.23, SE = 0.12, P < 0.01; Figure 2.7), a larger diameter at breast height (DBH; k = 29, SMD = 0.36 ± 0.21, SE = 0.11, P < 0.01; Figure 2.8), a lower decay class (k = 11, SMD = -0.69 ± 0.45, SE = 0.23, P < 0.01; Figure

2.9), and were taller (*k = 25*, SMD = 0.34 ± 0.22, SE = 0.12, P < 0.01; Fig 1-10). I found no significant evidence of selection regarding the density of snags within the stand (k = 14, SMD = 0.21 ± 0.22, SE = 0.11, P = 0.06; Figure 2.11), the distance to the nearest tree (k = 8, SMD = -0.12 ± 0.22, SE = 0.11, P = 0.27; Figure 2.12), the number of stems per hectare (k = 9, SMD = 0.37 ± 0.68, SE = 0.34, P = 0.29; Figure 2.13), the mean DBH of the stand (k = 10, SMD = -0.09 ± 0.22, SE = 0.11, P = 0.45; Figure 2.14), the stand basal area (k = 8, SMD = 0.11 ± 0.32, SE = 0.16, P = 0.51; Figure 2.15), the canopy cover at the roost tree (k = 22, SMD = 0.04 ± 0.31, SE = 0.16, P = 0.78; Figure 2.16), or slope (k = 15, SMD = 0 ± 0.14, SE = 0.07, P = 0.9; Figure 2.17). A Cochran's *Q*-test revealed significant heterogeneity not explained by sampling variation for all roost-tree characteristics except for slope and distance to nearest tree (p > 0.05).

META-REGRESSION

Latitude, the ratio of softwood roosts to overall roosts, and mean day of the year were the three moderators that best explained heterogeneity in tree-diameter effect size (< 2 ΔAICc of the top model; Table 2.4). Additionally, a three-term model that incorporated both latitude and softwood ratio was present in the final model set, but I rejected it due to lack of parsimony and 95% confidence intervals of the β-estimate overlapping zero. I determined the remaining models as equally likely and followed a "describe all models" approach rather than selecting one model or averaging (Arnold 2010). Tree diameter effect size was either positively associated with softwood ratio (β = 0.76, SE = 0.39) or positively associated with latitude (β = 0.05, SE = 0.30), while the mean day of the year of which a study occurred, produced a β-estimate with 95% confidence intervals overlapping zero. Surprisingly, both temperature$_{\text{mean}}$ (averaged from ~1960-1990) and the

$\text{temperature}_{\text{study}}$ performed worse than the null intercept model. This is despite having a Pearson's correlation coefficient of -0.67 and -0.48 respectively with latitude. QE tests of both models indicate that significant inter-study heterogeneity is still unaccounted for by the moderators (Softwood Ratio: QE = 84.8, $p < 0.001$, df = 22; Latitude: QE = 84.2, $p < 0.001$, df = 22).

Discussion

This is the first meta-analysis to summarize behavioral findings associated with roosting behavior of northern long-eared bats. My findings are comparable to most individual studies in that northern long-eared bats are generally roosting within 0.75 km of their capture site, switching roosts after ~2 days, and locating their subsequent roost nearby. However, I believe it is important to place these findings within context of current regulation and best management practices. Within the United States, the current 4(d) rule for the protection and recovery of the northern long-eared bat provides protection for any tree within a 45-meter buffer around a known maternity roost (Fish and Wildlife Service 2016). My findings indicate that the distance between subsequent roost trees is 327 ± 123 meters, which is well outside of this protected buffer distance. While stand-level or seasonal effects likely contribute to variation to this distance, a buffer of only 45-meters fails to protect many undetected or future roosts.

I found evidence that across the range of the species, northern long-eared bats selected for roost trees that are greater in height and diameter with low amounts of decay of and high bark retention when compared to assumed non-roost trees. Previous meta-analyses that combined multiple bat species, however, concluded roost trees are also in stands with greater snag density, have canopies that are more open, are closer to water, and are at lower elevation (Kalcounis-Rueppell et al. 2005, Fabianek et al. 2015). I lacked adequate sample size to examine proximity to water or elevation, however, canopy closure clearly showed no evidence of selection (SMD = 0.04, $K = 22$, $p = 0.78$). This suggests that relative to the stand, northern long-eared bats are not selecting for roost trees within canopy gaps that receive greater solar exposure.

When I applied a meta-regression approach to the effect size of diameter at breast height (DBH) selection, the results did not repeat the findings reported by Fabianek et al. (2015), which concluded mean summer temperature was the top predictor of DBH effect size when they combined species. Surprisingly, both historical average temperature and study-period temperature failed to account for any variation in effect size (pseudo-$R^2 < 0.01$), despite having a Pearson's coefficient of -0.67 ($p < 0.001$) and -0.47 ($p = 0.02$) respectively with my top predictor, latitude only accounted for 19% of variation between my studies. It is beyond this study's scope to explain the causal factor for this direct relationship between latitude and effect size, however, one possible explanation is day length. *Eptesicus nilssonii,* for example, reduces both its home range size and foraging time as the days grow longer at far northern latitude (Frafjord 2013) with nightly activity periods being as short as 4 hours during periods of 24-hour sunlight in July (Speakman et al. 2000). If northern long-eared bats exhibit similar behavior and are also shortening their foraging times at northern latitudes, they would be spending increased time in the roost and may be selecting for larger roosts that provide added thermal stability. An additional likely explanation could be an autocorrelation with latitude and forest composition. Northern forests are dominated with conifers and aspen (*Populus* sp.) and I observed a slight correlation between the ratio of softwood roosts and latitude ($r = 0.34$, $p = 0.096$).

The second predictor within my confidence set (<2 ΔAICc) was the ratio of softwood roosts relative to total roosts. Evidence supports a positive relationship between the effect size for DBH and the ratio of softwood roosts. This was counter to my expectations. If tree diameter were solely linked to the thermal properties of roosts, then one would expect an inverse relationship as softwoods have a lower thermal conductivity and thus a higher R-value compared to hardwoods (Forest Products Laboratory 2010). In other words, bats would need a relatively thicker cavity wall in a hardwood tree to provide the same thermal stability as in a softwood roost. One possible explanation of the positive correlation I observed is bark thickness. For a given a diameter, a generic hardwood will have a bark thickness approximately twice that of a generic softwood (Miles and Smith 2009). Following the equation and values provided by Miles and Smith (2009), a generic hardwood species would reach an arbitrary bark thickness of 1.5 cm at 43 cm in diameter. A generic softwood, however, would not reach this bark thickness until it grew to 111 cm in diameter. Particular tree species obviously play a considerable role in bark thickness, but because I did not distinguish between softwood/hardwood species in my analysis, I used estimates of generic softwoods and generic hardwoods (Miles and Smith 2009).

When compared to both previous multi-species meta-analyses (Kalcounis-Rueppell et al. 2005, Fabianek et al. 2015), the effect sizes for DBH, height, canopy closure, and snag density are all consistently closer to zero, with zero indicating no selection (Figure 2.18). Although there was overlap in the 95% confidence intervals of all comparisons of effect size, the consistency of the effect-size being nearer to zero suggests northern long-eared bats are less selective in regards to the variables researchers in my sample are measuring. Additionally, following the interpretation of Cohen (1988), all effect sizes were below 0.5; a level deemed a “medium effect” where differences are visually recognizable under careful scrutiny. Previous researchers have posited two possible explanations for similar findings, either northern long-eared bats are roost generalists or structural measurements taken by researchers fail to serve as proxies for microclimatic conditions within the roost.

A common explanation is that northern long-eared bats are roost generalists or have greater roost plasticity in various roost measures when compared to congeners (Kunz 1982). A generalist roosting behavior has been suggested for the following characteristics: roost type (Foster and Kurta 1999), diameter at breast height (Lacki et al. 2009), tree height (Lacki et al. 2009), forest treatment (Timpone et al. 2010), and decay class/condition (Foster and Kurta 1999). When directly compared to the Indiana myotis (*Myotis sodalis*), another U.S. federally protected species that co-occurs, both field studies (Foster and Kurta 1999, Timpone et al. 2010) and a meta-analysis (Lacki et al. 2009) concluded greater plasticity when easily measured structural characteristics are concerned. This species-level flexibility of northern long-eared bats could result from a variety of sources. Perry and Thill (2007) noted a sex-related plasticity with males having greater flexibility in snag size compared to females, while Foster and Kurta (1999) noted high amounts of variation within an individual’s roosting habits rather than simply between individuals. Additionally after comparing roosting results between two consecutive years, Silvis et al. (2015*a*) suggests variation is potentially related to annually variable environmental conditions.

A second, less explored, explanation for increased plasticity is the unknown ability for structural characteristics (proximal measures) to serve as proxies to microclimatic characteristics (causal measures) within roosts (Boyles 2007). This assumption serves as the basis for comparative studies that measure roost characteristics (Kunz 1982, Vonhof and Barclay 1996, Cryan et al. 2001), but it has been poorly tested to understand the accuracy of these assumptions (Boyles 2007). The ability of these measurements to serve as a proxies are also likely not constant between species. For example, *M. sodalis* primarily roosts under exfoliating bark slabs and in comparably large aggregations (Carter and Feldhamer 2005, Timpone et al. 2010). In this situation, diameter at breast height may be highly correlated with roosting selection, as a tree must grow large enough to have exfoliating bark plates of sufficient size to contain large aggregations. Northern long-eared bats, however, are known to utilize tree cavities, crevices, exfoliating bark (Foster and Kurta 1999, Carter and Feldhamer 2005), man-made structures (Timpone et al. 2010), and even cracks within cliff faces (Keinath and Abernethy 2016). Compounding the issue, crevice and cavity roosts are often not located on the main trunk of the tree and are instead located where limbs meet the main bole or in crevices along limbs. It is unlikely in these cases that structural measurements taken at the base of the tree are directly associated with either microclimate or other proxies for selection and may even be misleading (Boyles 2007) or simply associated with local conditions within a site or study year (Silvis et al. 2015*a*).

The relative importance of an individual roost tree is questionable given that northern long-eared bats switch roosts approximately every 2 days and utilize structurally variable roosts. Initially researchers considered roost availability a limiting factor and thought their protection critical to maintaining viable populations (Kunz 1982, Fenton 1997). This idea is present in current regulation, which protects individual current or historical roost trees (Fish and Wildlife Service 2016). Research into roosting networks reveals that northern long-eared bats aggregate into social groups that utilize a network of roosts within a forest patch (Johnson et al. 2012). These roost networks contain a central node tree and non-central node roosts, which display reduced connectivity within the network (Johnson et al. 2012, Silvis et al. 2014). The targeted removal of single maternity roost trees within these networks revealed the ability to modify their roosting and adapt to these changes (Silvis et al. 2014). However, the removal of multiple roost trees began to fragment the social network (Silvis et al. 2014). Evidence from these network studies suggested that northern long-eared bats are resistant to impacts from the loss of a limited number of maternity roosts (Johnson et al. 2009, Silvis et al. 2014, 2015*b*, Ford et al. 2016), and roosts may not be a limiting factor within the local stands due to the species' flexibility (Menzel et al. 2002). The rapid decline in populations due to white-nose syndrome may also further reduce the limiting effects of roost availability due to decreases in population densities (Ford et al. 2016).

Whether northern long-eared bats display a generalized selection because they simply lack strict requirements or because researchers have not been adequately measuring the causal (versus proximal) factors that the species is selecting, single-tree management may be impractical and potentially ineffective. Silvis (2012) recommends moving “beyond individual tree concepts and incorporate larger forest establishment conditions that create and maintain suitable long-term roosting opportunities and networks”. This is also a practical approach, as individual roost trees are often short-lived, with as many as 25-30% naturally falling within 1 year of use (Carter and Feldhamer 2005). Additionally, northern long-eared bats appear to respond favorably or at least tolerate some forest management practices (Silvis et al. 2014). For example, a study in the central Appalachians found no discernable negative effects of burning historically unburned stands (Ford et al. 2016) and others reported similar results from mechanical harvest studies (Pauli et al. 2015). Additionally, multiple studies found maternity colonies associated with recently (<10 years) harvested stands (Cryan et al. 2001, Menzel et al. 2002) even when unharvested stands were readily available (Perry and Thill 2007). Due to the lack of evidence supporting strong roost selectivity across the species range, forest management practices which allow for diverse age classes will be more likely to provide for the roosting needs of Northern long-eared bats. Additionally, recommendations solely built upon snag retention or creation (Perry and Thill 2007, Fabianek et al. 2015), fail to take into account selection of trees in early stages of decay with large percentages of bark retention, or the frequent use of live trees.

CONCLUSION

By combining previous studies that examined northern long-eared bat roost selection, evidence supports the use of roost trees that are larger in diameter, taller, and in early stages of decay. However, none of the effects sizes for these characteristics are of large enough magnitude to indicate strong selection when compared to available trees within stands. The lack of strong selection may be because researchers are not measuring adequate proxies for thermal requirements or because northern long-eared bats have increased plasticity in requirements when compared to congenerics. In softwood stands, relatively larger diameter trees may have an increased importance as potential roost trees, but we need further studies to understand the mechanisms for this phenomenon. I did not find evidence of a relationship between mean summer temperature and effect size of selection in regards to diameter at breast height in this species although it has been described in multi-species studies. Forest management practices that maintain diverse size and decay classes will provide increased roosting structure for the species. Additionally, management actions should take into consideration regular roost switching, complex social roost networks, and moderate distances between subsequent roosts.

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Tables and Figures

Table 2.1. Moderator variables and corresponding justification included in a meta-regression analysis to account for the heterogeneity in the standardized mean differences of diameter at breast height between roost trees and available trees reported by northern long-eared bat roost studies.

Moderator	Justification
Max $\text{Temp}_{\text{mean}}$	Lactation requires high temperatures to reduce torpor and promote milk production. Females cluster to maintain high temperatures within a roost. This model assess if historical temperatures are associated with roost diameter as bats may require thicker trees in cooler climes in increase heat retention.
Max $\text{Temp}_{\text{study}}$	The temperature of the study period was included to assess if bats were responding to historical temperature averages (Max $\text{Temp}_{\text{mean}}$) or modify behavior based upon experienced temperatures.
Latitude	I included latitude to address potential unaccounted for factors that vary with latitude yet are correlated. Potential effects include day length, forest type, and number of days without a frost.
Softwood ratio	Softwood contains a higher r-value (i.e. insulation) than hardwood (Forest Products Laboratory 2010). We hypothesize that due to higher insulative properties of softwoods, bats can satisfy their thermal demands without selecting for relatively larger trees that may be rarer.
Day of Year	Bats have different thermal requirements as reproductive condition of females change throughout the year.
Distance of avail. tree from roost (Dist. of avail.)	I divided studies based upon whether or not the available tree could be greater than or equal to 250 meters from the roost tree. This separated the “random walk” studies from studies that randomly selected coordinates within a study area to select available trees, as the spatial scale at which selection is occurring is different.
$\text{DBH}_{\text{Available}}$	To assess if bats are maximizing or satisficing in regards to diameter selection, I included the mean DBH of available trees in the stand. For example, if a stand is predominately all large diameter trees capable of meeting thermal demands, a result supporting satisficing would be little to no difference in DBH.
Sex	Northern long-eared bats separate during the maternity season with males roosting often solitarily while females cluster. Females have increased thermal demands and potentially require larger space to accommodate a colony.
Latitude + Softwood Ratio	This model tests if unaccounted for variation in latitude-encompassed factors is accounted for by occurrence in softwood roost use.
Softwood Ratio + $\text{DBH}_{\text{Available}}$	This model tests if variation in the above-mentioned satisficing/maximizing potential may be accounted for by the prevalence of softwood roosts.
Max $\text{Temp}_{\text{mean}}$ + Softwood Ratio	While softwood roosts may provide additional insulative properties relative to hardwoods, they may be unnecessary in warmer climates.

Table 2.1. Continued.

$DBH_{Available}$ + Dist. of avail.	I included this model to account for the possibility of studies describing diameter of roosts trees in immediate proximity of the roost tree or if these measurements or indicative of the study site as a whole.
Max $Temp_{mean}$ + Sex	Mean summer temperatures may affect roosting habits of sexes differently as thermal demands vary based upon sex.
Max $Temp_{study}$ + Sex	Mean summer temperatures may affect roosting habits of sexes differently as thermal demands vary based upon sex and this may vary based upon a summer's actual temperatures.

Table 2.2. Percentage of northern long-eared bat roost studies occurring in each U.S. Forest Service ecological division relative to division area within the species range. If a division contains greater percentage of studies than is represented by area, the difference column contains a negative difference.

USFS Division	Percentage by area	Percentage by study	Difference
Subarctic Division	32.8	7.1	-
Hot Continental Division	16.4	32.1	+
Warm Continental Division	13.5	17.9	+
Prairie Division	10.2	7.1	-
Temperate Steppe Division	9.9	10.7	+
Subtropical Division	8.2	0.0	-
Hot Continental Mountains	3.2	17.9	+
Warm Continental Mountains	2.8	3.6	+
Temperate Steppe Mountains	1.6	3.6	+
Subarctic Mountains	0.9	0.0	-
Subtropical Mountains	0.4	0.0	-

Table 2.3. Combined effect size and their corresponding confidence intervals of eleven roost characteristics reported by studies of northern long-eared bats. K = number of contributing datasets, SMD = standardized mean difference, LCI/UCI = 95% lower and upper confidence interval, Z = test statistic for intersect, P = p-value of the test statistic, τ^2 = estimated amount of residual between-study heterogeneity, I^2 = estimate of the percentage of total variability in the SMD that can be attributed to the heterogeneity among the true effects. Q = test statistic for a Q-test of residual heterogeneity and their corresponding degrees of freedom and P-value.

			SMD (95% CI)						**Q**		
Characteristic[a]	**K**	**SMD**	**LCI**	**UCI**	**Z**	**P**	**τ^2**	**I^2**	**Q**	**df**	**P**
Bark Cover	14	0.48	0.25	0.70	4.13	<0.01	0.12	68.6	39.1	13	<0.01
DBH	29	0.36	0.15	0.58	3.27	<0.01	0.27	81.7	113.1	28	<0.01
Decay Class	11	-0.69	-1.14	-0.24	-3.03	<0.01	0.50	90.8	150.8	10	<0.01
Roost Tree Height	25	0.34	0.12	0.57	2.97	<0.01	0.25	80.1	99.3	24	<0.01
Snag Density	14	0.21	-0.01	0.43	1.87	0.06	0.11	64.9	35.3	13	<0.01
Dist. to Nearest Tree	8	-0.12	-0.34	0.09	-1.10	0.27	0.04	41.7	12.8	7	0.08
Stand Density	9	0.37	-0.31	1.04	1.07	0.29	0.95	93.8	46.0	8	<0.01
Mean Stand DBH	10	-0.09	-0.31	0.14	-0.76	0.45	0.06	49.2	17.5	9	0.04
Stand Basal Area	8	0.11	-0.21	0.42	0.65	0.51	0.15	72.0	24.1	7	<0.01
Canopy Cover	22	0.04	-0.27	0.35	0.27	0.78	0.49	90.7	136.8	21	<0.01
Slope	15	0.00	-0.14	0.14	-0.04	0.97	0.02	23.1	19.5	14	0.15

[a] Bark Cover = percentage of bark remaining on the bole; DBH = diameter at breast height; Decay class = state of decay between 1-5; Roost tree height = height of the roost/random tree; Snag density = number of snags per hectare; Distance to nearest tree = distance (m) from roost/random tree to the nearest neighboring tree; Stand Density = trees per hectare; Mean stand DBH = mean diameter at breast height of trees surrounding the roost/random tree; Stand basal area = basal area (cm^2) of trees surrounding the roost/random tree; Canopy cover = % of area above the roost/random tree occupied by woody structure; Slope = steepness (%) of slope where the roost/random tree is present.

Table 2.4. Candidate model set for the meta-regression analysis of variables accounting for the between study heterogeneity in the standardized mean difference in roost tree diameter of northern long-eared bats. I considered all models within a ΔAICc ≤ 2 equivalent and considered these models as the confidence set indicated in bold. Number of estimated parameters (*K*), pseudo-R^2 (R^2), Akaike's Information Criterion for small samples (AICc), difference between the corresponding models (ΔAICc) and the top performing models AICc (ΔAICc), Akaike weight (weight), and cumulative sum of the weights (Σ_{weight}).

Rank	Model	*K*	R^2	AICc	ΔAICc	Weight	Σ_{weight}
1	**Latitude**	**3**	**18.66**	**48.11**	**0.00**	**0.22**	**0.22**
2	**Softwood Ratio**	**3**	**16.49**	**48.74**	**0.63**	**0.16**	**0.38**
3	**Latitude + Softwood Ratio**	**4**	**23.11**	**48.93**	**0.82**	**0.15**	**0.53**
4	**Day of Year**	**3**	**6.66**	**50.09**	**1.98**	**0.08**	**0.61**
5	Null Model	2	-	50.23	2.12	0.08	0.69
6	Scale of Available Tree	3	0.77	50.91	2.79	0.05	0.74
7	Softwood Ratio + $DBH_{Available}$	4	10.32	51.00	2.89	0.05	0.80
8	Max $Temp_{mean}$ + Softwood Ratio	4	9.66	51.16	3.05	0.05	0.84
9	Max $Temp_{mean}$	3	0.00	51.26	3.15	0.05	0.89
10	$DBH_{Available}$	3	0.00	51.92	3.80	0.03	0.92
11	Max $Temp_{study}$	3	0.00	52.05	3.94	0.03	0.95
12	$DBH_{Available}$ + Scale of Avail. Tree	4	0.00	52.94	4.82	0.02	0.97
13	Sex	4	0.00	53.21	5.10	0.02	0.99
14	Max $Temp_{mean}$ + Sex	5	0.00	55.83	7.72	0.00	1.00
15	Max $Temp_{study}$ + Sex	5	0.00	56.02	7.91	0.00	1.00

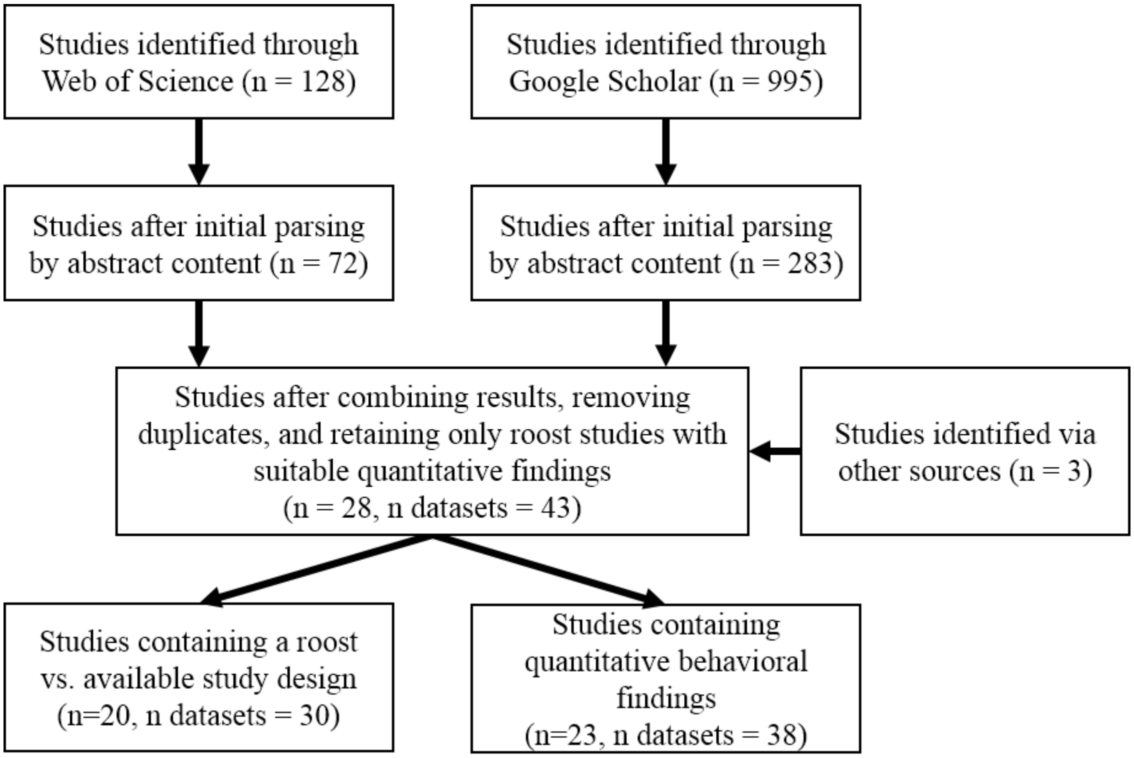


Figure 2.1. Data flow diagram for the identification and selection of northern long-eared bat roost studies included in a species-specific meta-analysis.

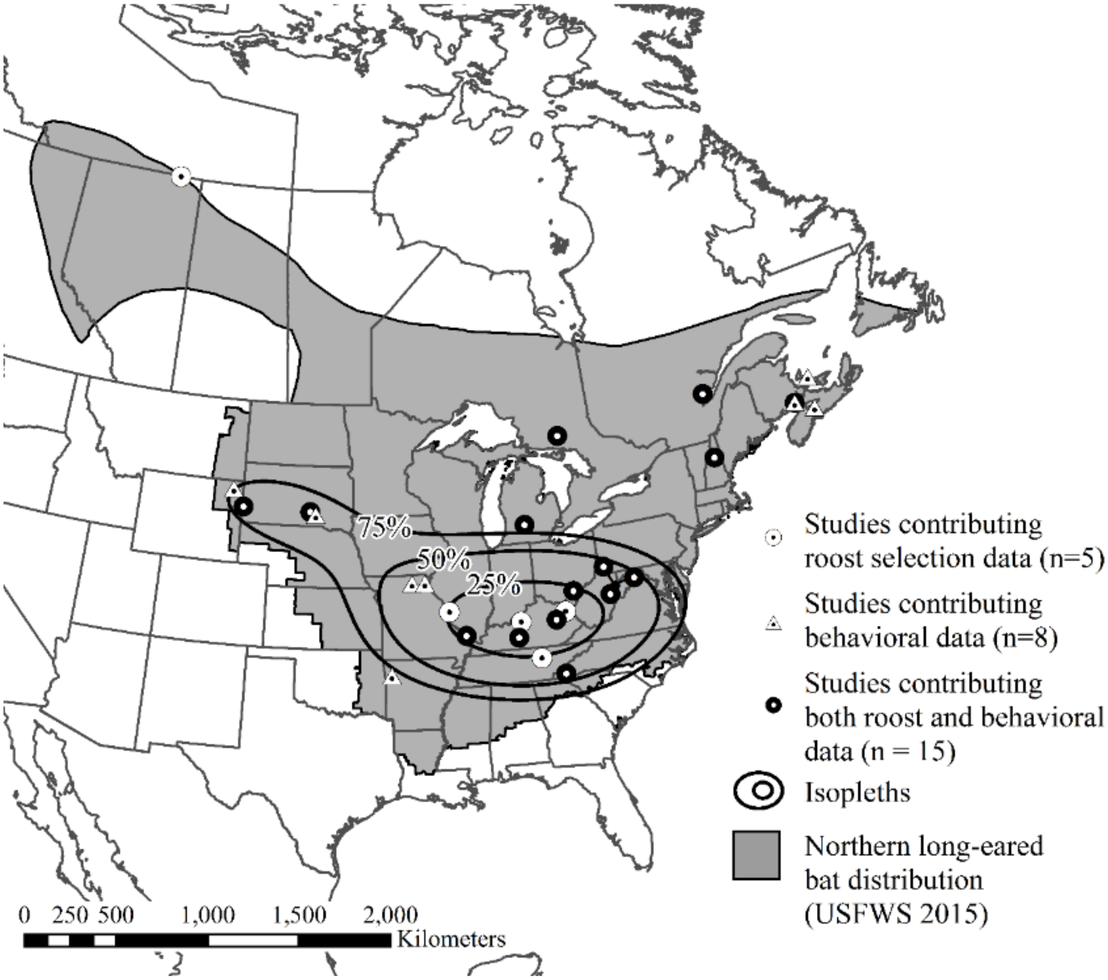
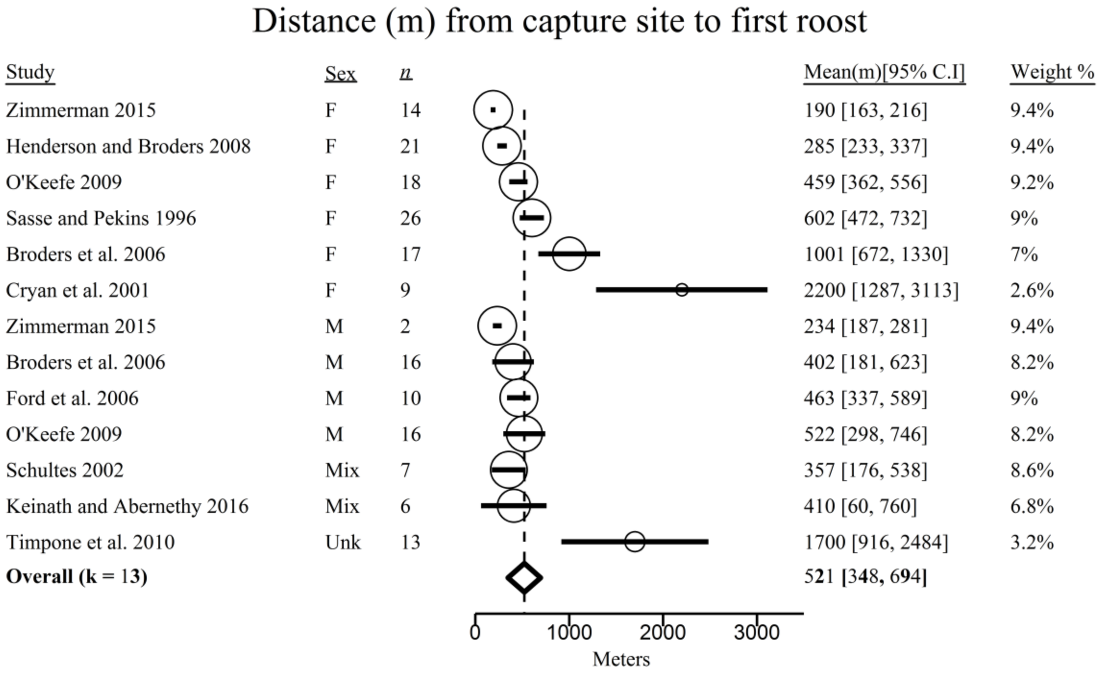


Figure 2.2. Study site locations of northern long-eared bat roost studies included in a species-specific meta-analysis. Kernel density analysis indicates 50% of studies are concentrated within the Ohio River Valley.


Distance (m) from capture site to first roost

Study	Sex	*n*	Mean(m)[95% C.I]	Weight %
Zimmerman 2015	F	14	190 [163, 216]	9.4%
Henderson and Broders 2008	F	21	285 [233, 337]	9.4%
O'Keefe 2009	F	18	459 [362, 556]	9.2%
Sasse and Pekins 1996	F	26	602 [472, 732]	9%
Broders et al. 2006	F	17	1001 [672, 1330]	7%
Cryan et al. 2001	F	9	2200 [1287, 3113]	2.6%
Zimmerman 2015	M	2	234 [187, 281]	9.4%
Broders et al. 2006	M	16	402 [181, 623]	8.2%
Ford et al. 2006	M	10	463 [337, 589]	9%
O'Keefe 2009	M	16	522 [298, 746]	8.2%
Schultes 2002	Mix	7	357 [176, 538]	8.6%
Keinath and Abernethy 2016	Mix	6	410 [60, 760]	6.8%
Timpone et al. 2010	Unk	13	1700 [916, 2484]	3.2%
Overall (k = 13)			**521 [348, 694]**	

Figure 2.3. Forest plot of the meta-analysis of all studies that reported the mean distance (meters) of the first roost tree from the capture site for northern long-eared bats. Overall effect, indicated by the rhombus, is the result of an intercept-only random effects model of *n* studies. The circle is centered over the study's mean and its size is relative to the weight that the study contributes to the overall estimate. The horizontal bar spans the 95% C.I. of the mean. Following release, the first located roost of northern long-eared bats are approximately 521 ± 173 meters from their capture site based upon a meta-analysis of previously published literature and unpublished theses/dissertations.

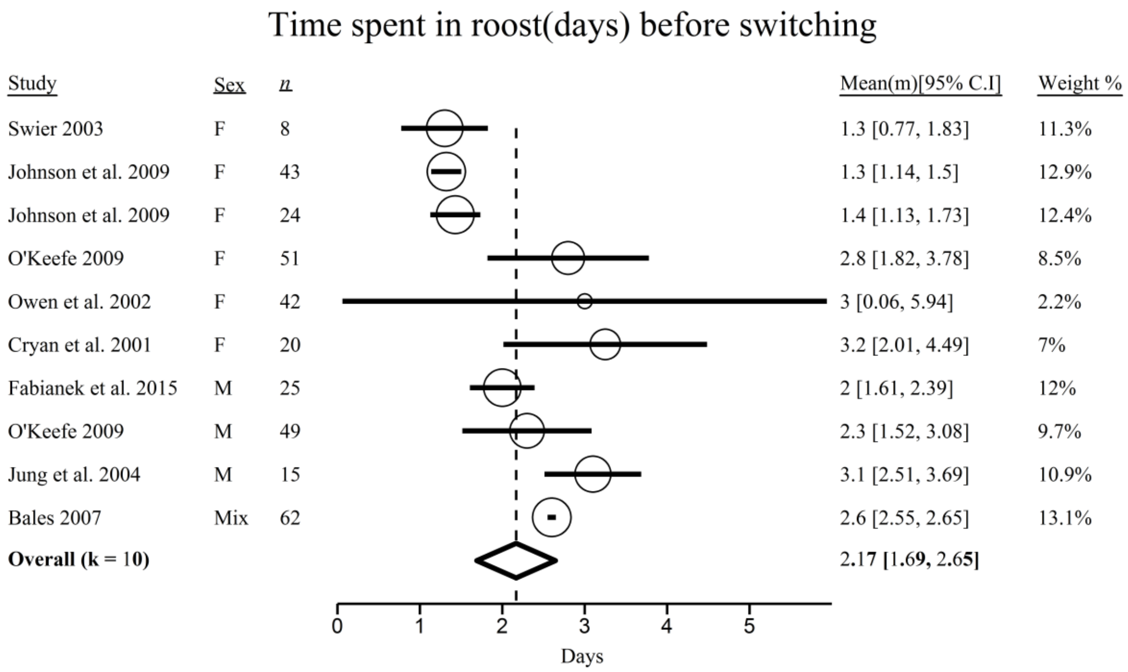


Figure 2.4. Forest plot of the meta-analysis of all studies that reported the mean number of day northern long-eared bats utilized a roost tree before switching to another roost. Overall effect, indicated by the rhombus, is the result of an intercept-only random effects model of *n* studies. The circle is centered over the study's mean and its size is relative to the weight that the study contributes to the overall estimate. The horizontal bar spans the 95% C.I. of the mean. Individuals relocated to another roost every 2.17 ± 0.48 days based upon a meta-analysis of previously published literature and unpublished theses/dissertations.

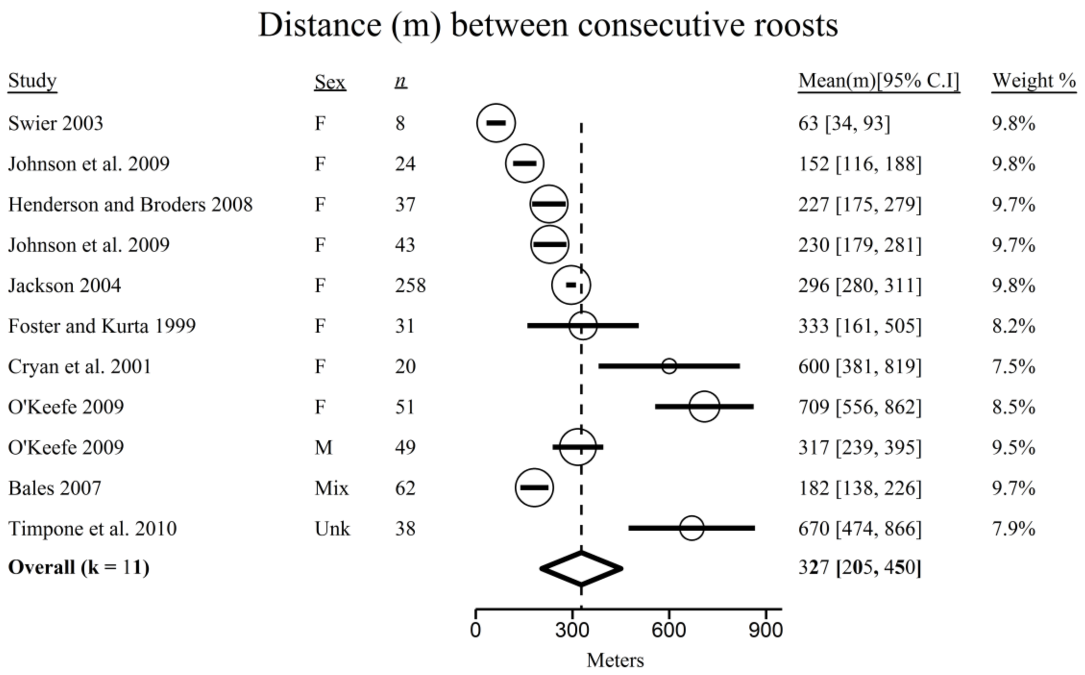


Figure 2.5. Forest plot of the meta-analysis of all studies that reported the mean distance between consecutive roosts utilized by northern long-eared bats. Overall effect, indicated by the rhombus, is the result of an intercept-only random effects model of *n* studies. The circle is centered over the study’s mean and its size is relative to the weight that the study contributes to the overall estimate. The horizontal bar spans the 95% C.I. of the mean. Consecutive roosts were located approximately 327 ± 123 meters apart based upon a meta-analysis of previously published literature and unpublished theses/dissertations.

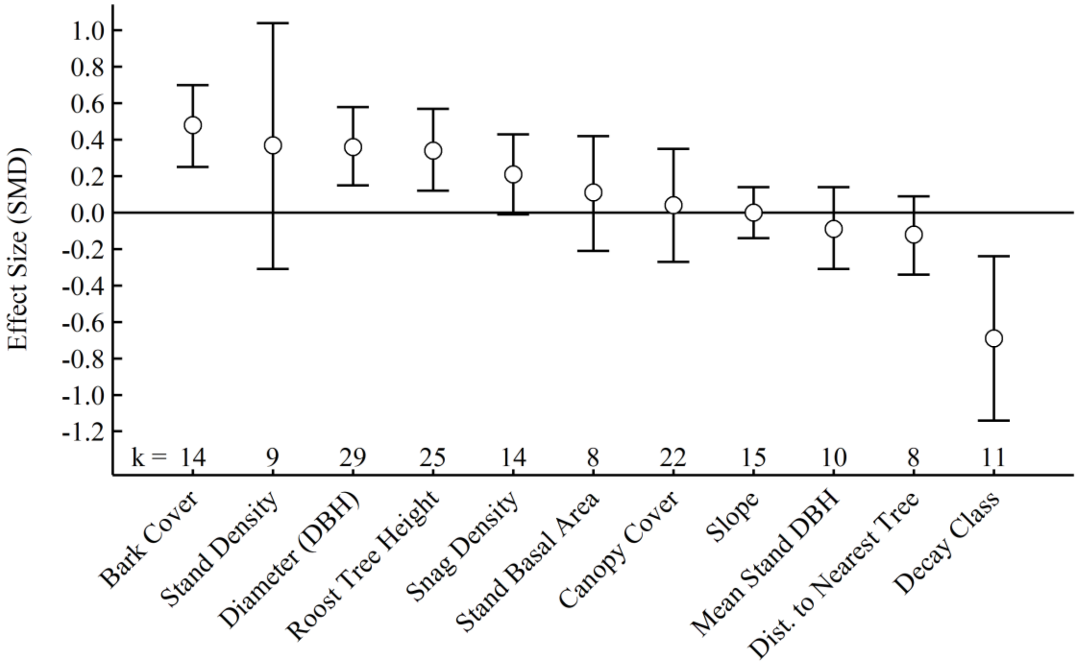


Figure 2.6. Effect sizes of all roost characteristics examined in a meta-analysis of northern long-eared bat roost selection studies. All estimates are the result of a random effects analysis of *k* populations with standardized mean differences indicated by the white circle. Brackets indicate 95% confidence intervals of the estimate. Evidence supported a significant selection for bark cover, diameter, decay class, and roost tree height when compared to available trees.

Study	**Sex**	**R**	$\mathbf{n_{roosts}}$	$\mathbf{n_{avail.}}$	**SMD [95%C.I]**	**Weight**
Lacki et al. 2009	F	Mx	35	57	1.10 [0.65, 1.55]	7.6%
Thalken 2017	M	Mx	14	82	1.09 [0.50, 1.68]	6.3%
Schultes 2002	MF	Mx	21	21	0.96 [0.32, 1.59]	5.8%
Thalken 2017	F	NR	38	82	0.80 [0.40, 1.19]	8.1%
Lacki et al. 2009	F	Mx	16	11	0.61 [-0.18, 1.39]	4.7%
Fabianek et al. 2015	M	Mx	26	40	0.56 [0.06, 1.06]	7.0%
Thalken 2017	F	Mx	30	82	0.55 [0.12, 0.97]	7.8%
Sasse and Pekins 1996	F	Mx	47	104	0.45 [0.10, 0.79]	8.6%
Broders and Forbes 2004	M	Mx	57	57	0.44 [0.07, 0.81]	8.4%
Carter and Feldhamer 2005	F	Mx	19	43	0.43 [-0.12, 0.97]	6.6%
Johnson et al. 2009	F	Mx	25	25	0.31 [-0.25, 0.87]	6.5%
Broders and Forbes 2004	F	Mx	55	55	0.15 [-0.22, 0.52]	8.3%
Johnson et al. 2009	F	Mx	44	45	-0.12 [-0.53, 0.30]	7.9%
Jung et al. 2004	M	Mx	15	52	-0.52 [-1.11, 0.06]	6.3%
Combined Effect (k = 14)					**0.48 [0.25, 0.70]**	

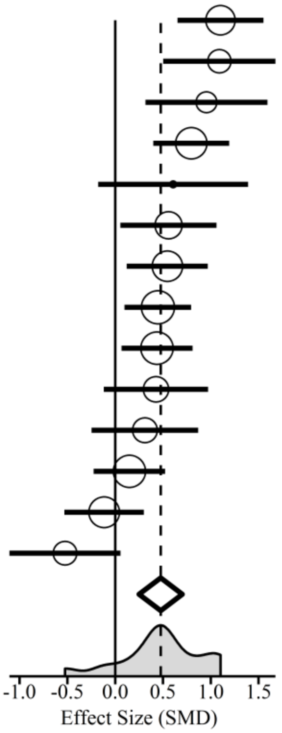


Figure 2.7. Forest plot of a northern long-eared bat meta-analysis of bark remaining on the bole of roost trees (%) when compared to randomly selected available trees. Reported is the sex of the study populations, reproductive condition (R), number of roost trees (n_{roosts}), number of available trees ($n_{avail.}$), standardized mean difference (SMD), 95% confidence interval around the SMD (95% C.I), and weight that the study contributes to the combined effect. The circle indicates the standardized mean difference of the study that I calculated from the reported means of the roost trees and available trees. The diameter of the circle is relative to the weight that the study contributes to the overall estimate with larger circles indicating greater weight. The length of the horizontal bar spans the 95% confidence intervals of the mean. An SMD greater than zero supports a claim that roost trees are greater than what is available.

Study	Sex	R	n_{roosts}	$n_{avail.}$	SMD [95%C.I]	Weight
Swier 2003	F	Mx	9	52	2.09 [1.29, 2.89]	2.8%
Jung et al. 2004	M	Mx	15	52	1.68 [1.04, 2.32]	3.2%
Ford et al. 2006	M	Mx	10	40	1.58 [0.82, 2.34]	2.9%
Fabianek et al. 2015	M	Mx	26	40	0.92 [0.40, 1.44]	3.6%
Kaupas 2016	F	L	22	22	0.77 [0.15, 1.38]	3.3%
Foster and Kurta 1999	F	Mx	17	14	0.77 [0.03, 1.50]	3.0%
O'Keefe 2009	F	Mx	33	33	0.76 [0.26, 1.26]	3.6%
Cryan et al. 2001	F	Mx	21	30	0.66 [0.09, 1.23]	3.4%
Sasse and Pekins 1996	F	Mx	47	104	0.58 [0.23, 0.93]	4.0%
Thalken 2017	M	Mx	14	82	0.58 [0.00, 1.15]	3.4%
Thalken 2017	F	NR	38	82	0.47 [0.08, 0.86]	3.9%
Silvis et al. 2015	F	Mx	220	108	0.42 [0.18, 0.65]	4.3%
Broders and Forbes 2004	M	Mx	57	57	0.41 [0.04, 0.78]	4.0%
Thalken 2017	F	Mx	30	82	0.40 [-0.02, 0.83]	3.9%
Broders and Forbes 2004	F	Mx	55	55	0.40 [0.02, 0.78]	4.0%
Schultes 2002	MF	Mx	21	21	0.28 [-0.33, 0.89]	3.3%
Badin 2014	F	Mx	6	29	0.20 [-0.68, 1.08]	2.6%
Lacki et al. 2009	F	Mx	35	57	0.16 [-0.26, 0.58]	3.9%
O'Keefe 2009	M	Mx	35	35	0.15 [-0.32, 0.62]	3.7%
Carter and Feldhamer 2005	F	Mx	19	44	0.14 [-0.40, 0.68]	3.5%
Lacki et al. 2009	F	Mx	16	11	0.14 [-0.63, 0.90]	2.9%
Johnson et al. 2009	F	Mx	44	45	0.08 [-0.34, 0.50]	3.9%
Foster and Kurta 1999	F	Mx	12	16	0.05 [-0.69, 0.80]	2.9%
Badin 2014	F	Mx	65	80	-0.13 [-0.46, 0.19]	4.1%
Johnson et al. 2009	F	Mx	25	25	-0.34 [-0.90, 0.21]	3.5%
Owen et al. 2002	F	Mx	43	43	-0.48 [-0.91, -0.06]	3.8%
Lereculeur 2013	M	Mx	9	21	-0.54 [-1.33, 0.26]	2.8%
Lereculeur 2013	F	Mx	12	21	-0.61 [-1.33, 0.12]	3.0%
Ford et al. 2006	M	Mx	6	24	-1.04 [-1.97, -0.11]	2.5%
Combined Effect (k = 29)					**0.36 [0.15, 0.58]**	

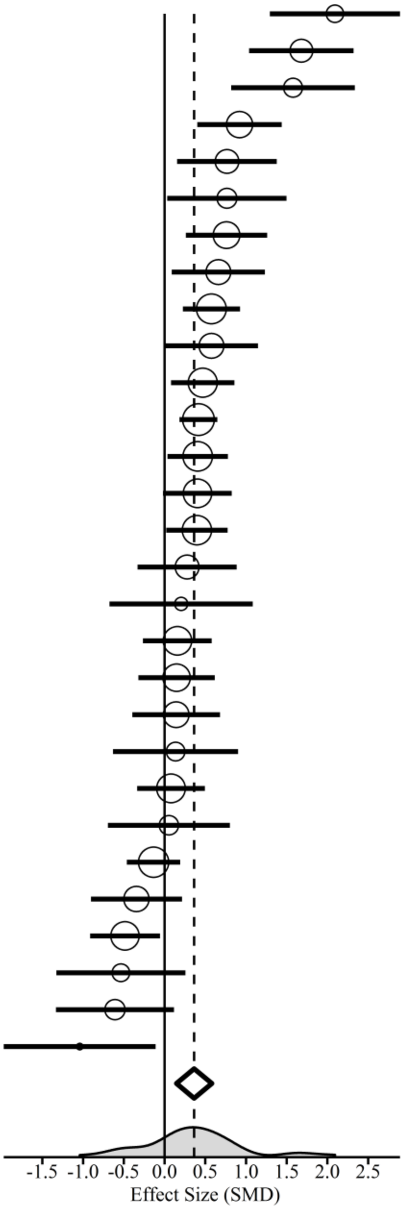
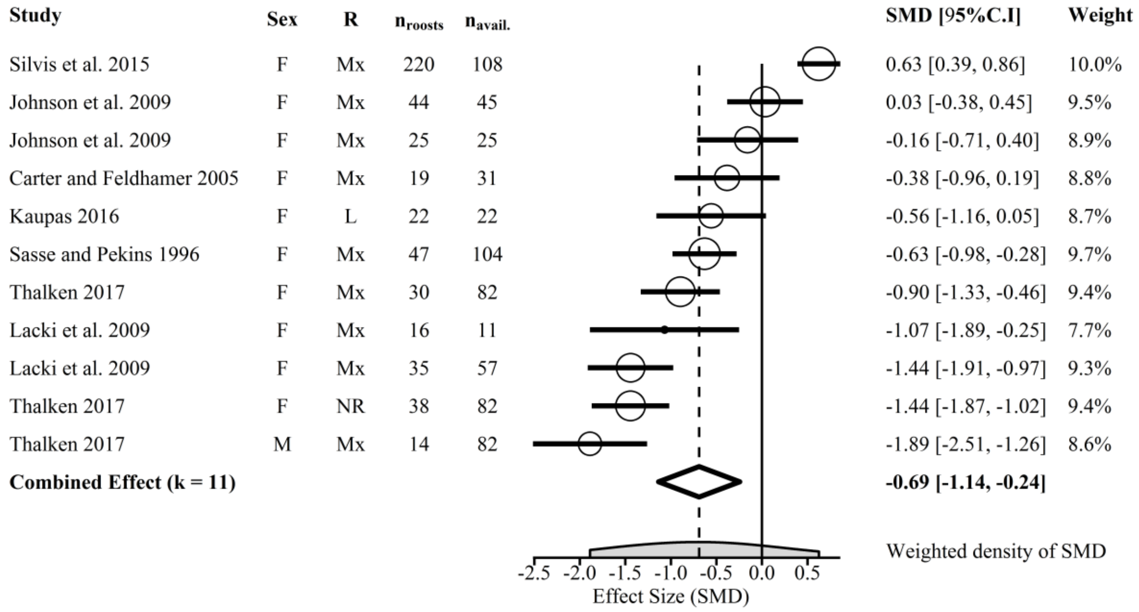
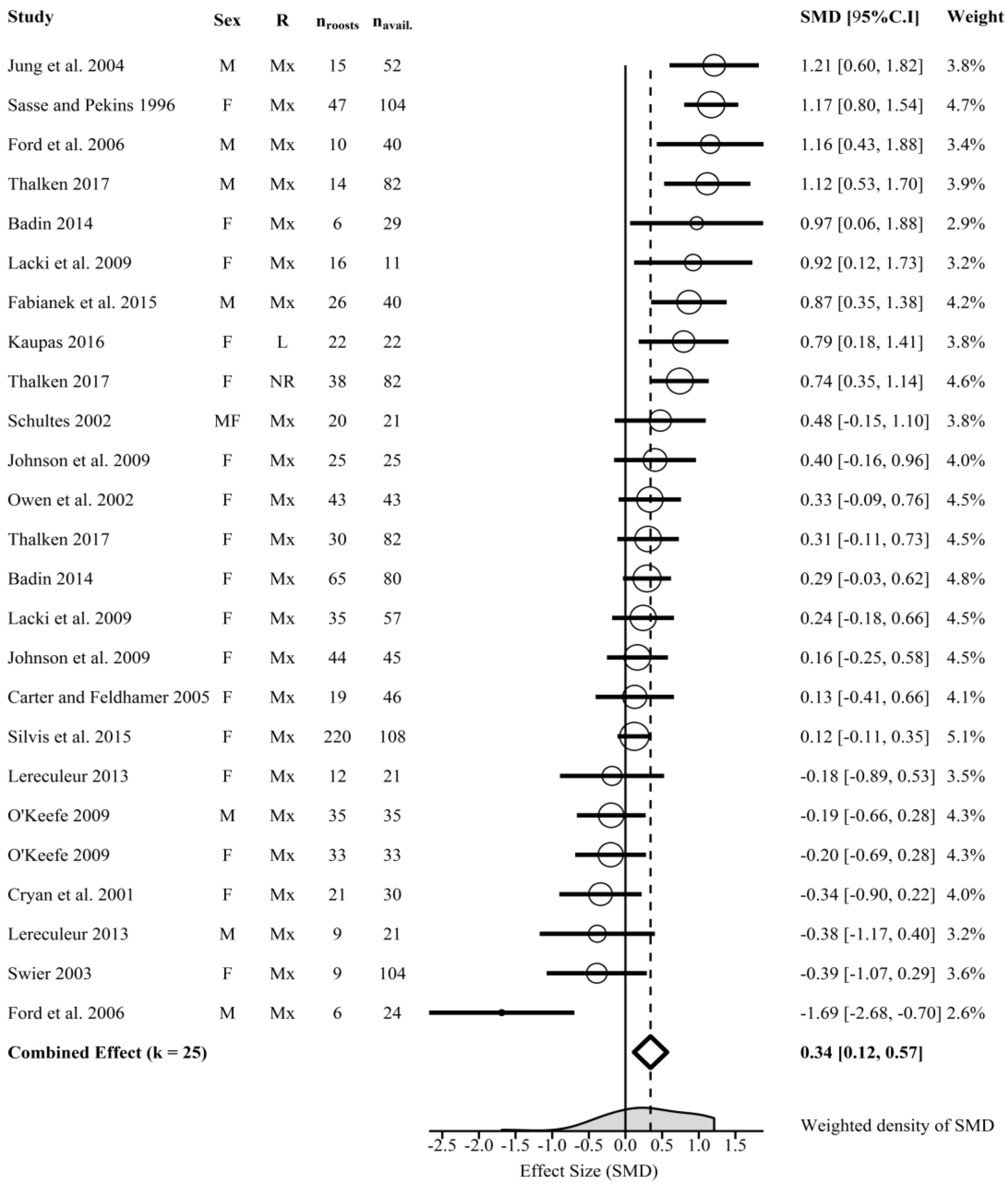


Figure 2.8. Forest plot of a northern long-eared bat meta-analysis of diameter at breast height (cm) of roost trees when compared to randomly selected available trees. Reported is the sex of the study populations, reproductive condition (R), number of roost trees (n_{roosts}), number of available trees ($n_{avail.}$), standardized mean difference (SMD), 95% confidence interval around the SMD (95% C.I), and weight that the study contributes to the combined effect. The circle indicates the standardized mean difference of the study that I calculated from the reported means of the roost trees and available trees. The diameter of the circle is relative to the weight that the study contributes to the overall estimate with larger circles indicating greater weight. The length of the horizontal bar spans the 95% confidence intervals of the mean. An SMD greater than zero supports a claim that roost trees are greater than what is available.



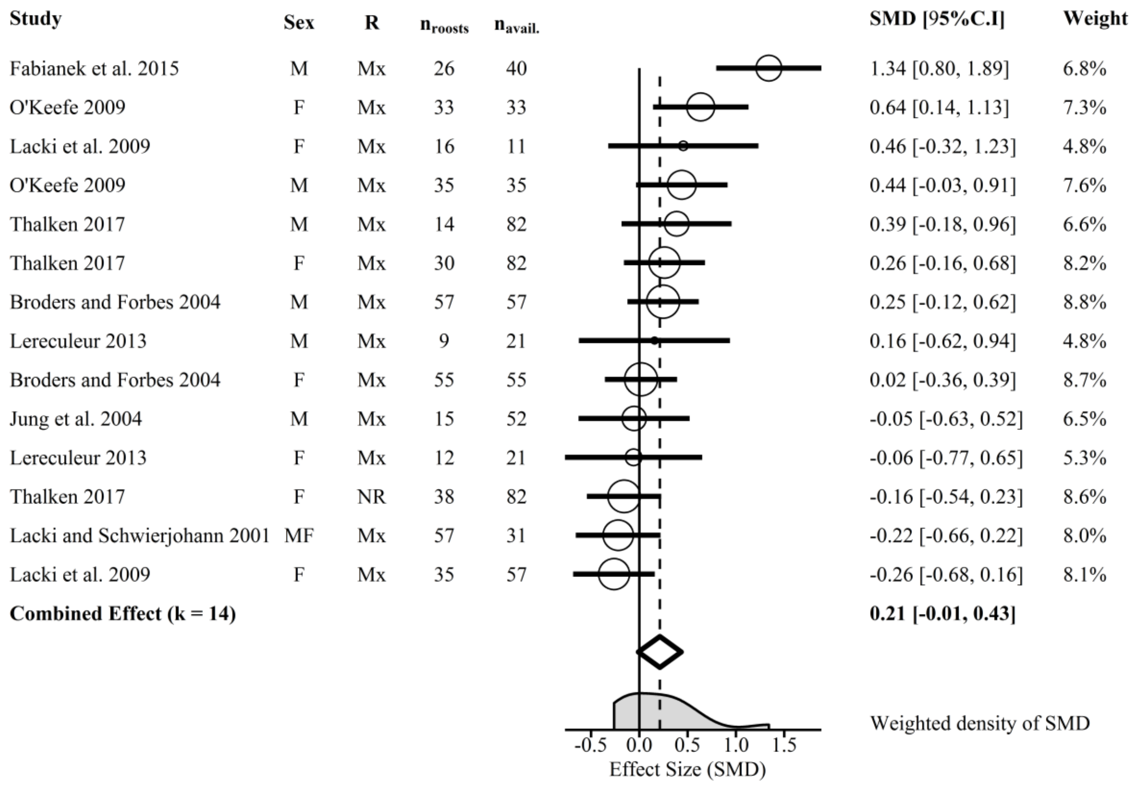
Study	Sex	R	n_{roosts}	$n_{avail.}$	SMD [95%C.I]	Weight
Silvis et al. 2015	F	Mx	220	108	0.63 [0.39, 0.86]	10.0%
Johnson et al. 2009	F	Mx	44	45	0.03 [-0.38, 0.45]	9.5%
Johnson et al. 2009	F	Mx	25	25	-0.16 [-0.71, 0.40]	8.9%
Carter and Feldhamer 2005	F	Mx	19	31	-0.38 [-0.96, 0.19]	8.8%
Kaupas 2016	F	L	22	22	-0.56 [-1.16, 0.05]	8.7%
Sasse and Pekins 1996	F	Mx	47	104	-0.63 [-0.98, -0.28]	9.7%
Thalken 2017	F	Mx	30	82	-0.90 [-1.33, -0.46]	9.4%
Lacki et al. 2009	F	Mx	16	11	-1.07 [-1.89, -0.25]	7.7%
Lacki et al. 2009	F	Mx	35	57	-1.44 [-1.91, -0.97]	9.3%
Thalken 2017	F	NR	38	82	-1.44 [-1.87, -1.02]	9.4%
Thalken 2017	M	Mx	14	82	-1.89 [-2.51, -1.26]	8.6%
Combined Effect (k = 11)					**-0.69 [-1.14, -0.24]**	

Figure 2.9. Forest plot of a northern long-eared bat meta-analysis of decay class compared to randomly selected available trees. Reported is the sex of the study populations, reproductive condition (R), number of roost trees (n_{roosts}), number of available trees ($n_{avail.}$), standardized mean difference (SMD), 95% confidence interval around the SMD (95% C.I), and weight that the study contributes to the combined effect. The circle indicates the standardized mean difference of the study that I calculated from the reported means of the roost trees and available trees. The diameter of the circle is relative to the weight that the study contributes to the overall estimate with larger circles indicating greater weight. The length of the horizontal bar spans the 95% confidence intervals of the mean. An SMD greater than zero supports a claim that roost trees are greater than what is available.



Study	Sex	R	n_{roosts}	$n_{avail.}$	SMD [95%C.I]	Weight
Jung et al. 2004	M	Mx	15	52	1.21 [0.60, 1.82]	3.8%
Sasse and Pekins 1996	F	Mx	47	104	1.17 [0.80, 1.54]	4.7%
Ford et al. 2006	M	Mx	10	40	1.16 [0.43, 1.88]	3.4%
Thalken 2017	M	Mx	14	82	1.12 [0.53, 1.70]	3.9%
Badin 2014	F	Mx	6	29	0.97 [0.06, 1.88]	2.9%
Lacki et al. 2009	F	Mx	16	11	0.92 [0.12, 1.73]	3.2%
Fabianek et al. 2015	M	Mx	26	40	0.87 [0.35, 1.38]	4.2%
Kaupas 2016	F	L	22	22	0.79 [0.18, 1.41]	3.8%
Thalken 2017	F	NR	38	82	0.74 [0.35, 1.14]	4.6%
Schultes 2002	MF	Mx	20	21	0.48 [-0.15, 1.10]	3.8%
Johnson et al. 2009	F	Mx	25	25	0.40 [-0.16, 0.96]	4.0%
Owen et al. 2002	F	Mx	43	43	0.33 [-0.09, 0.76]	4.5%
Thalken 2017	F	Mx	30	82	0.31 [-0.11, 0.73]	4.5%
Badin 2014	F	Mx	65	80	0.29 [-0.03, 0.62]	4.8%
Lacki et al. 2009	F	Mx	35	57	0.24 [-0.18, 0.66]	4.5%
Johnson et al. 2009	F	Mx	44	45	0.16 [-0.25, 0.58]	4.5%
Carter and Feldhamer 2005	F	Mx	19	46	0.13 [-0.41, 0.66]	4.1%
Silvis et al. 2015	F	Mx	220	108	0.12 [-0.11, 0.35]	5.1%
Lereculeur 2013	F	Mx	12	21	-0.18 [-0.89, 0.53]	3.5%
O'Keefe 2009	M	Mx	35	35	-0.19 [-0.66, 0.28]	4.3%
O'Keefe 2009	F	Mx	33	33	-0.20 [-0.69, 0.28]	4.3%
Cryan et al. 2001	F	Mx	21	30	-0.34 [-0.90, 0.22]	4.0%
Lereculeur 2013	M	Mx	9	21	-0.38 [-1.17, 0.40]	3.2%
Swier 2003	F	Mx	9	104	-0.39 [-1.07, 0.29]	3.6%
Ford et al. 2006	M	Mx	6	24	-1.69 [-2.68, -0.70]	2.6%
Combined Effect (k = 25)					**0.34 [0.12, 0.57]**	

Figure 2.10. Forest plot of a northern long-eared bat meta-analysis of roost tree height (m) compared to randomly selected available trees. Reported is the sex of the study populations, reproductive condition (R), number of roost trees (n_{roosts}), number of available trees ($n_{avail.}$), standardized mean difference (SMD), 95% confidence interval around the SMD (95% C.I), and weight that the study contributes to the combined effect. The circle indicates the standardized mean difference of the study that I calculated from the reported means of the roost trees and available trees. The diameter of the circle is relative to the weight that the study contributes to the overall estimate with larger circles indicating greater weight. The length of the horizontal bar spans the 95% confidence intervals of the mean. An SMD greater than zero supports a claim that roost trees are greater than what is available.



Study	Sex	R	n_{roosts}	$n_{avail.}$	SMD [95%C.I]	Weight
Fabianek et al. 2015	M	Mx	26	40	1.34 [0.80, 1.89]	6.8%
O'Keefe 2009	F	Mx	33	33	0.64 [0.14, 1.13]	7.3%
Lacki et al. 2009	F	Mx	16	11	0.46 [-0.32, 1.23]	4.8%
O'Keefe 2009	M	Mx	35	35	0.44 [-0.03, 0.91]	7.6%
Thalken 2017	M	Mx	14	82	0.39 [-0.18, 0.96]	6.6%
Thalken 2017	F	Mx	30	82	0.26 [-0.16, 0.68]	8.2%
Broders and Forbes 2004	M	Mx	57	57	0.25 [-0.12, 0.62]	8.8%
Lereculeur 2013	M	Mx	9	21	0.16 [-0.62, 0.94]	4.8%
Broders and Forbes 2004	F	Mx	55	55	0.02 [-0.36, 0.39]	8.7%
Jung et al. 2004	M	Mx	15	52	-0.05 [-0.63, 0.52]	6.5%
Lereculeur 2013	F	Mx	12	21	-0.06 [-0.77, 0.65]	5.3%
Thalken 2017	F	NR	38	82	-0.16 [-0.54, 0.23]	8.6%
Lacki and Schwierjohann 2001	MF	Mx	57	31	-0.22 [-0.66, 0.22]	8.0%
Lacki et al. 2009	F	Mx	35	57	-0.26 [-0.68, 0.16]	8.1%
Combined Effect (k = 14)					**0.21 [-0.01, 0.43]**	

Figure 2.11. Forest plot of a northern long-eared bat meta-analysis of snag density (snags/ha) compared to randomly selected available trees. Reported is the sex of the study populations, reproductive condition (R), number of roost trees (n_{roosts}), number of available trees ($n_{avail.}$), standardized mean difference (SMD), 95% confidence interval around the SMD (95% C.I), and weight that the study contributes to the combined effect. The circle indicates the standardized mean difference of the study that I calculated from the reported means of the roost trees and available trees. The diameter of the circle is relative to the weight that the study contributes to the overall estimate with larger circles indicating greater weight. The length of the horizontal bar spans the 95% confidence intervals of the mean. An SMD greater than zero supports a claim that roost trees are greater than what is available.

Study	Sex	R	n_{roosts}	$n_{avail.}$	SMD [95%C.I]	Weight
Jung et al. 2004	M	Mx	15	52	0.79 [0.20, 1.38]	9.4%
Johnson et al. 2009	F	Mx	44	45	-0.05 [-0.46, 0.37]	14.4%
Broders and Forbes 2004	M	Mx	57	57	-0.08 [-0.45, 0.28]	16.3%
Kaupas 2016	F	L	22	22	-0.13 [-0.72, 0.46]	9.3%
Johnson et al. 2009	F	Mx	25	25	-0.21 [-0.76, 0.35]	10.2%
Broders and Forbes 2004	F	Mx	55	55	-0.25 [-0.63, 0.12]	16.0%
O'Keefe 2009	F	Mx	33	33	-0.38 [-0.86, 0.11]	12.0%
O'Keefe 2009	M	Mx	35	35	-0.46 [-0.93, 0.02]	12.4%
Combined Effect (k = 8)					**-0.12 [-0.34, 0.09]**	

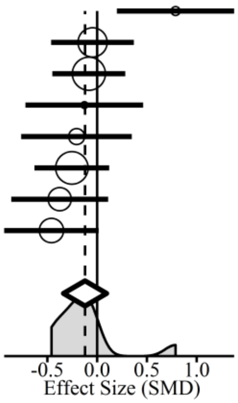
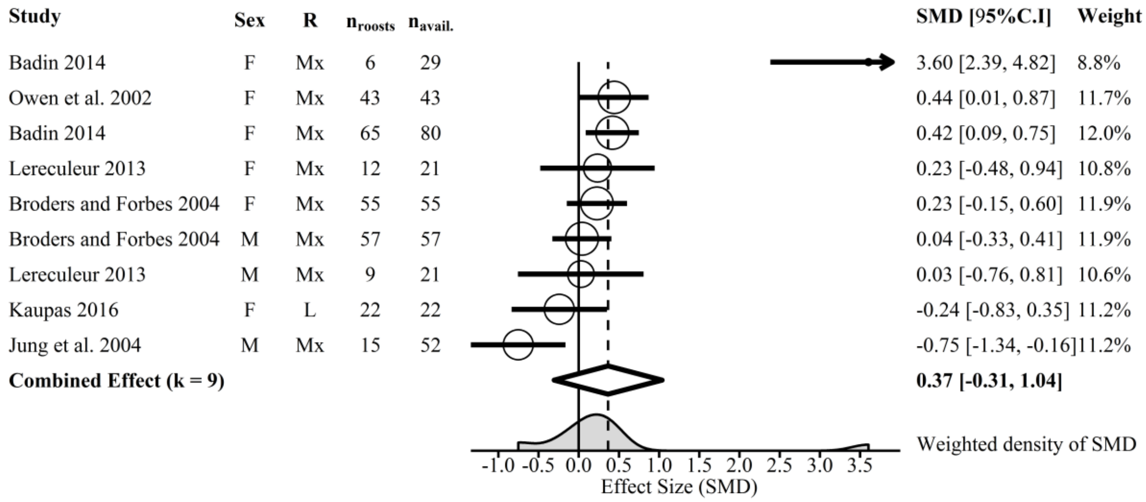
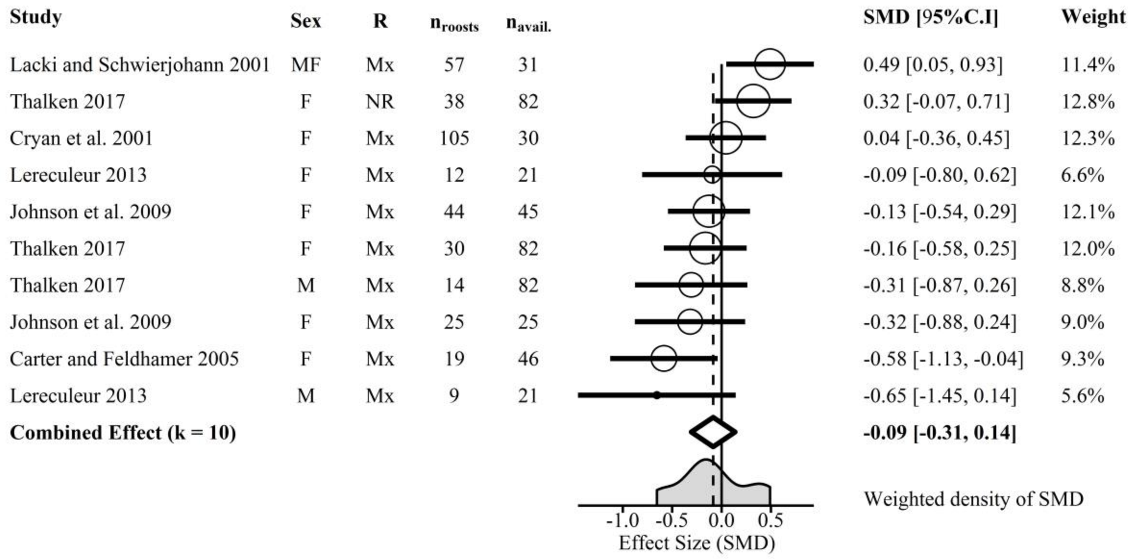


Figure 2.12. Forest plot of a northern long-eared bat meta-analysis of average distance to nearest tree (m) compared to randomly selected available trees. Reported is the sex of the study populations, reproductive condition (R), number of roost trees (n_{roosts}), number of available trees ($n_{avail.}$), standardized mean difference (SMD), 95% confidence interval around the SMD (95% C.I), and weight that the study contributes to the combined effect. The circle indicates the standardized mean difference of the study that I calculated from the reported means of the roost trees and available trees. The diameter of the circle is relative to the weight that the study contributes to the overall estimate with larger circles indicating greater weight. The length of the horizontal bar spans the 95% confidence intervals of the mean. An SMD greater than zero supports a claim that roost trees are greater than what is available.



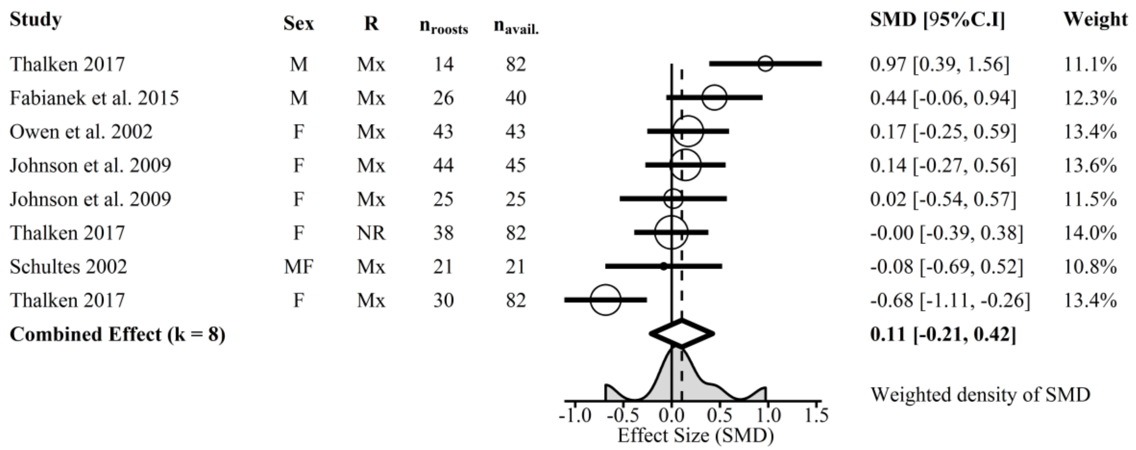
Study	Sex	R	n_{roosts}	$n_{avail.}$	SMD [95%C.I]	Weight
Badin 2014	F	Mx	6	29	3.60 [2.39, 4.82]	8.8%
Owen et al. 2002	F	Mx	43	43	0.44 [0.01, 0.87]	11.7%
Badin 2014	F	Mx	65	80	0.42 [0.09, 0.75]	12.0%
Lereculeur 2013	F	Mx	12	21	0.23 [-0.48, 0.94]	10.8%
Broders and Forbes 2004	F	Mx	55	55	0.23 [-0.15, 0.60]	11.9%
Broders and Forbes 2004	M	Mx	57	57	0.04 [-0.33, 0.41]	11.9%
Lereculeur 2013	M	Mx	9	21	0.03 [-0.76, 0.81]	10.6%
Kaupas 2016	F	L	22	22	-0.24 [-0.83, 0.35]	11.2%
Jung et al. 2004	M	Mx	15	52	-0.75 [-1.34, -0.16]	11.2%
Combined Effect (k = 9)					**0.37 [-0.31, 1.04]**	

Figure 2.13. Forest plot of a northern long-eared bat meta-analysis of stand density (stems/ha) compared to randomly selected available trees. Reported is the sex of the study populations, reproductive condition (R), number of roost trees (n_{roosts}), number of available trees ($n_{avail.}$), standardized mean difference (SMD), 95% confidence interval around the SMD (95% C.I), and weight that the study contributes to the combined effect. The circle indicates the standardized mean difference of the study that I calculated from the reported means of the roost trees and available trees. The diameter of the circle is relative to the weight that the study contributes to the overall estimate with larger circles indicating greater weight. The length of the horizontal bar spans the 95% confidence intervals of the mean. An SMD greater than zero supports a claim that roost trees are greater than what is available.



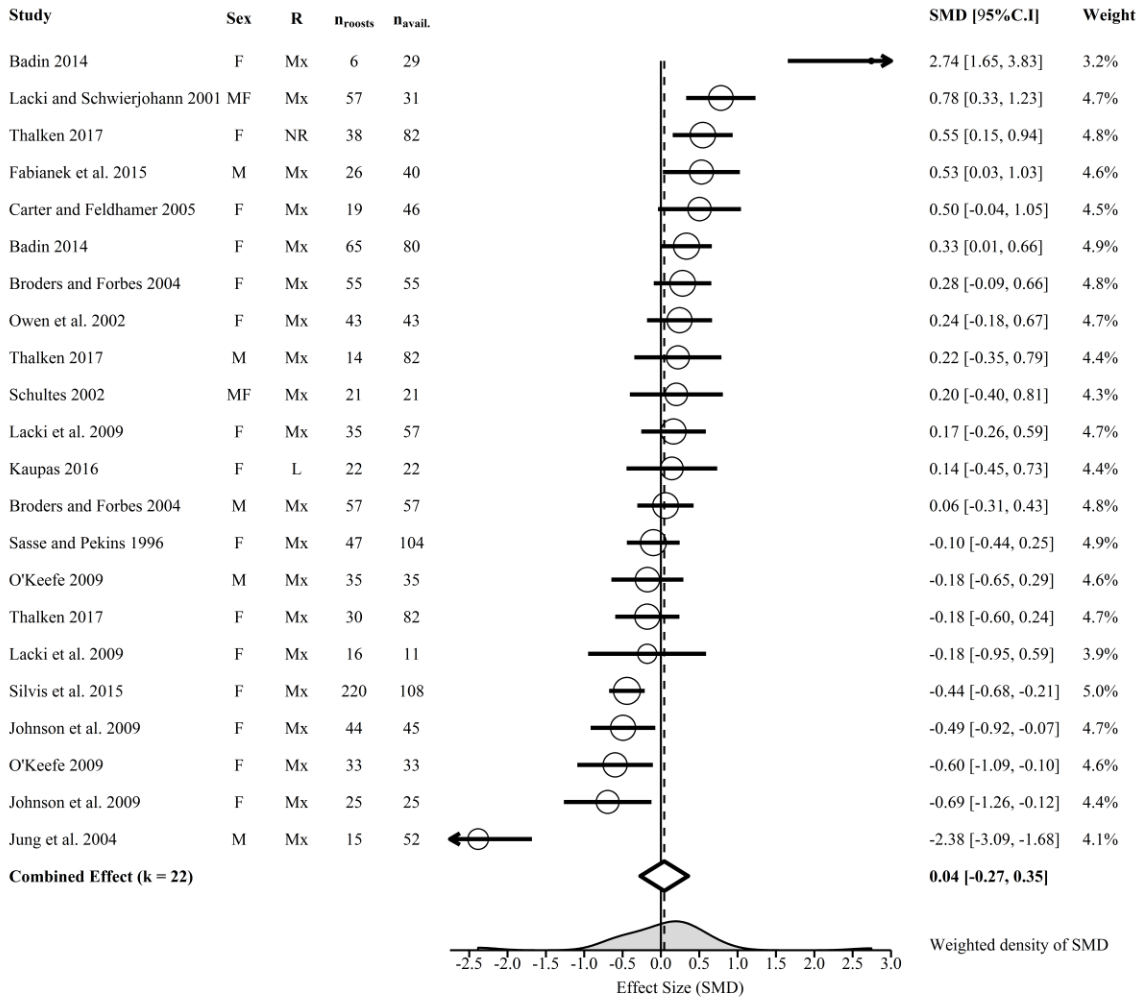
Study	Sex	R	n_{roosts}	$n_{avail.}$	SMD [95%C.I]	Weight
Lacki and Schwierjohann 2001	MF	Mx	57	31	0.49 [0.05, 0.93]	11.4%
Thalken 2017	F	NR	38	82	0.32 [-0.07, 0.71]	12.8%
Cryan et al. 2001	F	Mx	105	30	0.04 [-0.36, 0.45]	12.3%
Lereculeur 2013	F	Mx	12	21	-0.09 [-0.80, 0.62]	6.6%
Johnson et al. 2009	F	Mx	44	45	-0.13 [-0.54, 0.29]	12.1%
Thalken 2017	F	Mx	30	82	-0.16 [-0.58, 0.25]	12.0%
Thalken 2017	M	Mx	14	82	-0.31 [-0.87, 0.26]	8.8%
Johnson et al. 2009	F	Mx	25	25	-0.32 [-0.88, 0.24]	9.0%
Carter and Feldhamer 2005	F	Mx	19	46	-0.58 [-1.13, -0.04]	9.3%
Lereculeur 2013	M	Mx	9	21	-0.65 [-1.45, 0.14]	5.6%
Combined Effect (k = 10)					**-0.09 [-0.31, 0.14]**	

Figure 2.14. Forest plot of a northern long-eared bat meta-analysis of the mean DBH of the surrounding trees (cm) compared to randomly selected available trees. Reported is the sex of the study populations, reproductive condition (R), number of roost trees (n_{roosts}), number of available trees ($n_{avail.}$), standardized mean difference (SMD), 95% confidence interval around the SMD (95% C.I), and weight that the study contributes to the combined effect. The circle indicates the standardized mean difference of the study that I calculated from the reported means of the roost trees and available trees. The diameter of the circle is relative to the weight that the study contributes to the overall estimate with larger circles indicating greater weight. The length of the horizontal bar spans the 95% confidence intervals of the mean. An SMD greater than zero supports a claim that roost trees are greater than what is available.



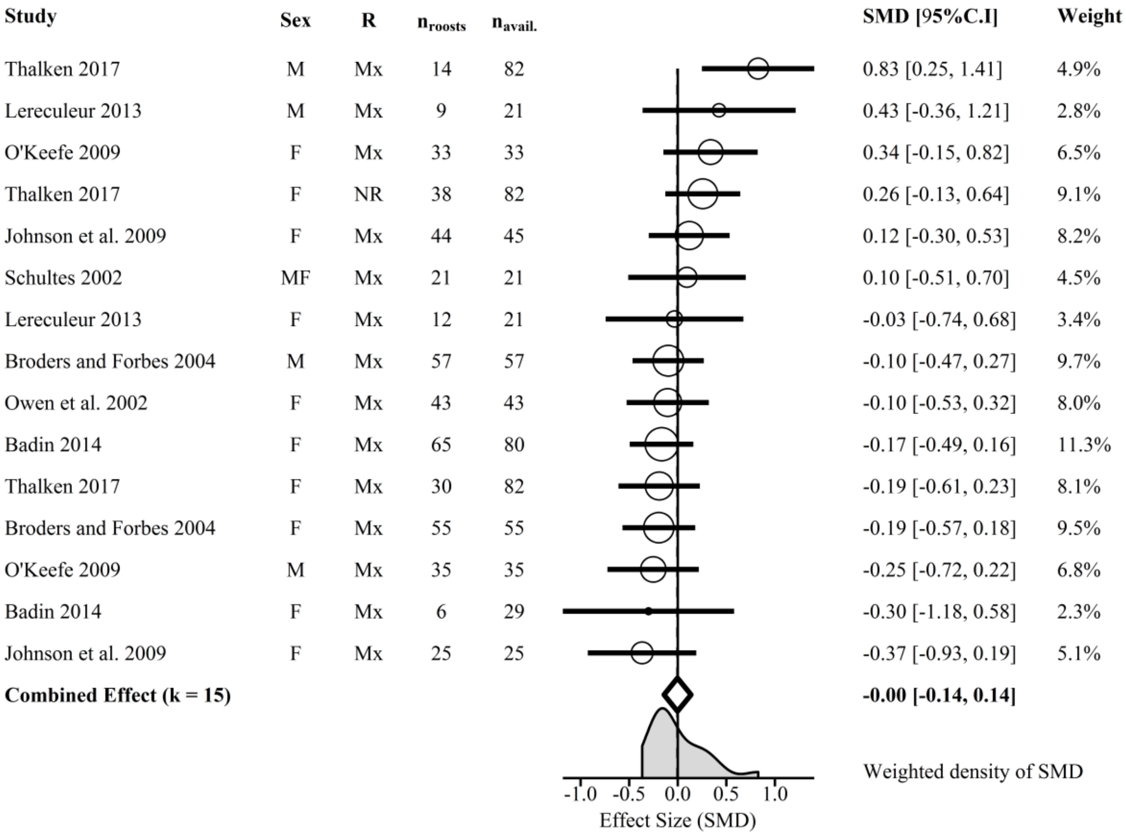
Study	Sex	R	n_{roosts}	$n_{avail.}$	SMD [95%C.I]	Weight
Thalken 2017	M	Mx	14	82	0.97 [0.39, 1.56]	11.1%
Fabianek et al. 2015	M	Mx	26	40	0.44 [-0.06, 0.94]	12.3%
Owen et al. 2002	F	Mx	43	43	0.17 [-0.25, 0.59]	13.4%
Johnson et al. 2009	F	Mx	44	45	0.14 [-0.27, 0.56]	13.6%
Johnson et al. 2009	F	Mx	25	25	0.02 [-0.54, 0.57]	11.5%
Thalken 2017	F	NR	38	82	-0.00 [-0.39, 0.38]	14.0%
Schultes 2002	MF	Mx	21	21	-0.08 [-0.69, 0.52]	10.8%
Thalken 2017	F	Mx	30	82	-0.68 [-1.11, -0.26]	13.4%
Combined Effect (k = 8)					**0.11 [-0.21, 0.42]**	

Figure 2.15. Forest plot of a northern long-eared bat meta-analysis of stand basal area (m^2/ha) compared to randomly selected available trees. Reported is the sex of the study populations, reproductive condition (R), number of roost trees (n_{roosts}), number of available trees ($n_{avail.}$), standardized mean difference (SMD), 95% confidence interval around the SMD (95% C.I), and weight that the study contributes to the combined effect. The circle indicates the standardized mean difference of the study that I calculated from the reported means of the roost trees and available trees. The diameter of the circle is relative to the weight that the study contributes to the overall estimate with larger circles indicating greater weight. The length of the horizontal bar spans the 95% confidence intervals of the mean. An SMD greater than zero supports a claim that roost trees are greater than what is available.



Study	Sex	R	n_{roosts}	$n_{avail.}$	SMD [95%C.I]	Weight
Badin 2014	F	Mx	6	29	2.74 [1.65, 3.83]	3.2%
Lacki and Schwierjohann 2001	MF	Mx	57	31	0.78 [0.33, 1.23]	4.7%
Thalken 2017	F	NR	38	82	0.55 [0.15, 0.94]	4.8%
Fabianek et al. 2015	M	Mx	26	40	0.53 [0.03, 1.03]	4.6%
Carter and Feldhamer 2005	F	Mx	19	46	0.50 [-0.04, 1.05]	4.5%
Badin 2014	F	Mx	65	80	0.33 [0.01, 0.66]	4.9%
Broders and Forbes 2004	F	Mx	55	55	0.28 [-0.09, 0.66]	4.8%
Owen et al. 2002	F	Mx	43	43	0.24 [-0.18, 0.67]	4.7%
Thalken 2017	M	Mx	14	82	0.22 [-0.35, 0.79]	4.4%
Schultes 2002	MF	Mx	21	21	0.20 [-0.40, 0.81]	4.3%
Lacki et al. 2009	F	Mx	35	57	0.17 [-0.26, 0.59]	4.7%
Kaupas 2016	F	L	22	22	0.14 [-0.45, 0.73]	4.4%
Broders and Forbes 2004	M	Mx	57	57	0.06 [-0.31, 0.43]	4.8%
Sasse and Pekins 1996	F	Mx	47	104	-0.10 [-0.44, 0.25]	4.9%
O'Keefe 2009	M	Mx	35	35	-0.18 [-0.65, 0.29]	4.6%
Thalken 2017	F	Mx	30	82	-0.18 [-0.60, 0.24]	4.7%
Lacki et al. 2009	F	Mx	16	11	-0.18 [-0.95, 0.59]	3.9%
Silvis et al. 2015	F	Mx	220	108	-0.44 [-0.68, -0.21]	5.0%
Johnson et al. 2009	F	Mx	44	45	-0.49 [-0.92, -0.07]	4.7%
O'Keefe 2009	F	Mx	33	33	-0.60 [-1.09, -0.10]	4.6%
Johnson et al. 2009	F	Mx	25	25	-0.69 [-1.26, -0.12]	4.4%
Jung et al. 2004	M	Mx	15	52	-2.38 [-3.09, -1.68]	4.1%
Combined Effect (k = 22)					**0.04 [-0.27, 0.35]**	

Figure 2.16. Forest plot of a northern long-eared bat meta-analysis of canopy cover (%) compared to randomly selected available trees. Reported is the sex of the study populations, reproductive condition (R), number of roost trees (n_{roosts}), number of available trees ($n_{avail.}$), standardized mean difference (SMD), 95% confidence interval around the SMD (95% C.I), and weight that the study contributes to the combined effect. The circle indicates the standardized mean difference of the study that I calculated from the reported means of the roost trees and available trees. The diameter of the circle is relative to the weight that the study contributes to the overall estimate with larger circles indicating greater weight. The length of the horizontal bar spans the 95% confidence intervals of the mean. An SMD greater than zero supports a claim that roost trees are greater than what is available.



Study	Sex	R	n_{roosts}	$n_{avail.}$	SMD [95%C.I]	Weight
Thalken 2017	M	Mx	14	82	0.83 [0.25, 1.41]	4.9%
Lereculeur 2013	M	Mx	9	21	0.43 [-0.36, 1.21]	2.8%
O'Keefe 2009	F	Mx	33	33	0.34 [-0.15, 0.82]	6.5%
Thalken 2017	F	NR	38	82	0.26 [-0.13, 0.64]	9.1%
Johnson et al. 2009	F	Mx	44	45	0.12 [-0.30, 0.53]	8.2%
Schultes 2002	MF	Mx	21	21	0.10 [-0.51, 0.70]	4.5%
Lereculeur 2013	F	Mx	12	21	-0.03 [-0.74, 0.68]	3.4%
Broders and Forbes 2004	M	Mx	57	57	-0.10 [-0.47, 0.27]	9.7%
Owen et al. 2002	F	Mx	43	43	-0.10 [-0.53, 0.32]	8.0%
Badin 2014	F	Mx	65	80	-0.17 [-0.49, 0.16]	11.3%
Thalken 2017	F	Mx	30	82	-0.19 [-0.61, 0.23]	8.1%
Broders and Forbes 2004	F	Mx	55	55	-0.19 [-0.57, 0.18]	9.5%
O'Keefe 2009	M	Mx	35	35	-0.25 [-0.72, 0.22]	6.8%
Badin 2014	F	Mx	6	29	-0.30 [-1.18, 0.58]	2.3%
Johnson et al. 2009	F	Mx	25	25	-0.37 [-0.93, 0.19]	5.1%
Combined Effect (k = 15)					**-0.00 [-0.14, 0.14]**	

Figure 2.17. Forest plot of a northern long-eared bat meta-analysis of slope (%) compared to randomly selected available trees. Reported is the sex of the study populations, reproductive condition (R), number of roost trees (n_{roosts}), number of available trees ($n_{avail.}$), standardized mean difference (SMD), 95% confidence interval around the SMD (95% C.I), and weight that the study contributes to the combined effect. The circle indicates the standardized mean difference of the study that I calculated from the reported means of the roost trees and available trees. The diameter of the circle is relative to the weight that the study contributes to the overall estimate with larger circles indicating greater weight. The length of the horizontal bar spans the 95% confidence intervals of the mean. An SMD greater than zero supports a claim that roost trees are greater than what is available.

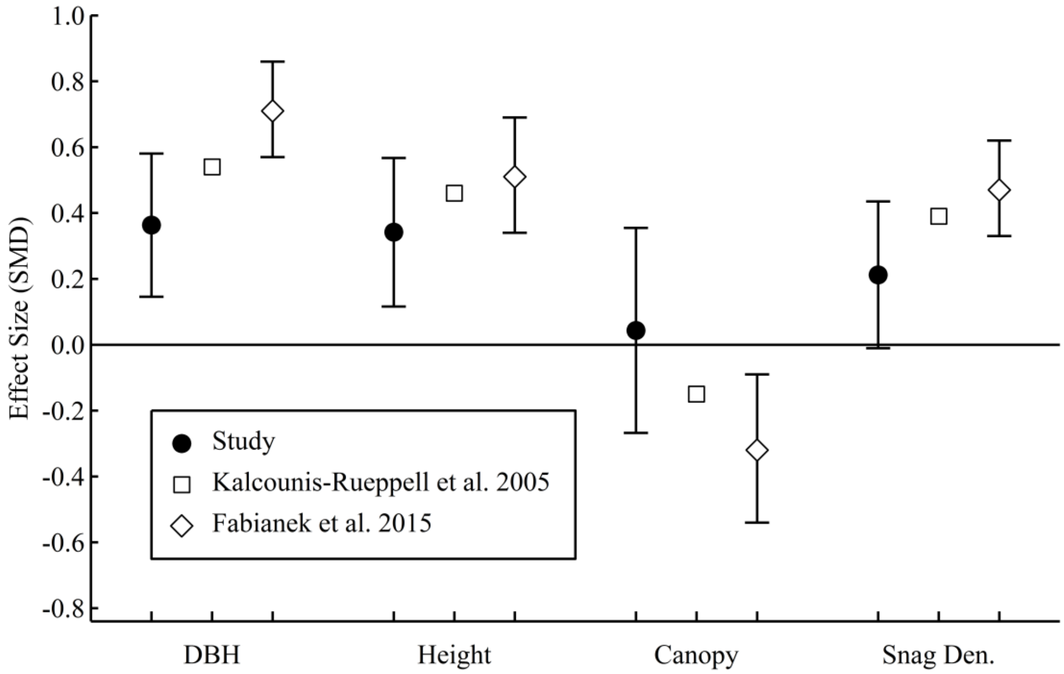


Figure 2.18. Comparison of the northern long-eared bat specific meta-analysis (Study) with previously published quantitative multi-species meta-analyses results. For all variables, evidence supported an effect size for northern long-eared bats nearer zero although overlap in 95% confidence intervals did occur. Kalcounis-Rueppell et al. (2005) did not report standard error or confidence intervals so they are not present in plot.

CHAPTER 3: THE SPATIAL DISTRIBUTION OF NORTHERN LONG-EARED BATS DURING MATERNITY SEASON IN NEBRASKA

Introduction

Due to anthroprogenic impacts, habitat conversion is occurring globally across ecological scales and despite regulatory initiatives, future projections of conversion trends appear bleak (Tittensor et al. 2014). Globally, processes such as climate change can exert pressures on species' distributions across latitudinal or elevation gradients (La Sorte and Jetz 2010, Tingley et al. 2012) or constrict local distributions when temperature constraints combine with biotic interactions (Merrill et al. 2008). At a finer scale, local initiatives such as channelizing streams and rivers, wildland fire suppression, agricultural expansion, or the planting of forested windbreaks can all effect the local distribution and abundance of species (Brooker 1985, Pierce II et al. 2001, Backer et al. 2004, Jetz et al. 2007). Additionally, landscape changes seemingly occurring at one scale can often times have unpredicted cross-scale impacts due to complex multi-scale interactions (Peterson et al. 1998). This multi-scale landscape change makes predicting the impacts to species difficult, as habitat use at one scale often does not transfer to inference at other scales (Schneider 2001, Mayor et al. 2009, Gallo et al. 2018), therefore studies incorporating multiple scales often times provided a better picture of the potential impacts of landscape change (Poizat and Pont 1996).

Understanding how species experiencing population declines respond to landscape changes require rigorous survey designs over large geographic extents. However, designing studies to accurately survey rare species is difficult due to the sampling intensity required to detect the presence of rare or cryptic species (Thompson

2004, MacKenzie and Royle 2005). Occupancy modeling provides a statistical methodology to incorporate imperfect detection with presence/absence data in order to estimate the proportion of sites occupied through repeated sampling (Tyre et al. 2003, MacKenzie and Royle 2005). By conducting repeated visits, it is possible to estimate the probability of false absences and reduce detection biases for rare species (MacKenzie and Royle 2005). Additionally, researchers can include covariates that account for variation in detection to improve occupancy estimates and gain an understanding of factors that affect species detection (MacKenzie and Royle 2005, Kaiser and O'Keefe 2015). Estimating site occupancy also provides a method for understanding habitat relationships, responses to management practices, or species responses to projected gloabal changes (Tyre et al. 2003, Gu and Swihart 2004, Zuckerberg et al. 2011).

Traditional single-season occupancy analysis, however, often only allows inference at a single spatial scale determined by the selection of the individual sampling locations. Multi-scale occupancy analysis, however, is an approach that incorporates a hierarchical sampling design where spatially replicated survey stations are nested within larger sampling units (Nichols et al. 2008, Pavlacky et al. 2012, Hagen et al. 2016). These survey stations then receive multiple visits to estimate detection probability. This modeling approach estimates occupancy at two distinct scales by simultaneously utilizing presence/absence observations and accounts for the non-independence of detections between the scales while also addressing the closure assumption for spatially replicated survey stations (Pavlacky et al. 2012). This approach estimates three parameters; large-scale occupancy (ψ; hereto referred to as grid occupancy), small-scale occupancy (θ; site occupancy for the purpose of this manuscript), and detection probability of the survey station (*p*). Multi-scale occupancy thus allows for the prediction of covariate relationships at two spatial extents to which a species may be responding differently (Mutter et al. 2015, Hagen et al. 2016).

Hibernating bats are an example of a relatively small mammal that interacts with its environment across distinctively different spatial scales (Gallo et al. 2018). Upon exiting a hibernation site (e.g., caves or buildings) a 7g bat may travel more than 300 km to its summer maternity site where it will remain until late summer after rearing its young (Griffin 1940). During the maternity season, a forest-associated species, such as the northern long-eared bat (*Myotis septentrionalis*), is relatively stationary within a forest stand (Owen et al. 2003). As an interior forest species (LaVal et al. 1977, Brack, Jr. and Whitaker Jr. 2001, Carroll et al. 2002), home ranges and habitat use of the species is affected by forest management practices that modify the density of trees at least at the stand level (Owen et al. 2003, Patriquin and Barclay 2003).

Globally, declines in bat populations are primarily the result of land conversion due to a growing human population and increased demands for space, food, and resource (Mickleburgh et al. 2002). Increased temperatures due to climate change also negatively influence future population projections (Adams and Hayes 2008). North America bats species are facing the aforementioned impacts along with an additional driver of population decline, white-nose syndrome (WNS); a fungal caused disease responsible for mortality rates often exceeding 95% in certain hibernating bat species (Frick et al. 2010). The northern long-eared bat is a species heavily affected by WNS and, as of 2018, is the only species federally listed under the United States Endangered Species Act as threatened as a direct result of the disease (Frick et al. 2015, Fish and Wildlife Service 2016).

The objective of this study was to predict northern long-eared bat occupancy within the state of Nebraska, determine environmental variables associated with this occupancy, and gain an understanding of factors that contribute to detection probability. To achieve these objectives, I applied multi-scale occupancy modeling to data collected from a hierarchical probabilistic sampling framework. I deployed multiple acoustic bat detectors nested within 10 km x 10 km grids within the state of Nebraska. This modeling approach allows for the testing of covariates that are associated with variation in detection probability, occupancy of grid, and occupancy of the survey station contingent upon detection within the larger grid unit. Additionally, I utilized landscape variables across the study area to predict grid occupancy spatially across the state.

Methods

STUDY AREA AND SITE SELECTION

I defined the study area as the geographical boundaries of Nebraska. I divided the state into a 10 x 10 km grid and then randomly selected cells using a generalized random tessellation stratified (GRTS) selection algorithm (Stevens and Olsen 2004). I biased the GRTS algorithm upon forest cover within a potential cell. In other words, the algorithm was more likely to select a cell with greater forest cover. Previous research has indicated that northern long-eared bats are highly associated with forest cover (Broders et al. 2006), therefore I biased the selection to maximize the likelihood of detecting the species as much of the state is not forested. I also balanced the selection to sample all level IV ecoregions (Omernik and Griffith 2014) relative to their area. This ensured I sampled every level IV ecoregion in Nebraska with at least one 10km x 10km grid.

Once a 10 x 10 km cell was selected using GRTS, I initially preselected potential habitat blocks from aerial images following a predefined selection framework (Figure 3.1). I established this framework to satisfy the following objectives: 1) reproducible (between survey units and surveyors), 2) easy application in the field without computer access, 3) based upon easily defined features, 4) incorporate species-specific information to maximize detection potential, 5) incorporate uncertainty of a species' habitat preferences, 6) modifiable to fit future needs of other species. Following my framework, I rejected and replaced a cell if it lacked roads, or at least one patch of trees ≥120m x 120m in at least two quadrants of the cell.

Once I selected a habitat block via the framework, personnel on the ground made the stand-level site selection decisions. By observing the habitat block from the road and through the utilization of plat maps, field personnel contacted the applicable landowner for access. If a preselected habitat block was not accessible due to lack of landowner permission, access, or any other extenuating circumstances, I utilized the decision framework to select a replacement habitat block within the cell. If field crew members were unable to deploy the targeted number of detectors within a cell (n=4) due to unforeseen circumstances, the cell was not rejected from analysis or replaced due to time constraints in the field season.

After I obtained landowner permission, I selected the actual deployment location within the habitat block. To select a site, I made my best attempts to adhere to the following dichotomous decision criteria:

1. Site contains a forested ridgeline ……………………………………..…...……… 2

   Site does not contain a forested ridgeline………………………...…………… 3

2. Ridgeline contains an area with reduced clutter………..….. Select site and deploy

   Ridgeline does not contain an area with reduced clutter………………………… 3

3. Within the forest block, an open corridor is present……..… Select site and deploy

   No corridor is present……………………………………….....…………… 4

4. Pond or stream present within block………………………...Select site and deploy

   No pond or stream is present……………………………….... Select site with the least amount of clutter while staying within forest block.

I based deployment location criteria upon previous findings pertaining to habitat usage and the constraints of recording bats in a cluttered setting. Previous research has concluded that northern long-eared bats forage on forested ridgelines and hillsides rather than along stream corridors (LaVal et al. 1977, Brack, Jr. and Whitaker Jr. 2001). By observing light-tagged individuals, LaVal (1977) observed northern long-eared bats only in the space between the forest canopy and the understory. This foraging behavior makes recording the species particularly difficult because recording in a cluttered environment has substantial limitations such as reduced recording quality and increased ambiguity of echolocations (Broders et al. 2004). If I was unable to locate a suitable recording environment within a habitat block, I rejected that block and replaced it following the selection framework.

DETECTOR DEPLOYMENT

At each sampling point, I recorded bat echolocations using AnaBat Express bat detectors (www.titley-scientific.com) mounted on a telescopic pole between 2.4 m and 7 m above the ground. I adjusted the height of the detector to place the detector between the understory and the canopy operating under the assumption that foraging occurs primarily in this open zone (Nagorsen et al. 1993) and to maximize the number of quality recordings (Weller and Zabel 2002). I oriented the microphone in the direction with the least amount of clutter (Weller and Zabel 2002). In cases where there was no understory, I positioned the detector at the minimum of 2.4 meters above the ground. Sampling began 30 minutes before sundown and continued until 30 minutes after sunrise. Detectors remained deployed for a minimum of 6 nights. Due to access constraints (i.e. inclement weather, road conditions, or vehicle damage), detectors often remained deployed for additional days. Additionally, issues with battery longevity sometimes resulted in recording periods less than 6 days. I accounted for this variation in survey time later in the statistical analysis.

ACOUSTIC ANALYSIS AND DETECTION HISTORY

I analyzed all recordings using Kaleidoscope v4.1.0 with the Bats of North America 4.1.0 classifier set to “-1 More Sensitive” (Wildlife Acoustics, Concord, MA, USA; www.wildlifeacoustics.com). I set the signal of interest parameters as follows: 16-120 kHz, 2-20ms, maximum inter-syllable gap = 500 ms, minimum number of pulses = 5, and advanced signal processing = ON. Prior to analysis, I divided the state into 17 regions of unique potential species assemblages using historical capture records and expert knowledge allowing buffers for potential distribution error due to a lack of survey effort. These species assemblages determined which auto-classifiers I activated in Kaleidoscope with northern long-eared bat activated in all regions. I performed this division to increase accuracy of identification and to simplify the confusion matrix within Kaleidoscope.

Once I auto-classified calls using Kaleidoscope, I applied additional conservative criteria to reduce false positives when determining detection or non-detection for a given night. For clarity, in my study I defined a pulse as an individual emission of echolocation and a call-sequence as a series of pulses within a single digital recording. I categorized each auto-classified call sequence as either high, medium, or low quality based upon the Kaleidoscope reported metrics. Specifically I used the number of pulses within the call sequence, the match ratio (a ratio of pulses matching the auto-assigned species vs the total number of pulses), and the software-generated maximum likelihood estimator (MLE; a test of the null hypothesis of a species not being detected within a given night). If a call-sequence contained at least 10 pulses and a match ratio of 0.9 or greater, I categorized it as a high quality call-sequence and awarded it a score of 0.5. A call-sequence with at least 5 pulses and a match ratio greater than 0.75 received a score of 0.33, a call-sequence with at least 5 pulses and a match ratio greater than 0.5 received a score of 0.25, and lastly a call-sequence with a match ratio below 0.5 received a score of 0 regardless of the number of pulses. I totaled the scores assigned to the northern long-eared bat for each night at a given deployment location. If a single night’s total score was at least 1.0 and the night’s MLE was less than or equal to 0.05, I scored that night as detected. If it did not meet the above criteria, it was determined to be non-detected for a given night. Additionally, I hand-vetted any detections occurring outside of the U.S. Fish and Wildlife estimated distribution (Fish and Wildlife Service 2016) of the species due to the implications of a range expansion.

DETECTION (P) PROBABILITY COVARIATES

To understand factors that contribute to detection probability, I recorded site characteristics at each microphone deployment **(**Table 3.1). To quantify the amount space in the recording environment (an inverse of the amount of clutter), I visually estimated distances to dense clutter as either <2.5m, 2.6-5m, 5.1-10m, or >10m from the front, back, left, right, above, and below relative to the microphone. I also calculated nightly mean temperature (°C), relative humidity (%), and wind speed (m/s), and total rain fall (mm) from Rapid Refresh (RAP) data during each nightly recording period. RAP data is an hourly updated weather model for North American at the 13-km resolution (Benjamin et al. 2016). I obtained recording length (decimal hours) for a given night from the auto-generated log files created by the recording units. This covariate accounts for battery failures that occurred partway through a recording night or for variations in night length throughout the summer. Lastly, I also incorporated day of the study season to account for the influence of volancy (pups gaining the ability to fly) mid-way through the study.

LOCAL OCCUPANCY (THETA) COVARIATES

I included habitat covariates at the detector (site) level that account for variation in site occupancy (Table 3.2). These are specific for each detector deployment nested within the 10km grids. To understand how anthropogenic landscape features affect local occupancy, I included the minimum distances of the nearest major road to each detector deployment. The minimum distance to major water sources as defined by the Landfire 2014 dataset was also included in my model set (LANDFIRE 2014). To understand the effects of landscape context, I calculated the area of forests within 125, 250, 500, and 1000 m buffers radiating outward from the deployment location. I chose 125 m as the starting value because the pixel resolution of the landcover raster (30 m) reduced the variation between buffer distances and the accuracy of the estimate. I increased the buffer distances multiplicatively rather than additively to reduce the number of models. I chose the distance of 1000 meters as the largest distance as this was roughly twice the average distance the species roosted from capture sites (see Chapter 2).

GRID OCCUPANCY (PSI) COVARIATES

I derived 11 continuous covariates that pertained to grid occupancy (psi) using digitally available landscape variables (Table 3.3). I used FRAGSTATS (McGarigal et al. n.d.) and the Landfire 2014 existing vegetation layer (LANDFIRE 2014) to calculate landscape metrics within the boundaries of the 10 km grid. Subsetting the LANDFIRE (2014) data to include patches with lifeform only equal to “tree”, I calculated the total core area of forest (HA), connectedness index of forest patches, clumpiness index of forest patches, and number of disjunct core areas of forest. Core area metrics require user-provided values of the depth of edge influence into forest from a neighboring patch. I set this value at 40m for all adjacent landcover classes per Jantzen and Fenton (2013). Additionally, connectedness metrics require a defined search distance around a forested patch to estimate connectedness of a grid cell. For this analysis, I set the search distance at 450 m as it was the upper 95% confidence interval for the distance between consecutive roosts following a quantitative meta-analysis on northern long-eared bat roosting behavior (see Chapter 2). Subsetting the LANDFIRE (2014) data to include patches with lifeform only equal to “water”, I estimated the total area of water (HA). I obtained the mean summer temperature (°C) and mean summer precipitation (mm) for the combined months of May, June, July, and August using WorldClim 1.4 data which averages weather observations from 1960 – 1990 at a 1km resolution. I also incorporated the geographic coordinates of the grid centroids into the model set to account for the spatial auto-correlation of the species distribution in Nebraska. It has been demonstrated that this approach improves predictive performance as a broad-scale environmental gradient may exist that is not adequately captured by other covariates (Václavík et al. 2012).

The aforementioned covariates all pertain to summer maternity distribution. To examine the proximity to potential winter hibernacula habitat, I created a covariate to serve as a proxy for potential non-traditional hibernacula availability. I calculated terrain position indices (TPI) using a 1 arc-second digital elevation model and the package Raster (Hijmans 2017). A raster pixel’s TPI is the difference between the pixel’s elevation and the mean elevation of all neighboring cells in a moving window approach (Wilson and Gallant 2000). I considered all terrain with a TPI of 4 or greater as potential ridge habitat for smaller hibernacula either in rocky cliff roosts or eroded bluff faces. I then extracted all terrain with a TPI of 4 or greater and a soil depth less than 5m derived from a global thickness of soil, regolith, and sedimentary deposit layer (Pelletier et al. 2016). While northern long-eared bats are traditionally considered cave hibernating bats, the rarity of Nebraska caves/mines and the documented occurrence of hibernation in Nebraska bluff faces led me to explore this approach (Lemen et al. 2016). I buffered the centroid of each sampled grid 89km as this was the longest reported distance the authors could locate of a northern long-eared bat traveling from its hibernacula (Griffin 1940) in late spring or early summer.

MODELING APPROACH

I applied a multi-scale occupancy modeling approach as first described by Nichols (2008) for use with multiple sampling devices. Rather than multiple devices, my replication within a sampling unit was individual survey stations similar to Pavlacky's (2012) analysis using point count transects. Survey stations were primary occasions for estimating site occupancy (θ), and nightly temporal replicates were secondary occasions for estimating detection probability (*p*) (Pavlacky et al. 2012, Hagen et al. 2016). This modeling approach decomposes the probabilities of θ and *p* to improve the inference of grid occupancy (ψ) (Nichols et al. 2008, Hagen et al. 2016). This approach contains the following assumptions: 1) there was no un-modeled heterogeniety in the probabilities of detections or occupancy, 2) each quadrant was closed to changes in occupancy during the course of sampling, 3) the nightly detections of northen-long eared bats were independent between survey stations, and 4) there were no false detections of the species (Nichols et al. 2008, Pavlacky et al. 2012). For all model sets, I ranked models according to Akaike's Information Criterion (Akaike 1973) adjusted for small sample sizes (AICc) (Hurvich and Tsai 1989), assessed the strength of evidence for a given model *i* using AICc model weights (w_i), and estimated the plausibility of a particular model *i* using evidence ratios (w_i / w_j).

MODEL FITTING

I fit all models in R using the package RMARK 2.2.4 (Laake 2013), an interface between MARK v8.0 (White and Burnham 2009) and R (R Development Core Team 2018). To access the need to include latitude and longitude to account for spatial autocorrelation, I fit three competing models, a global model without latitude and longitude, a global model with latitude and longitude as additive terms, and a global model with latitude and longitude as an interaction. I considered the top supported model based upon AICc as the global model for grid occupancy.

After incorporating the top spatial autocorrelation model, I fit four competing site occupancy (θ) models to assess the scale at which forest area most strongly correlated with site occupancy. The four models contained global p, global ψ, distance to road and water, and one of the four buffer distances at which the area of forest was calculated. To capture the spatial scale at which forest most strongly influenced site occupancy, I selected the top model based upon the largest β coefficient rather than the lowest AICc and included this term into the global θ model. I z-scored all covariates prior to fitting to allow direct comparison of β-estimates.

Once I had a global model for all three parameters, I grouped covariates for p and ψ into 1 – 2 additive term groupings corresponding to discrete themes and hypotheses. There were 5 term groupings for both p and ψ. For p these groupings corresponded to atmospheric conditions (temperature and RH), atmospheric interference (rain and wind), recording space, recording length, and day of season. For ψ, these groupings corresponded to forest area (forest core area and number of disjoint core areas), forest aggregation (forest clumpiness and connectivity), landscape features (developed area and water), climate (summer temperature and precipitation), and cliff area. I did not group any terms for θ. I then fit all possible models for *p*, θ, and ψ simultaneously in an all-combinations approach (Doherty et al. 2012). This resulted in 8,192 potentials models. I defined the final model set as all models within 2 ΔAICc. Rather than model averaging the β-coefficients of model variables and their respective standard errors, I unconditionally averaged the predicted real values from the models within 2 ΔAICc and included confidence intervals of 95%. I used the delta method to approximate the sampling variance and standard error when I estimated overall site occupancy and detection probability (Oehlert 1992, Powell 2007). To spatially predict grid occupancy across the state, I held all *p* and θ covariates constant at their means and applied covariate values for all possible 10 km x 10 km grids within the Nebraska range of the northern long-eared bat. I then *unconditionally* averaged the predicted real values from all models in the final confidence set. This resulted in an estimate of occupancy for all grids bound between 0 and 1. I arbitrarily defined 4 cut points for visualization purposes at 0-0.25, 0.25-0.5, 0.5-0.75, 0.75-0.90, 0.90-1.0 in ArcGIS (ESRI 2011).

Results

SURVEY RESULTS

I surveyed 101 grids and detected the northern long-eared bat at 22 grids (Figure 3.2). Prior to model fitting and z-scoring covariates, I removed 19 grids from consideration to limit modeling and prediction to within the range of the northern long-eared bat, as my observations did not warrant expanding the range and to limit the effects of zero-inflation of data. Although the target number of survey stations per grid was 4, I averaged 3.72 ± 0.06 SE survey stations per grid due to lack of suitable sites or landowner permission. I defined the number of primary samples as K=4 to correspond to the maximum number of survey stations within a grid, and L=8 as the number of secondary samples to correspond to the maximum number of nights sampled. This resulted in an encounter history of $K*L = 32$.

EFFECT OF SPATIAL AUTOCORRELATION TERMS ON GIRD OCCUPANCY

The best approximating model within the spatial autocorrelation model set for ψ included the additive effects of latitude and longitude (Table 3.4). The evidence ratio (w_i/w_j) indicated that this model was ~5.7 times more plausible than the next ranked model that included an interaction between latitude and longitude, and was ~7 times more plausible than the global ψ-model that lacked latitude and longitude. Due the strong support for including the additive terms of latitude and longitude, I included these terms in all subsequent models to account for the effects of spatial auto correlation or unforeseen landscape effects that varied with a latitude and longitude gradient but were not present in the model set.

EFFECT OF FOREST SCALE ON SITE OCCUPANCY

The best approximating model within the forest scale model set for θ included the effect of forest area within a buffer of 125 meters from the survey station; however, all models were within 2 AICc of each other (Table 3.5). The evidence ratio (w_i/w_j) indicated that this model was ~1.5 times more plausible than the next ranked model and ~2.4 times more plausible than the last ranked model in the set. The value of the model's β-coefficients provided support of a declining relationship in the effect of forest area on site occupancy as distances radiate outward from the survey station; however, all 95% confidence intervals indicated overlap of all estimates. Due to this relationship, I included the covariate representing the area of forest within a 125-meter buffer from the survey station in further model fitting.

FINAL FITTING OF ALL MODELS

The final confidence set, as defined by all models within 2 AICc of the top ranked model, contained 14 of the 8,192 potential models (Table 3.6). Other than latitude and longitude, which was included in all fitted models to account for spatial autocorrelation, the ψ-covariates included in the confidence set with β-estimates that did not overlap zero with 95% confidence included forest clumpiness, mean summer temperature (°C), and area of potential cliff terrain (HA) within 89 km (Table 3.7). Evidence supported a positive relationship with grid occupancy for all of these covariates.

The only θ-covariate that did not show overlap with zero with 95% confidence was a positive relationship with forest area (HA) within 125 meters of the survey station (Table 3.8). The *p*-covariates present in the confidence set with β-estimates that did not overlap zero with 95% confidence included an index of open recording space relative to the microphone, mean nightly temperature (°C), and day of the season (Table 3.9, Table 3.10). It is noteworthy that these covariates were present in all top models and contained β-estimates that did not overlap zero with 95% confidence in all models. Also of note, β-estimates indicate a negative relationship between nightly temperature and detection probability which was opposite of my expectations (Table 3.9). Evidence supported a positive correlation between day of season and detection, which met my expectations as volancy occurred in the latter half of the study season. Results also supported a negative relationship with recording space, which is consistent with some previous findings (Kaiser and O’Keefe 2015) (Table 3.9**)**.

The estimated nightly detection probability for acoustically surveying the northern long-eared bat using my study design was $\hat{p}$ = 0.52 which is well above the moderate range of 0.3 estimated by MacKenzie (2002) to provided unbiased estimates of occupancy (Table 3.11). Using the equation $1 - (1-p)^k$ to estimated overall detection probability (*d*) for night (*k*), overall detection exceeded 95% after four nights. With covariates set at their means, northern long-eared bats occupied 70% of the survey stations ($\hat{\theta}$), conditional on grid occupancy, but only 6% of the grid units ($\widehat{\Psi}$) (Table 3.11). This indicates that the species is locally common but occupies a relatively small percentage of the USFWS defined distribution within Nebraska. The naïve estimate of grid occupancy was 27%, which is considerably greater than the adjusted occupancy estimate when adjusted for detection and site occupancy. This is potentially due to a relatively high likelihood of detecting the species during my survey, combined with grid occupancy being associated with covariate values well outside of their respective means for the study area.

SPATIAL PREDICTION

Holding covariates for theta and *p* constant at their mean values, I predicted grid occupancy across estimated Nebraska range of the species using covariate values for all sampling units (Figure 3.4). The models averaged to predict grid occupancy across Nebraska included the following ψ covariates: latitude, longitude, cliff area with 89 km, forest clumpiness, forest connectivity, mean summer precipitation, and mean summer temperature. I held all values for θ and ψ constant at their means. To visualize the distribution of error across the study area, I also visualized standard error. Although I sampled all ecoregions relative to their area, the pine ridge area in the northwest panhandle received little sampling (Figure 3.2). Extremes in latitude and longitude combined with relatively little sampling, likely contributed to high standard error in this region.

Discussion

Applying a multi-scale occupancy approach was useful for determining the factors associated with occupancy at two distinct spatial scales while also providing insight into factors associated with detection probability of the northern long-eared bat across its Nebraska distribution. Our results suggest that by establishing multiple survey stations within larger sampling units, one can account for heterogeneous sampling availability of a species within the larger sample unit. The recording space around a bat detector's microphone, day of the season, and mean nightly temperature significantly influenced detection probabilities. The area of forest within 125 m of a survey station had a significant relationship with site occupancy. Latitude, longitude, cliff area with 89 km, forest clumpiness, and mean summer temperature significantly influenced larger-scale grid occupancy of the 10 km grids.

Opposite of my expectations, temperature showed a significant inverse relationship with detection probability. While the rate of sound temperature attenuation and air temperature are positively correlated (Griffin 1971), the relatively small range of nightly temperatures experienced during the course of the study season likely had little effect on sound attenuation (Lawrence and Simmons 1982). Previous studies have mostly reported a positive relationship with temperature and activity or detection probability (Hayes 1997, Yates and Muzika 2006, Kaiser and O'Keefe 2015), however, a weak negative relationship was observed between temperature and detection probability in evening bats (*Nycticeius humeralis*) (Hein et al. 2009). A possible explanation for this inverse relationship could be the effects of insect noise on the recording environment. Both insect abundance and insect call volume exhibit a positive relationship with ambient temperature (Anthony et al. 1981, Sueur and Sanborn 2003). Because the zero-cross recording technology used in this study only records the frequency of the most intense sound within the recording environment, insect noise could be essentially outcompeting northern long-eared bat echolocations and limiting the detectors ability to record the species. This effect may be less noticeable in lower frequency bats as lower frequency echolocations travel further distances (Lawrence and Simmons 1982, Adams et al. 2012). To account for the influence of insect noise, future studies could potentially use the number of non-bat recordings for a given night as a covariate for detection probability to reduce bias in the parameter estimate.

The other dominant detection probability covariate, recording space, is essentially an inverse of clutter; as clutter increases, recording space thus decreases. Clutter in a recording environment is generally thought to reduce detection rates (Broders et al. 2004) but studies assessing the relationship between detection probability offer mixed conclusions. O'Keefe and colleagues (2014) concluded that detection probability of high frequency bats, such as the northern long-eared bat, decreased as midstory live-stem count increased. However, they found the opposite relationship occurred between canopy crown volume and detection. Additionally, an occupancy study on Indiana bats (*M. sodalis*), concluded that detection probability was positively correlated with forest closure, a "principal component derived from mean canopy closure, mean mid-story closure, and number of trees ≥ 10 cm DBH" (Kaiser and O'Keefe 2015). The authors in that study speculated two possible explanations for this relationship. The first possible explanation was that closed forests contained reduced understory structure and thus provided greater foraging habitat and a possible increased availability of roost structures. Therefore, this closed forest habitat resulted in an increased abundance of bats and thus a greater detection probability. The second proposed explanation is that closed forest sites may simply limit the amount of available area around a microphone for a bat to fly resulting in a higher concentration of bats within the recording space (Kaiser and O'Keefe 2015). My study's estimate of recording space did not include forest cover but instead estimated the amount of 3-dimensional uncluttered space around the microphone. It is likely that at least two possible explanations exist for my observations of an inverse relationship between recording space and detection probability. The simplest explanation is comparable to Kaiser and O'Keefe (2015) in that reduced recording space simply forces bats to fly closer to the microphone. Because northern long-eared bats are a high frequency bat, their echolocation does not travel as far as lower frequency bats, due to high frequency sounds attenuating at a faster rate (Lawrence and Simmons 1982). In a large open recording environment, their echolocations may simply attenuate before being reaching the microphone. The second possibility, also proposed by Kaiser and O'Keefe (2015) is that the abundance of northern long-eared bats in denser forest sites is greater and thus the species has a greater probability of detection on a given night (Royle and Nichols 2003). While previous studies define the species as an interior forest bat (LaVal et al. 1977, Brack, Jr. and Whitaker Jr. 2001, Carroll et al. 2002), effort was always made to deploy detectors within suitable recording environments in the interior of forest patches. Therefore, even low clutter sites were often within the forest patches and should have received the added increase to abundance that preferred habitat deployments would allot. A third possible explanation for this relationship, and not proposed by others to the authors knowledge, is the possibility of false detections due to co-occuring species being falsely classified as the target species. High clutter (i.e. low recording space) sites cause shifts in the echolocations characteristics (Broders et al. 2004). Even with expert hand vetting of recordings, echolocations from co-occurring species, such as little brown bats (*Myotis lucifugus*), in a cluttered environment could be indiscernible from northern long-eared bats (Broders et al. 2004). To account for this possibility, I only selected suitable low-clutter survey locations in this study making this possibility unlikely. In future studies, especially with probabilistic site selection, the selected sampling area should be large enough to facilitate selecting a suitable site, or researchers should conduct oversampling of potential survey sites to allow substitution of replacement sites.

The final covariate associated with detection probability was day of the survey season. In the latter half of the survey season, juveniles become volant (Geluso et al. 2004) and there becomes a resulting increase in abundance (Agosta et al. 2005). My results are consistent with previous studies and indicate a positive relationship between day of season and detection probability (Kaiser and O’Keefe 2015, Pauli et al. 2017). This is likely due to the aforementioned increase in abundance (Royle and Nichols 2003, Kaiser and O’Keefe 2015). Future studies should take into account time of year when designing bat surveys, especially clearance surveys where inferring absence rather than presence is the goal.

The strongest relationship of forest area to site occupancy was the area of forest within a 125 m radius around the survey station. This corresponds to an area of approximately 4.9 hectares. Beyond this distance, data supported a consistent decline in β – estimates. This area of 4.9 ha corresponds with findings of previous roost selection studies which, when averaged, report a mean minimum roosting area of 5.2 ha ± 1.44 SE (Henderson 2008, Broders 2006, Johnson 2012, Badin 2014, Lereculeur 2013, O'Keefe 2009). Because 125 m was the smallest buffer I investigated, it is possible that forest area within a smaller radius could potentially result in a greater effect. These results suggest that the northern long-eared bat can occupy forest patches of relatively small size at least in the short term.

The site occupancy covariate, distance to major road was present in the confidence set but contained β–estimates with 95% confidence intervals overlapping zero. Bats regularly use roads for commuting and foraging and occupancy has been positively influence by proximity of roads (Hein et al. 2009). However, in some species, proximity to major roads negatively influences activity (Berthinussen and Altringham 2012). Although I restricted distances to only major roads, most nearby roads were rural paved roads that often received little nocturnal vehicle traffic. Bats may be utilizing roads through forested sites for foraging corridors but evidence does not support that the proximity of these roads was associated with occupancy of the site. The site occupancy covariate, distance to nearest water source, was not present in the confidence set. As a small, clutter-adapted species, these species likely only need small water sources (e.g., flooded road ditches, ephemeral pools, puddles) which are common in my study sites but were not documented in my data set as I was limited to large remotely sensed perennial water sources such as streams, rivers, and ponds. Additionally, unlike other *Myotis* species, the northern long-eared is not generally associated with riparian stream sites and is more encountered in the interior of the forest (Carroll et al. 2002).

The only grid occupancy covariate associated with forest was the clumpiness of forest patches. Studies conducted at finer spatial scales (e.g, within a single forest stand) report similar findings to my site occupancy results, with forest availability or stand density being correlated with northern long-eared bat presence or activity (Owen et al. 2003, Ford et al. 2005, Schirmacher et al. 2007, Johnson et al. 2008). At scales, however, availability becomes less predictive. A study in Ontario concluded that forest availability was not associated with northern long-eared bat abundance and instead reported a *positive* correlation between forest fragmentation and abundance of the species when forest area was held constant (Ethier and Fahrig 2011). Research in Paraguay also demonstrated that landscape fragmentation was positively associated with bat species richness (Gorresen et al. 2008). Ethier and Fahrig (2011) suggested their observations were due to an increase in “landscape complementation” which is the extent to which a landscape facilitates movement between habitat patches that fulfil various roles (e.g., foraging habitat and roosting habitat) (Dunning et al. 1992, Ethier and Fahrig 2011). In other words, if a bat species’ prefers to roost among dense forest stands but forages among clearings and road cuts, a more fragmented environment would be preferred as this places forest sites within closer proximity to open areas and reduces the energy expenditure of commuting. My results suggest that not all fragmentation is equal as the number of disjunct forest patches with the grids failed to predict occupancy. Instead, the aggregation of forest patches on the landscape, clumpiness, was positively associated with grid occupancy.

Another potential explanation for these results could be a reduction of the risk associated with site-fidelity. Female northern long-eared bats exhibit inter-annular site fidelity to their summer maternity grounds (Patriquin et al. 2010). If an individual bat exits a hibernacula in spring and travels potentially over 80 km to its historic summer grounds (Griffin 1940), it is placing a large bet in the form of energy expenditure that these roosting ground will be still be suitable and not impacted by disturbance. A landscape with an aggregation of disjunct habitat patches would thus offer an individual bat with neighboring options and reduce the costs of locating a new forest patch. While clumpiness was predictive of grid occupancy, my measurement of connectivity produced β-estimates with 95% confidence limits overlapping zero. It is possible that either my estimated search distance of 450 m when estimating connectivity was too restrictive or, if this risk-reduction hypothesis is correct, the distance they are capable of relocating to a new maternity site is further than they regularly travel when roost switching under favorable conditions.

Utilizing a multi-scale occupancy approach enabled inference at two distinct spatial scales. Evidence supported a conclusion that the northern long-eared bat is rare within it is regulatory range within the Nebraska but is highly available for sampling within forest patches in parts of the state where it occurs. This high availability combined with a favorable detection probability indicates that future acoustic surveys are well suited for determining species presence at a given site. This assumes, however, that researchers select survey sites within forest interiors and only at suitable recording locations. Additionally, researchers can transfer the site selection framework and hierarchy defined in this study to future northern long-eared bat surveys or modified to target other bat species.

My observation that forest area is predictive of site occupancy but not larger-scale grid occupancy provides an example of habitat associations occurring at one scale not scaling up to larger spatial scales. Multi-scale occupancy provides methodology for examining a species habitat relationship at these distinct scales while also reducing bias inherent in surveying for rare species. As white-nose syndrome continues to reduce bat populations (Frick et al. 2010), these hard to detect species may become even more difficult to document due to a reduced abundance (Royle and Nichols 2003). I conducted this study prior to the detection of white-nose syndrome in Nebraska, and thus provide a baseline of occupancy estimates that researchers can compare to future occupancy studies to track species impacts. Additionally, a multi-scale occupancy approach would reveal population declines in local availability even if large-scale grid occupancy across the state remains constant.

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Tables and Figures

Table 3.1. Detection probability (p) covariates used to assess the factors associated with detection probability of Northern long-eared bats in Nebraska.

Abbreviation	**Covariate**	**Description**	**Source**
RecLnHr	Recording Length (Hrs)	Length in decimal hours from when a night's recording started to when it stopped; either because of battery failure or a scheduled stop-recording time.	Anabat Express log files
RHPer	Relative Humidity (%)	Mean relative humidity during a night's recording window.	NOAA Rapid Refresh Data (Benjamin et al. 2016)
TempC	Temperature (°C)	Mean temperature during a night's recording window.	NOAA Rapid Refresh Data (Benjamin et al. 2016)
YDay	Day of study season	Day of the study season	Author generated
WindMS	Wind Speed (m/s)	Mean wind speed during a night's recording window.	NOAA Rapid Refresh Data (Benjamin et al. 2016)
RainMm	Total rain (mm)	Total amount of recorded rainfall during a night's recording window.	NOAA Rapid Refresh Data (Benjamin et al. 2016)
RecSpce	Recording Space	An index of available recording space. I binned distance estimates and then calculated cubic area using assigned scores. This can be thought of as the inverse of clutter.	Author generated

Table 3.2. Covariates used to assess the factors associated with site occupancy (θ) of Northern long-eared bats in Nebraska. I included these covariates in a multi-scale occupancy analysis to describe effects in site occupancy of four detectors nested within larger spatially replicated 10km x 10km grids.

Abbreviation	**Covariate**	**Description**	**Source**
DstRoadM	Distance to nearest major road (m)	Geodesic distance from detector to a major road with an MTFCC code of S1100, S1200, S1400, or S1630 and an RTTYP code of C, I, O, S, or U	U.S. Census Bureau. TIGER/Line Shapefile, Nebraska, 2010 Census Block State-Based.
DstWatrM	Distance to nearest water source (m)	Geodesic distance from detector to nearest water at a 30m resolution as defined by the national Land Fire dataset.	Landfire 2014 – vegetation layer subset with life form equal to “water”
Frst125Ha	Forest within a 125m radius (HA)	Area of forest within a 125 m radius of the detector.	Landfire 2014 – vegetation layer subset with life form equal to “tree”
Frst250Ha	Forest within a 250m radius (HA)	Area of forest within a 250 m radius of the detector.	Landfire 2014 – vegetation layer subset with life form equal to “tree”
Frst500Ha	Forest within a 500m radius (HA)	Area of forest within a 500 m radius of the detector.	Landfire 2014 – vegetation layer subset with life form equal to “tree”
Frst1KHa	Forest within a 1km radius (HA)	Area of forest within a 1 km radius of the detector.	Landfire 2014 – vegetation layer subset with life form equal to “tree”

Table 3.3. Covariates used to assess the factors associated with grid occupancy (ψ) of northern long-eared bats in Nebraska. I included these covariates in a multi-scale occupancy analysis to describe effects in grid occupancy of spatially replicated 10km x 10km grids across Nebraska.

Abbreviation	**Covariate**	**Description**	**Source**
FrstCorHa	Total Core Area of Forest (HA)	Total core area of forest with a depth of edge influence set at 40m for all other neighboring habitat.	Landfire 2014 – vegetation layer subset with life form equal to “tree”
FrstConct	Connectedness index of forest patches	The number of functional connections between forest patches divided by the number of possible connections. I chose a threshold distance of 450m as this was the upper 95%C.I. of reported distances between consecutive MYSE roosts.	Landfire 2014 – vegetation layer subset with life form equal to “tree”
FrstClump	Clumpiness Index of forest patches	An index of the randomness of forest patches. The clumpiness index is equal to -1 when patches are maximally disaggregated, 0 when patches are arranged at random, and 1 when maximally clumped.	Landfire 2014 – vegetation layer subset with life form equal to “tree”
FrstNDCA	Number of disjunct core areas of forest	The sum of all disjunct core forest patches with a depth of edge influence set to 40m.	Landfire 2014 – vegetation layer subset with life form equal to “tree”
WtrAreaHa	Total area of water (HA)	The total area of water within the grid	Landfire 2014 – vegetation layer subset with life form equal to “water”
DevAreaHa	Total area of developed land (HA)	The total area of developed land within the grid	Landfire 2014 – vegetation layer subset with life form equal to “Developed”
CliffHA	Total area of cliffs (HA)	The total area of land within an 89 km buffer with both a terrain position index of 4 or greater and soil depth less than 5m. This provides an index of potential cliff habitat.	1. National Elevation Dataset digital elevation models (1 arc-second; USGS); and Global 1km gridded thickness of soil, regolith, and sedimentary deposit layer (ORNL DAAC, Oak Ridge, Tennessee, USA.)
Long	Longitude (°)	Longitude (°)	Author recorded
Lat	Latitude (°)	Latitude (°)	Author recorded

Table 3.4. Model selection for effects of latitude (Lat.) and longitude (long.) on grid occupancy (ψ). The model-selection metrics include the number of parameters (K), Akaike's Information Criterion adjusted for sample size (AICc), the difference between a model's AICc and the top ranked model's AICc (ΔAICc), AICc weight (w_i), and -2 log likelihood (-2log(L)).

Model	K	**AICc**	**ΔAICc**	w_i	**-2log(L)**
ψ(global + Lat. + Long.) θ(global) p(global)	23	640.17	0.00	0.76	575.13
ψ(global + Lat. * Long.) θ(global) p(global)	24	643.66	3.49	0.13	574.61
ψ(global) θ(global) p(global)	21	644.06	3.90	0.11	586.66

Table 3.5. Model set for assessing the relationship of forest area at various distances on site occupancy (θ) of the northern long-eared bat. The model-selection metrics include the number of parameters (*K*), the beta coefficient for the buffer distance (β), and its respective standard error (SE). The objective of this model comparison was to assess the scale at which forest area most strongly correlated with site occupancy. Therefore, I selected the covariate corresponding to area of forest within 125 m (Frst_125) for inclusion in further multi-scale occupancy modeling as this covariate contained the largest β-estimate.

Model	***K***	**β**	**SE**
ψ(global) θ(global + Frst_125) *p*(global)	24	0.52	0.36
ψ(global) θ(global + Frst_250) *p*(global)	24	0.46	0.38
ψ(global) θ(global + Frst_500) *p*(global)	24	0.35	0.36
ψ(global) θ(global + Frst_1000) *p*(global)	24	0.30	0.37

Table 3.6. Confidence set of all models within 2 AICc of the top ranked model. Models accessed the effects of covariates on grid occupancy (ψ), site occupancy (θ), and detection probability (p) . I grouped covariates into discrete thematic parings (forest aggregation, climate, water availability, etc.). An “X” below a covariate group indicates that the paring was included in that particular model. Number of estimated parameters (*K*), Akaike’s Incormation Criterion for small samples (AICc), difference between the corresponding models AICc and the top performing model’s AICc (ΔAICc), Akaike weight (weight), and -2 log-likelihood function (-2LnL) are included.

	Psi(ψ)					Theta(θ)			*p*									
Mod. Rank	Frst. Aggregation	Frst. Avail.	Other Features	Climate	Hibernacula	Water	Road	Frst. 125 m	Atmospheric	Masking	Rec. Space	Rec. Length	Day of Season	*K*	AICc	ΔAICc	Weight	-2LnL
1	X							X	X		X		X	12	615.52	0.0000	0.0500	587.00
2				X	X			X	X		X		X	13	615.53	0.0044	0.0499	584.17
3	X			X	X			X	X		X		X	15	615.89	0.3657	0.0417	578.62
4	X			X				X	X		X		X	14	616.54	1.0153	0.0301	582.27
5				X	X		X		X		X		X	13	616.63	1.1032	0.0288	585.27
6	X						X		X		X		X	12	616.64	1.1212	0.0286	588.12
7	X			X	X		X		X		X		X	15	616.86	1.3389	0.0256	579.59
8	X						X	X	X		X		X	13	616.90	1.3768	0.0251	585.55
9	X								X		X		X	11	616.93	1.4070	0.0248	591.16
10				X	X				X		X		X	12	616.93	1.4102	0.0247	588.41
11	X			X	X				X		X		X	14	616.96	1.4395	0.0244	582.69
12				X	X		X	X	X		X		X	14	617.02	1.4975	0.0237	582.75
13	X			X	X		X	X	X		X		X	16	617.46	1.9417	0.0190	577.09
14	X			X			X		X		X		X	14	617.49	1.9638	0.0187	583.22

Table 3.7. Covariate estimates pertaining to grid occupancy (ψ) included in the confidence set for a multi-scale occupancy analysis of northern long-eared bat occurrence in Nebraska. Table includes covariate terms occurring in the confidence set and their corresponding β-estimate and standard error in parenthesis. "N.S." represents estimates with 95% confidence intervals overlapping zero.

Rank	Cliff (Ha)	Frst. Clump	Frst. Connect	Summer Precip. (mm)	Summer Temp (°C)	Latitude	Longitude
1		2.47 (0.83)	N.S.			N.S.	1.88 (0.62)
2	2.82 (1.06)			N.S.	5.86 (2.21)	2.67 (1.05)	N.S.
3	N.S.	N.S.	N.S.	N.S.	4.89 (2.27)	2.70 (1.10)	N.S.
4		2.65 (1.01)	N.S.	N.S.	N.S.	2.26 (1.05)	N.S.
5	2.87 (1.04)			N.S.	5.89 (2.19)	2.68 (1.04)	N.S.
6		2.52 (0.84)	N.S.			N.S.	1.90 (0.62)
7	N.S.	N.S.	N.S.	N.S.	4.89 (2.26)	2.72 (1.10)	N.S.
8		2.52 (0.84)	N.S.			N.S.	1.90 (0.62)
9		2.49 (0.83)	N.S.			N.S.	1.88 (0.62)
10	2.83 (1.02)			N.S.	5.84 (2.17)	2.66 (1.03)	N.S.
11	N.S.	N.S.	N.S.	N.S.	4.85 (2.24)	2.68 (1.09)	N.S.
12	2.86 (1.06)			N.S.	5.91 (2.22)	2.68 (1.05)	N.S.
13	N.S.	N.S.	N.S.	N.S.	4.91 (2.29)	2.73 (1.11)	N.S.
14		2.73 (1.03)	N.S.	N.S.	N.S.	2.32 (1.07)	N.S.

Table 3.8. Covariate estimates pertaining to site occupancy (θ) included in the confidence set for a multi-scale occupancy analysis of northern long-eared bat occurrence in Nebraska. Table includes covariate terms occurring in the confidence set and their corresponding β-estimate and standard error in parenthesis. "N.S." represents estimates with 90% confidence intervals overlapping zero.

Rank	**Dist. Road (m)**	**Dist. Water (m)**	**Forest 125 m (Ha)**
1			N.S.
2			N.S.
3			N.S.
4			0.69 (0.35)
5	N.S.		
6	N.S.		
7	N.S.		
8	N.S.		N.S.
9			
10			
11			
12	N.S.		N.S.
13	N.S.		N.S.
14	N.S.		

Table 3.9. Covariate estimates pertaining to detection probability (p) included in the confidence set for a multi-scale occupancy analysis of northern long-eared bat occurrence in Nebraska. Table includes covariate terms occurring in the confidence set and their corresponding β-estimate and standard error in parenthesis. "N.S." represents estimates with 90% confidence intervals overlapping zero.

Rank	**Rec. Space**	**RH (%)**	**Temp. (°C)**	**Day of Season**
1	-1.16 (0.24)	N.S.	-0.35 (0.12)	0.47 (0.21)
2	-1.16 (0.24)	N.S.	-0.35 (0.12)	0.47 (0.20)
3	-1.16 (0.24)	N.S.	-0.35 (0.12)	0.47 (0.21)
4	-1.15 (0.24)	N.S.	-0.35 (0.12)	0.48 (0.21)
5	-1.09 (0.25)	N.S.	-0.35 (0.12)	0.45 (0.20)
6	-1.09 (0.25)	N.S.	-0.35 (0.12)	0.46 (0.20)
7	-1.09 (0.25)	N.S.	-0.35 (0.12)	0.45 (0.20)
8	-1.12 (0.24)	N.S.	-0.35 (0.12)	0.46 (0.21)
9	-1.15 (0.24)	N.S.	-0.35 (0.12)	0.47 (0.20)
10	-1.16 (0.24)	N.S.	-0.35 (0.12)	0.47 (0.20)
11	-1.15 (0.24)	N.S.	-0.35 (0.12)	0.47 (0.20)
12	-1.12 (0.25)	N.S.	-0.35 (0.12)	0.46 (0.20)
13	-1.12 (0.25)	N.S.	-0.35 (0.12)	0.46 (0.21)
14	-1.08 (0.25)	N.S.	-0.35 (0.12)	0.46 (0.21)

Table 3.10. Occurrence of covariates in the confidence set where 95% confidence intervals of the β-estimates did not overlap zero when assessing multi-scale occupancy of the northern long-eared bat in Nebraska. Confidence set was defined as all models within 2 AICc of the top ranked model. Model selection explored covariate effects on grid occupancy (ψ), site occupancy (θ), and detection probability (*p*). Summary metrics include the parameter associated with covariate, the covariate, the number of models within the confidence set that the covariate occurred (n Models), the percentage of models within the set containing the covariate (% of Models), and the percentage of models containing the covariate in which the 95% confidence interval of the β-estimates did not overlap with zero (% Significant).

Parameter	**Covariate**	**n Models**	**% of Models**	**% Significant**
ψ	Latitude[a]	14	1.00	0.71
ψ	Longitude[a]	14	1.00	0.29
ψ	Frst. Clumpiness	10	0.71	0.60
ψ	Summer Temp (°C)	10	0.71	0.80
ψ	Cliff (Ha)	8	0.57	0.50
θ	Frst. 125 m (Ha)	7	0.50	0.14
p	Recording Space	14	1.00	1.00
p	Nightly Temp (°C)	14	0.94	1.00
p	Day of Season	14	0.67	0.76

[a] Latitude and longitude was present in all fitted models to account for spatial autocorrelation.

Table 3.11. Parameter estimates and standard error for northern long-eared bat multi-scale occupancy within the Nebraska distribution of the species. Psi ($\widehat{\Psi}$) is the estimate of large-scale grid occupancy. Theta ($\hat{\theta}$) is the estimate of small-scale site occupancy contingent upon occupancy at the grid level. Detection ($\hat{p}$) is the estimate of detection probability for a given recording night starting at 30 minutes before sundown and continuing until 30 minutes after sunup. I estimated parameters by model averaging the real predictions of all models within 10% of the top model weight as defined by AICc. I averaged standard error following a delta method approach.

Parameter	**Estimate**	**SE**
Grid Occupancy ($\widehat{\Psi}$)	0.06	0.05
Site Occupancy ($\hat{\theta}$)	0.70	0.09
Detection ($\hat{p}$)	0.52	0.04

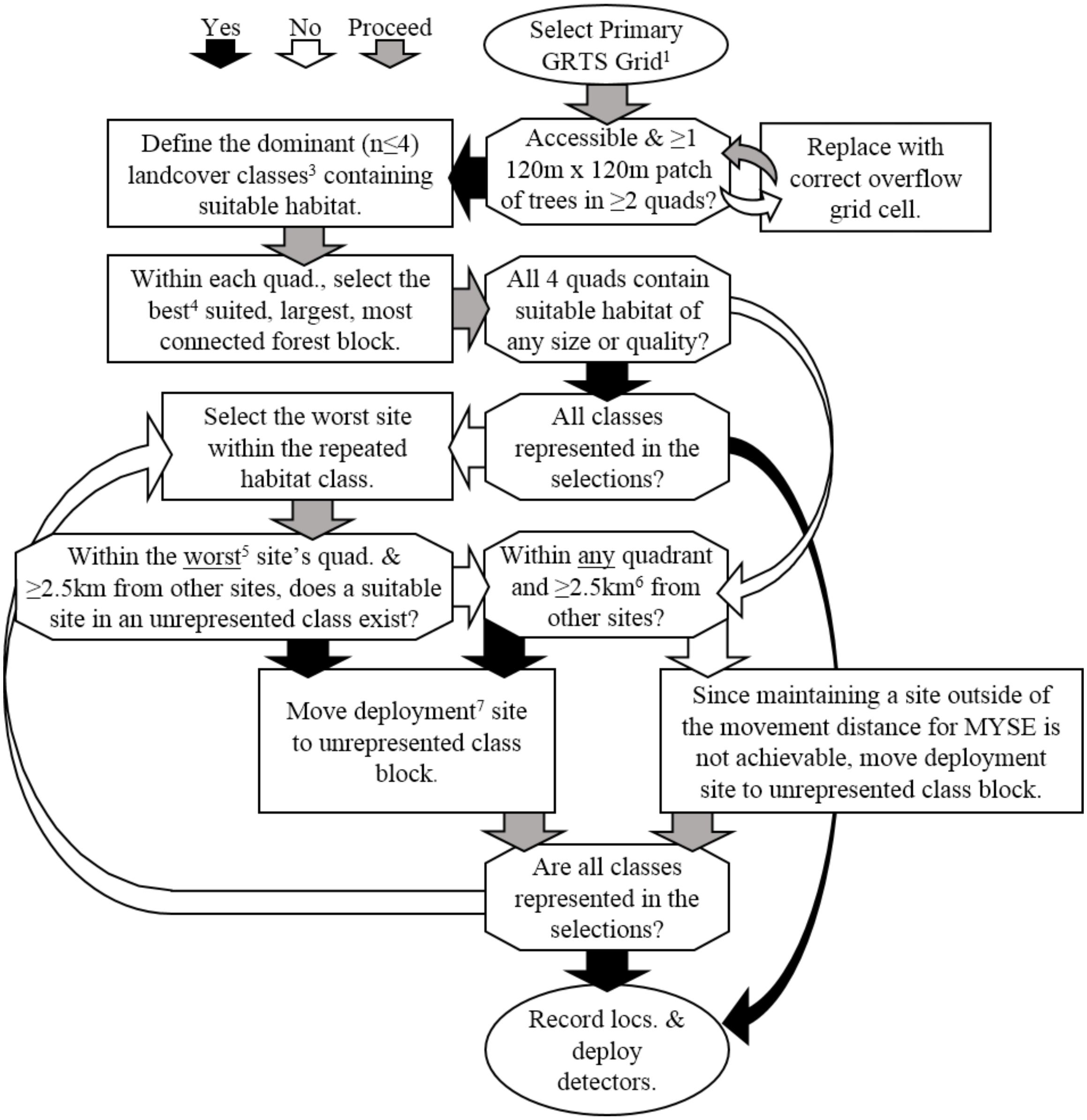

Figure 3.1. Predefined selection framework for selecting habitat blocks within 10 km grids to deploy acoustic detectors used to survey for northern long-eared bats in Nebraska. Grids were initially selected following a generalized random tessellation stratified (GRTS) survey design for a finite resources approach (Stevens and Olsen 2004). Once I selected a habitat blocks following the framework, I deployed four bat detectors within each grid.

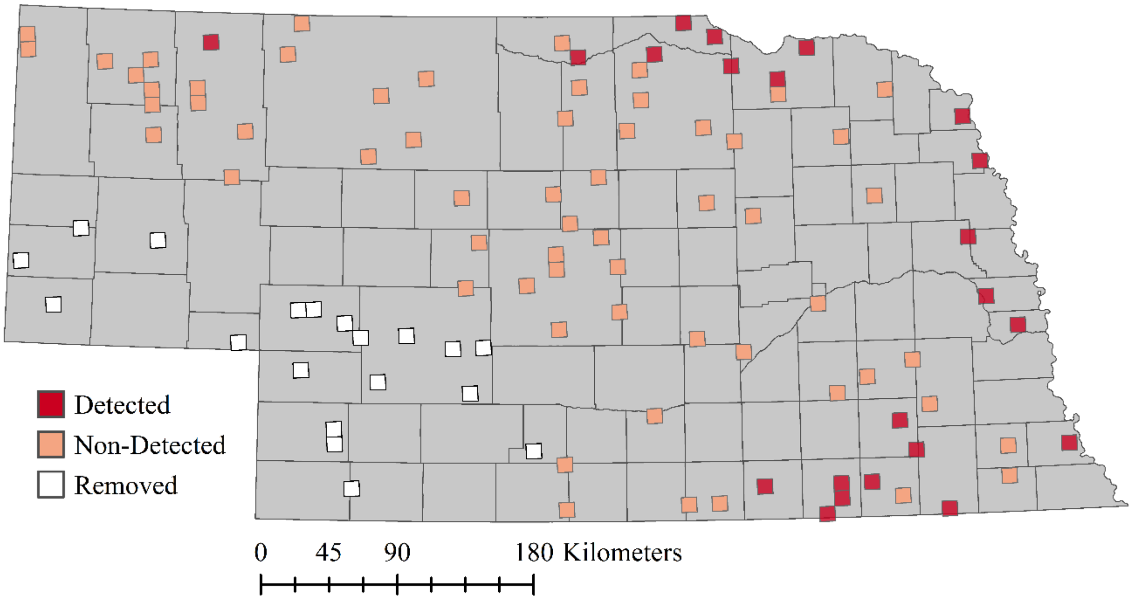

Figure 3.2. Sampling grids (n = 101) surveyed in 2015 for the northern long-eared bat to predict distribution within Nebraska. Prior to modeling, I removed 19 grids outside of the USFWS defined range to restrict inference to within the range and to reduce the effects of zero-inflation. Of the remaining 82 surveyed grids, I detected northern long-eared bats at 22 grids.

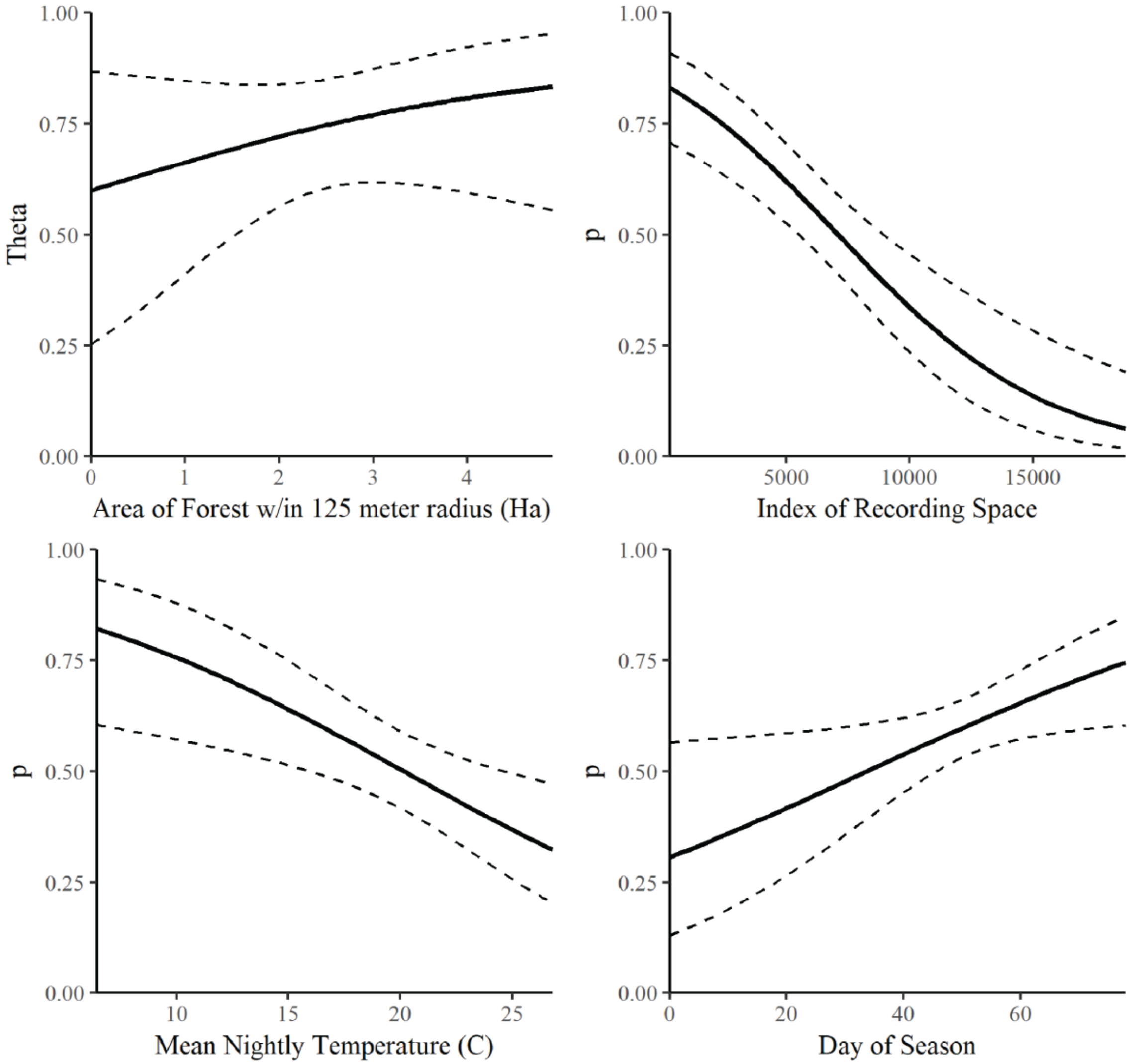

Figure 3.3. Predicted relationships of covariates associated with northern long-eared bat site occupancy and detection probability in Nebraska. Predictions are the results of unconditionally averaging the real estimates of all models within 2 AICc of the top ranked model. Dashed lines denote 95% confidence intervals around the parameter prediction.

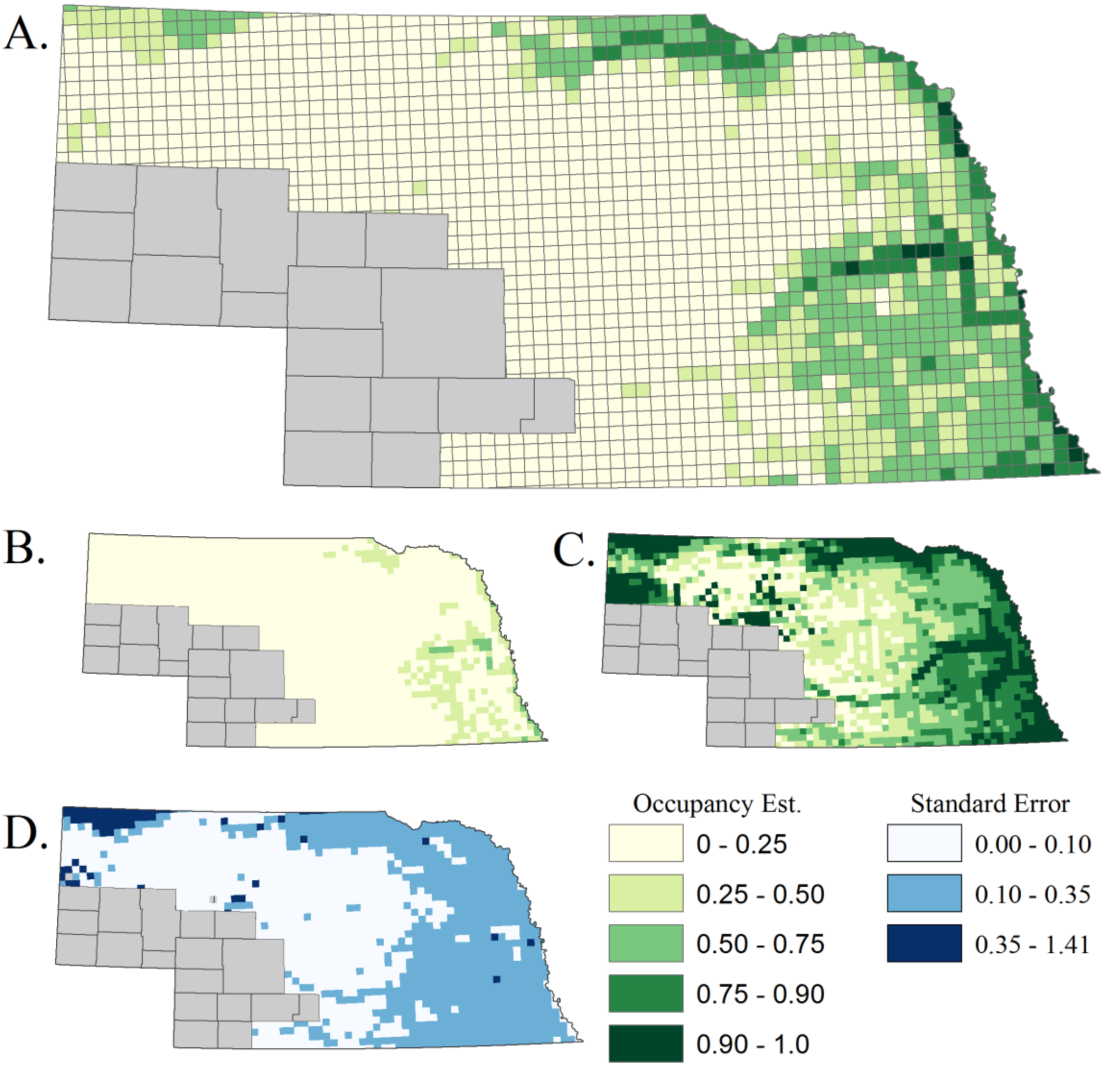

Figure 3.4. Predicted grid occupancy (ψ) of the northern long-eared bat within Nebraska (A). Predictions are the results of *unconditionally* averaging the real estimates for ψ of all models within 2 ΔAICc of the top ranked model with all covariates for θ, and *p* held constant at their z-scored means. Psi covariates used in the prediction were latitude, longitude, cliff area with 89 km, forest clumpiness, forest connectivity, mean summer precipitation, and mean summer temperature. To visualize the range of the parameter estimates, the lower 95% confidence interval (B), upper 95% confidence interval (C), and standard error (D) are also included. Counties excluded from prediction and outside of the recognized distribution of the species are represented in grey.

CHAPTER 4. UTILIZING A MULTI-SCALE OCCUPANCY APPROACH TO UNDERSTAND THE FACTORS THAT AFFECT OCCUPANCY AND DETECTION OF THE NORTHERN LONG-EARED BAT

Introduction

Forests serve a variety of roles in the life history of bats (Miller et al. 2003). They provide roosting sites to rear offspring (Carter and Feldhamer 2005), foraging areas (Bender et al. 2015), travel corridors (Hein et al. 2009), and wintering habitat (Boyles and Robbins 2006). While forests are important for most bat species, ideal habitat conditions for one species is often less than ideal for another (Patriquin and Barclay 2003). For example, two federally protected conspecifics may select for competing habitat types within the same forest stand, or afforestation may benefit bats while causing declines in grassland birds (Brennan and Kuvlesky 2005, Carter and Feldhamer 2005, Pauli et al. 2017). In order for managers to balance the requirements of multiple species, an understanding of habitat associations must first be developed (Miller et al. 2003).

To better understand the driving factors of bat occurrence, radiotelemetry studies have been the primary method for understanding bat habitat since the 1980s (Lacki and Schwierjohann 2001, Carter and Feldhamer 2005, Broders et al. 2006, Silvis et al. 2012). Major limitations of radiotelemetry studies however include low sample size, pseudoreplication, and limited inferential ability (Morris et al. 2011). Due to the intensive effort and resources required to conduct large-scale telemetry studies, we still know relatively little about difficult to study forest dwelling species, and much of what is known is based upon studies with very small sample sizes often occurring at single locations (Miller et al. 2003).

With the advent of acoustic bat detectors, researcher can conduct large-scale surveys with relatively little labor (Rodhouse et al. 2011, Frick 2013, Russo and Voigt 2016). Although acoustic surveys provide added sampling data, they are not the “silver-bullet” for bat researchers, and significant limitations stand in the way of determining habitat usage from acoustic surveys (Miller et al. 2003). For example, results from acoustic surveys reveal that bat activity varies substantially both temporally and spatially (Hayes 1997) and many factors contribute to the detection probability of a target species (Weller and Zabel 2002, Duchamp et al. 2006, Kaiser and O’Keefe 2015). For example, the amount of structural clutter in an environment can interfere with recording echolocations or cause bats to shift their pulse frequencies into unclassifiable patterns (Weller and Zabel 2002, Broders et al. 2004). The echolocation characteristics of a species can also affect the distance at which an individual detectable due to high frequency sounds attenuating faster than lower frequency sounds (Lawrence and Simmons 1982). Atmospheric conditions at a recording site can also effect detection due to changes in air density or bat activity levels (Griffin 1971).

One way to reduce the bias inherent in acoustic sampling is with occupancy modeling (MacKenzie 2006, Kaiser and O’Keefe 2015). By conducting repeated site visits (i.e. recording one site for multiple nights), the effect of false-absences can be reduced along with detection biases for rare species (Tyre et al. 2003, MacKenzie 2006). Additionally, in some cases, occupancy may provide more reliable estimates of populations compared with abundance estimates for rare or cryptic species and often requires reduced sampling especially at large scales (MacKenzie 2006). Occupancy analysis also provides insight into site usage, habitat associations, and population trends over time (Yates and Muzika 2006, Gorresen et al. 2008, Kaiser and O’Keefe 2015).

Traditional single-season occupancy analysis, however, often only allows inference at a single spatial scale determined by the selection of the individual sampling locations. Multi-scale occupancy analysis, however, is an approach that incorporates a hierarchical sampling design where spatially replicated survey stations are nested within larger sampling units (Nichols et al. 2008, Pavlacky et al. 2012, Hagen et al. 2016). These survey stations then receive multiple visits to estimate detection probability. This modeling approach estimates occupancy at two distinct scales by simultaneously utilizing presence/absence observations and accounts for the non-independence of detections between the scales while also addressing the closure assumption for spatially replicated survey stations (Pavlacky et al. 2012). This approach estimates three parameters; large-scale occupancy (ψ; hereto referred to as grid occupancy), small-scale occupancy (θ; site occupancy for the purpose of this manuscript), and detection probability of the survey station (p). Multi-scale occupancy thus allows for the prediction of multi-scale covariate relationships at two spatial extents for which a species may be responding differently (Mutter et al. 2015, Hagen et al. 2016). For bat species, this modeling multi-scale modeling approach is likely well suited. For example, a species such as the northern long-eared bat, a forest associated species, may be associated with closed forest stands but within those stands it is more available for sampling at openings in the forest that provide suitable foraging habitat (Carter and Feldhamer 2005, Ethier and Fahrig 2011).

The goal of my study was to conduct a multi-scale occupancy study on the northern long-eared bat to evaluate the habitat factors that could contribute to occupancy at two spatial scales. Additionally, due to the inherent biases of acoustic sampling, I also assessed factors that potentially affect detection probability. Accounting for these factors reduces biases in occupancy estimates and provides researchers and managers insight into future study designs.

Methods

SITE SELECTION

I selected five random spatially balanced points along with 10 oversampled points for each selection following a generalized random tessellation stratified (GRTS) survey design for a finite resources approach (Stevens and Olsen 2004). This resulted in 4 initial sites and 40 reserve sites. The oversampling allowed for replacement of sites if obtaining landowner permission was an impediment or if access was not possible due to lack of roads.

STUDY SITES

I conducted my study at 5 separate study sites located in eastern Nebraska during the summer of 2016 (Figure 4.1). The majority of sampling locations occurred on rural privately owned land that supported crop production and cattle grazing. The first study site was located approximate 14 miles north of Rushville, NE (42.92°N, -102.49°E) and sampling occurred between June 4 and June 11. This site was dominated by ponderosa pine (*Pinus ponderosa*), and to a lesser extent ash (*Fraxinus* sp.), juniper (*Juniperus* sp.), and hackberry (*Celtis occidentalis*). The second study site was located 6 miles southeast of Naper, NE (42.90 N, -99.00 E) along the Keya Pahe River and sampling occurred between June 18 and June 25. The most common species were oak (*Quercus* sp.), juniper, ash, and elm (*Ulmus* sp.). The third study site was located approximately 2.5 miles east of Union, Nebraska (40.81 N, -95.85 E) and sampling occurred between July 1 and July 11. This site was predominantly deciduous hardwoods with oak, hackberry, elm, and honey locust (*Gleditsia tricanthos*). The fourth study site was located 3 miles northeast of Fairbury, NE (40.19 N, -97.22 E) and sampling occurred between July 18 and July 24. The dominate species were juniper, elm, hackberry, and oak. The fifth study site was located immediately west of Ft. Calhoun, Nebraska (41.45 N, -96.06 E) and sampling occurred between July 31 and August 6. The dominant tree species at this location were elm, hackberry, black locust (*Robinia pseudoacacia*), and ash.

LARGE-SCALE SAMPLING LOCATIONS

Within a 4.3 km radius around each study site, I created a 150 m buffer surrounding all forest locations as defined by the LANDFIRE v.14 landcover dataset (LANDFIRE 2014) in ArcGIS (ESRI 2011). Following the GRTS sampling approach, I generated 216 primary points and 648 oversample points (three overflow points for each primary point) within the 150 m forest buffer. I conducted initial point sampling over such a large area to allow the sampling locations to vary based upon landowner permissions once surveyors were in the field as computer access was limited. The GRTS method assigns a selection number to each location. Once I received sufficient access to at least 23 sampling locations, I selected the lowest numbered 23 locations and began deployment. If two preselected sampling locations occurred less than 250 m apart, I deployed at the lowest numbered location and then selected a replacement point beginning with the lowest numbered overflow sampling point. This was to ensure an even spatial distribution between sampling locations as per the GRTS framework. If a sampling location lacked any forested habitat, I rejected the location and replaced it with an overflow site. Deployment of acoustic detectors occurred within 100m of this selected point.

SMALL-SCALE DETECTOR LOCATION

Within 100 m of each of the 23 sampling locations, I ranked suitable recording locations based upon clutter in the recording environment, available flyways, and proximity to water. I selected the best-ranked recording site as the first detector deployment location. If the second best location was less than 50 meters from this point, I chose the next best-ranked location and so forth until I selected two sampling locations within the 100 m buffer.

DETECTOR DEPLOYMENT

At each secondary sampling location, I recorded bat echolocations using AnaBat Express units (www.titleyscientific.com). I mounted each unit on a telescopic pole between 2.4 m and 7 m above the ground. I adjusted the height of the detector to place it between the understory and the canopy operating under the assumption that northern long-eared bats forage primarily in this open zone (Nagorsen et al. 1993). I oriented the microphone in the direction with the least amount of clutter to reduce interference, maximize recording space, and prevent false-detections of conspecifics (Weller and Zabel 2002, Broders et al. 2004). In cases where there was no understory, I elevated the detector a minimum height of 2.4 m as this was the collapsed height of the pole. I deployed all 46 detectors over the course of 2 - 4 days. Once I deployed all detectors, they remained recording for at least five rain-free days before retrieval began which took 2 - 3 additional days. Detectors recorded 30 minutes before sundown and continue until 30 minutes after sunrise.

ECHOLOCATION ANALYSIS

I analyzed all recordings using Kaleidoscope v4.1.0 with the Bats of North America 4.1.0 classifier set to "-1 More Sensitive" (Wildlife Acoustics, Concord, MA, USA; www.wildlifeacoustics.com). I set the signal of interest parameters as follows: 16-120 kHz, 2-20ms, maximum inter-syllable gap = 500ms, minimum number of pulses = 5, and advanced signal processing to ON. Prior to analysis, I divided the state into 17 regions of unique potential species assemblages using historical capture records and expert knowledge allowing buffers for potential distribution error due to a lack of survey effort. These species assemblages determined which auto-classifiers I activated in Kaleidoscope with northern long-eared bat activated in all regions. I performed this division to increase accuracy of identification and to simplify the confusion matrix within Kaleidoscope.

Once I auto-classified calls using Kaleidoscope, I applied additional conservative criteria to reduce false positives when determining detection or non-detection for a given night. For clarity, in my study I defined a pulse as an individual emission of echolocation and a call-sequence as a series of pulses within a single digital recording. I categorized each auto-classified call sequence as either high, medium, or low quality based upon the Kaleidoscope reported metrics. Specifically I used the number of pulses within the call sequence, the match ratio (a ratio of pulses matching the auto-assigned species vs the total number of pulses), and the maximum likelihood estimator (MLE; a test of the null hypothesis of a species not being detected within a given night). If a call-sequence contained at least 10 pulses and a match ratio of 0.9 or greater, I categorized it as a high quality call-sequence and awarded it a score of 0.5. A call-sequence with at least 5 pulses and a match ratio greater than 0.75 received a score of 0.33, a call-sequence with at least 5 pulses and a match ratio greater than 0.5 received a score of 0.25, and lastly a call-sequence with a match ratio below 0.5 received a score of 0 regardless of the number of pulses. I totaled the scores assigned to the northern long-eared bats for each night at a given deployment location. If a single nights total score was at least 1.0 and the night's MLE was less than or equal to 0.05, I scored that night as detected. If it did not meet the above criteria, it was determined to be non-detected for a given night.

HABITAT SAMPLING

At each sampling point, I delineated a circular plot (25m radius, 0.2 hectares) centered at the microphone location. Within this plot, I counted the number of snags with ≥10cm diameter at a height of 130 cm (D_{130}) (Brokaw and Thompson 2000). The microphone location also served as the sampling point for plotless point-quarter vegetation sampling (Cottam and Curtis 1956, Brower et al. 1998). I based sampling quadrants upon the pre-set direction of the microphone and a truncated the sampling distance to a maximum of 25m as described in Mitchell (2015). I recorded distances to the nearest tree with a D_{130} of 10cm or greater and then documented D_{130} and tree species. At the microphone location, and 25 m out following the quadrat directions, canopy and mid-story closure was estimated as either open (0%), low (1-25%), medium (26-50%), high (51-75%), or very high (76-100%).

SMALL-SCALE OCCUPANCY (Θ) COVARIATES

I included habitat covariates at the detector level that potentially account for variation in small-scale occupancy. These are specific for each detector deployment nested within the 100 m sampling buffers. Using the measurements collected from the point-quarter sampling, I calculated mean basal area (cm^2), tree density (stems/ha) adjusted for truncated sampling distances (Warde and Petranka 1981), and relative abundance of juniper (%). The relative abundance of juniper was included as this is species has received increased management attention due to juniper invasion in the Great Plains (Briggs et al. 2002). I estimated midstory closure and canopy closure separately by assigning scores of 0 (open), 25 (1-25%), 50 (26 – 50%), 75 (51 – 75%), or 100 (75-100%) based upon the closure estimates at the 5 points within the plot and then averaging the five scores to estimate a single value. I calculated the distance to the nearest available water source by digitizing all available water sources within 2 km of the sampling locations using aerial imagery and on-the-ground site observations. These water sources included natural sources as well as anthroprogenic sources such as stock tanks (Jackrel and Matlack 2010) and swimming pools (Bowles et al. 1990). I also calculated the distance from the detector to the nearest non-forest 30 m pixel using the LANDFIRE 14 dataset with landcover classes degraded to “forest” or ”non-forest” using lifeform equal to “tree” in the dataset (LANDFIRE 2014).

LARGE-SCALE OCCUPANCY (Ψ) COVARIATES

I included 9 covariates that pertained to large-scale occupancy (ψ) using digitally available landscape variables and on-the-ground habitat measurements. To assess if occupancy varied with site location, I included study site as a factor covariate in the model set for large-scale occupancy. Using the measurements collected from the point-quarter sampling, I calculated mean basal area (cm^2), tree density (stems/ha) adjusted for truncated sampling distances (Warde and Petranka 1981), and relative abundance of juniper (%). I combined measurements from the two sampling locations within 100 m buffer for these estimates to describe the overall primary sampling location. I also combined the averages of the canopy scores to obtain to single mean canopy closure for the forest within the primary sampling site. The density of snags (stems/ha) was calculated by summing the number of snags observed within the two sampling plots and dividing by the area of the two plots combined (0.4 ha). I calculated the mean geodesic distance to the nearest bridge/box culvert from the two detectors locations (Munson 2017). I included snag density and bridge distance to assess if potential roost availability influenced large-scale occupancy (Carter and Feldhamer 2005, Geluso et al. 2018). I also calculated the mean distance to available water using the measurements derived from the individual detector locations. Finally, I calculated the area of forest within a 125 m buffer centered on the geographic centroid between the two detector locations. I chose this distance as it contained the strongest association with occupancy in previous analyses when compared other distances (see Chapter 2).

DETECTION PROBABILITY COVARIATES

To understand factors that contribute to detection probability, I recorded site characteristics at each microphone deployment. To quantify the amount space in the recording environment (an inverse of the amount of clutter), I visually estimated distances to dense clutter as either <2.5m, 2.6-5m, 5.1-10m, or >10m from the front, back, left, right, above, and below relative to the microphone. Cluttered was defined as any structure that could interfere with the flight path of a bat or cause echoes or interruption of an emitted echolocation pulse. Examples included trees, structures, and bluff faces. I measured the height of the microphone above the average understory vegetation within 10 m of the microphone to nearest 0.1 m. I extracted the minimum nightly temperature from Express unit log files that records internal ambient temperature in 5-minute intervals. Additionally, I subtracted the minimum temperature at a sampling location from the mean minimum temperature of all detectors at the study site on the same night. This was to test if detection probability was associated with microclimate differences between sites independent of nightly temperature effects. I also calculated mean nightly relative humidity (%) from Rapid Refresh (RAP) data during each nightly recording period. RAP data is an hourly updated weather model for North American at the 13-km resolution (Benjamin et al. 2016). To access the effects of insect or other environmental noise on detection probability, I quantified the number of files autoclassified as non-bat "noise" recordings for each recording night at each detector. Rather than including recording length to account for nights in which detectors ceased recording due to battery failure, I removed all partial nights from the analysis.

MODELING APPROACH

I applied a multi-scale occupancy modeling approach as first described by Nichols (2008) for use with multiple sampling devices. Rather than multiple devices, my replication within a sampling unit was individual detector deployments similar to Pavlacky's (2012) analysis using point count transects. Detector deployments constituted primary occasions for estimating small-scale occupancy (θ), and nightly temporal replicates were secondary occasions for estimating detection probability (p) (Pavlacky et al. 2012, Hagen et al. 2016). This modeling approach decomposes the probabilities of θ and p to improve the inference of grid occupancy (ψ) (Nichols et al. 2008, Hagen et al. 2016). For all model sets, I ranked models according to Akaike's Information Criterion (Akaike 1973) adjusted for small sample sizes (AICc) (Hurvich and Tsai 1989), assessed the strength of evidence for a given model *i* using AICc model weights (w_i), and estimated the plausibility of a particular model *i* using evidence ratios (w_i / w_{top}).

MODEL FITTING

I fit all models in R using the package RMARK 2.2.4 (Laake 2013), an interface between MARK v8.0 (White and Burnham 2009) and R (R Development Core Team 2018). I z-scored all covariates except temperature difference of a detector, to improve likelihood of convergence. I grouped covariates for p, ψ, and θ into 1 – 3 additive term groupings corresponding to discrete themes and hypotheses. For p these groupings corresponded to atmospheric conditions (minimum nightly temperature, difference in detector temperature from the nightly site mean, and relative humidity), recording environment (recording space and height above vegetation), and extrinsic noise (number of noise recordings for a given night and detector). For ψ these groupings corresponded to study site, relative abundance of red cedar, forest structure (mean basal area, mean tree density, and mean canopy closure), resource availability (forest area within 125 m and distance to water), and roost availability (snag density and distance to nearest bridge). For θ these groupings corresponded to stand structure (basal area and tree density), relative abundance of red cedar, resource proximity (distance to open area and distance to water), and forest closure (midstory closure and canopy closure). Prior to model fitting, I z-scored all covariate values to improve convergence and comparison of β-estimates across covariates. I then fit all possible models for *p*, θ, and ψ simultaneously in an all-combinations approach (Doherty et al. 2012). This resulted in 4,096 potentials models. I defined the confidence set as all models 2 ΔAICc of the top ranked model. Rather than model averaging the β coefficients and their respective standard errors, I *unconditionally* averaged the predicted real values of occupancy from the models and included confidence intervals of 95%. I used the delta method to approximate the sampling variance and standard error when estimated overall site occupancy and detection probability (Oehlert 1992, Powell 2007).

Results

SURVEY RESULTS

Between the 5 study sites, I sampled a total of 1,547 complete recording nights. Although the minimum target number of recordings nights per deployment was 5, I averaged 6.7 ± 0.09 SE recording nights stations per deployment due to number of days it took to deploy and retrieve detectors. Additionally, detectors remained deployed for additional days if I observed rain during a deployment schedule. The maximum number of recording nights for a deployment was 10 nights. Therefore, I defined the number of primary samples as K=2 to correspond to the maximum number of survey stations within a sampling buffer, and L=10 as the number of secondary samples to correspond to the maximum number of nights sampled. This resulted in an encounter history of $K*L = 20$.

MODELLING RESULTS

The final confidence set, as defined by all models within 2 ΔAICc the top ranked model, contained 2 of the 4,096 potential models (Table 4.1). The only ψ-covariates included in the confidence set with β-estimates that did not overlap zero with 95% confidence was an effect of study site (Table 4.2). This failure to generate predictive covariates is likely an effect of the high naïve occupancy across sites and small sample size. Similarly, the only θ-covariate in the confidence that did not show overlap with zero with 95% confidence was a positive relationship with canopy closure (%) (Table 4.3, Figure 4.2). The *p*-covariates present in the confidence set with β-estimates that did not overlap zero with 95% confidence included an index of open recording space relative to the microphone, height of the microphone above vegetation, and the number of non-bat "noise" recordings for a given night (Table 4.4). Evidence supported a negative correlation between all covariates and detection probability with the strongest relationship between the number of noise files and detection (Figure 4.2).

The estimated nightly detection probability for acoustically surveying the northern long-eared bat was $\hat{p}$ = 0.37 which was above the moderate range of 0.3 estimated by MacKenzie (2002) to provided unbiased estimates of occupancy. Using the equation $1 - (1-p)^k$ to estimated overall detection probability (*d*) for night (*k*), overall detection exceeded 95% after 6 nights. Northern long-eared bats occupied 68% of the survey stations ($\hat{\theta}$) and 75% of the larger sampling units ($\hat{\Psi}$) (Table 4.5). This indicates that northern long-eared bats are both locally common and occupied a large portion of the forests within my study sites. Large-scale occupancy was not consistent across all study sites. The Ft. Calhoun site and the Naper site contained 100% large-scale occupancy and likely contributed to difficulties in predictive ability. The Union, Fairbury, and Rushville sites exhibited lower estimates of large-scale occupancy with Fairbury and Rushville significantly lower than the Union site at 95% confidence (Table 4.2, Table 4.5).

Discussion

The effect of structural clutter on detection probability is mixed across bat species with some studies indicating a positive relationship while others report negative relationships (Weller and Zabel 2002, Broders et al. 2004, Ford et al. 2006, Yates and Muzika 2006, Bender et al. 2015, Kaiser and O’Keefe 2015). Due to these mixed results, it is probable that wing aspect ratio, echolocation call characteristics, and foraging behavior all potentially affect the relationship between clutter and detection probability through acoustic surveys (Aldridge and Rautenbach 1987). The northern long-eared bat is a high frequency, clutter-adapted species that exhibits gleaning foraging behavior, a foraging strategy where an individual listens for insect noise and captures prey off a substrate (Faure et al. 1993). This likely reduces the distance at which recording equipment can detect their echolocations (Lawrence and Simmons 1982, Adams et al. 2012). This has lead others to suggest that a positive relationship between clutter and detection probability may simply be an effect of clutter causing bats to fly closer to the microphone (Kaiser and O’Keefe 2015). To provide additional evidence for this possible explanation, the height of the microphone above the understory vegetation was negatively associated with detection probability meaning microphones placed nearer the top of the understory were more likely to detect the northern long-eared bat. If the species is flying between the canopy and the understory and gleaning insects off vegetation (Nagorsen et al. 1993), a microphone placement nearer to this vegetation may increase the likelihood of it being located between the bat and the direction of its echolocating. However, this deployment strategy is not without costs as a lower deployment height reduces the recording area of the microphone (Weller and Zabel 2002).

Others have mentioned extrinsic sound (e.g., insects, flowing water, wind, etc.) as possible interference in the recording environment, but to the author’s knowledge, its relationship with detection probability has yet to be assessed (Schnitzler and Kalko 2001, Broders et al. 2004). Evidence from this study indicate that, of the covariates included in the model set, the number of noise files recorded in a night had the strongest association with detection probability (Figure 4.2, Table 4.4). At extremely high numbers of noise files, nightly detection probability even neared zero. This is likely due to extrinsic sounds masking bat echolocations thus preventing the zero-cross recording technology used in this study from recording identifiable echolocation pulses. Future studies should consider limiting deployments during periods of high insect noise or include this factor to in modeling to reduce bias in detection probability estimates. In contrast with previous occupancy studies, minimum nightly temperature failed to provide predictive estimates (Kaiser and O’Keefe 2015). The same was true for temperature differences between a detector location and the average minimum temperature of the site.

Due to this study detecting the northern long-eared bat at a majority of sampling locations, the predictive ability of both large-scale and small-scale occupancy covariates was poor. The study, however, still provides some insights into multi-scale habitat use of the northern long-eared bat. For example, at the larger scale, evidence does not support a relationship between canopy closure and occupancy but results did support a significant positive relationship at the smaller scale. This suggests that within an occupied forested habitat patch, the northern long-eared is more available for sampling within closed canopy forests. This is consistent with prior habitat use studies of the species and supports the generalization of the species as an interior forest species (LaVal et al. 1977, Brack, Jr. and Whitaker Jr. 2001, Carroll et al. 2002, Patriquin and Barclay 2003). However, my results suggest that it will occupy sparsely treed habitat patches as two of my study sites had an estimated 100% large-scale occupancy. Future researchers and managers should consider the observed relationship between small-scale occupancy and canopy closure when selecting survey locations within forest patches as others have also described the relationship between fine-scale sampling location selection and perceived species assemblages (Carroll et al. 2002). It is worth noting that evidence did not support a relationship, either positive or negative, between occupancy and red cedar abundance. This warrants future studies to assess the relationships between northern long-eared bats and encroaching juniper in the Great Plains. Additionally, although reports describe northern long-eared bat to both day and night roost within bridge structures, I found no evidence to support an effect of bridge proximity to occupancy; however, my predictive ability was likely low in this study.

Immediately prior to this study, managers detected the fungus responsible for the disease white-nose syndrome within Nebraska, and the next winter, the state observed the first die offs due to the disease (U.S. Fish and Wildlife Service 2017). Research indicates that of the eastern bat species, the northern long-eared bat experiences the highest rates of mortality prior to infection (Frick et al. 2015). This study provides a baseline of occupancy estimates to which researchers can compare futures studies and determine the population effects of the disease. While this study indicates that the northern long-eared bat was locally common at the study sites, it unlikely this will remain post-infection (Frick et al. 2010).

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Tables and Figures

Table 4.1. Confidence set of all models within 10% of the top ranked model’s weight assessing multi-scale occupancy of the northern long-eared bat at 5 study sites across Nebraska. Models accessed the effects of covariates on grid occupancy (ψ), site occupancy (θ), and detection probability (p). I grouped covariates into discrete thematic parings (roost availability, forest closure, stand structure, resource availability, etc.). An “X” below a covariate group indicates that the paring was included in that particular model. Number of estimated parameters (K), Akaike’s Incormation Criterion for small samples (AICc), difference between the corresponding models AICc and the top performing model’s AICc (ΔAICc), Akaike weight (weight), and -2 log-likelihood function (-2LnL) are included.

Rank	**ψ(Study Area)**	**ψ(Cedar)**	**ψ(Roost Avail.)**	**θ(Frst. Closure)**	**θ(Stand Structure)**	**θ(Resource Prox.)**	***p*(Rec. Environment)**	***p*(Noise)**	***p*(Atmospheric)**	***K***	**AICc**	**ΔAICc**	**weight**	**-2LnL**
1	X			X			X	X		10	1186.56	0.00	0.31	1164.45
2	X	X		X			X	X		11	1187.70	1.14	0.17	1163.13

Table 4.2. Covariate estimates pertaining to large-scale occupancy (ψ) included in the confidence set for a multi-scale occupancy analysis of northern long-eared bat occurrence at five study sites in Nebraska. Table includes covariate terms occurring in the confidence set and their corresponding β-estimate and standard error in parenthesis. "N.S." represents estimates with 90% confidence intervals overlapping zero.

Rank	**ψ(Site:Ft.Calhoun)**	**ψ(Site:Fairbury)**	**ψ(Site:Naper)**	**ψ(Site:Rushville)**	**ψ(Bridge Dist.)**	**ψ(Cedar Abund.)**	**ψ(Snag Density)**
1	N.S.	-2.18 (1.0)	N.S.	-1.69 (0.95)	-	-	-
2	N.S.	-2.26 (1.0)	N.S.	-1.67 (0.95)	-	-	-

Table 4.3. Covariate estimates pertaining to small-scale occupancy (θ) included in the confidence set for a multi-scale occupancy analysis of northern long-eared bat occurrence at five study sites in Nebraska. Table includes covariate terms occurring in the confidence set and their corresponding β-estimate and standard error in parenthesis. "N.S." represents estimates with 90% confidence intervals overlapping zero.

Rank	**θ(Basal Area)**	**θ(Canopy Closure)**	**θ(Cedar Abund.)**	**θ(Tree Density)**	**θ(Dist. to Open)**	**θ(Dist. to Water)**	**θ(Midstory Closure)**
1	-	0.71 (0.25)	-	-	-	-	N.S.
2	-	0.86 (0.28)	N.S.	-	-	-	N.S.

Table 4.4. Covariate estimates pertaining to detection probability (p) included in the confidence set for a multi-scale occupancy analysis of northern long-eared bat occurrence at five study sites in Nebraska. Table includes covariate terms occurring in the confidence set and their corresponding β-estimate and standard error in parenthesis. “N.S.” represents estimates with 90% confidence intervals overlapping zero.

Rank	**p(Temp. Dif.)**	**p(Height Above Vegetation)**	**p(Min. Nightly Temp.)**	**p(Noise)**	**p(Recording Space)**	**p(Relative Humidity)**
1	-	-0.16 (0.08)	-	-1.02 (0.14)	-0.18 (0.08)	-
2	-	-0.16 (0.08)	-	-1.01 (0.14)	-0.18 (0.08)	-

Table 4.5. Parameter estimates and standard error for northern long-eared bat multi-scale occupancy and detection probability at 5 study sites across Nebraska. Psi ($\widehat{\Psi}$) is the estimate of large-scale occupancy and is reported for each of the 5 study sites and as an overall estimate of large-scale occupancy. Theta ($\widehat{\theta}$) is the estimate of small-scale occupancy contingent upon occupancy at the large-scale level. Detection ($\hat{p}$) is the estimate of detection probability for a given recording night starting at 30 minutes before sundown and continuing until 30 minutes after sunup. I estimated parameters by model averaging the real predictions of all models within 10% of the top model weight as defined by AICc. I averaged standard error following a delta method approach.

Parameter	**Estimate**	**Standard Error**
Large-scale occupancy ($\widehat{\Psi}$)	0.75	0.04
Psi:Union ($\widehat{\Psi}$)	0.85	0.11
Psi:Ft.Calhoun ($\widehat{\Psi}$)	1.00	0.00
Psi:Fairbury ($\widehat{\Psi}$)	0.39	0.14
Psi:Naper ($\widehat{\Psi}$)	1.00	0.00
Psi:Rushville ($\widehat{\Psi}$)	0.52	0.13
Small-scale occupancy ($\widehat{\theta}$)	0.68	0.05
Detection probability ($\hat{p}$)	0.37	0.02

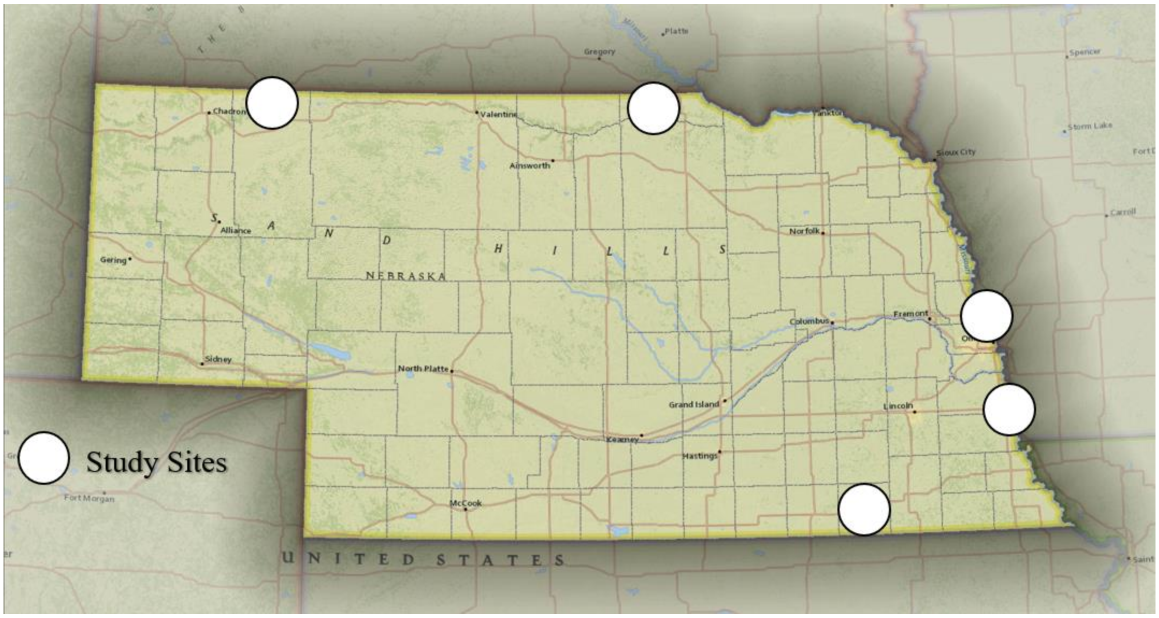

Figure 4.1 Study site locations (n=5) surveyed in 2016 for the northern long-eared bat to assess multi-scale occupancy and detection probability.

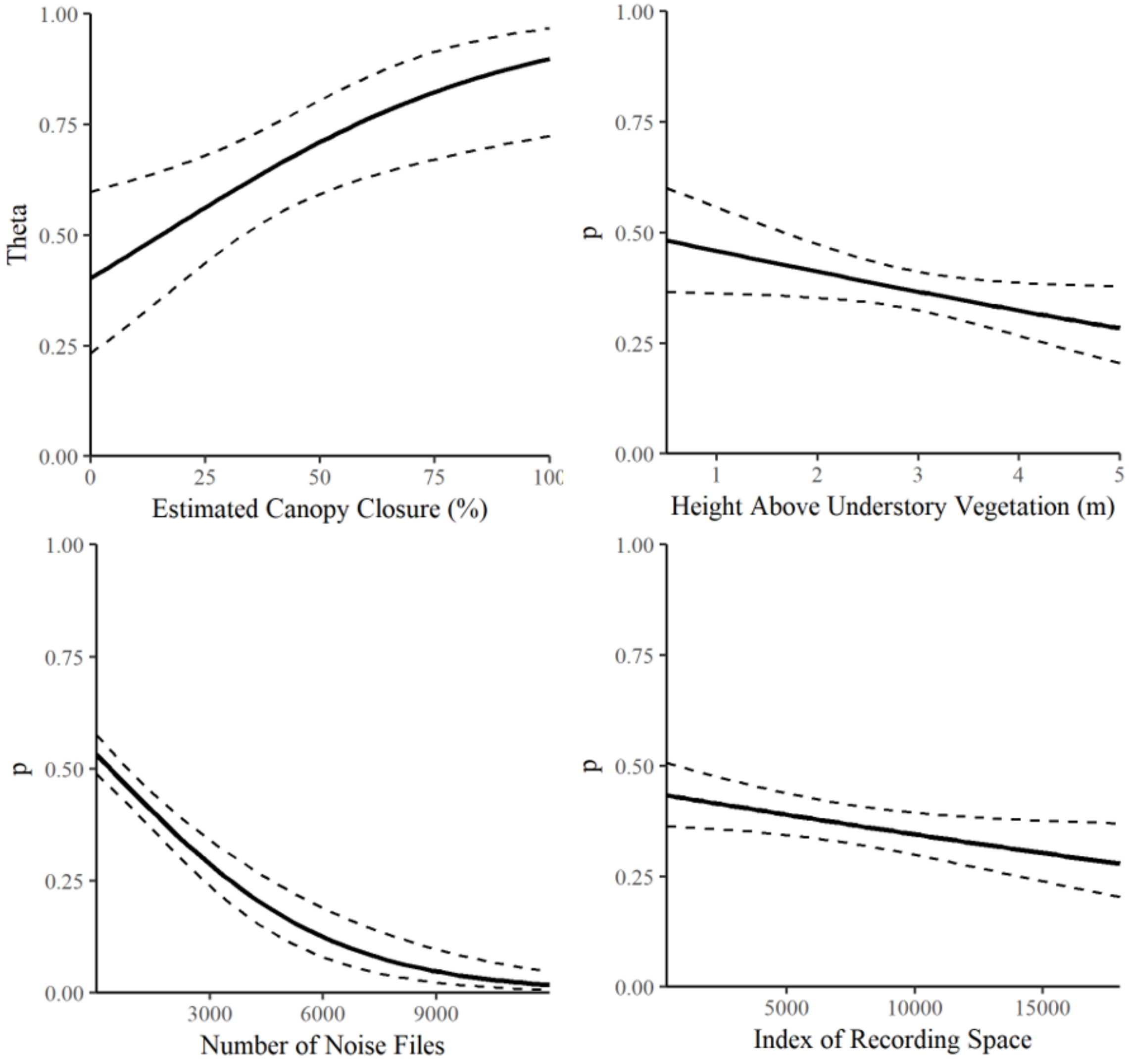

Figure 4.2. Predicted relationships of covariates associated with northern long-eared bat site occupancy and detection probability for all covariates in the confidence set that contained confidence intervals not overlapping with zero in at least one model. Predictions are the results of unconditionally averaging the real estimates of all models within 2 AICc of the top ranked model. Dashed lines denote 95% confidence intervals around the parameter prediction. To assess occupancy and detection probability, I applied a multi-scale occupancy approach to acoustic data collected during the summer of 2016 at 5 study sites within the northern long-eared bat distribution in Nebraska. Covariate relationships includr the height in meters of the microphone above the dominant understory vegetation, the number of non-bat noise files recorded on a given night, an index of 3-dimensional recording space, and the relationship between small-scale occupancy and forest area. All covariates contained β-estimates that did not overlap with zero. Unconditional averaging the real estimates results across the confidence set results in a flattening of the effect.

CHAPTER 5: SYNTHESIZING THE FACTORS ASSOCIATED WITH ROOST TREE SELECTION AND HABITAT USE OF THE NORTHERN LONG-EARED BAT

Introduction

Insight into the northern long-eared bat’s habitat associations is a necessity to ensure biologically relevant management practices (Morrison et al. 2006). Understanding these relationships, however, requires a holistic approach that addresses the multiple levels at which the species is interacting with its environment (Miller et al. 2003). The objective of my thesis was to address these relationships following a multi-scale approach that assessed the factors associated with roost tree selection, distribution, and intra-forest habitat use.

To expand the inferential range beyond a traditional single-site roost study, I mined the current corpus of studies across the northern long-eared bat’s distribution and quantified the structural characteristics associated with roost tree selection. As expected, evidence of selection for many roost tree characteristics varied greatly among studies, further highlighting the importance of caution when extrapolating results from single studies to the species as a whole (Miller et al. 2003). Even with this variation, however, results supported species-wide conclusions pertaining to roost tree selection and roosting behavior. To move beyond traditional observation-based range maps, I sought to understand the factors associated with the northern long-eared distribution in Nebraska. Results from this study enabled the prediction of the likelihood of occupancy across the state and thus provided insight into unsampled portions of Nebraska. Lastly, in an attempt to assess factors associated with occupancy at finer spatial scales, I combined spatially concentrated survey efforts with on-the-ground habitat measurements. While this third study failed to provide insight into these habitat associations, it did provide an understanding of forest structure associated with species availability within occupied survey locations. Additionally, the two habitat studies provided insight into factors that are associated with detection probability of the northern long-eared. This provides guidance to future studies while also reducing bias in occupancy estimates.

Study Methods and Results

To determine the roost tree characteristics that support evidence of selection by the northern long-eared bat across its range, I gathered published studies, dissertations, theses, and grey literature using research search engines and *a priori* search operators. I extracted reported means of all roost tree characteristics and means of all available non-roost trees for all studies that employed a use-versus-available study design. For roost tree characteristics with ≥5 studies, I calculated Hedges' *g* Standardized Mean Difference to compare effect sizes (Hedges 1981). I then applied an intercept-only random effects model to assess evidence of selection (i.e. statistically significant deviation from a zero effect size). When compared to available trees, selected roost trees had a greater amount of bark remaining on the bole, a larger diameter at breast height, a lower decay class, and were taller. Compared to results from meta-analyses that pooled studies from multiple of species, the effect size for the 4 most common roosting characteristics showed closer proximity to zero indicating a reduce strength of selection (Kalcounis-Rueppell et al. 2005, Fabianek et al. 2015). I then applied a multi-model meta-regression approach to determine which external variables explained the most variation in the standardized mean difference of roost tree diameter as this was the most commonly reported characteristic. Evidence supported a positive relationship with relative abundance of softwood roost trees and the square root of latitude. Additionally, I generated intercept-only random effects estimates for each of the following behavior characteristics: the distance from the first roost to the capture site (m), the distance between subsequent roosts (m), and the number of days spent in a roost before switching. A northern long-eared bats first roost following capture was approximately 521 ± 173 m (SE = 88.3) from its capture site. It spends an average of 2.17 ± 0.48 days (SE = 0.24) in a roost before switching, and consecutive roosts were approximately 327 ± 123 meters (SE = 62.6) apart. This is the first meta-analysis to summarize roosting behavior and provides species-wide movement estimates of behavioral characteristics referenced in federal regulations (Fish and Wildlife Service 2016).

In the summer of 2015, I acoustically surveyed 101 10 km x 10 km grids distributed across the state. I applied a multi-scale occupancy approach to assess factors associated with large-scale occupancy (ψ), small-scale occupancy (θ), and detection probability (p) (Nichols et al. 2008, Pavlacky et al. 2012). Evidence supported a positive relationship between large-scale occupancy and mean summer temperature (°C), forest clumpiness, and availability of potential cliff habitat within 89km. Within occupied grids, evidence supported a positive relationship between small-scale occupancy and the area of forest within 125 m. By conducting repeated visits, I assessed the relationship between various covariates and nightly detection probability. Evidence supported a negative relationship between detection probability and recording space around the microphone and mean nightly temperature, and a positive relationship with the day of the season. I then predicted large-scale occupancy across the state using remotely available covariates. Estimates of ψ, θ, p, provided by this modeling approach suggested the northern long-eared bat is rare within its previously estimated geographic range, but locally common and easily detected.

Since I conducted the 2015 study over a large geographic scale with the intent to create a predictive occupancy map, I was restricted to remotely sensed covariates in the form of GIS layers. To understand the relationship between occupancy and forest structure, resource availability, and invasive species abundance, I intensively sampled 5 study sites within the Nebraska range of the northern long-eared bat. At each of these sites, I simultaneously deployed 23 pairs of acoustic detectors for multiple nights. High naïve large-scale occupancy at sites approaching 100% at some sites, likely contributed to a failure to generate predictive models for large-scale occupancy (ψ). However, there was support for a positive relationship between canopy closure and small-scale occupancy (θ), with greater availability of northern long-eared bats at deployment locations with increased canopy closure. Additionally, evidence supported a negative correlation between detection probability (p) and the number of noise files during a given night, recording space, and the height of the detector above understory vegetation. Averaging large-scale occupancy across all sites revealed an estimate comparable to the small-scale occupancy in the 2015 study with an overlap of their 95% confidence limits (2015: $\theta = 0.70 \pm 0.18$, 2016: $\psi = 0.76 \pm 0.10$).

Conclusion

Results from all three studies are inconsistent with previous descriptions of the northern long-eared bat as a specialist species and uncommon on the western expanse of their range (Jung et al. 1999, Caceres and Barclay 2000). While still exhibiting evidence of roost selection for multiple characteristics, the species shows a reduced strength of selection and greater plasticity when compared to multi-species meta-analyses and in comparative studies with other congenerics (Foster and Kurta 1999, Lacki et al. 2009, Timpone et al. 2010). This observation could be the result of greater roost plasticity or the failure accurately capture microclimatic characteristic through the measurement of structural proxies such as diameter at breast height (Boyles 2007). Regardless of the explanation, traditional singletree management strategies may be impractical and potentially ineffective (Silvis et al. 2012), especially considering the regularity of roost switching.

Evidence from both field studies supports describing the northern long-eared bat as locally common, occupying ~70% of treed habitats within its distribution. Additionally, the high large-scale occupancy estimates at multiple sites in 2016, indicated the northern long-eared bat occupied even sparsely treed habitats contrary to previous descriptions as an interior forest species (LaVal et al. 1977, Brack, Jr. and Whitaker Jr. 2001, Carroll et al. 2002). The majority of comparative habitat studies of the northern long-eared bat are located in portions of the range that overlaps with multiple forest dwelling *Myotis* species. Much of the northern long-eared distribution in Nebraska, however, only overlaps with a single other congeneric, the little brown bat (*M. lucifugus*), and in portions of its state range it is the only *Myotis* species known to occur. When designing future studies, researchers should consider comparing the species habitat use relative to the co-occurrence of other Myotids in Nebraska as reduced competition could be enabling a broadening of the species niche breadth into more open habitats than traditionally observed further east.

I wish emphasize that I conducted these field studies prior to the detection of white-nose syndrome in Nebraska and the observation of subsequent die-offs (U.S. Fish and Wildlife Service 2017). As such, one should consider my reported occupancy estimates as pre-white-nose estimates of occupancy. It is likely that the effects of the disease have substantially reduced northern long-eared bat populations since this data was collected (Frick et al. 2010). My occupancy estimates, however, should serve as baseline estimates to compare against future occupancy studies to estimate population trends post-white-nose syndrome (MacKenzie 2006).

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