SUMMER OCCUPANCY AND HABITAT CHARACTERISTICS OF THE NORTHERN LONG-EARED BAT IN NORTHERN GEORGIA

by

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(Under the Direction of Steven B. Castleberry and Jeff Hepinstall-Cymerman)

ABSTRACT

Mass mortality from white-nose syndrome (WNS) has resulted in increased conservation concerns for bats in North America and the federal listing of the northern long-eared bat (*Myotis septentrionalis*). To better manage *M. septentrionalis* in northern Georgia, which represents the southern extent of its range, we identified the species' regional distribution and roost habitat. We used mist-netting records from 2007-2017 to develop dynamic occupancy models relating occurrence to habitat and geographic features at two spatial scales. Models estimated *M. septentrionalis* occupancy prior to WNS presence in the study area (2007-2011) and allowed for annual changes in occupancy through estimates of extinction and colonization. Prior to WNS, *M. septentrionalis* occupancy was positively associated with percent deciduous forest at the home range scale and elevation at both the home range and landscape scales. Post-WNS *M. septentrionalis* occupancy was associated with large patches of deciduous forest and areas of higher elevation at the landscape scale, resulting in the extirpation of peripheral populations. Patterns in *M. septentrionalis* roosting habitat selection were assessed by comparing roosts to surrounding vegetation and topographic characteristics at two spatial scales. *M. septentrionalis* disproportionately roosted in snags relative to their availability and selected snags with larger diameters. At the home range scale, we observed an interactive effect of slope and aspect, with both reproductive females and all bats selecting west facing aspects on low angle slopes and showing no aspect preference as slope increased. In addition to mortality from WNS, millions of bats in North America have died due to collisions with wind energy facilities. However, only *M. septentrionalis* has received federal protection as a result of these mortality sources. To evaluate the potential for *M. septentrionalis* to act as an umbrella species for the bat community, we constructed a community occupancy model for species in northern Georgia. Protection was implied based on co-occurrence with *M. septentrionalis*, with only the hoary bat (*Aeorestes cinereus*) and silver-haired bat (*Lasionycteris noctivagans*) found to confer adequate protection through protection of habitat for *M. septentrionalis*. However, a small number of species, preferably those with limited co-occurrence, likely could confer protection to the larger bat community.

INDEX WORDS: Occupancy, Hierarchical Modeling, Northern Long-eared Bat, *Myotis septentrionalis*, Georgia, Roost, Bats, Community Modeling, Habitat Selection, Peripheral Population, Landscape Ecology, Population Decline

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TABLE OF CONTENTS

CHAPTER

APPENDICES

LIST OF TABLES

Page

LIST OF FIGURES

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

Historically bats in eastern North America have suffered from habitat loss and disturbance at hibernacula (Fenton 1997). However, more recently, white-nose syndrome (WNS) and collisions at wind energy facilities have become the greatest threats to bats in North America, with both sources estimated to have killed millions of bats (Blehert et al. 2009, Frick et al. 2010, Arnett and Baerwald 2013). While WNS poses the more immediate threat, as it can cause > 90% population declines in 2-3 years after arrival of the fungus (Blehert et al. 2009), collisions at wind energy facilities represent a long-term and potentially permanent threat given the push for renewable energy (Kunz et al. 2007).

Mortality from WNS and wind energy primarily occurs at hibernacula and along migratory corridors, respectively (Blehert et al. 2009, Arnett and Baerwald 2013). However, protecting these areas likely will not aid in the recovery of populations, because declines are not associated with habitat degradation or loss. Therefore, population recovery may be best accomplished through protection and enhancement of summer habitat. During summer in eastern North America, most bat species forage and roost in forests (Lacki et al. 2007a). Protection and enhancement of summer habitat may aid in recovery of populations experiencing elevated mortality, by improving body condition and increasing recruitment. Improved body condition could be particularly important for species experiencing mortality from WNS, as higher fat stores decrease WNS-related mortality (Cheng et al. 2019).

Traditionally, population declines were thought to result in range retractions, resulting in core populations persisting longer than those on the periphery (Lawton 1995). However, during disease outbreaks, populations may persist based on isolation from disease, suggesting peripheral populations may be the last to experience perturbation from WNS (Channell and Lomolino 2000, Maher et al. 2012, Thogmartin et al. 2012). Additionally, bats on the range periphery may display localized variation in behavior that warrants specific or amended conservation strategies. For example, Indiana bat (*Myotis sodalis*) populations at the range periphery exhibits variation in roost selection and diet composition not observed in more centrally located populations (Britzke et al. 2003, Kurta et al. 1993, Kurta and Whitaker 1998). Further, bats in the southeastern United States exhibit variation in wintering strategies not observed in other parts of their range, including increased levels of winter activity, shorter hibernation periods, or forgoing hibernation altogether (Rice 1957, Grider et al. 2016). Shortened hibernation in southern peripheral populations may allow increased survival from WNS as the disease has less time to develop in individuals. Habitat associations of bats within our study area, northern Georgia, may be of particular interest, as it contains the southern range limit for several bat species.

LITERATURE REVIEW

Distribution and Habitat Associations

Understanding habitat associations and occurrence patterns for species of conservation concern is fundamental to recovery efforts. Early attempts to delineate species distributions resulted in the idea of niche theory, which predicts that every species has a set of environmental conditions for which it is best adapted (Grinnell 1917). Since, distribution models have proven well suited for addressing a number of conservation problems, including: determining potential spread of invasive species, assessing impacts of climate change on species occurrence, proposing new survey areas for rare species, and understanding coexistence of multiple species (Peterson 2003, Thuiller 2004, Engler et al. 2004).

Regardless of the intended use, species distribution models all seek to relate abiotic and or biotic factors to species occurrence. Explanatory variables commonly considered for predicting distribution include distance to water availability, elevation, land cover, forest canopy, and vertical forest structure (Jaberg and Guisan 2001, Ford et al. 2005, Watrous et al. 2006). When delineating species distributions, appropriate predictor variables as well as the spatial scale at which the species responds to predictor variables must be considered (Holland et al. 2004). Determining the appropriate scale(s) is necessary because an animal can be affected not only by the patch in which it exists but also by surrounding patches (Aberg et al. 1995, Saab 1999). The most common method for selecting scales is to apply various sized polygons around sample locations with the polygon size reflecting species movement potential (Wheatley and Johnson 2009, Thornton and Fletcher 2014). However, this method relies on arbitrary decisions regarding the number and range of scales to consider and lacks the ability to draw statistical inference for selected scales (Chandler and Hepinstall-Cymerman 2016). Additionally, scale of habitat selection can fluctuate temporally, making factors such as seasonal resource availability, reproductive status, and sex an important consideration (Beasley et al. 2007, Henry et al. 2002).

There are ubiquitous assumptions across distribution models, including no false positives within species identification, the population being at equilibrium, and all represented habitat being sampled (Kery and Schaub 2012, Guisan et al. 2017). If any of these assumptions are violated, habitat may be misidentified potentially leading to poor quality habitat being set aside for conservation. While false positives and representative sampling can be accounted for through adequate training, statistical methodologies, and proper study design, the issue of population equilibrium still can be difficult to ascertain (Clement et al. 2014). Assuming a population is at equilibrium requires individuals in the population to be in habitat conducive to long-term population stability (Sinclair et al. 2010). However, species can occur in areas where populations would not exist without immigration or be absent from suitable areas due to a lack dispersal ability (Shaffer 1981, Sinclair et al. 2010). Therefore, to accurately estimate a species distribution ecologists must consider factors such as dispersal ability and site fidelity.

Bats and Habitat Modeling

Distribution models for bats have proven useful for determining habitat relationships, community composition, and discovery of bats outside of their known range (Jaberg and Guisan 2001, Greaves et al. 2006, Rebelo and Jones 2010). While bats occur in many different regions and habitat types, globally bats rely heavily on forests. At course spatial scales bat distribution is often distinguished with features such as land cover types, elevation, and distance to water (Jaberg and Guisan 2001, Kaminski et al. 2020), while at small spatial scales bats occurrence may be driven by forest type, distance to water, canopy height and gaps, and vertical forest structure (Kalcounis et al. 1999, Ford et al. 2005). However, in the absence of known habitat relationships inference on a bats ecological niche can be deduced from wing shape, body size, and echolocation call structure (Lacki et al. 2007, Arita and Fenton 1997). For example, in forests of the eastern United States bats with high wing aspect ratios (i.e., long narrow wings) and low frequency calls use more open areas, due to lower maneuverability and low frequency being beneficial at longer ranges (Aldridge and Rautenbach 1987, Arita and Fenton 1997).

Roost Tree Selection

Roost structures, particularly maternity roosts, play a critical role in bat life history through facilitating social interaction, providing refuge from predators and weather, and as a place for gestation and rearing of young (Racey and Swift 1981, Kunz 1982, Johnson and Lacki 2014). In eastern North America, bats use a variety of roost structures ranging from rock outcrops to buildings, but most species predominantly use trees for at least part of the year (Barclay and Kurta 2007). Tree roosting bats generally can be broken into two groups: those that roost in loose bark, hollow boles, or cavities and those that roost in foliage. Meta-analysis of North American roost tree selection suggests bats generally select tall, large-diameter trees in areas of open canopy (Kalcounis-Rueppell et al. 2005, Barclay and Kurta 2007). Selection of large exposed trees is often attributed to increased roost temperature, which facilitates thermoregulatory needs (Kalcounis-Rueppell et al. 2005). However, roost temperatures can be influenced by several factors, and studies using exact measurements to characterize roost microclimates are limited (Boyles 2007). Additionally, bats prefer to roost in snags, likely because they are more likely to contain desirable features for roosting, such as loose bark and crevices (Kalcounis-Rueppell et al. 2005).

Selection for roosting habitat also occurs beyond the roost structure, with factors influencing roost selection at the landscape scale including distance to water (Ormsbee and McComb 1998, Miles et al. 2006), slope (Perry et al. 2008), forest age (Perry et al. 2008), snag density (Lacki and Schwierjohann 2001), forest type (Perry et al. 2007 and Cryan et al. 2001), and distance to forest edge (Boonman 2000). Reports of bats preferring to roost on steeper slopes and in older forest stands are thought to be linked to greater occurrence of large diameter trees, a roost characteristic preferred across bat species (Kalcounis-Rueppell et al. 2005). Roost being located close to linear landscape features such as roads and forest edges likely facilitate movement and foraging, as many species use forest edge to forage and move between habitat patches (Henderson and Broders 2008, Morris et al. 2010, Jantzen and Fenton 2013). Selection for stands with greater snag density has been reported in colonial bats that require a network of roosts (Lacki and Schwierjohann 2001). Lastly, selecting roosts within close proximity to water should reduce daily commuting costs to resources, saving bats energy (Miles et al. 2006).

Community Based Conservation

Given limited effort and funding, species in the United States are often not directly protected until listed under the Endangered Species Act (ESA). Although several million bats have died from WNS and wind energy, only *M. septentrionalis* has been listed under the ESA as a direct result of these losses (Fish and Wildlife Service 2016). While several other bat species are being evaluated for protection, there can be a lag time of several years from a listing proposal to final listing (U. S. Fish & Wildlife Service 2019). Given the ability of WNS to cause > 90% mortality to infected populations within 2-3 years after arrival of the fungus, any delay in listing could be detrimental to long term viability of susceptible populations (Blehert et al. 2009, Frick et al. 2010). One solution for protecting a group of vulnerable species, which would otherwise see little to no protection, is through the use of an umbrella species.

The term umbrella species first appeared in the literature in 1984 to describe a species whose minimum habitat requirements encompassed the need of multiple species in the larger community (Wilcox 1984). In the intervening years, the utility of umbrella species has been debated, with evidence suggesting an umbrella species can be an effective management strategy (Caro 2003, Dunk et al. 2006, Hecker 2008). Utilization of the umbrella species approach can be particularly effective when a suite of species is available for use as an umbrella or little is known about the life history of the species for which protection is needed (Fleishman et al 2000, Roberge and Angelstam 2004). However, protection via an umbrella species is often implied via co-occurrence and studies assessing the utility of umbrella species often lack long term data detailing population trends after the implementation of conservation activities targeted at the umbrella species (Copeland et al. 2014, Malso et al. 2016).

OBJECTIVES AND GUIDE TO THE DISSERTATION

Elevated mortality from wind energy installations and WNS have called increased attention to the need for conservation and management of North American bats. However, uncertainty regarding how mortality will influence community structure and habitat relationships make conservation for bats difficult. To help address these issues, we identified critical summer habitat for *M. septentrionalis* along the southern periphery of its range. Additionally, we assessed *M. septentrionalis* co-occurrence with other bat species to determine its ability to confer protection to species yet to receive federal protection.

This dissertation is presented in a series of manuscript-style chapters addressing habitat associations of and conservation for *M. septentrionalis* in northern Georgia. Chapter 2 investigates shifts in *M. septentrionalis* occupancy as the species experienced mortality from WNS. We used dynamic occupancy models to relate habitat metrics at multiple scales to bat occurrence records from 2007-2017. In Chapter 3, we evaluate underlying patterns of *M. septentrionalis* roost tree selection based on roost structure and location. Roost preference was determined by comparing roosts to their immediate surrounding as well as pseudo-non-roost structures on the landscape.

Lastly in Chapter 4, we assess the ability of *M. septentrionalis* to act as an umbrella species for the larger bat community. The ability of *M. septentrionalis* to confer protection to other species was assessed by building a community occupancy model involving nine bat species in north Georgia. The area occupied by each species was overlaid with the occupied area of *M. septentrionalis* to determine if an appreciable portion of the target species occupied area could conferred protection through co-occurrence.

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CHAPTER 2

DYNAMIC OCCUPANCY DURING DISEASE RELATED POPULATION DECLINES IN PERIPHERAL POPULATIONS OF MYOTIS SEPTENTRIONALIS[1]

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[1] Grider, J. F., S. B. Castleberry, and J. Hepinstall-Cymerman. To be submitted to Landscape Ecology

ABSTRACT

Mortality from White-nose Syndrome (WNS) has led to several species of bats becoming a conservation priority. *Myotis septentrionalis* became the first species listed under the Endangered Species Act due to WNS-related mortality. However, developing conservation strategies for this species can be difficult due to limited knowledge regarding its distribution and habitat associations. To aid in making land-use decisions that minimize impacts to *M. septentrionalis*, we determined summer distribution and habitat associations in northern Georgia. We used 10 years (2007-2017) of mist-netting records to construct multi-season site occupancy models, allowing for variation in area occupied between years. Initial occupancy and extinction between years were assessed with predictor variables related to percent land cover, metrics quantifying forest patch arrangement, year since WNS, distance to karst, and distance to nearest WNS positive county. Detection probability was estimated using Julian date, sampling effort, and year since WNS. Because the scale at which bats respond to landscape composition and arrangement was unknown, predictor variables were assessed at the home range (65 ha) and landscape (491 ha) scales. Initial (pre-WNS) site occupancy was positively associated with percent deciduous forest cover at the home range scale and elevation at both scales. Post-WNS, *M. septentrionalis* became restricted to large patches of deciduous forest and higher elevations at the landscape scale. While larger patches of high elevation deciduous forests may be a likely location for *M. septentrionalis* to persist, there is potential for any habitat loss to be critical for long term viability due to site fidelity. Additionally, our study demonstrated that while peripheral populations may persist longer than core populations due to isolation, populations closest to the range edge were most vulnerable once the fungus arrived. We recommend managers on the periphery of *M. septentrionalis*' range focus conservation on areas where this species was known

to previously occur with preference given to large patches of deciduous forest away from the range periphery.

INTRODUCTION

Precipitous declines in several temperate bat species in North America, primarily due to White-nose Syndrome (WNS), have highlighted the need to better understand bat habitat and species occurrence (Blehert et al. 2009, Frick et al. 2010). The northern long-eared bat (*Myotis septentrionalis*), once one of the most common forest bats in the eastern United States (Caceres and Barclay 2000), was listed as Threatened in 2015 due to mortality associated with WNS (U.S. Fish and Wildlife Service 2015). The severity of mortality experienced by *M. septentrionalis* is evident from declines in capture rates, including 98% and 95% reductions in New Hampshire (Moosman et al. 2013) and Virginia (Reynolds et al. 2016), respectively. Furthermore, initial reports showed proportion of juveniles in the population is declining, making long term population viability questionable (Francl et al. 2012, Reynolds et al. 2016). High mortality and subsequent listing has made management for *M. septentrionalis* a priority throughout its range and created a greater need to understand habitat associations.

Previous studies relating landscape scale and forest stand features to *M. septentrionalis* occurrence have shown selection for large areas of contiguous forest (Yates and Muzika 2006, Henderson et al. 2008), deciduous forests (Henderson et al. 2008, Henderson and Broders 2008), forest stands with partial harvests that leave a cluttered understory (Owen et al. 2003), closed forest canopy (Owen et al. 2003, Ford et al. 2005), linear features to facilitate movement (Owen et al. 2003, Henderson and Broders 2008, Jantzen and Fenton 2013), and aversion to open areas (Henderson and Broders 2008, Jantzen and Fenton 2013). Additionally, roosting habitat studies generally have shown that *M. septentrionalis* roosts are associated with areas of high canopy cover (Sasse and Perkins 1996, Foster and Kurta 1999, Menzel et al. 2002), high snag density (Lacki and Schwierjohann 2001), and in deciduous forest stands, although use of coniferous trees has been documented (Foster and Kurta 1999, Lacki and Schwierjohann 2001, Broders and Frobes 2004).

The southern edge of *M. septentrionalis* range occurs in the southeastern U.S., and peripheral bat populations are known to exist in different habitats and display variation in behavior (Kurta et al. 1993, Grider et al. 2016). Once largely ignored or underrepresented in conservation planning due to ideas that fragmentation and isolation would lead to extinction, there is now evidence that peripheral populations may persist longer than core populations during population declines (Lomolino and Channell 1995, Channell and Lomolino 2000). Additionally, peripheral populations are known to possess greater regional genetic variation, which is important to the long term species adaptability and survival (Millar and Libby 1991, Lesica and Allendorf 1995, Hampe and Petit 2005). Habitat and behavioral variation across *M. septentrionalis*' range, combined with high mortality from WNS and the potential importance of peripheral populations for conservation, emphasize the need to develop distinct habitat associations for *M. septentrionalis* in the southeastern U.S (Grider et al. 2016).

A common method to establish species habitat preferences is occupancy modeling, which relates predictor variables to occurrence records while allowing for imperfect detection (Mackenzie et al. 2002). However, standard occupancy models are static in time and unable to track changes in occupancy that may be occurring as bats experience elevated mortality from WNS. Conversely, dynamic occupancy models allow for colonization and extinction between years (Mackenzie et al. 2003), making them more appropriate for determining occupancy before and after disease-related mortality events such as WNS. While this modeling approach accommodates change in occupancy from disease related mortality, there is uncertainty as to whether areas remaining occupied are a result of habitat associations or resistant/tolerant individuals (Thompson 1996). Research on persistence and recovery of European rabbit (*Oryctolagus cuniculus*) populations post-rabbit hemorrhagic disease concluded rabbit density was positively associated with high quality habitat, suggesting that areas occupied post-disease are those that best satisfy species niche requirements (Fernandez 2005, Calvete et al. 2006).

Existing knowledge on habitat selection, combined with morphological traits associated with maneuverability and foraging in cluttered habitat, demonstrate *M. septentrionalis* selection for and adaptation to cluttered forest environments (Ratcliffe and Dawson 2003, Broders et al. 2004). However, how or if habitat associations of peripheral *M. septentrionalis* populations change as they experience mortality from WNS is unknown. To better understand occupancy during WNS-associated population declines, we used land cover and geographic characteristics to track shifts in *M. septentrionalis* occupancy before WNS and through the first six years of decline following the arrival of WNS to our study region. We hypothesized that *M. septentrionalis* occupancy prior to WNS would be positively associated with forest cover, and as the population declined, occupancy would be highest in larger patches of forest, particularly deciduous forest (Yates and Muzika 2006, Henderson and Broders 2008, Henderson et al. 2008). Further, we expected sites further away from WNS positive areas to experience lower extinction rates.

METHODS

Study Area

Our study covered approximately 45,000 km^2 in northern Georgia, USA and included the Blue Ridge, Valley and Ridge, Appalachian Plateau, and northern portion of the Piedmont physiographic provinces: an area representing the southeastern extent of *M. septentrionalis* historic range (Figure 2.1). Most of our sampling was conducted on public land in the Chattahoochee National Forest and state managed wildlife areas, however, only 11.1% of the study area was publicly owned. Much of the study area, 55.9%, was forested, with mesophytic (*Quercus* and *Acer*) and southern mixed forest (*Quercus* and *Pinus*) being the dominate forest types (Dyer 2006). Common tree species encountered included loblolly (*Pinus taeda*), shortleaf (*Pinus echinata*), white (*Pinus strobus*), and Virginia (*Pinus virginiana*) pine, white oak (*Quercus alba*), northern red oak (*Quercus rubra*), yellow poplar (*Liriodendron tulipifera*), chestnut oak (*Quercus prinus*), and red maple (*Acer rubrum*). Topography varied across the study area with elevations ranging from 1,563 m in the mountains of the Blue Ridge and to 94 m in the Piedmont (Hodgkins 1965).

Field Data Collection

Mist-net surveys occurred on public lands from mid-May through early August, 2015-2017. Sites were randomly generated using ArcMap (ESRI 2014) in patches of forest >20 ha (derived as an 8-way neighborhood from 2011 National Land Cover Database (U.S. Geological Survey 2014 [NCLD]) classes: deciduous [41], evergreen [42], and mixed [43]) that contained unimproved or low traffic roads, stream road intersections, and small bodies of water that could accommodate mist-netting. We followed the Indiana bat (*Myotis sodalis*) survey protocol (U.S. Fish and Wildlife Service 2015), which included mist-netting in temperatures >10° C beginning at sunset and continuing for five hours on nights with no precipitation or sustained high winds using predominately double high mist-nets. We mist-netted no more than 2-3 consecutive nights at a single location. Supplemental capture data (2007-2017) was obtained from the Georgia Department of Natural Resources’ Rare Species and Natural Community Database. These data were collected by private contractors and agency biologists in areas where environmental impact statements were required, or in areas thought to be suitable habitat for threatened or endangered bat species. Much of the supplemental data followed the Indiana bat survey protocol, but some sites had variation in the duration of sampling and number of nights sampled.

Statistical Analysis

We used dynamic occupancy models to delineate the distribution of *M. septentrionalis* prior to WNS and through the first six years of disease presence in the study area (Mackenzie et al. 2003). Data from 2007-2011 (pre-WNS) was combined and treated them as a closed single-season occupancy model allowing for imperfect detection. Results from this pre-WNS portion of the model are referred to as initial occupancy. Although WNS was not documented in Georgia until winter 2012-2013, two counties directly bordering the northwest edge of our study area and one county 7.2 km from the northeast corner of our study areas tested positive for WNS in the winter of 2011-2012, and could have influenced *M. septentrionalis* in our study area. Subsequently the model updated annually, estimating imperfect detection and the likelihood that a site was colonized or became extinct.

Predictor variables used to estimate initial occupancy and subsequent extinction and colonization events included percent forest cover for NLCD forest classes, percent total forest, forest landscape metrics (detailed below), physiographic province, years since WNS, mean elevation, distance to karst topography, and distance to nearest WNS positive county. Because no colonization events were observed during sampling and bats were known to be experiencing high mortality from WNS, colonization was left null in the model. Land cover percentages and mean elevation were calculated using NLCD and DEM data layers and a circular moving window within ArcMap. Forest landscape metrics relating forest configuration to bat occurrence included number of forest patches, largest patch, edge density, total core area, mean forest patch size, largest patch index, and perimeter to area ratio of patches (Table 2.1). Landscape metrics were derived individually for NLCD forest cover classes (41, 42, and 43) as well as total forest cover using FRAGSTATS 4.2 (McGarigal et al. 2012). Distance to karst topography and nearest WNS positive county were derived by measuring straight line distance between sample locations and the closest polygon on the USGS karst map (Weary and Doctor 2014) and U.S. county layer, respectively. Detection probability was estimated using Julian date, duration of sampling events (hours), years since WNS, *M. septentrionalis* captures per night, and area of mist-net (m^2).

Due to uncertainty regarding the scale at which *M. septentrionalis* selects habitat (Chandler and Hepinstall-Cymerman 2016), predictor variables were derived at two spatial scales: home range (65 ha) and landscape (491 ha). Home range scale was based on home range size of pregnant *M. septentrionalis* from the literature (Owen et al. 2003, Lacki et al. 2009), which we assumed represented the species smallest daily movements. Landscape scale was based on the furthest distance we tracked a bat from capture location to roost (1.25 km).

Correlation between predictor variables was assessed using Pearson's correlation, with variables with $| r | >0.7$ being excluded from the same models. Model fit was assessed using area under curve values (AUC), with AUC > 0.7 considered capable of distinguishing occupied from unoccupied areas (Pearce and Ferrier 2000). Models were ranked using AIC values with all models ΔAIC < 2 of the highest ranked model considered to have support (Burnham and Anderson 2002). We concluded no support for model estimates in cases where models did not outperform the null model. A single parsimonious model was obtained by model averaging all supported models. Predictor variables and their 95% confidence intervals were calculated based on the averaged model, with influential predictor variables being those whose confidence interval did not include zero. All models were constructed using function colext in package *unmarked* within program R (Fiske and Chandler 2011, R Core Team 2019).

RESULTS

In total, 1,093 mist-netting nights at 533 unique locations were included in the analysis, with *M. septentrionalis* captured at 68 (12.8%) sites (Table 2.2). Mean number of sites sampled/time period was 90.3 (SD = 53.3, range 2 - 159). During the study, 80 sites (15%) were sampled in multiple time periods with no site sampled in >5 time periods. When a site was sampled within a time period it was visited for an average of 1.7 (SD = 1.0, range 1-8) nights. Despite increased capture effort post-WNS, naïve occupancy declined in every subsequent year, with the exception of 2015 to 2016, where naïve occupancy remained the same (Table 2.2).

Four models were supported by our data (< 2 ΔAIC) containing effects of deciduous forest at the home range scale, and mean elevation at the home range and landscape scales as predictors of initial occupancy (Table 2.3). Model averaged parameter estimates indicated that influential predictor variables were percent deciduous forest and elevation for initial occupancy (Table 2.4). Initial site occupancy was 1.16 times more likely for every one percent increase in deciduous forest at the home range scale, and 5.38 and 4.58 times more likely to be initially occupied for every 195 m increase in elevation at the landscape and home range scales, respectively. Initial occupancy indicated *M. septentrionalis* occupied deciduous forest patches in the northern portion of the study area and smaller more fragmented patches towards the southern extent (Figure 2.2).

As *M. septentrionalis* experienced mortality from WNS, site extinction was best explained by largest patch index of deciduous forest, mean elevation at the landscape scale, and sampling year (Table 2.4). Based on 95% confidence intervals, no predictor variables were influential in explaining site extinction (Table 2.4). Sites were 2.52 times less likely to go extinct for every 195 m increase in mean elevation and 1.06 time more likely to be occupied for every one percent increase in largest patch of deciduous forest. Further, with each year a site became 2.56 times more likely to become unoccupied. Detection probability was influenced by sampling year, with *M. septentrionalis* 1.69 times less likely to be detected in each subsequent year (Table 2.4). Over time, the model predicted severe declines in site occupancy that coincided with movement of WNS into and throughout the study area (Figures 2.2 & 2.3). As mortality from WNS became more prevalent, smaller forest patches at lower elevations in the southern extent of the study area became unoccupied. By 2016, *M. septentrionalis* range had retracted toward more core areas, with only high elevation deciduous forests remaining occupied.

DISCUSSON

Our results support previous studies emphasizing the importance of deciduous forest patches as *M. septentrionalis* habitat (Yates and Muzika 2006, Henderson et al. 2008). Initial occupancy was positively associated with percent deciduous forest and following presence of WNS in the region, site extinction was negatively associated with large patches of deciduous forest. Before arrival of WNS, total forest cover likely influenced *M. septentrionalis* occupancy (Yates and Muzika 2006, Kaminski et al. 2020), however, to maximize likelihood of bat capture, sampling prior to WNS focused on areas of contiguous forest cover, resulting in areas of low forest cover being underrepresented in the sampling effort. Therefore, total forest cover between sites was statistically indistinguishable and resulted in perfect separation when applied to initial occupancy. Regardless, deciduous forests being positively associated with initial occupancy and negatively associated with site extinction coincides with previous work demonstrating the importance of forest habitat to *M. septentrionalis* presence (Henderson and Broders 2008, Henderson et al. 2008, Kaminski et al. 2020).

Mean elevation was a driver of occupancy, with *M. septentrionalis* initially occupying higher elevations at both spatial scales and experiencing lower extinction at higher elevations at the landscape scale after arrival of WNS. Previous studies have not reported a relationship between *M. septentrionalis* occupancy and elevation, which could be due to our study covering an elevation gradient (~1,450 m) over twice as large the next largest elevation gradient studied (~650 m) (Owen et al. 2003, Ford et al. 2005, Henderson and Broders 2008, Jantzen and Fenton 2013). Within our study area, elevation decreased from north to south and coincided with elevated temperature (PRISM Climate Group 2015). Lower temperature at higher elevations also could explain the positive correlation between *M. septentrionalis* occupancy and elevation. Given that *M. septentrionalis* in our study exist at the southern range limit, potentially approaching its thermal tolerance, individuals may be less suited to low elevations where temperatures are higher. In addition to elevated temperatures, lower elevations in our study area are correlated with decreased precipitation, transition into the Piedmont physiographic province, and shifts in the plant community, all of which likely limit the dispersal of *M. septentrionalis* further south (Dyer 2006, PRISM Climate Group 2015). Similar patterns of occurrence have been reported from Virginia to Alabama, where *M. septentrionalis* occupy high elevation forests of the Appalachian Mountains but are not present in the Piedmont (Morris et al. 2009, White et al. 2018).

The only influential predictor for detection probability was year since WNS arrival. While year since WNS infection was not expected to directly affect detection probability, we considered it a surrogate for abundance, which is positively associated with detection probability

(Royle and Nichols 2003). The correlation between year since WNS infection and abundance is due to population decline associated WNS morality that occurred in a predictable temporal pattern between annual sampling events (Blehert et al. 2009, Frick et al. 2010). Additionally, evidence of temporal declines in detection post-WNS have been reported in Virginia, where a 95% decrease in capture rate of *M. septentrionalis* was observed two years after the arrival of WNS (Reynolds et al. 2016).

The rate of population decline predicted by our model is consistent with previous studies that reported high mortality in bat populations during the first 2-3 years following initial WNS detection (Blehert et al. 2009, Frick et al. 2010). However, because *M. septentrionalis* site extinction was negatively correlated with larger patches of deciduous forest at higher elevations, area occupied by *M. septentrionalis* contracted into core populations where WNS was first observed in our study area. An explanation for the observed range retraction could be linked to the majority of known hibernacula being located in the northern portion of the state (Culver et al. 1999), causing bats at the southern edge of the range to make longer seasonal migrations to hibernacula. The physical stress of longer migrations combined with weakened physical condition from WNS may have made spring migrations to summer habitat in the southern reaches of the range insurmountable. The inability to make longer spring migration post–infection would result in the furthest reaches of habitat experiencing the lowest occupancy rate, which coincides with our findings (Figure 2.2). Studies of birds infected with avian influenza (H5N1) demonstrated that seasonal migration is energetically expensive and reduces immune function, making long distance migration of infected individuals unlikely (Weber and Stilianakis 2007). Further, WNS is known to cause damage to the wing membrane of affected individuals and could make spring migration difficult (Reichard and Kunz 2009).

Our observation of occupancy retracting from south to north also could be attributed to marginal habitat in the southern range periphery. After severe population declines from rabbit hemorrhagic disease, *Oryctolagus cuniculus* populations were most prevalent in areas associated with higher habitat quality (Fernandez 2005, Calvete et al. 2006). Additionally, abundance typically is positively related to habitat quality (Denoël and Lehmann 2006, Johnson 2007), and peripheral populations tend to have lower abundance relative to more centrally located populations (Brown 1984, Lawton 1993, Lomolino and Channell 1995). Although we did not directly measure habitat quality across the study area, similar patterns of disease-related decline would suggest that peripheral *M. septentrionalis* populations were occupying marginal habitat. Given the positive relationship between habitat quality and body condition (Bearhop et al. 2004, Sztatecsny and Schabetsberger 2005), and bats with better body conditions being more likely to survive WNS (Cheng et al. 2019), we conclude that northern centrally-located populations were existing in higher quality habitat, thus improving their physical condition and likely increasing their ability to survive WNS infection.

Patterns of WNS-related bat population declines across North America follow expected patterns in an epizootic disease, with mortality radiating from a focal area and spreading based on proximity and connectivity to known occurrences (Hudson et al. 2002, Russell et al. 2005, Wilder et al. 2011, Thogmartin et al. 2012). In this scenario, peripheral bat populations affected by white-nose syndrome may be more likely to survive due to their relative isolation. However, while WNS took longer to reach southern *M. septentrionalis* populations, once it arrived our results indicated that individuals occupying the outer margins of the range were less likely to persist. These conflicting patterns of decline highlight the importance of scale and location when monitoring population declines. Had management decisions in our study area been based on protecting populations least likely to be exposed to WNS, i.e., the most isolated individuals, managers would overvalue low-quality habitat where individuals were least likely to survive. While all areas where *M. septentrionalis* were once known to inhabit should be considered for conservation due to site fidelity (Patriquin et al. 2010, Perry 2011), we suggest conservation efforts should prioritize high quality habitat where individuals were once abundant, as these populations have a greater chance at long-term survival from WNS.

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Table 2.1: Name, units, and description of landscape metrics generated in FRAGSTATS and used in modeling *M. septentrionalis* occupancy and extinction in northern Georgia, 2007-2017.

Coefficient Name	Description
Edge Density	Sum of edge (m) divided by square meters.
Largest Patch Index	Percent of landscape comprised of the largest habitat patch.
Number of Patches	Number of patches of each habitat type.
Total Core Area	Total area (ha) of all habitat area inside a fixed edge depth* from the habitat patch perimeter.
Largest Patch	Area (ha) of the largest habitat patch of the specified habitat type.
Mean Patch Size	Area (ha) of the corresponding habitat type, divided by the total number of patches.
Perimeter to Area Ratios	Length (m) of habitat perimeter divided by the area of habitat (m^2).

* Edge depths were set at 60, 90, and 120 meters to specify which areas of the raster where to be treated as edge and which parts were to be treated as core. Example: An edge depth of 60 meters would mean that an area was not considered a core area unless it was surrounded on all sides by at least 60 meters of the same habitat type.

Table 2.2: Number of nights sampled, number sites surveyed, and occupied sites (sites with a detection) for *M. septentrionalis* mist-net surveys conducted in northern Georgia, 2007-2017. Pre-WNS is defined as a 5-year period (2007-2011) before WNS was likely affecting bats on the study area. Naïve occupancy rate was calculated as the number of sites occupied out of the total number sites sampled in each year.

	Pre-WNS	2012	2013	2014	2015	2016	2017
Nights sampled	47	16	241	190	314	179	111
Sites surveyed	43	12	143	110	159	101	64
Occupied sites	21	3	27	9	8	5	1
Naïve occupancy	0.49	0.25	0.19	0.08	0.05	0.05	0.02

Table 2.3: The top supported models (ΔAIC <2), number of predictor variables, Akaike's Information Criterion (AIC), AIC difference between a model and the model with the lowest AIC (ΔAIC), AIC weighted average (ω_i) and area under curve values (AUC) used to predict changes in *Myotis septentrionalis* initial occupancy, (ψ) seasonal colonization (γ), seasonal local extinction (ε), and probability of detection (p) in northern Georgia, 2007-2017. Largest patch index, LPI below, is the percent of landscape (here either the home range or landscape scales) comprised by the largest habitat patch.

Model	Predictor Variables	AIC	ΔAIC	ω_i	AUC
ψ (Percent Deciduous Forest^1), γ (Null), ε (Mean Elevation^2 + Year), p (Year)	8	428.559	0	0.32	0.87
ψ (Percent Deciduous Forest^1), γ (Null), ε (Mean Elevation^2 + LPI Deciduous Forest^2 + Year), p (Year)	9	428.987	0.428	0.26	0.873
ψ (Mean Elevation^2), γ (Null), ε (LPI Deciduous Forest^2 + Year), p (Year)	8	429.364	0.805	0.22	0.866
ψ (Mean Elevation^1), γ (Null), ε (LPI Deciduous Forest^2 + Year), p (Year)	8	429.47	0.91	0.20	0.866
Ψ(Null), γ (Null), ε (Null), p (Null)	4	474.107	45.548	0	0.783

[1] Home range scale (65 ha)

[2] Landscape scale (491 ha)

Table 2.4: Coefficient average estimates, standard error, 95% confidence intervals, and odds ratios from the model average of competing models used to predict changing *Myotis septentrionalis* initial occupancy (ψ), seasonal colonization (γ), seasonal local extinction (ε), and probability of detection (p) in northern Georgia, 2007-2017.

Coefficients	Estimate	Standard Error	LCL	UCL	Odds Ratio
ψ Intercept	-3.094	3.535	-10.024	3.835	
ψ Deciduous Forest	0.15	0.059	0.033	0.266	1.162
ψ Elevation^2	1.673	0.833	0.039	3.306	5.328
ψ Elevation^1	1.522	0.716	0.118	2.925	4.581
γ Intercept	-3.388	1.001	-5.351	-1.426	
ε Intercept	-1.603	1.337	-4.224	1.018	
ε Elevation^2	-0.926	0.475	-1.857	0.005	0.396
ε LPI^2	-0.06	0.051	-0.16	0.04	0.942
ε Year	0.94	0.647	-0.328	2.252	2.56
p Intercept	0.887	0.594	-0.278	2.052	
p Year	-0.526	0.173	-0.864	-0.187	0.591

^{1}Home range scale (65 ha)

^{2} Landscape scale (491 ha)

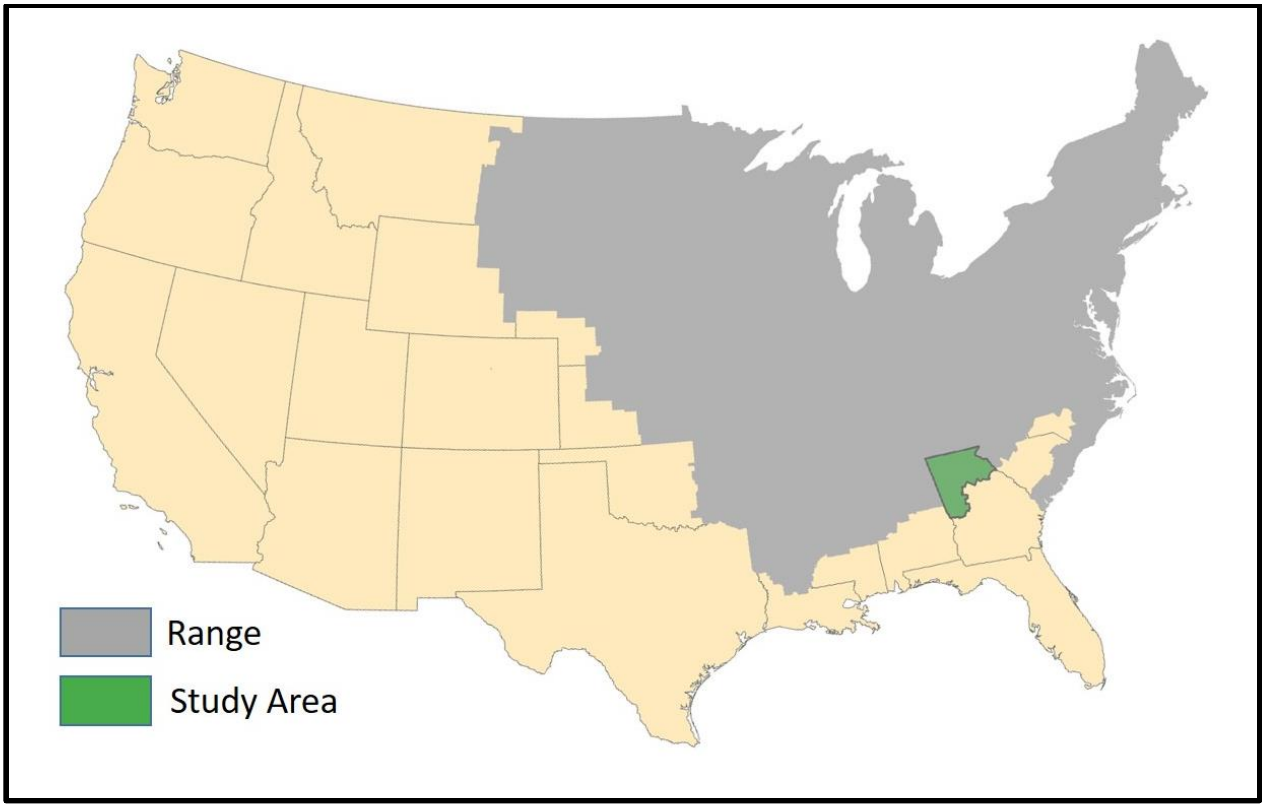

Figure 2.1: Range of *Myotis septentrionalis* in the contiguous United States and study area in northern Georgia

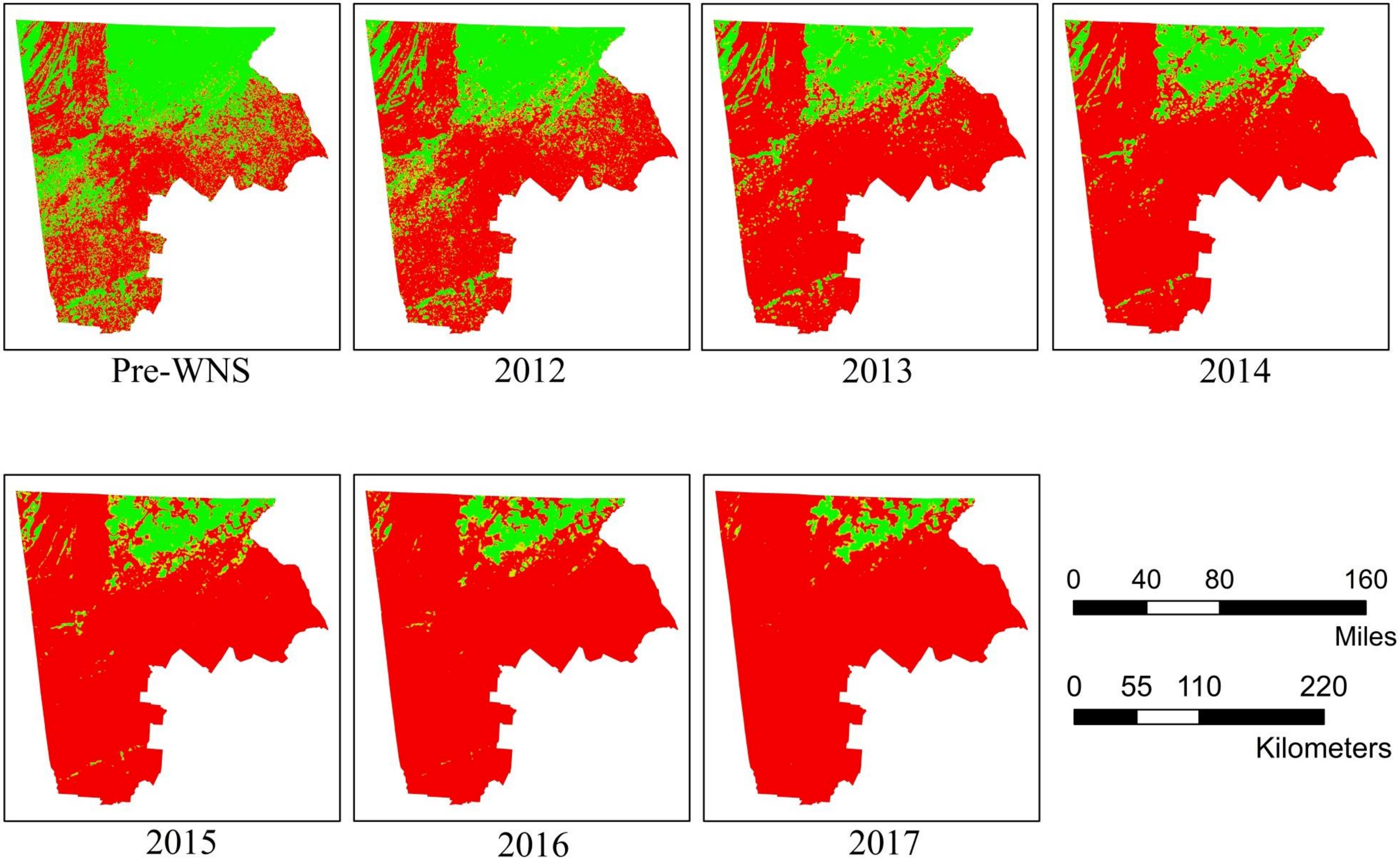

Figure 2.2: Predicted year-by-year range contraction of *Myotis septentrionalis* within their historically occupied range in northern Georgia. Models predicted occupied areas from time periods prior to the arrival of White-nose Syndrome (WNS) (Pre-WNS, 2007-2011) through 2017, when initial WNS mortality was occurring. Areas in green are predicted occupied in the given year.

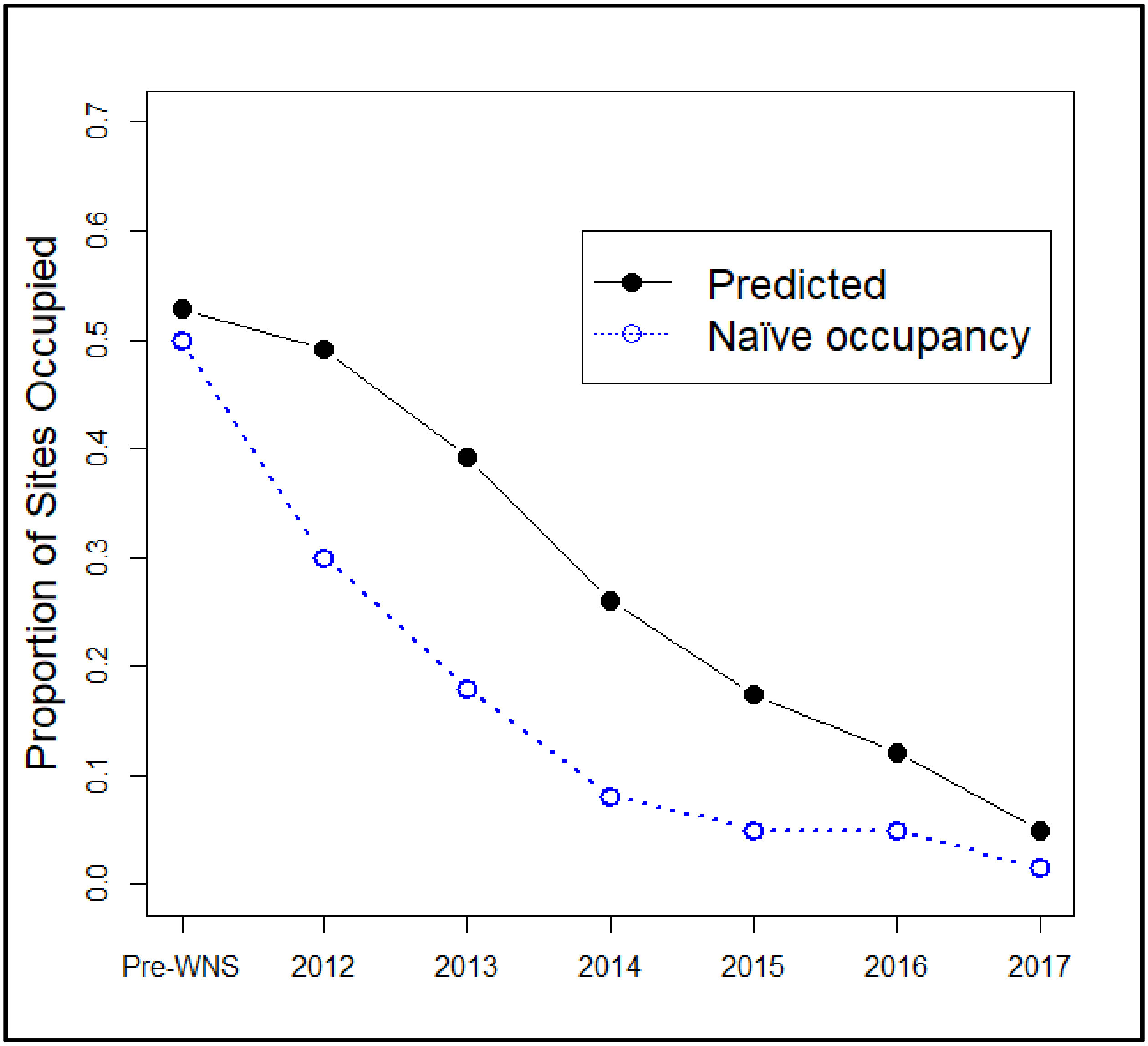

Figure 2.3: Proportion of sites occupied by *Myotis septentrionalis* in northern Georgia before effects of White-nose Syndrome (Pre-WNS, 2007-2011) and yearly post-WNS (2012-2107). Blue line represents data collected in the field (naïve occupancy) and the black line represents the predicted occupancy from the combined top models.

CHAPTER 3

DIURNAL ROOST SELECTION BY MYOTIS SEPTENTRIONALIS ON THE SOUTHERN EDGE OF THEIR RANGE[2]

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[2] Grider, J. F., S. B. Castleberry, and J. Hepinstall-Cymerman. To be submitted to Journal of Wildlife Management

ABSTRACT

Mortality from white-nose syndrome has made management and recovery of *Myotis septentrionalis* a priority. Successful recovery will ensure availability of diurnal summer roosts, where gestation and rearing of young occurs. However, variation in roost selection across the species' range, and limited studies on roost election at the southern range extent, makes extrapolating data across physiographic regions and habitat types difficult. Therefore, we examined *M. septentrionalis* diurnal roost selection at the southern extent of its range in northern Georgia, USA. We identified characteristics of desirable roosting habitat for all individuals and reproductive females by comparing roosts to vegetation and topographic characteristics of the surrounding area at the plot, home range, and landscape scale. From May to July 2014 through 2017 we radio tagged 16 *M. septentrionalis*, 12 females and 4 males, and located 37 roosts. Bats roosted in cavities, loose bark, and hollow boles of 16 different tree species. Roosts were often located below the canopy in trees with larger diameters than surrounding trees. While live trees were used as roosts, bats disproportionately roosted in snags, with relative probability of roosting in a snag increasing with snag density at the plot scale. On low degree slopes, roosts occurred more frequently on west facing aspects but as slope increased, bats showed no preference for aspect. Additionally, bats roosted more frequently on west facing than east facing slopes. *M. septentrionalis* preference for west facing aspects and less steep slopes while roosting on west facing aspects suggests that individuals in our study area may be indifferent to or actively avoid solar radiation when selecting roosts. The observed indifference or avoidance of solar radiation indicates *M. septentrionalis* may be reaching their upper thermal tolerance at the southern periphery of their range. However, there remains unexplored variables influencing roost solar exposure and microclimate that require further evaluation to substantiate our findings.

INTRODUCTION

For several bat species in the eastern United States and Canada, mortality from White-Nose Syndrome (WNS) has made long term population persistence uncertain (Blehert et al. 2009, Frick 2010). Persistence and recovery of bat populations in affected areas will require an understanding of life history requirements across their range, including roosting habitat. For bats, a substantial portion of their lives are spent in summer roosts where social interactions, gestation, rearing of young, and refuge from weather and predation occurs (Kunz 1982). Given that such critical life events are associated with summer roosts, understanding roosting habitat of bats species is of vital importance.

The federal listing of the northern long-eared myotis (*Myotis septentrionalis*) has made conservation of summer roosting habitat for this species a priority (Fish and Wildlife Service 2016). While *M. septentrionalis* summer roots are predominantly located in trees (Sasse and Perkins 1996, Foster and Kurta 1999), identifying critical summer roosting habitat is difficult due to variation in roost preferences depending on location, sex, forest type, and reproductive status (Broders and Frobes 2004,Carter and Feldhamer 2005, Perry and Thill 2007, Garroway and Broders 2008). Reproductive female bats often select roosts with high solar exposure during pregnancy and rearing of young, which is thought to aid in meeting thermoregulatory requirements (Kalcounis-Rueppell et al. 2005). Studies assessing effects of solar exposure on *M. septentrionalis* roosts, regardless of reproductive status, have been inconclusive, with roosts located in areas with high solar exposure and below the canopy where solar exposure is reduced (Menzel et al. 2002, Perry and Thill 2007, Rojas et al. 2017). Studies in northern portions of *M. septentrionalis'* range have shown that individuals select roosts with high solar exposure during energetically expensive life stages, such as lactation (Garroway and Broders 2008). However, Silvis et al. (2012) found that female *M. septentrionalis* in the central portion of the range consistently roosted below the canopy where solar radiation is reduced, regardless of reproductive status. Further variation in roost selection exists in the types of trees used by *M. septentrionalis*, with some studies showing exclusive use of hardwood trees (Foster and Kurta 1999, Menzel et al. 2002, Carter and Feldhamer 2005) whereas others demonstrate strong preference for conifers (Perry and Thill 2007). Size of roost trees selected by female bats also varies, with either no preference for tree size (Menzel et al. 2002, Carter and Feldhamer 2005) or selection for larger diameter roost trees (Sasse and Perkins 1996, Foster and Kurta 1999, Silvis et al. 2015a).

Consistent across *M. septentrionalis* roost studies is use of bark, cavities, and crevices in snags and live trees, with bats displaying a preference for snags (Sasse and Perkins 1996, Lacki and Schwierjohann 2001, Lacki et al. 2009, Silvis et al. 2015a). Additionally, reproductive female *M. septentrionalis* are reported to utilize a network of roosts (Johnson et al. 2009, Silvis et al. 2015b). Female networks have been reported to contain 4-42 roosts and can occupy up to 58.3 ha (Silvis et al. 2015b). Within the network roost switching is frequent, with means days spent in a roost before switching ranging from 1.3 to 5.3 and most bats switching roost every 2-3 days (Menzel et al. 2002, Johnson et al. 2009). Movement between roosts is typically ≤ 0.2 km (Carter and Feldhamer 2005, Johnson et al. 2009, Silvis et al. 2015b), but mean distances up to 0.6 km and individual movements up to 2.0 km have been reported (Foster and Kurta 1999, Cryan et al. 2001). Although previous studies have focused on differences between *M. septentrionalis* roost structures, the use of roost networks across their range indicates the importance of, and potential selection pressure for, roost habitat on a landscape scale.

The large latitudinal range encompassed by *Myotis septentrionalis'* distribution results in a wide temperature gradient, with individuals at the northern and southern peripheries encountering their thermal limits (Stevens 1989, Sunday et al. 2012). Importance of ambient temperature and optimal thermoregulatory strategies have been demonstrated, with *M. septentrionalis* selecting for increased canopy cover in warmer years (Silvis et al. 2015b). A closely related species, the Indiana bat (*Myotis sodalis*), displays variation in roost selection at its northern and southern range limits. On the northern edge of the range, *M. sodalis* were only found in roosts with direct solar exposure (Kurta et al. 1993), whereas individuals at the southern extent of the range have primary roosts with high solar exposure as well as secondary roosts below the canopy or in areas of higher canopy cover (Britzke et al. 2003). These studies suggest that variation likely exists in *M. septentrionalis* roost selection at the thermal extremes of their range and highlights the need to understand variation in roost selection occurring at range limits.

Currently, there are few published data available on roosting habitat of *M. septentrionalis* in the southeastern portion of its range, with most studies occurring in the core of the range. Given variation in roost selection observed across the range, results from previous roost studies may not apply at the southern periphery. Our goal was to identify characteristics of *M. septentrionalis* roosting habitat at their southern range limit to inform land managers tasked with protecting and promoting habitat. We characterized roost location relative to the surrounding environment to determine factors that affect roost and roost area selection within the expected home range and the larger landscape. Additionally, we examined characteristics of individual roost trees and the immediately surrounding area to identify important roost tree features. On the home range and landscape level, we hypothesized bats would select for increased solar radiation and forest cover, with the former providing a greater number of roost structures and the latter thought to decrease costs associated with thermoregulation.

METHODS

Study Area

Our study was located in northern Georgia, USA, which is the southern extent of *M. septentrionalis'* historic range (Figure 3.1). The study area includes the Blue Ridge, Valley and Ridge, Appalachian Plateau, and northern portion of the Piedmont physiographic provinces, and ranges topographically from mountainous in the Blue Ridge to rolling hills in the Piedmont (Hodgkins 1965). Forests in these regions are comprised of mesophytic and southern mixed forest, with both regions containing oak (*Quercus*) dominate sections (Dyer 2006). Tree species commonly encountered included softwood species such as loblolly (*Pinus taeda*), shortleaf (*P. echinata*), white (*P. strobus*), and Virginia (*P. virginiana*) pine, and hardwood tree species including white (*Q. alba*), northern red (*Q. rubra*), and chestnut (*Q. prinus*) oak, yellow poplar (*Liriodendron tulipifera*), and red maple (*Acer rubrum*).

Field Data Collection

Bat capture occurred on state and federally managed lands from mid-May through early August 2015 – 2017. We followed the Indiana bat survey protocol (U.S. Fish and Wildlife Service 2015), which included mist-netting beginning at sunset and continuing for five hours on nights with no precipitation, no sustained high winds, and temperature above 10°C. We netted sites for 2-3 consecutive nights and used predominately double high mist-nets. We fitted all captured *M. septentrionalis* with radio transmitters (LB- 2X, 0.27 g, Holohil Systems, Ontario, CA) between the scapulae using surgical adhesive. Transmitter mass did not exceed 5% of body mass (mean body mass = 6.8, range 5.5 - 8 g, Aldridge and Brigham 1988). We released individuals at the capture site and tracked them to diurnal roost daily until the transmitter fell off or the individual could not be located for 3 days. When possible, we conducted emergence counts on roost trees to confirm roost locations and determine size of colonies. The Institutional Animal Care and Use Committee of the University of Georgia (A2014 04-022-Y3-A0, A2017 03-005-Y3-A2) approved bat capture, handling, and transmitter attachment.

We characterized roost trees by measuring height (m), decay stage (Anderson et al. 1979), crown class (Helms 1998), species, distance (m) from roost to nearest taller tree, and from roost to nearest canopy tree (Menzel et al. 2002). We defined canopy trees as those within the co-dominate or dominate crown class (Helms 1998). For nearest taller and nearest canopy tree, we recorded DBH (cm), height, and species. We characterized surrounding vegetation plots within a 10-m radius of roosts by measuring DBH of all woody stems > 2.54 cm and recording number of snags. We acquired additional roost locations from the Georgia Department of Natural Resources (GA DNR) that had been located by private contractors and agency biologists. In general, these roosts were located in areas where environmental impact statements were required, or in areas thought to have suitable habitat for threatened or endangered bat species. Data available on these roosts and surrounding vegetation varied, but DBH, crown class, and whether the roost was alive or dead was known for all but 2 roosts. Due to the lack of complete descriptions for surrounding habitat, we did not use roots supplied by the GA DNR in analyses pertaining to snag density.

Home Range Selection Model

Because the scale at which species were responding to predictor variables was unknown (sensu Chandler and Hepinstall-Cymerman 2016), we examined roost selection at the home range and landscape scales. We defined home range scale as a 67-ha circular buffer around the weighted central mean of all locations for each radio-tagged individual. Home range buffer area was based on mean home range of 23 individuals reported in Owen et al. (2003) and Lacki et al. (2009). For the analysis, we combined locations for two individuals because they were captured at the same site and roosted together.

We generated pseudo absences within each home range buffer at a 10:1 ratio using a random point generator in ArcMap 10.2 (ESRI 2014). A 10:1 ratio was selected because it is the approximate maximum number of pseudo absences to known locations that can be generated without negatively affecting the predictive accuracy of a generalized linear model (Barbet-Massin et al. 2012). For all roost trees and pseudo absences, we selected predictor variables related to hypotheses surrounding thermoregulation and snag generation, including slope (degrees), distance to ridge (m), and aspect. Aspect was derived using the USGS 10 m DEM (U.S. Geological Survey 2017), with east/west and north/south calculated using the sine and cosine of the aspect in radians, respectively. Distance to stream was straight-line distance (m) from roost trees and pseudo absences to nearest stream, river, canal, or artificial path within the National Hydrography Dataset flowlines layer (U.S. Geological Survey 2018). We included artificial paths because many major rivers are listed under this classification. Distance to ridge was straight-line distance (m) from each point/location to nearest ridge as defined by zero accumulation in a flow accumulation raster derived from 10 m DEM.

Landscape Selection Model

To examine landscape-scale roost area selection, we compared the area where bat roosts were located (hereafter, roost area) to total available roosting area. Roost area was defined as an 11-ha circular buffer centered on the weighted mean centroid of all roost locations for an individual. The roost area buffer size was equivalent to the mean of all 100% minimum convex polygons around groups of roost trees in our data and reported in Johnson et al. (2012). We defined total available roosting area as a 17.2 km^2 circular buffer centered on the weighted mean of all locations for that individual. The buffer size was based on a 2.4 km radius, which was the furthest movement we recorded between roosts.

Using ArcMap, we generated random pseudo absences at a 10:1 ratio within the total available roosting area. For all pseudo absences and roost areas, we derived percent deciduous forest, percent mixed forest, percent evergreen forest, mean slope, mean east/west aspect, and mean north/south aspect. Percent forest type and mean aspect were calculated using an 11ha circular moving window and the 2011 National Land Cover dataset (U.S. Geological Survey 2014) and 10 m DEM, respectively. Mean aspect was converted to east/west and north/south as described above.

Analysis

For roost-level analysis, we used all roost locations to compare DBH, distance to nearest taller tree, and distance to nearest over-story tree, between live and dead roosts as well as between roosts and their vegetative plot. We assessed differences using t-tests and considered significant if the 95% confidence interval surrounding the mean difference did not include zero. To determine the relative probability of roosting in a snag relative to snag density we used logistic regression with a response variable of live or snag roost and the dependent variable of snag density within the roost tree vegetative plot. We transformed logistic regression coefficients to odds ratios to interpret how the relative probability of roost use changes in relation to predictor variables. We compared Akaike Information Criterion (AIC) values of snag density and null models to ascertain if snag density explained use of live trees or snags as roosts, with $\Delta AIC < 2$ between the two models indicating that there was not overwhelming support for one model over the other. Lastly, to determine if *M. septentrionalis* disproportionately used snags as roosts, we used a chi-squared test comparing the number of live trees and snags in plots surrounding roosts to the number of live trees and snags used as roosts. For analyses related to snag density we removed one of the roost trees, a snag, from the analysis because the roost was located in a recent burn containing many trees of small DBH, resulting in a snag density five time higher than any other plot.

Due to low sample size, we pooled female bats across reproductive status and age (including one juvenile male that roosted in a maternity colony). At both scales we used logistic regression to fit null models as well as models relating solar exposure, snag generation, and forest cover. We used a Pearson's test (Pearson's $|r| \leq 0.70$) to ensuring no correlated predictor variables were in the same model. Predictor variables at the home range scale included east/west aspect, north/south aspect, degree slope, and distance to ridge. Landscape scale predictor variables included east/west aspect, north/south aspect, degree slope, and percent cover in evergreen, deciduous, and mixed forest types. Due to solar exposure being related to slope position and aspect, we included interactions of aspect and slope or distance to ridge in all models at both scales (Kumar et al. 1997).

Models were evaluated using AIC with those having ΔAIC < 2 of the top model considered to have support (Burnham and Anderson 2002). We concluded no support for model estimates in cases where no model outperformed the null model. Supported models were model-averaged based on weights derived from AIC values to obtain a single parsimonious model. We calculated model averaged predictor variables and their 95% confidence interval, with influential predictor variables defined as those having confidence intervals that did not include zero.

RESULTS

We tracked 16 *M. septentrionalis*, 12 females and 4 males, for a mean of 4.4 ± 2.7 days each (standard deviation [SD], range 1-9 days). We located 47 roosts consisting of 23 snags, 12 live trees, 2 unknown (unreported). Bats roosted in cavities, loose bark, and hollow boles. We identified 16 tree species used as roosts and 8 species were used more than once (Appendix A). Of the 35 roosts for which roost position relative to the canopy was determined, 19 roosts were below the canopy.

Bats switched roost trees every 1.8 ± 1.3 (mean ± SD) days and no individual stayed in a roost longer than 5 consecutive days. Mean movement distance between roosts was 427.8 ± 620.6 m (range 2.8-2,344.7 m). Reproductive females and juveniles of both sexes roosted in colonies whereas non-reproductive females and adult males always roosted alone. The largest roost observed, located in 2014, contained 31 individuals. Number of individuals in the largest colony decreased in every subsequent year (2015 – 19 individuals, 2016 – 3 individuals, and 2017 – 1 individual).

Snags were used as roosts more frequently than expected ($\chi^2 = 66.72$, $p < 0.001$) based on their prevalence. DBH of snags roosts (34.7 ± 24.4) was greater ($t = 3.71$, $p = 0.001$) than snags in the surrounding area (18.1 ± 6.1). Propensity to roost in a snag was positively correlated to snag density (0.026, 95% confidence intervals = 0.005 - 0.048 [Appendix B]), with the use of a snag as a roost being 1.03 times more likely for every 1 snag/ha increase in snag density (Figure 3.2). Roost tree DBH (29.8 ± 22.0) was greater ($t = 3.69$, $p = 0.001$) than mean tree DBH within the surrounding plot (14.7 ± 3.8).

Our most supported models (ΔAIC < 2) for all individuals and reproductive females at the home range scale indicated that effects of slope, aspect, the interaction of slope and aspect, and distance to ridge were important to roost tree selection (Table 3.1). For reproductive females and all individuals, two predictor variables, aspect and the interaction of slope and aspect, were influential (Table 3.2). Both reproductive females and all individuals disproportionately roosted on west facing slopes, with individuals being 10.9 and 9.09 times more likely to select a roost at 270° (west) than 90° (east), respectively. The interaction of slope and aspect revealed reproductive females and all individuals selected for west facing aspects on low-grade slopes, a preference that diminished as slope increased (Figure 3.3). While distance to ridge was in the top model, its effect on roost selection was small and the 95% confidence interval surrounding the estimate included zero. Models evaluating roost area selection for reproductive females and all individuals at the landscape scale failed to outperform the null model and thus were deemed to have no support.

DISCUSSION

While some studies have documented *M. septentrionalis* using specific tree species as roosts (Johnson et al. 2009, Silvis et al. 2015a), we documented no apparent preference for any one species. Indifference in roost tree species in our study could be explained by our larger study area relative to other studies, which included a wider range of habitats and tree species. Roost studies across *M. septentrionalis*' range reveal the species' ability to adapt roosting behavior to local conditions. Roosts have been found in pine forests (Perry and Thill 2007), hardwood forests (Silvis et al. 2012), and exclusively using Ponderosa pine (*Pinus ponderosa*, (Cryan et al. 2001)), a tree that occurs in only a small portion in the western reaches of the range of *M. septentrionalis*. Additionally, while roost tree species preference has been documented, the tree of preference varies among study sites (Johnson et al. 2009, Silvis et al. 2015a). Given the observed plasticity in tree species used as roosts across the range, *M. septentrionalis* species selection is likely tied to availability and local successional trajectories.

Similar to other research, we found *M. septentrionalis* roosting in live trees and snags, with snags selected more than expected based on their availability (Sasse and Perkins 1996, Lacki and Schwierjohann 2001, Lacki et al. 2009, Silvis et al. 2015a). While live trees can have cavities and loose bark used for roosting, snags are more likely to contain these features resulting in their disproportionate use as roosts. While DBH was variable, roosts tended to have a larger DBH than surrounding trees and snags. Larger trees and snags likely provide a more stable thermal environment, which is thought to decrease energetic demands and promote gestation and development of young (Kunz and Lumsden 2003, Barclay and Kurta 2007, Coombs et al. 2010). Selection for larger snags also may allow for greater roost retention between years, as larger snags often take longer to decay, are less likely to be downed during extreme weather events, and are more prone to develop or retain cavities and loose bark needed for roosting (Vanderwel et al. 2006, Barclay and Kurta 2007, Parish et al. 2010).

While previous studies have demonstrated no difference between snag densities of roost plots vs random plots (Lacki and Schwierjohann 2001, Lacki et al. 2009, Alston et al. 2019), the effect of snag density on selection of live tree vs snag roost has not been investigated. We found the relative probability of a roost being in a snag positively correlated with snag density surrounding the roost. The propensity of *M. septentrionalis* to use snags over live trees combined with their relative probability of using a snag as a roost increasing with snag density may indicate that live trees are only used when suitable snags are unavailable. However, it should be noted that *M. septentrionalis* have been documented using live trees as roosts even in areas of high snag density (Carter and Feldhamer 2005, Perry and Thill 2007).

During energetically demanding times, female *M. septentrionalis* have been found roosting in areas of high solar exposure which is thought to decrease thermoregulatory costs

(Perry and Thill 2007, Garroway and Broders 2008, Rojas et al. 2017). However, over half of the roosts in our study were located below the canopy, a roost selection attribute of *M. septentrionalis* previously reported to be more prevalent during warmer years in the central portion of their range (Silvis et al. 2015a). The positive correlation between roosts below the canopy and warmer temperatures combined with the prevalence of below canopy roosts in our study indicates that *M. septentrionalis* in northern Georgia may be selecting for reduced roost temperatures. Additionally, bats in our study preferred west-facing aspects on low-grade slopes and had no preference for aspect on steeper slopes, the former of which coincides with low solar exposure in the afternoon and the latter an apparent indifference to solar exposure. If selection for roosts was based on increased solar exposure, we would expect bats to disproportionally select south facing slopes which receive the most solar exposure (Willis and Brigham 2007, Hammond et al. 2016) or east facing slopes which receive solar exposure in the morning when temperatures are lowest (Riskin and Pybus 1998). Similar to Menzel et al. (2002) and Silvis et al. (2012), we found no relationship between roost selection and increased solar exposure, which could be because *M. septentrionalis* is reaching its upper thermal tolerance (Stevens 1989, Sunday et al. 2012). However, there are a number of factors, not evaluated in this study, that can influence roost temperature, including: canopy cover, ambient temperature, number of individuals present, and location of individuals within the roost structure (Boyles 2007).

Similar to other studies, we found *M. septentrionalis* utilized a network of roost trees (Johnson et al. 2012, Silvis et al. 2015b), but landscape scale analysis found no correlation between the central point of roost network and the surrounding landscape. Lack of preference in selecting roost network centers could be because individuals are not responding to roost habitat at the landscape scale. Instead, *M. septentrionalis* could be responding to non-roost related cues when selecting habitat on the landscape scale, then establishing a roost network within the selected area. Conversely, bats could be selecting for areas with diverse landscape features that accommodate all potential thermoregulatory needs, thus making the composite of landscape features within the roost network statistically indistinguishable from the surrounding landscape. Lastly, the lack of relationship between network centers and the surrounding landscape could be because we had a small sample size, 15 roost network centers, for comparison. The limited number of roost network centers likely made discerning patterns of selection more difficult. Additionally, several of our roost networks contained few roosts and may not accurately reflect the central point of the roost network.

M. septentrionalis in our study area occur at the southern extent of the range and higher temperatures in this region could change their thermoregulatory strategy, with solar exposure being unnecessary or avoided when selecting a roost. *M. septentrionalis* in Canada are at the northern range limit and select roosts to increase solar exposure during energetically expensive life history stages (Garroway and Broders 2008). In central portions of the species' range, Silvis et al. (2015a) found that in warmer years, bats roosted below the canopy more often, suggesting that selection for greater canopy cover could be an optimal strategy for thermoregulation. Variation in roost selection at the thermal extremes of a bats range has been documented in *M. sodalis*, with individuals at more northern latitudes roosting only in areas of high solar exposure (Kurta et al. 1993) and those in southern latitudes demonstrating greater variability in roost selection (Britzke et al. 2003). We note that our sample size precluded us from investigating variation in roost selection between female reproductive classes. Thus, we need more information on roosting habits of *M. septentrionalis* in the southern reaches of its range before a clear pattern of thermal requirements can be established.

Based on our results, land managers in the southern extent of *M. septentrionalis*' range should focus management efforts on snag creation and retention, providing snags across a range of DBH and canopy cover. Previous studies have demonstrated the benefits of fire to *M. septentrionalis* roost habitat (Johnson et al. 2009, Lacki et al. 2009, Ford et al. 2016), thus prescribed burning could be used to increase snag availability and promote roosting habitat. We recommend management strategies prioritizing areas where the species is known to occur following initial mortality, with additional effort afforded to areas where *M. septentrionalis* once occurred, as they are known to display site fidelity (Perry 2011). While landscape factors indicated that *M. septentrionalis* was indifferent to or avoided solar exposure, establishing this relationship can be difficult due to the number of factors that can influence roost temperature. Thus, more research is needed to obtain a comprehensive pattern of roost selection for *M. septentrionalis* in the southeastern US.

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Table 3.1: Number of samples (N), number of parameters (K), AIC value, difference in AIC from top model (Δ AIC), and AIC weight of all models with Δ AIC < 2 of the top model for all individuals and reproductive females. Models for each group were averaged based on the AIC weights and used to predict the *Myotis septentrionalis* roost occurrence in north Georgia from 2014-2017.

Model	N	K	AIC	Δ AIC	Weight
All Individuals					
East/West Aspect x Slope	407	4	246.37	0	0.7
East/West Aspect x Slope + Distance to Ridge	407	5	248.09	1.71	0.3
Reproductive Females					
East/West Aspect x Slope	308	4	186.99	0	0.71
East/West Aspect x Slope + Distance to Ridge	308	5	188.8	1.8	0.29

Table 3.2: Estimates, standard errors, 95% lower (LCL) and upper (UCL) confidence limits, and odds ratios of predictor variables used to estimate the relative probability of roost occurrence for all individuals and reproductive females in north Georgia from 2014-2017.

Predictor Variable	Estimate	SE	LCL	UCL	Odds Ratio
All Individuals					
Intercept	-2.646	0.496	-3.618	-1.675	
Aspect East/West	-1.519	0.544	-2.586	-0.452	0.212
Slope	0.005	0.011	-0.016	0.026	1.005
Distance to Ridge	0	0.001	-0.001	0.002	1.001
Aspect East/West x Slope	0.029	0.014	0.002	0.056	1.023
Reproductive Females					
Intercept	-2.612	0.521	-3.633	-1.59	
Aspect East/West	-1.694	0.61	-2.89	-0.497	0.184
Slope	0	0.013	-0.022	0.028	1.003
Distance to Ridge	0.001	0.001	-0.001	0.002	1.001
Aspect East/West x Slope	0.035	0.015	0.005	0.066	1.036

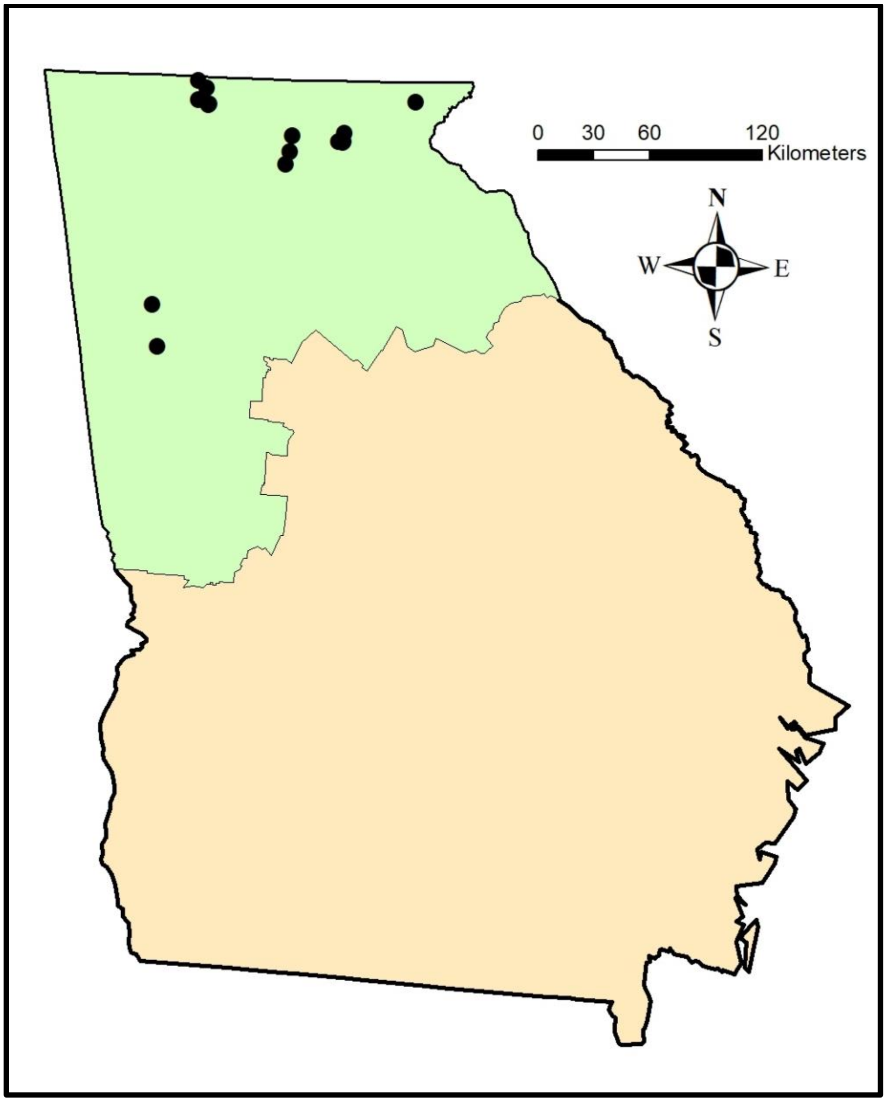

Figure 3.1: Locations (black dots) of roost centers used to characterize *Myotis septentrionalis* roost habitat at the landscape scale in northern Georgia from 2014-2017. The green area represents the historic range of *Myotis septentrionalis* within Georgia.

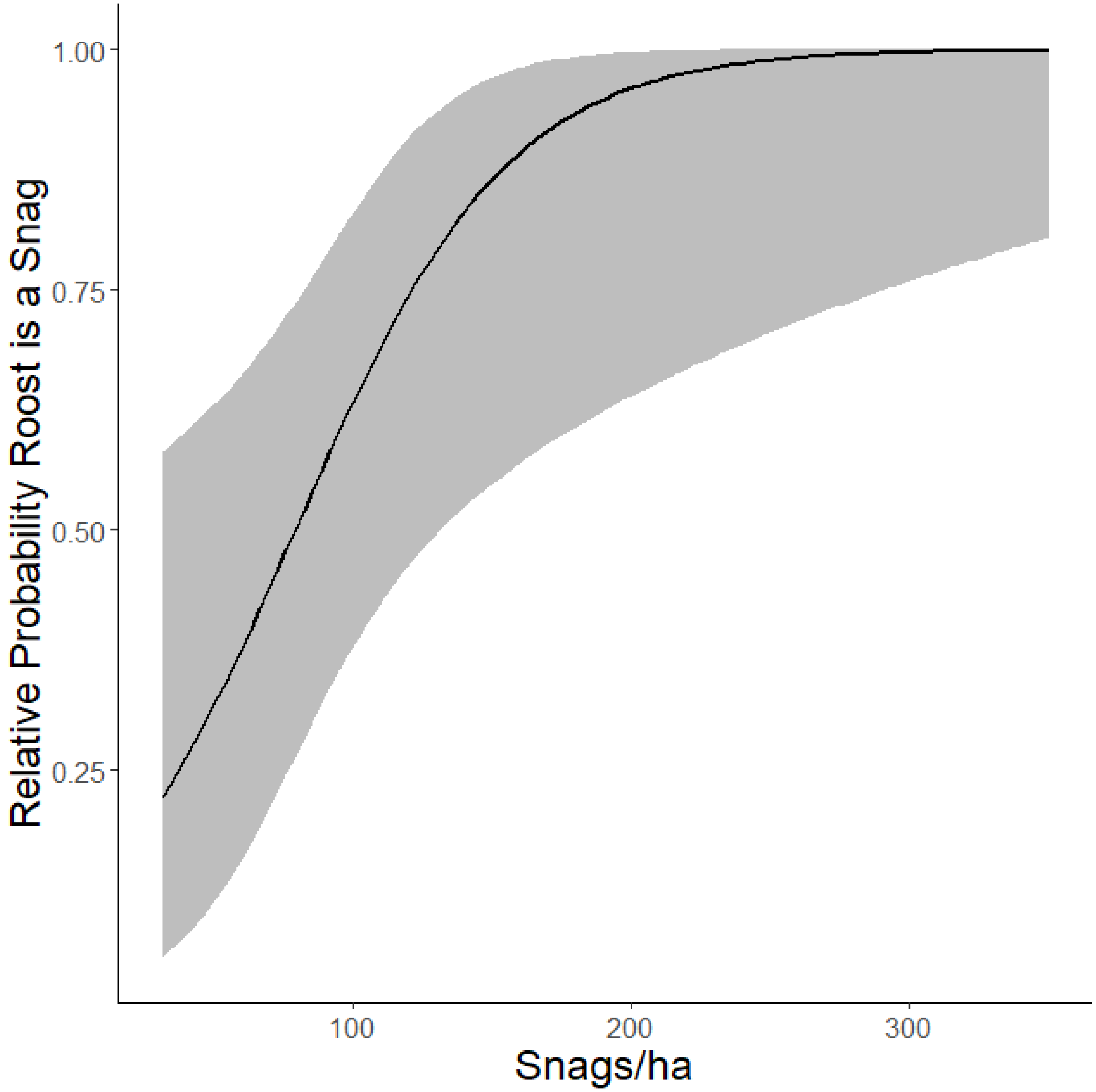

Figure 3.2: Relative probability (black line) and 95% confidence interval (gray band) that a *Myotis septentrionalis* roost in north Georgia between 2014 and 2017 was located in a snag based on the snag density per hectare.

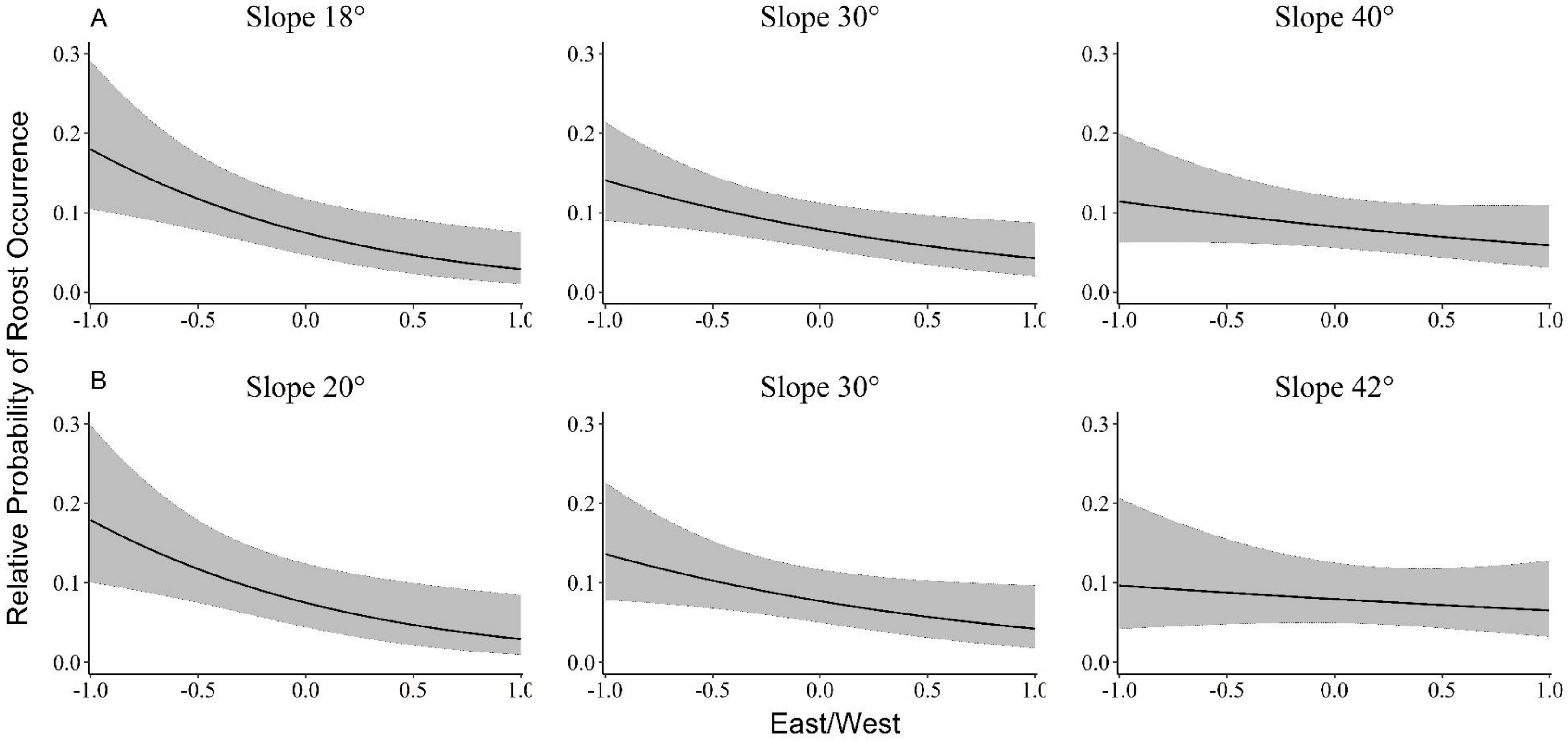

Figure 3.3: Relative probability of roost occurrence at the home range scale for all individuals (A) and Female (B) *Myotis septentrionalis* in north Georgia from 2014-2017, based on the interactive effect between aspect and slope. The black line represents the mean effect of the predictor variable and the grey band the 95% confidence interval. Above each subplot is the slope value constant, which represent the 25th percentile, mean, and 75th percentile of the slope values for each group. X-axis values are the sine of the radians for the roost or pseudo root aspects.

CHAPTER 4

MYOTIS SEPTENTRIONALIS AS AN UMBRELLA SPECIES FOR BAT CONSERVATION IN NORTHERN GEORGIA[3]

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[3] Grider, J. F., S. B. Castleberry, and J. Hepinstall-Cymerman. To be submitted to Biological Conservation

ABSTRACT

Recent mortality from white-nose syndrome and wind energy facilities has resulted in growing conservation concerns for bat species in temperate North America. Although these perturbations have affected numerous bat species, only *M. septentrionalis* has been afforded protection under the Endangered Species Act as a result. While conservation efforts are often focused on a single species, management decisions for target organisms can impact habitat for co-occurring species. We used capture records from 2007-2017 in a Bayesian community occupancy modeling framework to determine the ability of *M. septentrionalis* to confer protection to other species in northern Georgia, USA. We assessed bat occupancy using the covariates percent forest cover, elevation, and distance to karst topography, and probability of detection was explained by sampling period and duration of sampling event. Model fit and conferred protection were assessed using area under curve and co-occurrence with *M. septentrionalis*, respectively. Our models accurately predicted occupancy for five species. *Aeorestes cinereus* and *Lasionycteris noctivagans* had near 100% co-occurrence with *M. septentrionalis* while *Myotis grisescens* and *Nycticeius humeralis* had <15%. Potential protection afforded by *M. septentrionalis* to *A. cinereus* and *L. noctivagans* would be minimal because our study area does not encompass their primary summer habitat. However, the striking difference in *M. grisescens* and *N. humeralis* co-occurrence with *M. septentrionalis* highlights the potential to use multiple species as umbrellas to protect the larger community. While our results provide insight into the ability of a single species or subset of species to protect the larger community, it only implies protection via co-occurrence, which could be inadequate for the long-term success of all species due to critical habitat potentially being omitted from the protected area.

INTRODUCTION

Historically, disturbance at hibernacula and habitat loss were the largest drivers of population declines in North American temperate bats (Pierson 1998, Lacki et al. 2007). Recently, interactions with wind turbines and white-nose syndrome (WNS) have become the leading causes of mortality in bat populations. In the United States and Canada, WNS has killed millions of bats and threatens several species with regional extirpation (Frick 2010, Thogmartin et al. 2013). Additionally, wind turbines are estimated to have killed 1.3 million bats from 2000 to 2011 (Frick 2010, Arnett and Baerwald 2013, Reynolds et al. 2016). Mortality from these sources is widespread taxonomically and geographically. At least 21 species have experienced mortality from wind turbines and diagnostic symptoms of WNS have been documented in 12 North American species. Further, the effects are intensifying as WNS continues to spread annually causing additional mortality and infecting new species (White-Nose Syndrome Response Team 2019), and with wind energy production in the United States increasing every year since 1998 (WINDExchange 2019).

Despite elevated mortality, only one species, the northern long-eared bat (*Myotis septentrionalis*), has been listed under the U.S. Endangered Species Act (ESA) in response to recent declines. The listing took six years from the time of first petition (Matteson 2010, Fish and Wildlife Service 2016). A major hurdle for listing is that a species must be "in danger of extinction throughout all or a significant portion of its range" (U.S. Congress 1973), which makes protecting wide ranging species difficult. For example, tri-colored bats (*Perimyotis subflavus*) and little brown bats (*Myotis lucifugus*), which both experienced severe mortality from WNS over much of their range, are not proposed for listing until 2021 and after 2023, respectively (U. S. Fish & Wildlife Service 2019). Given delays in protection, high mortality rates, and ever-increasing mortality threats, species could be beyond the point of recovery and or functionally extinct by the time of their listing (Scott et al. 1987).

In accordance with 16 U.S.C. § 1533(f) of the ESA, recovery plans for threatened and endangered species are designed for protection and conservation of listed species (U.S. Congress 1973). However, these efforts are not limited to species in the recovery plan and the protection provided can be a critical conservation tool when knowledge of habitat requirements is uncertain or with delays in federal listing, as is the case with some temperate bat species (Caro 2003, Barrows et al. 2005). One approach to confer protection to the larger community is by utilizing an “umbrella species” approach (Caro and O’Doherty 1999). An umbrella species strategy relies on conservation efforts targeted at a species or small group of species, the umbrella, whose habitat requirements can encompass the needs of a larger group (Simberloff 1998).

The umbrella species concept has been applied and its efficacy assessed in ecological communities around the world. In the Pacific northwest, distribution of the northern spotted owl (*Strix occidentalis caurina*) was used in the delineation of protected areas, and resulted in greater species richness than would be expected by random selection of an equal area of land for protection (Dunk et al. 2006). A study examining large mammals as umbrella species in east Africa concluded that while benefits were not equivalent cross taxa, use of umbrella species was effective in recovery of non-target species (Caro 2003). While the above studies provide evidence of protection via umbrella species, management efforts for a single species do not necessarily benefit all taxa in the community. For example, recovery efforts for the red-cockaded woodpecker (*Leuconotopicus borealis*), whose habitat restoration requires frequent fires, can negatively affect bird species commonly associated with understory and dense vegetation (Allen et al. 2006).

To determine the potential ability of *M. septentrionalis* to act as an umbrella species for the larger bat community, we evaluated the following criteria often used when identifying a candidate species: requiring a large area, easily monitored, an existing understanding of its natural history and habitat requirements, co-occurrence with target species, moderate vulnerability to human disturbance, potential for management needs to benefit other species, and population persistence (Seddon and Leech 2008). With a range that covers most of the eastern United States and Canada and a mean home range of approximately 70 hectares, *M. septentrionalis* requires a relatively large area and co-occurs with many bat species (Caceres and Barclay 2000, Owen et al. 2003, Lacki et al. 2009). Additionally, knowledge of their natural history and summer habitat requirements have been documented across much of the range, with *M. septentrionalis* exhibiting a strong preference for forested habitat (Yates and Muzika 2006, Ford et al. 2006, Perry and Thill 2007, Henderson et al. 2008). Protection of forested habitat used by *M. septentrionalis* could potentially benefit bat species in the eastern United States, which all rely on forests for varying aspects of their life history (Lacki et al. 2007), likely leading to co-occurrence. While population persistence in the region is questionable given current declines, the aforementioned criteria demonstrate *M. septentrionalis* potential as an umbrella species for bat communities.

Within forested habitat, co-occurrence of bat species in eastern North American is enabled through physiological and morphological adaptations that allow for niche partitioning. The most notable of these adaptations is wing morphology and echolocation call structure, with low wing aspect ratio and high frequency calls suited for dense vegetation whereas high wing aspect ratio and low frequency calls being advantageous in open areas and above the canopy (Aldridge and Rautenbach 1987, Norberg and Rayner 1987, Kalcounis et al. 1999, Schnitzler and

Kalko 2001). Sympatric bat species with similar call structures and wing aspects further partition through selection of prey items relative to body size and subtle differences in call structure (Aldridge and Rautenbach 1987, Hickey et al. 1996). On a larger scale, bat occurrence is determined by topography, physiography, and land use history that influence abiotic factors and shape the biotic community (Dunson and Travis 1991, Cahill et al. 2014). Abiotic factors could be a significant influence on the bat community in our study area because several bat species, including *M. septentrionalis*, are at their range limit where abiotic factors are thought to disproportionately influence occupancy (Fenton and Barclay 1980, Decher and Choate 1995, Caceres and Barclay 2000, Cahill et al. 2014).

Recent mass mortality in temperate North American bat species highlights the need for effective conservation. However, time lags in species listing and inadequate knowledge of specific habitat requirements make conservation for all affected species difficult. An umbrella species may provide an effective conservation approach to protect bats across eastern North America. We examined the ability of *M. septentrionalis*, a federally protected bat species, to confer protection to the summer habitat of other bat species within its range. Protection was assessed via co-occurrence with *M. septentrionalis* using community occupancy modeling, which have previously been used to assess the effect of management action, land-use change, and identifying areas of species richness (Russell et al. 2009, Zipkin et al. 2009, Petracca et al. 2019). We hypothesized that protection provided by *M. septentrionalis* will be greatest for those species that exist in areas of high forest cover (Yates and Muzika 2006, Henderson et al. 2008, Kaminski et al. 2020) at higher elevation (Chapter 2 of this dissertation).

METHODS

We conducted our study in northern Georgia, USA including portions of the Blue Ridge, Valley and Ridge, Appalachian Plateau, and Piedmont physiographic regions (Figure 4.1). The study area is of interest because it includes the southeastern range limit for several species in the genus *Myotis,* including three federally protected species, Indiana bat (*Myotis sodalis*), *M. septentrionalis,* and gray bat (*Myotis grisescens*), and a species proposed for listing *M. lucifugus.* Sampling occurred primarily on national forests managed by the United States Forest Service and wildlife management areas managed by the Georgia Department of Natural Resources. Primary forest types on the study area are mesophytic (oak and maple) and southern mixed forest (oak and pine) (Dyer 2006). Elevation ranges from 290-1,562 m and rainfall is 127-213 cm/year (National Oceanic and Atmospheric Administration 2008, U.S. Geological Survey 2017).

We collected species occurrence records from mist-netting surveys conducted from mid-May through early August 2015-2017. Surveys followed the Indiana bat survey protocol (U.S. Fish and Wildlife Service 2015), which included mist-netting with double high mist-nets in temperatures >10° C beginning at sunset and continuing for five hours. Sampling was avoided during periods of precipitation or sustained high winds. Sites were netted no more than 2-3 consecutive nights at a single location.

Supplemental capture data from 2007-2017 were obtained from the Georgia Department of Natural Resources' Rare Species and Natural Community Database. These data were collected in areas where environmental impact statements were required, or areas thought to have suitable habitat for threatened or endangered bat species. All supplemental capture data followed the Indiana bat survey protocol regarding weather conditions, but some sites varied in duration of sampling and number of nights sampled.

Statistical Analysis

We used capture records to construct a community occupancy model which allowed for estimation of individual species summer occupancy and imperfect detection (Dorazio and Royle

2005). Nine species were considered in the model including the evening bat (*Nycticeius humeralis*), *M. grisescens, M. lucifugus, M. septentrionalis,* red bat (*Lasiurus borealis*), hoary bat (*Aeorestes cinereus*), silver-haired bat (*Lasionycteris noctivagans*), *P. subflavus,* and big brown bat (*Eptesicus fuscus*). Due to a limited number of capture records for some species, estimating all predictor variables of interest would not be possible if species were analyzed individually. Thus, we used community occupancy modeling which links single species occupancy models to the larger community under the assumption that species-specific predictor variables are random effects drawn from a single community distribution (Kery and Royle 2008). In community occupancy models, the community distribution ($\beta1$) is governed by "hyper-parameters" ($\mu_{\beta1}, \sigma_{\beta1}$) and can be written as: $\beta1 \sim$ Gaussian ($\mu_{\beta1}, \sigma_{\beta1}$), where $\mu_{\beta1}$ is the mean community level response to predictor variable $\beta1$ and $\sigma_{\beta1}$ the standard deviation of the community response (Kery and Royle 2009). Under this assumption, species are seen as similar but not identical, and using this method has been shown to reduce prediction error and improved estimates of species occupancy (Zipkin et al. 2009, Kery and Royle 2015).

The community occupancy model is a hierarchical model that predicts probability of occupancy for species of interest, *k*, at a given site, *i*, while accounting for imperfect detection. Model occurrence is specified using $z_{ik} \sim$ Bernoulli (ψ_{ik}), where ψ_{ik} is the probability of a species occurring at a given site. However, using this model alone, the state variable z_{ik} is not always known with certainty. To better account for uncertainty in the state variable and multiple sampling occasions, *j*, we instead modeled the observed state (x_{ijk}), which combines the state variable, z_{ik}, with probability of detection, P_{ijk} and can be written as $x_{ijk} \sim$ Bernoulli ($z_{ik} * P_{ijk}$). Under this model $x_{ijk} = 1$ only when $z_{ik} = 1$ and sampled zeros are allowed with probability $1\text{-}P_{ijk.}$ Note that sampled zeros can result in a true absence when $z_{ik} = 0$.

To estimate the state variable, $z_{ik,}$ we constructed a model that described the relationship between site-level habitat predictor variable *i* and species *k* occurrence. Site level predictor variables included in the model were those known to influence bat species within the study area, including: distance to karst topography, percent forest cover, and elevation (Ford et al. 2005, Yates and Muzika 2006, Pauli et al. 2017). Although we recognized that distance to karst topography would not be important for *L. Borealis, A. cinereus*, and *L. noctivagans*, all other bats considered use caves for a significant portion of the year in the study area, thus it was included in the model. Scale of effect for these predictor variables was assumed to be equivalent to the species' home range. However, home range estimates for species in this study can be difficult to calculate due to a paucity of knowledge and variation in home range size based on habitat, reproductive class, and analysis method used (Menzel et al. 2001, Mickaël et al. 2002, Mcloughlin et al. 2000). Therefore, a 1-km radius buffer (314.2 ha) was used to encompass the scale of effect of surrounding bat habitat. One-km radius moving windows were used on forest cover and elevation raster layers to derive mean vales of predictor variables across the study area. Source data for forest cover were all forest cover classes (41, 42, and 43) in the 2011 National Land Cover Data set (U.S. Geological Survey 2014). Elevation data were obtained using the10-m digital elevation model (DEM) from USGS national elevation dataset (U.S. Geological Survey 2017). Distance to karst topography was derived using straight-line distance from each site to the nearest polygon in the USGS karst topography data layer (Weary and Doctor 2014). Effects of species and site-level predictor variables were used to estimate the state variable using the following equation, where I is the species-specific intercept and β1- β3 the species-specific parameter estimates for site occupancy:

$$\text{logit}\ (\psi_{ik}) = I_k + \beta1_k\text{Forest}_i + \beta2_k\text{Elevation}_i + \beta3_k\text{Karst}_i$$

Species probability of detection (P_{ijk}) was expected to vary by years since the arrival of WNS and duration of sampling event. We assumed that the bat community was closed over the study duration but recognized that mortality from WNS and seasonal variation could influence probability of detection. Therefore, we included a temporal predictor variable. Points sampled before 2012 were pooled and considered a single time period (pre-WNS). In subsequent years, we allowed detection to vary by year because some species were experiencing mortality from WNS, which likely influenced detection. Although WNS was not documented in our study area until 2013, two counties directly bordering the northwest edge of our study area and one county 7.2 km from the northeast of our study area tested positive for WNS in the winter of 2011 – 2012, and could have influenced *M. septentrionalis* in our study area. We defined duration of sampling event as the number of hours elapsed during each night of sampling. Probability of detection estimates were derived using the following equation, where I is the species-specific intercept and β1- β2 the species-specific parameter estimates for detection probability:

$$\text{logit}(P_{ijk}) = I_k + \beta 1_k \text{Year}_{ij} + \beta 2_k \text{Duration}_{ij}$$

We estimated the effects of seven predictor variables for each species using a Bayesian analysis of the model with non-informative priors on the hyper-parameters. Using package rjags (Plummer et al. 2019) in R (R Core Team 2019), the model was run for 41,000 iterations with a burn-in of 21,000 iterations to ensure all samples from the Markov chains were drawn from the target distribution (Ravenzwaaij et al. 2018). We ran three Markov chains to ensure distribution of samples from all chains was similar and convergence was met. Convergence of chains was additionally monitored using a Gelman diagnostic (Brooks and Gelman 1998). Model fit was assessed using area under curve values (AUC), with AUC > 0.7 considered capable of distinguishing occupied from unoccupied areas (Pearce and Ferrier 2000). Predictor variables were determined to significantly affect occupancy and detection if the 95% credible intervals around mean estimates did not include zero. Cutoffs indicating occupancy were derived using package ROCR (Sing et al. 2005) by selecting values that achieved the shortest distance to top-left corner of the receiver operator characteristic curve (ROC curve) (Liu et al. 2005).

The ability of *M. septentrionalis* to act as an umbrella species was assessed by the percent of each species' occupied area that fell within areas occupied by *M. septentrionalis.* A species was considered protected if ≥70% of its occupied area fell within *M. septentrionalis* occupied area. While the true threshold for habitat needed to persist is unknown, 70% was selected based on bat ecology and factors known to influence the amount of habitat needed for a species to persist, such as emigration rate and survival (Fahrig 2001). Those species whose AUC values did not meet the 0.7 minimum were not considered for *M. septentrionalis* co-occurrence due to uncertainty surrounding estimates of their occupied area.

RESULTS

We sampled 533 unique sites for 1,093 nights, with sites sampled an average of 2.1 nights (standard deviation = 1.1, range 1-9 nights [Figure 4.1]). Of the nine species modeled, the most prevalent species, *L. borealis* and *E. fuscus*, were captured at 390 and 325 sites, respectively, while the three least observed species, *L. cinereus*, *L. noctivagans*, and *M. lucifugus*, were captured at 14, 27, and 24 sites, respectively (Figure 4.2). *M. septentrionalis* and *P. subflavus* captures declined from pre-WNS to 2017 whereas captures of other species were relatively consistent across sampling years (Table 4.1).

L. borealis and *M. septentrionalis* were the only species whose site occupancy was significantly affected by forest cover within 1 km^2 (Table 4.2). Both species were positively associated with forest cover, with *L. borealis* being 1.07 and *M. septentrionalis* 1.17 times more likely to occur for every one percent increase in forest cover. Distance to karst topography significantly affected site occupancy of *E. fuscus* and *M. grisescens*, however, these species responded to the predictor variables differently, with *M. grisescens* 2.76 times less likely to occur and *E. fuscus* 1.53 times more likely to occur with every 15 km from karst topography. Occupancy of five species were significantly correlated with mean elevation. *M. septentrionalis, L. cinereus,* and *L. noctivagans* were 4.00, 5.42, and 2.08 times more likely to occur with every 195 m increase in mean elevation. Conversely, *N. humeralis* and *M. grisescens* were 7.93 and 2.61 times less likely to occur with every 195 m increase in mean elevation. Two species, *M. lucifugus*, and *P. subflavus*, were not significantly influenced by any occupancy predictor variable we examined.

Sample year had a significant effect on detection for four species (Table 4.2). *M. lucifugus*, *P. subflavus,* and *M. septentrionalis* were 2.32, 1.69, and 2.27 times less likely and *A. cinereus* was 1.55 times more likely to be detected with each subsequent year. *M. septentrionalis* and *E. fuscus* detection was positively associated with duration of sampling event, with probability of detection 1.38 and 1.33 times higher for each additional hour of sampling, respectively. Neither year nor duration of sampling event significantly explained detection probability of the four remaining species.

Gelman diagnostic values for all model parameters was <1.09 indicating model convergence. AUC values indicated that the model's ability to accurately predict areas occupied by *M. lucifugus, E. fuscus, L. borealis,* and *P. subflavus* was poor (Table 4.2). For the remaining five species, the model was capable of distinguishing occupied from unoccupied areas (AUC values > 0.7) and were thus considered for protection under the umbrella of *M. septentrionalis* (Figure 4.3). Only *L. noctivagans* and *A. cinereus* were conferred protection, with the area occupied by both species being 99.7% and 100% within the occupied area of *M. septentrionalis* (Table 4.3). Adequate protection could not be conferred for *N. humeralis* and *M. grisescens*, with 8% and 12% of their occupied areas, respectively, occurring within the areas occupied by *M. septentrionalis.*

DISCUSSION

Our study provides evidence that listing of a wide-ranging species can confer protection to the habitat of other bat species, however, protection provided within our study area was limited to a small number of species in the community. The only species afforded protection, *A. cinereus* and *L. noctivagans,* are long distance migrants that generally are not present in the southeastern region in summer (Cryan 2003), making summer habitat in the region a low priority for both species. The remaining two species for which occupancy could be predicted, *M. grisescens* and *N. humeralis*, infrequently co-occurred with *M. septentrionalis,* and are thus afforded little protection from its federal listing. However, neither species is currently in need of protection from *M. septentrionalis* as the former is a federally protected species and the latter a common species that faces no major threats to persistence (U. S. Fish & Wildlife Service 1976).

Accurately distinguishing between occupied and un-occupied areas was only possible when a species was significantly influenced by mean elevation. Although, more commonly occurring at more northern latitudes in summer (Cryan 2003), *A. cinereus* and *L. noctivagans* were found at high elevation sites within our study area, which are known to maintain lower summer temperatures (PRISM Climate Group 2015). Temperatures at higher elevations in northern Georgia are comparable to temperatures at northern latitudes and may allow for small numbers of *A. cinereus* and *L. noctivagans* to remain in northern Georgia during summer. Conversely, occupancy of *M. grisescens* and *N. humeralis* was negatively correlated with elevation. *M. grisescens* aversion to higher elevations could be because high elevations were largely void of karst topography required for roosting (Weary and Doctor 2014) or their propensity to forage over lager streams and rivers (LaVal et al. 1977, Johnson et al. 2010), which are more likely to occur at lower elevations. Similar to our study, previous occurrences of *N. humeralis* were positively correlated with lower elevations (Menzel et al. 2000, Johnson et al. 2010). Reasons for *N. humeralis* inability to occupy higher elevation sites is less clear, but could be related to competitive exclusion, lack of suitable habitat, and or lower temperatures.

Several species not restricted by elevation, *E. fuscus, L. borealis,* and *P. subflavus*, were ubiquitous across the study area which makes predicting species occurrence difficult (McPherson et al. 2004, Luoto et al. 2005, Elith et al. 2006). Additionally, because these species appear to occupy large areas beyond *M. septentrionalis'* occupied area, they likely would have received inadequate protection. Additionally, *M. lucifugus* only occurred at the most northern and southern extremes of the study area and was rarely encountered (19 of 533 sites), providing limited ability to make inferences about occupancy (Stockwell and Peterson 2002, McPherson et al. 2004). Distinguishing between occupied and un-occupied areas for these species would require a more comprehensive sampling effort, accounting for fine-scale habitat selection, or constructing individual models with species-specific effects of scale and predictor variables.

While all bats modeled use forested habitat (Lacki et al. 2007), only *L. borealis* and *M. septentrionalis* were positively associated with percent forest cover. Forest cover's lack of influence on occupancy could be due to concentrated sampling in forested areas, which limited sample variation, making sites less distinguishable. Additionally, our study did not account for variation in forest habitat, which is known to influence habitat selection in bats (Ford et al 2005, Yates and Muzika 2006). Further refinement of forest habitat by species composition, vertical structure, age classes, or arrangement would likely result in a greater effect of forest cover on species occupancy.

As expected, occupancy of *M. grisescens,* a year-round cave obligate, was restricted to areas in proximity to karst topography (Decher and Choate 1995). *M. grisescens* dependence on karst restricted their co-occurrence with *M. septentrionalis,* whose occupancy was fragmented in karst areas. *E. fuscus,* the only other bat for which distance to karst topography had a significant effect on occupancy, had an aversion to karst topography. Reasons for this relationship are unknown but could be due to un-modeled factors correlated with karst topography. While other species in the community rely on caves, their lack of fidelity to karst topography in our model is not surprising because our model predicted summer habitat and caves are primarily used in winter.

Bats in our study area with the highest reported mortality from WNS, *M. septentrionalis, M. lucifugus,* and *P. subflavus*, experienced a decrease in detection over the study period (Ingersoll et al. 2013). Decrease in detectability of *M. septentrionalis, M. lucifugus,* and *P. subflavus* corroborates previous findings linking detection with abundance (Royle and Nichols 2003), as over the course of the study these species experienced the greatest declines in abundance and were the only species in which we observed temporal declines in detectability. Conversely, *A. cinereus* was the only species that was more likely to be captured with each passing year. *A. cinereus* increased in detectability was unexpected, but due low overall capture rates, only a marginal increase in capture rate was needed for a significant effect. Increasing sampling duration significantly increased *M. septentrionalis* and *E. fuscus* detection rates, but there was no effect of mist-netting duration on detection of other species. The lack of effect could be attributed to periods of highest activity being the first and last hours of the night, making capture efforts in the middle of the night less productive (Hayes 1997). However, post-WNS activity patterns of bat species are altered with most species experiencing a more even distribution of activity across early evening hours (Jachowski et al. 2014). Shifts to more temporally uniform activity would result in every hour of effort seeing more comparable bats captures, and could potentially explain the positive correlations between detection and nightly effort seen in *M. septentrionalis* and *E. fuscus*.

The ability of *M. septentrionalis* to serve as an umbrella for the larger bat community is questionable given that the only species with significant co-occurrence, *A. cinereus* and *L. noctivagans*, were not prevalent on the landscape. However, *M. septentrionalis* covered a large area of mesophytic forests in northern Georgia that contains some of highest salamander, freshwater fish, and freshwater mussel diversity on Earth, with many endemic species (Lydeard and Mayden 1995, Warren et al. 2000, Petranka 2010). Additionally, many species are limited to small geographic areas, vulnerable to disturbance, and have severely limited dispersal ability, making them prone to extinction (Işik 2011). Given co-occurrence of *M. septentrionalis* with this areas of high global biodiversity, protection afforded to *M. septentrionalis* could act as an umbrella for these taxonomic groups.

While *M. septentrionalis* alone would not provide adequate protection, the larger bat community could likely be protected through the conservation of two or more species (Fleishman et al 2000, Roberge and Angelstam 2004). An optimal set of focal species for use as a multi-species umbrella would have little co-occurrence, thus maximizing conservation areas and covering a wider range of habitats. Such is the case for M. *grisescens* and *M. septentrionalis,* the two federally protected species in our study area. On their own, *M. grisescens* and *M. septentrionalis* are predicted to occur in 16.6% and 26.4% of the study area, respectively, but in combination the two species occur on 40.1% of the study area. However, because federal protection of *M. grisescens* is focused on the protection of caves, its ability to confer protection to other species is limited (Brady et al. 1982). Nonetheless, this example highlights the potential for conservation of a few species to protect the larger community.

In our study, as well as others assessing the potential of umbrella species, protection is implied via co-occurrence (Fleishman et al. 2001, Copeland et al. 2014, Malso et al. 2016). Umbrella species may not cover all necessary habitat for co-occurring species within the protected area, leading to inadequate protection (Noss et al. 1997). Therefore, fully understanding protection conferred by an umbrella species would require long term monitoring and extensive sampling of several species within a study area. While studies implying protection through the use of an umbrella species are numerous, long term assessments of population growth and species occupancy with implied protection are limited (Caro 2003). Further, because our sampling occurred during summer, implied protection would only pertain to summer habitat requirements of these species. While summer habitat is critical for the recruitment of young into the population, an ideal umbrella species would provide protection for all habitat relevant to each species life history. Despite the potential shortcomings, the use of a single or multi-species umbrella may be the best conservation strategy given the severity of bat mortality and potentially long process for federally listing a species.

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Table 4.1: Total and annual bat captures by species during sampling conducted in northern Georgia, USA, 2007-2017. Captures from 2007 through 2011 are combined because to represent the period before the influence of white-nose syndrome on the study area. Species abbreviations are as follows: EPFU (*Eptesicus fuscus*), NYHU (*Nycticeius humeralis*), MYSE (*Myotis septentrionalis*), MYLU (*Myotis lucifugus*), MYGR (*Myotis grisescens*), PESU (*Perimyotis subflavus*), LABO (*Lasiurus borealis*), LACI (*Aeorestes cinereus*), and LANO (*Lasionycteris noctivagans)*

	2007-2011	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**
EPFU	45	47	462	434	351	496	209
NYHU	8	6	41	110	35	44	6
MYSE	117	6	50	13	10	6	1
MYLU	10	1	33	9	2	0	0
MYGR	2	0	43	7	9	12	6
PESU	67	0	101	96	60	22	1
LABO	93	43	373	358	443	301	151
LACI	1	0	1	6	0	6	0
LANO	0	0	4	0	4	17	11
Sites Visited	43	12	143	110	159	101	64
Sampling Occasions	47	16	241	190	314	179	111

Table 4.2: Mean predictor variable estimates and 95% credible intervals for bat occupancy and detection in community occupancy models determined from bat sampling conducted in northern Georgia, USA, 2007-2017. Bold predictor variable estimates indicate significance based on 95% credible intervals. Species abbreviations are as follows: EPFU (*Eptesicus fuscus*), NYHU (*Nycticeius humeralis*), MYSE (*Myotis septentrionalis*), MYLU (*Myotis lucifugus*), MYGR (*Myotis grisescens*), PESU (*Perimyotis subflavus*), LABO (*Lasiurus borealis*), LACI (*Aeorestes cinereus*), and LANO (*Lasionycteris noctivagans*).

	Occupancy				**Detection**			
	Intercept	**Forest**	**Karst**	**Elevation**	**Intercept**	**Year**	**Time**	**AUC**
EPFU	1.896	-1.046	**0.426**	0.38	-0.503	-0.045	**0.287**	0.596
	(1.02, 2.875)	(-2.32, 0.17)	(0.07, 0.903)	(-0.022, 0.842)	(-1.434, 0.448)	(-0.152, 0.06)	(0.106, 0.474)	
NYHU	-1.75	0.727	-0.16	**-2.07**	-0.691	-0.113	0.102	0.748
	(-2.842, -0.668)	(-0.573, 2.056)	(-0.476, 0.168)	(-3.015, -1.291)	(-2.104, 0.698)	(-0.281, 0.056)	(-0.167, 0.37)	
MYSE	-2.229	**2.819**	-0.177	**1.386**	0.207	**-0.819**	**0.322**	0.734
	(-3.785, -0.574)	(0.82, 5.008)	(-0.771, 0.372)	(0.58, 2.686)	(-1.236, 1.648)	(-1.04, -0.618)	(0.026, 0.666)	
MYLU	-0.884	-0.056	0.693	0.997	-0.363	**-0.842**	0.22	0.658
	(-2.574, 1.313)	(-2.384, 2.216)	(-0.025, 1.706)	(-0.071, 2.883)	(-2.203, 1.411)	(-1.232, -0.524)	(-0.125, 0.642)	
MYGR	-3.151	0.447	**-1.015**	**-0.96**	-0.357	-0.234	0.127	0.814
	(-4.604, -1.771)	(-1.263, 2.142)	(-1.922, -0.3)	(-2.016, -0.088)	(-2.248, 1.508)	(-0.492, 0.006)	(-0.248, 0.5)	
PESU	-0.13	-0.074	0.21	-0.219	0.861	**-0.526**	0.163	0.559
	(-0.95, 0.758)	(-1.255, 1.103)	(-0.101, 0.574)	(-0.595, 0.135)	(-0.483, 2.218)	(-0.701, -0.36)	(-0.086, 0.43)	
LABO	1.22	**1.948**	-0.269	0.285	0.421	-0.049	0.08	0.596
	(0.137, 2.466)	(0.264, 3.92)	(-0.638, 0.121)	(-0.322, 1.096)	(-0.429, 1.371)	(-0.141, 0.042)	(-0.1, 0.242)	
LACI	-2.998	1.61	0.09	**1.69**	-1.242	-0.185	-0.137	0.826
	(-5.485, -0.633)	(-0.78, 4.488)	(-0.902, 1.008)	(0.319, 3.87)	(-3.518, 0.656)	(-0.474, 0.105)	(-0.557, 0.24)	
LANO	-3.47	1.957	-0.049	**0.732**	-2.701	**0.436**	-0.233	0.806
	(-5.65, -1.532)	(-0.189, 4.595)	(-0.708, 0.517)	(0.148, 1.598)	(-5.996, -0.039)	(0.08, 0.841)	(-0.792, 0.224)	

Table 4.3:
Total area occupied (ha) and area (ha) and percent of summer habitat co-occurrence with *M. septentrionalis* for bat species in northern Georgia, USA, 2007-2017. Species abbreviations are as follows: MYGR (*Myotis grisescens*), NYHU (*Nycticeius humeralis*), LACI (*Aeorestes cinereus*), and LANO (*Lasionycteris noctivagans*).

Species	Area Occupied (ha)	Area of Co-occurrence	Percent Co-occurrence
MYGR	608,019	73,830	12.1
NYHU	2,606,943	218,381	8.4
LACI	522,856	522,854	100
LANO	1,009,172	1,006,016	99.7

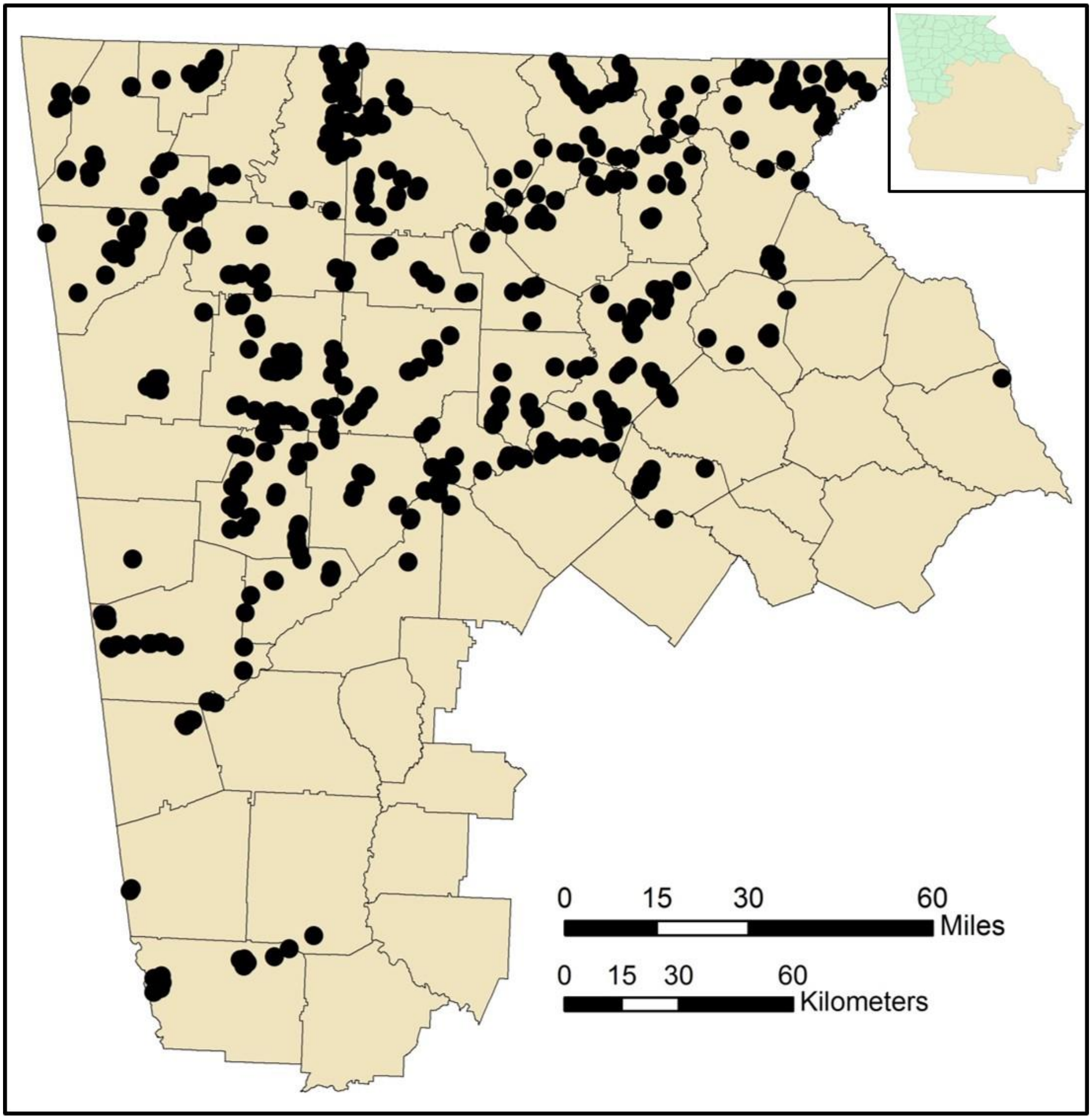

Figure 4.1: Sites sampled (black dots) to examine bat species occupancy and co-occurrence with *M. septentrionalis* in northern Georgia, USA, 2007-2017.

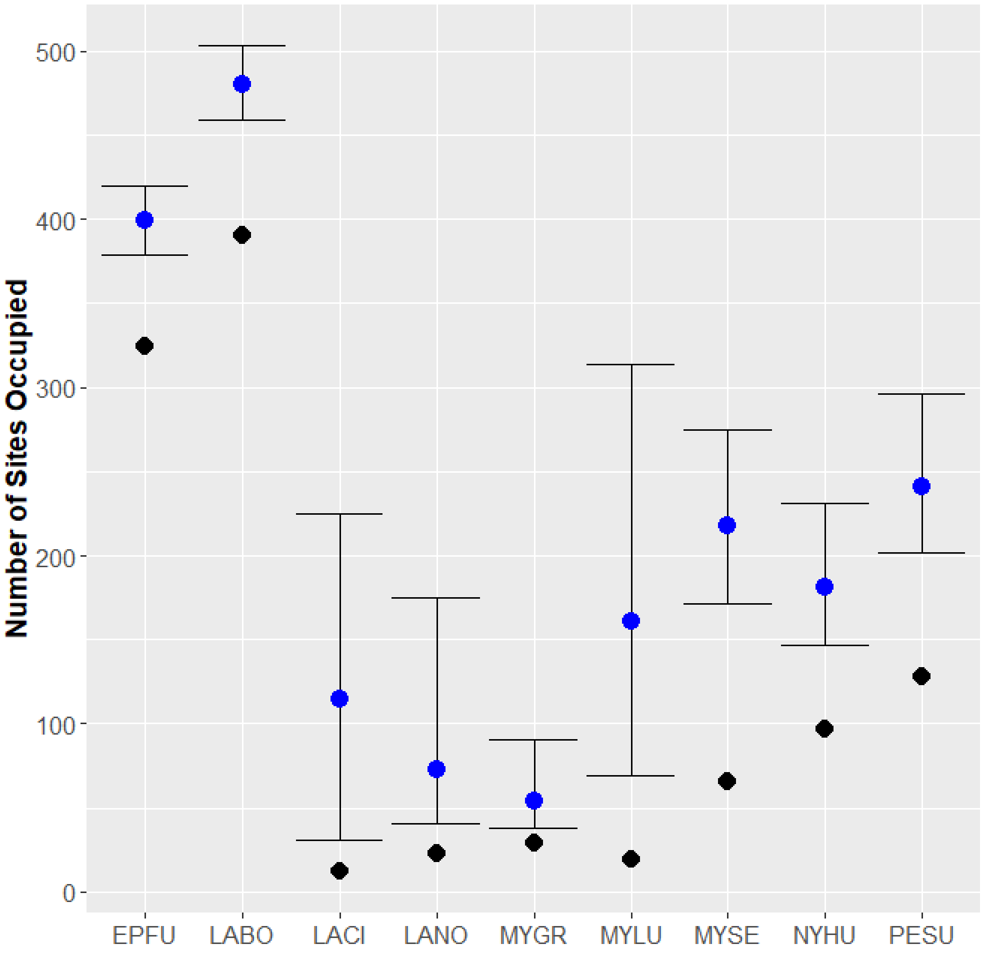

Figure 4.2: Number of sites where a species was captured (black dots), mean estimate (blue dots), and 95% credible intervals for sites occupied by nine bat species in northern Georgia, USA, 2007-2017. Four letter species abbreviations are as follows: EPFU (*Eptesicus fuscus*), NYHU (*Nycticeius humeralis*), MYSE (*Myotis septentrionalis*), MYLU (*Myotis lucifugus*), MYGR (*Myotis grisescens*), PESU (*Perimyotis subflavus*), LABO (*Lasiurus borealis*), LACI (*Aeorestes cinereus*), and LANO (*Lasionycteris noctivagans*).

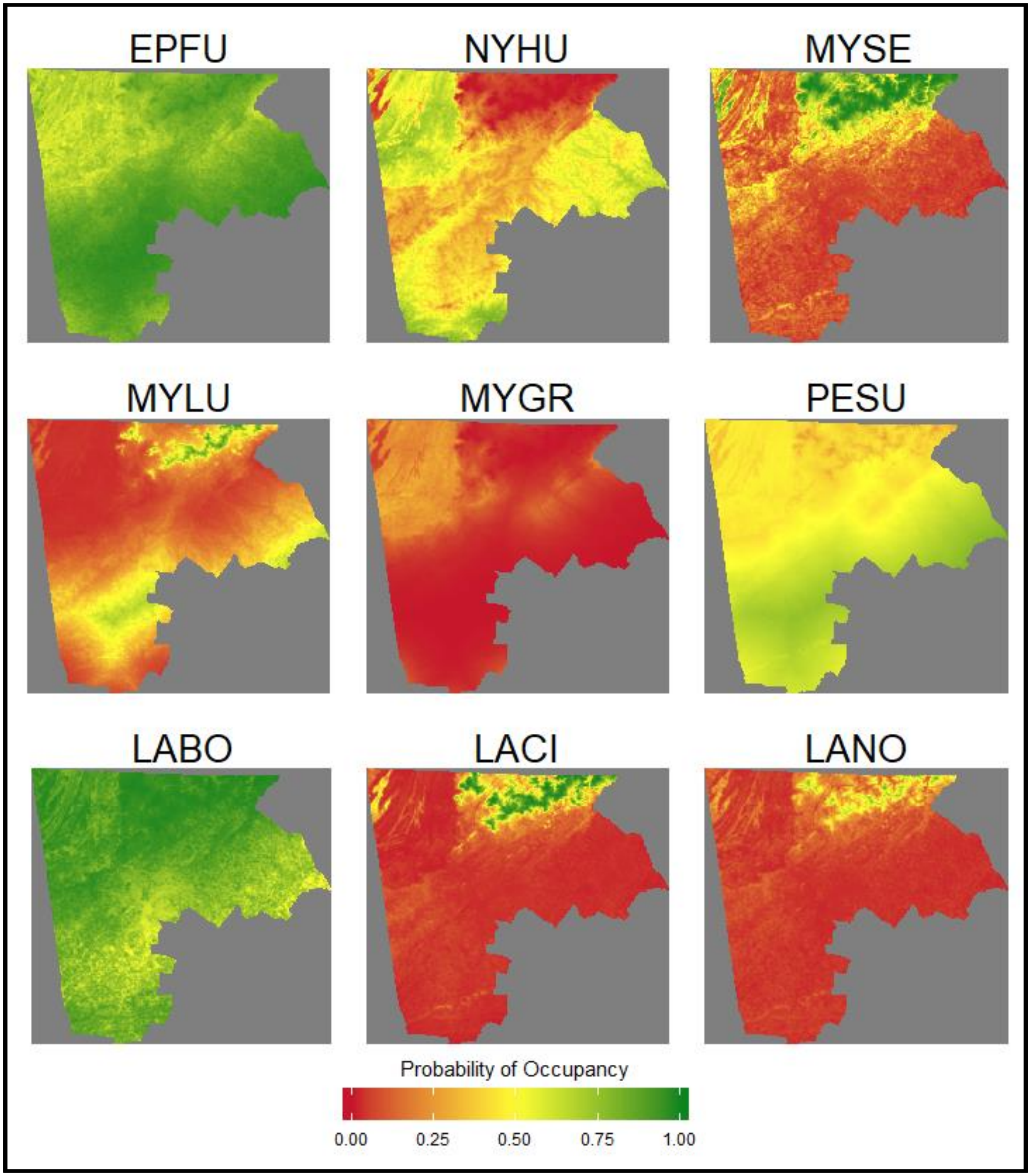

Figure 4.3: Predicted probability of occupancy for nine bat species in northern Georgia, USA, 2007-2017, derived from community occupancy models. Species abbreviations are as follows: EPFU (*Eptesicus fuscus*), NYHU (*Nycticeius humeralis*), MYSE (*Myotis septentrionalis*), MYLU (*Myotis lucifugus*), MYGR (*Myotis grisescens*), PESU (*Perimyotis subflavus*), LABO (*Lasiurus borealis*), LACI (*Aeorestes cinereus*), and LANO (*Lasionycteris noctivagans*).

CHAPTER 5

SUMMARY AND MANAGEMENT IMPLICATIONS

Mortality associated with white-nose syndrome (WNS) and wind energy facilities has ushered in a new zeitgeist and sense of urgency for bat conservation in North America. As species are listed and proposed to be listed, there is no clear understanding of how occurrence and life history requirements for species will change across their range. Once one of the most common bats in eastern North America, *M. septentrionalis* was the first species listed under the Endangered Species Act (ESA) due to mortality from WNS (Caceres and Barclay 2000, Fish and Wildlife Service 2016).

Throughout much of the range, *M. septentrionalis* is dependent on forest cover even in patchy forest networks (Yates and Muzika 2006, Henderson and Broders 2008, Jantzen and Fenton 2013). Further, diurnal summer roosts are almost exclusively in trees, with patterns of roost use varying with land use history (Cryan et al. 2001, Menzel et al. 2002, Perry and Thill 2007). While this information has been crucial for initial management actions, published data on summer habitat requirements of *M. septentrionalis* along the southern extremes of their range are limited. To address this paucity of knowledge, we investigated landscape factors driving roost and habitat selection of *M. septentrionalis* in northern Georgia, which represents the southern extent of the species range. The objective of this study was to provide land managers and government agencies with summer distribution and habitat associations of *M. septentrionalis* so they can better plan for and mitigate habitat loss at the southern range limit.

Occupancy

Understanding basic habitat associations and occurrence patterns of a species is fundamental to its conservation. To inform management for *M. septentrionalis*, we investigated shifts in habitat use and area occupied as the species experienced mortality from WNS. Changes in occupancy were estimated using dynamic occupancy models, which related predictor variables of land cover and topography at the home range (65 ha) and landscape scale (491 ha) to initial occupancy, site extinction, and site colonization. The model was partitioned into seven time periods, with initial occupancy derived from captures from multiple years before WNS arrived in the study area and with each subsequent year modeled independently.

Our findings indicated that, prior to the arrival of WNS, *M. septentrionalis* was positively associated with both deciduous forest cover at the home range scale and mean elevation at the home range and landscape scales. Our findings are consistent with previous studies which related *M. septentrionalis* occurrence to forest cover even when forest patches were highly fragmented (Ford et al. 2005, Jantzen and Fenton 2013). While most studies relate occupancy to forest cover and not specifically deciduous forest cover, we were unable to do so because sites sampled prior to WNS were all forested making them indistinguishable to our model. Previous associations between *M. septentrionalis* occupancy and elevation have not been reported. However, the observed relationship likely is due to our study area having twice the topographic relief (~1400 m) reported in other studies (~650 m) (Owen et al. 2003, Ford et al. 2005, Henderson and Broders 2008). Additionally, the positive correlation between higher elevations and occupancy along the southern range limit could be due to higher elevations having cooler temperatures (PRISM Climate Group 2015) that are more ideal for *M. septentrionalis'* thermoregulation.

Our results indicate that as *M. septentrionalis* experienced declines from WNS, site extinction was inversely related to large patches of deciduous forest and higher mean elevation at the landscape scale. While deciduous forest and elevation were the primary drivers of occupancy before and after the arrival of WNS, the scale of selection shifted post-WNS and habitat selection was only detected at the landscape scale. Additionally, we found that bats were selecting for large patches of deciduous forest rather than percent deciduous forest across the landscape, suggesting that larger patches of deciduous forest may be higher quality habitat for this species. These habitat association post-WNS resulted in the area occupied by *M. septentrionalis* retracting northward toward higher elevations and larger expanses of forest, areas likely representing core habitat.

The observed northward range retraction was unexpected. Previous research indicated that proximity to known infection played a significant role in WNS susceptibility (Wilder et al. 2011, Maher et al. 2012, Thogmartin et al. 2012), thus I hypothesized that bats closest to the periphery would have a buffer from disease related perturbation. However, while WNS took longer to reach peripheral populations, once present these populations appeared to be disproportionately vulnerable. We speculate this vulnerability is due to reduced body condition in peripheral populations, a factor linked to reduced WNS survival (Cheng et al. 2019). Better body condition in core habitat likely would result from large patches of deciduous forest at higher elevations providing higher quality habitat resulting in improved body condition. Further, peripheral populations may have reduced body condition due to longer energetically expensive migrations to and from hibernacula.

The ability to track range retraction of *M. septentrionalis* using land cover and topography indicates that bat populations are persisting due to habitat relationships and not genetic resistance alone. Given the importance of habitat to population persistence, effective management and conservation of quality habitat likely will aid in *M. septentrionalis* recovery. Knowing this, we suggest land managers in northern Georgia and surrounding areas protect large patches of high elevation deciduous forest, with habitat on the outer periphery being lower management priority.

Roost Habitat

While recent mass mortality of *M. septentrionalis* has occurred at hibernacula, population recovery is impossible without recruitment of young, for which summer roosts play an integral role (Kunz 1982). Roost tree selection is influenced by thermoregulatory needs, with bats favoring tall trees in more open canopies with a larger diameter at breast height (DBH) relative to random trees (Kalcounis-Rueppell et al. 2005, Boyles 2007). While *M. septentrionalis* almost exclusively roosts in trees, there is variation in roost selection across its range, making conservation for roosting habitat difficult (Cryan et al. 2001, Lacki and Schwierjohann 2001, Perry and Thill 2007). To better understand summer diurnal roosting habitat of *M. septentrionalis* on the southern periphery of the range, we compared known roosts and center points of roost networks to surrounding habitat and landscape. Landscape analysis was conducted on all bats for which we had data and separately for reproductive female bats.

We tracked 14 female and 4 male *M. septentrionalis* to 37 roost, all of which were in snags or live trees. Bats displayed no preference for tree species, utilizing 16 species throughout the study. Similar to other studies, we found snags were used more often relative to their abundance (Sasse and Perkins 1996, Lacki and Schwierjohann 2001, Silvis et al. 2015).

Preference for snags over live trees is likely because they provide loose bark, hollow boles, and cavities *M. septentrionalis* requires for roosting. Additionally, use of snags as roosts was positively associated with snag density, indicating that live trees may only be selected as roosts when snags are limited. Lastly, snags used as roosts had a significantly larger diameter than immediately surrounding snags. Use of larger diameter trees has been a previously documented characteristic of bat roosts and is thought to increase the likelihood of roost retention between years and/or provide a more stable thermal environment for rearing young (Kunz and Lumsden 2003, Vanderwel et al. 2006, Barclay and Kurta 2007).

Comparing roosts to pseudo-absences at the home range and landscape scale revealed that roost selection of all bats and reproductive females was influenced by the interaction of slope and aspect at the home range scale. Both groups disproportionately selected west facing aspects on low slopes with preference diminishing as slope increased. Given west facing aspects and low slopes are associated with reduced solar exposure and no preference was observed on steeper slopes, bats seem to be displaying an indifference to or are potentially avoiding high solar exposure. Solar exposure may be less important for *M. septentrionalis* on our study area, which represents the southern range periphery, because they are potentially reaching their thermal limit (Stevens 1989, Sunday et al. 2012).

Our results suggest that to promote *M. septentrionalis* summer roosting habitat in northern Georgia and surrounding areas at the southern periphery, land managers should encourage snag generation and retention. While our results indicate that *M. septentrionalis* is not selecting roost locations that promote solar exposure, there remains a number of unexplored factors that potentially influence the thermal environment of a roost, including ambient temperature, roost location, and/or number of individuals present (Boyles 2007). However, based on our data, *M. septentrionalis* at the southern periphery may avoid or may be indifferent to roosts with increased ambient temperature.

Community Level Management

Wildlife recovery in the United States is overwhelmingly centered around individual target species, however, management actions for a single species influence the larger community (Caro 2003, Barrows et al. 2005). Currently, many bats are experiencing severe declines from wind energy and WNS (Blehert et al. 2009, Arnett and Baerwald 2013), but the listing process under the ESA can take many years. Due to the large range extent and area required for protection of bat species, as well as the reliance of many eastern bats species on forested habitat, we hypothesized that protection afforded to *M. septentrionalis* could allow it to act as an umbrella species to the larger bat community (Seddon and Leech 2008). To assess the ability of *M. septentrionalis* to confer protection to the summer habitat of other bat species, we used community occupancy models to determine if an appreciable portion of a given species occupied area fell within the occupied area of *M. septentrionalis*.

Our model predicted occupancy of nine species, evening bat (*Nycticeius humeralis*), gray bay (*Myotis grisescens*), little brown bat (*Myotis lucifugus*), *M. septentrionalis*, eastern red bat (*Lasiurus borealis*), hoary bat (*Aeorestes cinereus*), silver-haired bat (*Lasionycteris noctivagans*), tri-colored bat (*Perimyotis subflavus*), and big brown bat (*Eptesicus fuscus*), using mean elevation and percent forest cover within 1 km^2 and nearest distance to karst topography. Species whose occupancy could not be accurately estimated were not considered for protection due to uncertainty surrounding their co-occurrence with *M. septentrionalis.* Of the four species for which occupancy could be accurately estimated, only two species, *A. cinereus* and *L. noctivagans*, received adequate protection, with nearly 100% of their occupied area encompassed by the occupied area of *M. septentrionalis*. However, protection of summer habitat for *A. cinereus* and *L. noctivagans* in northern Georgia is of low priority because the majority of individuals migrate from this area in summer (Cryan 2003). The occupied areas of the remaining two species, *M. grisescens* and *N. humeralis*, had <15% overlap with areas occupied by *M. septentrionalis.*

Our findings provide limited evidence that management for *M. septentrionalis* habitat will confer adequate habitat protection to the larger bat community. However, limited overlap between *M. septentrionalis* and several species highlight the potential for multiple bat species to confer protection to the larger community. Alone *M. grisescens* and *M. septentrionalis* are predicted to occupy 16.6% and 26.4% of the study area respectively, but in combination they occupy 40.1%, covering more area and habitat types than *M. septentrionalis* alone. While a species or group of species could provide protection to the larger community, protection is only implied and there is no certainty that management for target species will promote habitat for co-occurring species (Copeland et al. 2014, Malso et al. 2016). Additionally, implied protection in this study only includes summer habitat, leaving migratory habitat and hibernacula unprotected. A more suitable umbrella species would confer protection to all habitat necessary throughout a species life history. However, if elements of required habitat are not covered by the umbrella species conservation efforts could be amended to allow for additional protection.

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Appendix A: Roost used by *M. septentrionalis* over the course of our study. Species name was not determined for 5 of the roost trees. Count represents the number of times tree species was used as a roost with living and dead denoting the live state of the trees for that species.

Common Name	**Scientific Name**	**Count**	**Live**	**Dead**
Sourwood	*Oxydendrum arboreum*	4	2	2
Chestnut Oak	*Quercus prinus*	3	2	1
Loblolly Pine	*Pinus taeda*	3	1	2
Red Maple	*Acer rubrum*	3	1	2
Tulip Poplar	*Liriodendron tulipifera*	3	1	2
White Oak	*Quercus alba*	3	1	2
White Pine	*Pinus strobus*	3	0	3
Pignut Hickory	*Carya glabra*	2	1	1
Black Locust	*Robinia pseudoacacia*	1	0	1
Black Tupelo	*Nyssa sylvatica*	1	1	0
Eastern Hophornbeam	*Ostrya virginiana*	1	1	0
Flowering Dogwood	*Cornus florida*	1	1	0
Sassafras	*Sassafras albidum*	1	0	1
Scarlet Oak	*Quercus coccinea*	1	0	0
Short Leaf Pine	*Pinus echinata*	1	0	1
Virginia Pine	*Pinus virginiana*	1	0	1
Hickory sp.	Carya sp.	1	0	1
Unknown	Unknown	4	0	3

Appendix B: Model relating probability of a roost being in a snag based on snag density and the corresponding null model. For each model, the top number is the parameter estimate and the range below is the 95% confidence interval around the estimate.

Model	**Intercept**	**Snag Density**	**AIC**
Snag Density	-2.087 (-4.236, 0.061)	0.026 (0.005 - 0.048)	26.956
Null	0.747 (-0.046, 1.540)		37.165