ROOSTING BEHAVIOR, HABITAT USE, AND RELATIVE ABUNDANCE OF THE NORTHERN LONG-EARED BAT (*MYOTIS SEPTENTRIONALIS*) FOLLOWING ARRIVAL OF WHITE-NOSE SYNDROME TO MAMMOTH CAVE NATIONAL PARK

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ROOSTING BEHAVIOR, HABITAT USE, AND RELATIVE ABUNDANCE OF THE NORTHERN LONG-EARED BAT (MYOTIS SEPTENTRIONALIS) FOLLOWING ARRIVAL OF WHITE-NOSE SYNDROME TO MAMMOTH CAVE NATIONAL PARK

Thesis

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in the College of Agriculture at the University of Kentucky

By

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Lexington, Kentucky

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2017

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ABSTRACT OF THESIS

ROOSTING BEHAVIOR, HABITAT USE, AND RELATIVE ABUNDANCE OF THE NORTHERN LONG-EARED BAT (MYOTIS SEPTENTRIONALIS) FOLLOWING ARRIVAL OF WHITE-NOSE SYNDROME TO MAMMOTH CAVE NATIONAL PARK

White-Nose Syndrome (WNS; Pseudogymnoascus destructans) is responsible for the regional population collapse of many cave-hibernating bat species, including the northern long-eared bat (Myotis septentrionalis), in eastern United States and Canada. I evaluated roosting behavior, habitat selection, and landscape-scale distribution of roosts of the northern long-eared bat during spring emergence and the early maternity season in Mammoth Cave National Park, Kentucky, USA, from 2015 to 2016. Logistic regression analysis comparing habitat features of roosts with random plots indicated selection of roosts reflected the costs of energetic demands by sex and reproductive status. Relative abundance of local bat species was assessed pre- and post-arrival of WNS in the Park during the summer season, with capture rates observed during the progression of WNS indicating that the fungal disease led to declines in the overall abundance of several bat species on the summer landscape, especially the northern long-eared bat. Distributional trends were quantified using spatial point pattern analysis which indicated that bats had clear roosting patterns associated with landscape level features and habitat resources. Monitoring bat populations regionally and at local scales will be imperative to helping conservation efforts for several bat species most affected by WNS.

KEYWORDS: bats, habitat use, Myotis septentrionalis, roost selection, species assemblage, white-nose syndrome

Marissa M. Thalken

April 6, 2017
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CHAPTER 1: BATS AND THEIR IMPORTANCE

Bats (Order: Chiroptera) are second only to rodents (Order: Rodentia) in numbers and constitute approximately one-fifth of all mammal species (Martin et al. 2011). Fossil records from the Eocene have shown that bats have been around for over 52 million years (Fenton and Simmons 2015). They are the only mammal that is capable of sustained flight, unquestionably influencing their broad distribution and diversity worldwide (Martin et al. 2011). They can be found on every continent, with the exception of Antarctica, and in many different types of terrestrial habitats. They have been found roosting in caves, rock shelters, talus slopes, trees, tree stumps, forest litter, mines, and human dwellings. Insectivory, carnivory, frugivory, nectivory, piscivory and sanguivory are the diverse dietary habits that bats have evolved (Fenton and Simmons 2015). There are 20 extant family groups of bats, 19 of which use echolocation (Fenton and Simmons 2015).

Bats are divided into two suborders: Yinpterochiroptera and Yangochiroptera. Until recently, the two suborders were called Megachiroptera and Microchiroptera, respectively. With the help of evolutionary studies of DNA, scientists were able to better classify various species of bats into the new suborders (Fenton and Simmons 2015). Yinpterochiropterans or as they were formally known, Megachiropterans, feed mainly on plant material such as fruit, nectar or pollen (Francis et al. 1999). They are found only in the Old World and the majority do not rely on echolocation but instead use vision to navigate and locate food. Yangochiroptera or Microchiroptera are much more broadly distributed and exclusively use echolocation to orient and capture prey (Fenton and Simmons 2015).
In the United States, there are approximately 45 species of bats, all belonging to the Suborder Yangochiroptera. Within the Suborder Yangochiroptera, the Family Vespertilionidae makes up the largest contribution of North American bat species (Martin et al. 2011). Vespertilionid bats are insectivorous, nocturnal, and navigate with the aid of echolocation. Many eat flying insects that are captured in mid-air while others glean insects from foliage, rock substrates, the ground or surfaces of water (Martin et al. 2011). Within the Vespertilionidae, *Myotis* is the largest and most broadly distributed genus.

Bats are considered to be one of the least studied and misunderstood groups of mammals. Bats benefit and influence many other species including humans, plants, and other wildlife (Francis et al. 1999). They play a large role in seed dispersal, pollination, and insect control. In the tropics, fruit bats are important seed dispersers and help promote diversity of fruiting trees. There are important commercial crops such as Agave and bananas that are pollinated by bats (Wund and Myers 2005). In temperate regions, insectivorous bats influence insect control and likely have long term effects on agricultural and natural ecological systems. They consume tons of insects per year including insects that transmit disease or are crop pests such as noctuid moths (Whitaker et al. 2007). Bats around the world are facing substantial threats from habitat loss and fragmentation. Destruction of roost sites and pesticide use indirectly affecting insects or plants are problematic for many bat species (Wund and Myers 2005). Many bat populations in eastern North America are especially strained by white-nose syndrome (WNS; *Pseudogymnoascus destructans*) that arrived in 2006. In recent years, awareness of the beneficial role that bats play in ecosystems has increased and allowed for many successful conservation projects to help restore bat populations around the world.
1.1 Project Objectives and Hypotheses Tested

This project evaluated the roosting behavior, habitat selection, and landscape-scale distribution of roosts during spring emergence and the early maternity season of the northern long-eared bat in Mammoth Cave National Park (MCNP), Kentucky, USA. This document also elaborates on summer patterns in relative abundance of bat species pre- and post-arrival of WNS. This project builds upon an existing data set started in 2010 (J. Johnson, Ohio University, unpublished data) and worked in conjunction with MCNP staff to help assess the effects of WNS on the northern long-eared bat within Park boundaries. The specific project objectives are:

1) Objective 1: To determine roost characteristics and habitat use of female northern long-eared bats during staging and early maternity season.

2) Objective 2: To evaluate effects of WNS on emergence behavior and population counts of northern long-eared bats at documented roosts during staging and early maternity seasons.

3) Objective 3: To document shifts in bat assemblages at MCNP following the arrival of WNS.

4) Objective 4: To determine landscape-level distribution of roosts for northern long-eared bats during spring emergence and the early maternity season at MCNP.

These objectives played an integral role in addressing the following hypotheses for northern long-eared bats:

\[ H_0: \text{Roost characteristics and habitat use differ between staging and the early maternity season post-WNS.} \]
$H_0$: Colony size and emergence counts should decrease following arrival of WNS relative to historic patterns observed for the species elsewhere.

$H_1$: Shifts in the abundance of foraging bats should occur in the bat assemblage at MCNP after the onset of WNS, with species less affected by WNS being relatively more common after arrival of WNS.

$H_2$: Roosts should be locally distributed within intact upland deciduous forests and clustered across MCNP close to known overwintering caves, especially during spring staging.
CHAPTER 2: STUDY AREA

The study site is located at MCNP and is part of the Green River Valley in south central Kentucky, USA. The Park is approximately 212 km² and is situated on a karst landscape recognized for the world’s longest known cave system. The limestone rocks were dated to 325 million years ago; formed during the Mississippian period (Livesay 1953). Much of the landscape on and around the Park is pitted by depressions called sinkholes. The average rainfall in the area is about 130 cm annually but there are very few surface streams in the Park other than the Green and Nolin Rivers. Due to the karst topography, most of the streams have an underground course, running through sinkholes, and cannot be seen from the surface (Livesay 1953). Mammoth Cave National Park ranges in elevation from 128 to 281 m above sea level and has a mean annual temperature of 14.9°C (U.S. Climate Data 2016).

Mammoth Cave was established as a National Park in 1941, named a World Heritage site in 1981 and became the core area for an International Biosphere Reserve in 1990. It is dominated by second-growth oak-hickory forest (U.S. National Park Service 2016). Due to MCNP’s location, the area is considered to be a transitional zone that lies between the open grasslands and oak-hickory forests to the west and the mesophytic forests to the east. Likewise, it is located between colder northern climates and the sub-tropical climates to the south. The different vegetation types create a mosaic of habitats across the Park that support a vast array of flora and fauna (U.S. National Park Service 2016). In 2002, a prescribed fire management plan was set in place for the Park to reduce fuel loads and restore the forest to pre-settlement conditions. Between 2002 and 2011, over 25% of the Park was burned with prescribed fire techniques (Figure 2.1; Lacki et al. 2014).
Mammoth Cave National Park is home to 203 species of birds, 43 mammal species, 29 amphibian species, 38 species of reptile, 50 species of mussel, 82 species of fish, 250 species of invertebrates and over a thousand kinds of plants (U.S. National Park Service 2001). Mammoth Cave National Park is home to a large number of bats that include 8 species year-round: Corynorhinus rafinesquii (Rafinesque’s big-eared bat), Eptesicus fuscus (big brown bat), Myotis grisescens (gray bat), M. leibii (eastern small-footed bat), M. lucifugus (little brown bat), M. septentrionalis (northern long-eared bat), M. sodalis (Indiana bat), and Perimyotis subflavus (tri-colored bat). During the growing season, the Park is also home to 5 other species of tree-roosting bats: Lasiurus borealis (eastern red bat), L. cinereus (hoary bat), L. seminolus (Seminole bat), Lasionycteris noctivagans (silver-haired bat), and Nycticeius humeralis (evening bat).
Figure 2.1. Map of Mammoth Cave National Park showing prescribed fire burn units from 2002-2011. Map courtesy of Lillian Scoggins, MCNP, U.S. National Park Service.
Figure 2.2. Map showing bat capture locations from 2009 to 2016 and male and female roost locations identified between 2015 and 2016 at Mammoth Cave National Park, Kentucky, USA.
CHAPTER 3: ROOSTING BEHAVIOR AND HABITAT SELECTION OF THE
NORTHERN LONG-EARED BAT (*MYOTIS SEPTENTRIONALIS*) DURING SPRING
EMERGENCE AND EARLY MATERNITY SEASON AT MAMMOTH CAVE
NATIONAL PARK

3.1 Abstract

The spring emergence season is one of the most poorly studied periods of the
seasonal cycle of North American cave-roosting bats, and is likely critical to the long-
term survival of species in regions affected by white-nose syndrome (WNS). WNS
reached cave-hibernating populations of bats in Mammoth Cave National Park (MCNP),
Kentucky, in 2013, with significant declines in several species of hibernating bats in the
Park during the winter of 2014-15, including the northern long-eared bat (*Myotis
septentrionalis*). To assess behavior and roost selection of individuals surviving to spring
emergence and the summer maternity season, I radio-tracked 21 northern long-eared bats
(19 female and 2 male) and an additional 5 males during the fall season captured at
various locations and habitats in MCNP during 2015 and 2016. Bats were tracked daily
to: identify roosting sites and patterns in use of roosts, describe habitat conditions
associated with roosting sites, and quantify variation in size of colonies occupying roost
trees. The average number of bats emerging from roost trees (3.58 bats ± 0.57) was lower
than estimates reported for the species in the literature for populations studied pre-WNS.
Adult female bats selected trees within 6 roost areas with no overlap in use of roost areas
between non-reproductive females in spring and pregnant and lactating females in
summer. I compared variation in roost tree and stand characteristics of non-reproductive
female, pregnant and lactating female, and male northern long-eared bats. Logistic
regression analyses comparing habitat features of roosts with random plots indicated roost selection by bats reflected the costs of energetic demands of different sex and reproductive classes. Males and pregnant and lactating females roosted at higher elevations than non-reproductive females. Comparisons of models of roosting habitat demonstrated the torpor model (decay class, diameter, percent canopy cover) to be parsimonious, regardless of sex and reproductive condition class, suggesting the potential importance of choosing roost trees that facilitate use of daytime torpor in these bats. Such a strategy is consistent with behaviors anticipated for bats vulnerable to WNS effects during winter hibernation, as these bats are potentially compromised in health and physiologic condition upon emergence from hibernation in spring. I encourage managers responsible for roost trees of northern long-eared bats, to consider strategies for these forests that account for seasonal variation in habitat needs of these bats.
3.2 Introduction

Several North American cave-hibernating bat species are rapidly declining in numbers since the onset of white-nose syndrome (WNS) in 2006 (Blehert et al. 2009; Frick et al. 2010; Ingersoll et al. 2013). Presumably, habitat selection is critical for species survival and fitness (Veilleux et al. 2004), especially now for cave-hibernating bats whose population numbers have declined from exposure to WNS, and the recovery of which inherently depends on successful reproduction during non-hibernating periods of the year. Many bat species, including the northern long-eared bat (*Myotis septentrionalis*), reside in forests during the growing season and depend on trees for protection from predators, spaces for social interactions and ambient environmental conditions for both adults and pups during the maternity season (Kunz and Lumsden 2003; Barclay and Kurtz 2007). Understanding a species’ life history strategies, especially roosting behavior, is imperative to develop effective conservation plans in light of arrival of WNS (Fenton 1997; Veilleux et al. 2004).

WNS has resulted in the loss of millions of hibernating bats in eastern North America and may lead to a dramatic restructuring of bat communities in many locales (Jachowski et al. 2014). For the northern long-eared bat, extinction risk is constant across winter colonies, suggesting that both large and small populations are at equal risk of local extinction (Frick et al. 2015). Evidence indicates that severe population declines are already in effect for the northern long-eared bat in many parts of its range (Moosman et al. 2013; Lacki et al. 2015; Reynolds et al. 2016). Population declines of this magnitude are problematic for a species that has long generation times and low reproductive rates (Jones et al. 2009; Badin 2014). Cave-hibernating bat populations have yet to show
substantial signs of recovery from WNS and are continuing to decline as the geographic range of the fungus expands (Jachowski et al. 2014).

Historically (i.e., pre-WNS), the northern long-eared bat was considered a common forest dwelling bat that ranged from the central and eastern United States to western Canada (Barbour and Davis 1969; Caceres and Barclay 2000). During summer, female northern long-eared bats formed maternity colonies that frequently exceeded 50 individuals (Foster and Kurta 1999; Owen et al. 2002; Menzel et al. 2002), roosting in dead and live trees under exfoliating bark or in crevices and cavities (Owen et al. 2002; Broders et al. 2004; Carter and Feldhamer 2005; Lacki et al. 2009a). Although less studied, males tended to roost alone or in small groups in trees that were smaller in diameter on average than female roosts (Perry and Thill 2007). Most studies demonstrated the importance of hardwoods for roosting by the northern long-eared bat but these bats also roost in conifers (Lacki and Schwierjohann 2001; Carter and Feldhamer 2005; Perry and Thill 2007). It is widely accepted that the northern long-eared bat has greater plasticity in choice of summer roost trees, suggesting that the structural complexity of the habitat or available resources nearby are potentially more important factors for roost selection than actual tree species (Carter and Feldhamer 2005; Lacki et al. 2009b). Clearly, a better understanding of the life history strategies of forest bat species, including roosting behavior, and how these patterns are affected by environmental change, such as wide-scale population collapse, is imperative to developing effective conservation plans for these bats (Fenton 1997, Veilleux et al. 2004).

Bats spend much of their lives roosting but few studies have examined the
relationship between thermoregulation costs and roost selection, which likely influences fetal development and juvenile growth rates (Chruszcz and Barclay 2002). General patterns of cavity-dwelling species appear to be preferentially choosing taller, large diameter roost trees surrounded by less percent canopy cover (Lacki and Baker 2003; Kalcounis-Ruppell et al. 2005). Warmer roost microclimates are hypothesized to occur in trees that protrude above the canopy, are located on southwestern slopes, and which do not sit adjacent to neighboring trees of greater or equal height, all of which theoretically lead to increased exposure to solar radiation (McComb and Noble 1981; Veilleux et al. 2004; Lacki et al. 2013). Dzal and Brigham (2013) theorized that reproductive status may even determine thermoregulation patterns in some bat species, and for small mammals that are slow to reproduce, torpor may be important in balancing the costs of reproduction (Dzal and Brigham 2013).

Few studies have examined the within-season variation in roost tree and stand characteristics selected by temperate zone bat species. Differential selection of roosting sites by big brown bats (Eptesicus fuscus) and western long-eared bats (Myotis evotis) was based on the importance of roost microclimates to various reproductive classes (Chruszcz and Barclay 2002, Lausen and Barclay 2002). Garroway and Broders (2008) demonstrated that reproductively active females of the northern long-eared bat choose roosts with open, dominant canopies and in low tree densities to help balance energy demands and reproductive output during the summer months. Tri-colored bat (Perimyotis subflavus) were shown to select day roost characteristics differently based on female reproductive status (Veilleux et al. 2004). Because internal roost microclimates can be difficult to measure for roosts high aboveground (Lacki et al. 2013), I used external
characteristics of roost trees as an indicator for identifying seasonal differences among
preferred roost site locations for northern long-eared bats. I hypothesized: (i) roost
characteristics and habitat use of northern long-eared bats should differ between spring
staging and the early maternity season, reflecting varying needs of bats for micro-
environmental conditions during these two seasons of the year; and, (ii) patterns in use of
roosting sites should differ between pre- and post-WNS periods, as reduced population
numbers of bats likely affect how and where bats select roosts, especially in response to
altered micro-environments inside roosts due to changes, if any, in population sizes of
roosting bats.

3.3 Methods

Data were collected from early April to late September across spring, summer and
fall of 2015, and spring and summer of 2016. During the fall season of 2015, no female
bat was tracked. Ephemeral ponds, cave entrances and backcountry roads at MCNP were
habitats used for capture of northern long-eared bats with mist-nets that measured 6-18 m
in length and were stacked 6-9 m high (Avinet, Dryden, NY). Upon capture, the mass (g),
right forearm length (mm), reproductive condition (females: pregnant, lactating or non-
reproductive; males: scrotal or non-scrotal), Reichard’s wing index score (Reichard and
Kunz 2009), sex, and age (Brunet-Rossinni and Wilkinson 2009) were collected for every
individual. Adult females were grouped as non-reproductive if no evidence of pregnancy
or lactation was visible; however, because all of these bats were captured in the post-
hibernation staging period, many likely were reproductively active and would have
demonstrated to be so if captured later in summer.
Northern long-eared bats receiving radio-transmitters were not banded to keep added weight <5% of their body mass (Aldridge and Brigham 1988). *Myotis* bats not receiving radio-transmitters were banded with 2.9 mm bands provided by the Kentucky Department of Fish and Wildlife Resources. Twenty-six (19 females, 7 males) northern long-eared bats were fitted with LB-2XT radio-transmitters (Holohil Systems, Ltd., Ontario, Canada), attached with surgical glue (Perma-Type Company, Inc., Plainville, CT) between the shoulder blades. Transmitters mass was ≤ 0.33 g to comply with the 5% rule (Aldridge and Brigham 1988). After completion of each survey night, recommended decontamination protocols from the U.S. Fish and Wildlife Service (USFWS) were used to minimize the spread of fungal spores (USFWS 2016). Bats were tracked for approximately 8-15 days, or until either the transmitter battery failed or the transmitter fell off the bat. A 3-element yagi antenna (Wildlife Materials, Inc., Murphysboro, IL) and an Icom IC-R20 radio-receiver (Icom America, Inc, Kirkland, WA) were used to track bats.

For each roost identified, the tree species, tree height (m), roost height (m), roost type (bark, crevice or cavity), roost orientation (°), decay class (Maser et al. 1979), diameter at breast height (cm; DBH), GPS location, bark remaining (%), canopy cover (%), and basal area (10-factor prism; m²/ha) were collected. I estimated percent slope at the plot center using a clinometer and derived elevation of the roost tree from topographic maps using GPS coordinates. Habitat characteristics associated with roost trees were measured within a 0.04-ha plot. All trees in the plot were identified to species, measured for DBH (cm) and assigned a decay class. Random compass bearings and distances ≥ 50 m from any known roost were used to locate random plots. At each random plot, centered
on the closest dead tree ≥ 10 cm, I measured all the same habitat characteristics as collected for known roost trees.

Exit count surveys were conducted for one or more nights at each known roost tree. Exit counts started 15 min prior to sunset and ended 15 min after the last bat emerged from the roost tree. To count bats, recorders were positioned to ensure emerging bats were silhouetted against the sky when the roost tree had an open canopy. For closed canopy or hard to see roosts, night vision goggles (Firefield, Mansfield, TX) were used to count bats.

3.3.1 Data Analysis

A one-way ANOVA (PROC GLM; SAS 9.4, SAS Inc., Cary, NC, USA) was used to test for differences in quantitative habitat characteristics for roost plots by sex and reproductive condition. When ANOVAs were significant, differences among sex and reproductive conditions were examined using Fisher’s LSD multiple comparison procedure. Prior to analysis, data for percent canopy cover, percent bark remaining, and percent slope were transformed using an arcsine transformation to account for possible non-normality, and data for aspect were transformed with a cosine function to linearize circular data. I compared mean colony size, as indexed by emergence counts, for roosts of pregnant and lactating females (maternity season) with that of non-reproductive females using a Student’s t-test (PROC GLM; SAS 9.4, SAS Inc., Cary, NC, USA). For each roost tree with multiple exit counts, I used the average colony size recorded across multiple nights in the analysis. This prevented non-independence among repeat counts at roosts from inflating sample sizes and erroneously increasing the power of the test (Type
To evaluate importance of roost condition and location relative to randomly available roosting habitats on the MCNP landscape, I developed competing models to account for why bats may have selected the roost trees I observed. Using logistic regression (PROC LOGISTIC; SAS 9.4, SAS Inc., Cary, NC, USA) and Akaike’s Information Criterion (AIC), competing habitat models of roosting habitats were compared with random plots to identify best fit models for each sex and reproductive condition class separately. Each of the four models selected for analysis were developed on the basis of existing data from prior research on roost selection of northern long-eared bats pre-WNS (Menzel et al. 2002; Carter and Feldhamer 2005; Johnson et al. 2009). This approach was chosen over comparisons of models comprised of all possible variable combinations, following recommendations for model selection and testing that discourage use of the latter approach (Burnham and Anderson 2002; Arnold 2010).

Importance of individual predictor variables were then evaluated based on their significance in the models and direction of effect (+ or – loading).

I developed 4 habitat models for analysis and AIC comparisons. The preferred roosting environment model (i.e., recognition) tested three roost characteristics believed to be important to northern long-eared bats: roost tree DBH (Lacki and Schwierjohann 2001; Johnson et al. 2009; Krynak 2010), height of the roost tree (Lacki and Schwierjohann 2001; Garroway and Broders 2008; Johnson et al. 2009), and the percent bark remaining on the tree (Johnson et al. 2009; Krynak 2010). This model reflected a bat’s ability to recognize trees that provided suitable micro-sites for roosting and rearing pups in summer. The preferred forest conditions model (i.e., stand) tested four variables:
basal area (Johnson et al. 2009), stand density, number of snags (Lacki and Schwierjohann 2001), and average stand DBH. This model reflected a bat’s preference for stand structural conditions surrounding roost trees, including the availability of alternate roosting sites nearby. The preferred geographic location model (i.e., landscape) tested three variables: elevation (Lacki et al. 2009a), slope position (Lacki and Schwierjohann 2001; Johnson et al. 2009), and aspect. This model reflected a bat’s choice of roosts across varying landscape positions, especially as these influence heating and cooling of roost structures. The final model, energy savings model (i.e., torpor), tested three variables: DBH, canopy cover (Carter and Feldhamer 2005; Krynak 2010), and decay class (Carter and Feldhamer 2005; Johnson et al. 2009). This model reflected a bat’s needs for roosting structures that facilitate use of torpor while also allowing for passive re-warming behaviors used to reduce energy expenditures.

3.4 Results

I tracked non-reproductive (staging period) female northern long-eared bats to 39 roost trees, pregnant and lactating female northern long-eared bats to 30 roosts trees and male northern long-eared bats to 14 roost trees (Figure 2.2). Bats roosted in 24 different tree species including red maple (Acer rubrum n= 16), red oak (Quercus rubra n= 8), yellow-poplar (Liriodendron tulipifera n= 7), white oak (Q. alba n= 6), sugar maple (A. saccharum n= 5), mockernut hickory (Carya tomentosa n= 5), unidentifiable trees (n= 5), sassafras (Sassafras albidum n= 4), chestnut oak (Q. montana n= 4), Virginia pine (Pinus virginiana n= 3), eastern red cedar (Juniperus virginiana n= 3), sourwood (Oxydendrum arboreum n= 3), black cherry (Prunus serotina n= 2), and one each of sweetgum
(Liquidambar styraciflua), blackgum (Nyssa sylvatica), white ash (Fraxinus americana), black walnut (Juglans nigra), slippery elm (Ulmus rubra), American sycamore (Plantanus occidentalis), flowering dogwood (Cornus florida), scarlet oak (Q. coccinea), southern red oak (Q. falcata), shagbark hickory (Carya ovata), eastern redbud (Cercis canadensis) and pignut hickory (Carya glabra). Roost trees classified as snags made up 46.2% of non-reproductive female roosts, 60% of pregnant and lactating female roosts, and 42.8% of male roosts. Habitat variables measured at roost trees of non-reproductive females, pregnant and lactating females, and male northern long-eared bats are provided (Table 3.1).

Despite historical evidence of successful capture of northern long-eared bats across the Park, roosts of female northern long-eared bats were largely clustered within 6 roost areas, ≥ 1 km apart, with no overlap in use of the same roost areas between non-reproductive and pregnant and lactating bats (Figure 2.2). Roosts of males were more widely distributed on the landscape and demonstrated overlap in use of roost areas with non-reproductive females, but not with pregnant and lactating females.

I conducted exit counts at all 83 roost trees, with a maximum estimated colony size of 40 bats emerging on 25 June 2016 from a cavity of a dead, 49 cm diameter yellow-poplar. The maximum exit counts (16 and 17 bats; 27 and 28 May 2015) observed during late spring staging were recorded from two separate yellow-poplars, located by following the signal of a single radio-tagged, non-reproductive female. These likely represented the early formation of summer maternity colonies, as no more than 4 bats were observed exiting any other roost of northern long-eared bats in April and May during either 2015 or 2016. The overall average number of bats exiting roost trees (3.58
bats \pm 0.57(\text{SE}) \) was low compared to most published estimates for mean summer exit counts of northern long-eared bats pre-WNS (mean = 17.8 bats \pm 3.16, \( n = 9 \) sources; Table 3.2). The average exit count for non-reproductive females (i.e., spring staging; 2.65 bats \pm 0.63) was lower (\( t_{1.67} = 8.89; \ P < 0.004 \) than the average for pregnant and lactating females (7.3 bats \pm 1.58).

The one-way ANOVAs and LSD comparisons indicated significant differences among sexes and reproductive conditions for several habitat characteristics (Table 3.1). Significant variation was detected for canopy cover (\( F_{2.80} = 3.1, \ P = 0.0504 \)), percent slope (\( F_{2.80} = 3.74, \ P = 0.0281 \)), tree density (\( F_{2.80} = 4.02, \ P = 0.0217 \)), mean diameter (\( F_{2.80} = 2.85, \ P = 0.0636 \)), and basal area (\( F_{2.80} = 19.6, \ P < 0.0001 \)). Decay class showed some potential for variation among sex and reproductive condition classes (\( F_{2.80} = 2.55, \ P = 0.0846 \)), but no Fisher’s LSD comparison was significant (\( P > 0.05 \)). Pregnant and lactating females selected trees in stands with the least amount of canopy cover and lowest basal area volumes compared with non-reproductive females and males. Roosts of non-reproductive females were in forested stands with the highest amounts of canopy cover and lowest tree densities. Males roosted in stands with the steepest slopes, highest tree densities, and the greatest volumes of basal area. Elevation was also important in roost selection (\( F_{2.80} = 11.1, \ P < 0.0001 \)), with roosts of pregnant and lactating females and males being located higher in elevation than roosts of non-reproductive females. Bats roosted in both cavities and beneath bark, with significant variation in roost height occurring among sex and reproductive condition classes (\( F_{2.79} = 3.18, \ P = 0.0471 \); Table 3.3). Males roosted higher up in the canopy (mean = 12.2 m aboveground) than pregnant and lactating females (7.4 m). Although not different across sex and reproductive
condition classes, the average roost aspect for all groupings was between 178° and 186°, indicating use of warmer, south-facing slopes.

Logistic regressions of roost trees with random snags indicated the torpor model was the best fit model for all sex and reproductive classes (Table 3.3 and 3.4). For pregnant and lactating females, however, the stand model ranked out as best-fit by a very slight margin over the torpor model (ΔAIC = 0.3). All remaining model/sex and reproductive condition class combinations received limited support (ΔAIC > 7), despite most having significant likelihood ratios (P < 0.05). Non-reproductive females were more likely to roost in larger diameter trees, in a lesser state of decay, located in forested stands with higher amounts of canopy cover than randomly-selected snags (AICc = 114.6). Pregnant and lactating females (AICc = 122.3) also selected trees in a lesser state of decay than random snags, but chose them within forested stands with lower volumes of basal area and reduced tree densities. Males (AICc = 54.8) showed the greatest response in decay class relative to random snags, reflecting their selection of live trees as roosting sites more frequently than other sex and reproductive condition classes of bats.
Table 3.1. Means ± SE of habitat variables measured at roost trees of non-reproductive females, pregnant and lactating females, and male northern long-eared bats at Mammoth Cave National Park, Kentucky, USA. Within rows, means without common letters are different ($P < 0.05$).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Non-reproductive Females</th>
<th>Pregnant/Lactating Females</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$X$ (SE) n= 39</td>
<td>$X$ (SE) n=30</td>
<td>$X$ (SE) n=14</td>
</tr>
<tr>
<td>Roost tree</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diameter (cm)</td>
<td>32.3 (3.4)</td>
<td>31.2 (4.3)</td>
<td>32.9 (5.9)</td>
</tr>
<tr>
<td>Decay Class (1-9)</td>
<td>2.46 (0.3)</td>
<td>3.23 (0.3)</td>
<td>2.14 (0.4)</td>
</tr>
<tr>
<td>Tree Height (m)</td>
<td>19.3 (1.5)</td>
<td>15.6 (2.1)</td>
<td>22.1 (2.8)</td>
</tr>
<tr>
<td>Roost Height (m)</td>
<td>10.03 (1.0)$^{a,b}$</td>
<td>7.43 (1.0)$^{b}$</td>
<td>12.2 (1.9)$^{a}$</td>
</tr>
<tr>
<td>Bark Remaining (%)</td>
<td>78.3 (5.1)</td>
<td>71.6 (6.4)</td>
<td>88.9 (4.4)</td>
</tr>
<tr>
<td>Stand</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canopy Cover (%)</td>
<td>79.4 (2.8)$^{a}$</td>
<td>66.7 (4.7)$^{b}$</td>
<td>75.4 (8.1)$^{a,b}$</td>
</tr>
<tr>
<td>Snag Density (#/ha)</td>
<td>4.33 (0.6)</td>
<td>6.03 (1.0)</td>
<td>6.5 (1.2)</td>
</tr>
<tr>
<td>Live Tree Density (#/ha)</td>
<td>35.1 (1.6)$^{b}$</td>
<td>38.9 (2.4)$^{a,b}$</td>
<td>46.5 (5.1)$^{a}$</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>210.6 (5.4)$^{b}$</td>
<td>240.3 (3.0)$^{a}$</td>
<td>235.1 (6.9)$^{a}$</td>
</tr>
<tr>
<td>Slope (%)</td>
<td>13.8 (4.8)$^{b}$</td>
<td>8.46 (0.8)$^{b}$</td>
<td>14.6 (2.3)$^{a}$</td>
</tr>
<tr>
<td>Aspect ($^{f}$)</td>
<td>178.03 (17.2)</td>
<td>186.5 (15.7)</td>
<td>186 (20.6)</td>
</tr>
<tr>
<td>Mean Diameter (cm)</td>
<td>12 (0.3)$^{a}$</td>
<td>11.2 (0.2)$^{a,b}$</td>
<td>10.9 (0.6)$^{b}$</td>
</tr>
<tr>
<td>Basal Area (m²/ha)</td>
<td>14.2 (1.9)$^{b}$</td>
<td>5.89 (1.4)$^{c}$</td>
<td>26 (2.3)$^{a}$</td>
</tr>
</tbody>
</table>
Table 3.2. Mean and maximum size of exit counts of northern long-eared bats inhabiting roost trees across the distribution of the species reported pre- and post WNS impacts.

<table>
<thead>
<tr>
<th>WNS Status</th>
<th>Source</th>
<th>Location</th>
<th>No. of Roosts (n)</th>
<th>Max</th>
<th>Mean</th>
<th>Reproductive Condition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-WNS</td>
<td>Sasse and Perkins 1996</td>
<td>New Hampshire</td>
<td>47</td>
<td>36</td>
<td>10.8</td>
<td>P</td>
</tr>
<tr>
<td></td>
<td>Foster &amp; Kurta 1999</td>
<td>Michigan</td>
<td>32</td>
<td>60</td>
<td>17</td>
<td>P, L, PL</td>
</tr>
<tr>
<td></td>
<td>Lacki &amp; Schwierjohann 2001</td>
<td>Kentucky</td>
<td>57</td>
<td>65</td>
<td>25.6</td>
<td>P</td>
</tr>
<tr>
<td></td>
<td>Menzel et al. 2002</td>
<td>West Virginia</td>
<td>12</td>
<td>65</td>
<td>31.3</td>
<td>L</td>
</tr>
<tr>
<td></td>
<td>Owen et al. 2002</td>
<td>West Virginia</td>
<td>43</td>
<td>88</td>
<td></td>
<td>P, L</td>
</tr>
<tr>
<td></td>
<td></td>
<td>New Brunswick, CAN</td>
<td>55</td>
<td>26</td>
<td>10.4</td>
<td>P, L, NR</td>
</tr>
<tr>
<td></td>
<td>Broders and Forbes 2004</td>
<td>Arkansas</td>
<td>49</td>
<td>51</td>
<td>17.8</td>
<td>P, L</td>
</tr>
<tr>
<td></td>
<td>Perry and Thill 2007</td>
<td>Kentucky</td>
<td>9</td>
<td>30</td>
<td>13.9</td>
<td>P, NR</td>
</tr>
<tr>
<td></td>
<td>Dickinson et al. 2009</td>
<td>Kentucky</td>
<td>54</td>
<td>56</td>
<td></td>
<td>P, L, PL, NR</td>
</tr>
<tr>
<td></td>
<td>Lacki et al. 2009</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Whitaker &amp; Mumford 2009</td>
<td>Indiana</td>
<td>100</td>
<td>30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Post-WNS</td>
<td>Lereculeur 2013</td>
<td>Tennessee</td>
<td>101</td>
<td>116</td>
<td>11</td>
<td>P, L</td>
</tr>
<tr>
<td></td>
<td>Badin 2014</td>
<td>Indiana</td>
<td>40</td>
<td>44</td>
<td>8</td>
<td>P, L, PL</td>
</tr>
<tr>
<td></td>
<td>This study</td>
<td>Kentucky</td>
<td>30</td>
<td>40</td>
<td>7.3</td>
<td>P, L</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>39</td>
<td>17</td>
<td>2.6</td>
<td>NR</td>
</tr>
</tbody>
</table>

* Reproductive conditions are: pregnant (P), Lactating (L), post-lactating (PL), and non-reproductive (NR).
Table 3.3. Logistic regression outcomes of four habitat models tested for non-reproductive female, pregnant/lactating female and male northern long-eared bats at Mammoth Cave National Park, Kentucky, USA.

<table>
<thead>
<tr>
<th>Sex/Reproductive Condition</th>
<th>Model</th>
<th>AICc</th>
<th>ΔAIC</th>
<th>Likelihood Ratio</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-reproductive Females</td>
<td>Torpor</td>
<td>114.6</td>
<td>0</td>
<td>46.6</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Recognition</td>
<td>133.9</td>
<td>19.3</td>
<td>27.3</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Landscape</td>
<td>150.5</td>
<td>35.9</td>
<td>8.55</td>
<td>0.0359</td>
</tr>
<tr>
<td></td>
<td>Stand</td>
<td>153.1</td>
<td>38.5</td>
<td>10.3</td>
<td>0.0357</td>
</tr>
<tr>
<td>Pregnant/Lactating Females</td>
<td>Stand</td>
<td>122.3</td>
<td>0</td>
<td>19</td>
<td>0.0008</td>
</tr>
<tr>
<td></td>
<td>Torpor</td>
<td>122.6</td>
<td>0.3</td>
<td>16.5</td>
<td>0.0009</td>
</tr>
<tr>
<td></td>
<td>Recognition</td>
<td>129.5</td>
<td>7.2</td>
<td>9.66</td>
<td>0.0217</td>
</tr>
<tr>
<td></td>
<td>Landscape</td>
<td>132.4</td>
<td>10.1</td>
<td>6.76</td>
<td>0.0798</td>
</tr>
<tr>
<td>Male</td>
<td>Torpor</td>
<td>54.8</td>
<td>0</td>
<td>33.7</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Recognition</td>
<td>63.4</td>
<td>8.6</td>
<td>25.1</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Landscape</td>
<td>76.2</td>
<td>21.4</td>
<td>12.3</td>
<td>0.0064</td>
</tr>
<tr>
<td></td>
<td>Stand</td>
<td>76.6</td>
<td>21.8</td>
<td>14.1</td>
<td>0.0069</td>
</tr>
</tbody>
</table>
Table 3.4. Means (SE), logistic regression $\beta$-values (SE), and significance of predictor variables in best fit models of habitat characteristics of roosts used by pregnant/lactating, non-reproductive female and male northern long-eared bats in Mammoth Cave National Park, Kentucky, USA. Data for random plots are provided for comparison.

<table>
<thead>
<tr>
<th>Sex/Reproductive Condition</th>
<th>Best-fit Model</th>
<th>Variables</th>
<th>Mean (SE)</th>
<th>$\beta$ (SE)</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-reproductive Females</td>
<td>Torpor</td>
<td>Decay Class (1-9)</td>
<td>2.46 (0.29)</td>
<td>-0.861</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Canopy Cover (%)</td>
<td>79.4 (2.57)</td>
<td>(0.92)</td>
<td>0.1199</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Diameter (cm)</td>
<td>32.3 (4.29)</td>
<td>0.033</td>
<td>0.0676</td>
</tr>
<tr>
<td>Pregnant/Lactating Females</td>
<td>Stand</td>
<td>Basal Area (m$^2$/ha)</td>
<td>5.89 (1.43)</td>
<td>-0.082</td>
<td>0.0019</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Live Tree Density (#/ha)</td>
<td>38.9 (2.38)</td>
<td>-0.049</td>
<td>0.0188</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mean Diameter (cm)</td>
<td>11.2 (0.21)</td>
<td>(0.19)</td>
<td>0.2351</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Snag Density (#/ha)</td>
<td>6.03 (0.97)</td>
<td>0.047</td>
<td>0.3473</td>
</tr>
<tr>
<td>Males</td>
<td>Torpor</td>
<td>Decay Class (1-9)</td>
<td>3.23 (0.32)</td>
<td>-0.612</td>
<td>0.0008</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Canopy Cover (%)</td>
<td>66.7 (4.68)</td>
<td>0.448</td>
<td>0.5588</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Diameter (cm)</td>
<td>31.2 (4.29)</td>
<td>(0.01)</td>
<td>0.7801</td>
</tr>
<tr>
<td>Random</td>
<td></td>
<td>Decay Class (1-9)</td>
<td>4.45 (0.13)</td>
<td>-1.501</td>
<td>0.0002</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Canopy Cover (%)</td>
<td>70.6 (2.18)</td>
<td>(0.32)</td>
<td>0.7835</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Diameter (cm)</td>
<td>24.8 (1.34)</td>
<td>(0.02)</td>
<td>0.4802</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Basal Area (m$^2$/ha)</td>
<td>13.9 (1.41)</td>
<td>(0.13)</td>
<td>0.501</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Live Tree Density (#/ha)</td>
<td>42.5 (1.54)</td>
<td>(0.13)</td>
<td>0.4502</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mean Diameter (cm)</td>
<td>11.4 (0.18)</td>
<td>(0.13)</td>
<td>0.337</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Snag Density (#/ha)</td>
<td>4.83 (0.47)</td>
<td>(0.13)</td>
<td>0.403</td>
</tr>
</tbody>
</table>
3.5 Discussion

Prior studies demonstrated northern long-eared bats selected roosts on the basis of individual roost trees and surrounding stand characteristics (Menzel et al 2002; Carter and Feldhamer 2005; Johnson et al. 2009). My findings were consistent in that northern long-eared bats used both live and dead trees (Sasse and Pekins 1996; Foster and Kurta 1999; Lacki and Schwierjohann 2001) and were likely to roost in trees in earlier stages of decay compared to randomly selected snags (Carter and Feldhamer 2005; Johnson et al. 2009; Lacki et al. 2009b). Northern long-eared bats in our study used a high diversity of tree species for roosting in both spring staging and the summer maternity season, consistent with documented patterns in tree species selection by this species (Sasse and Pekins 1996; Lacki and Schwierjohann 2001; Menzel et al. 2002). Despite capture records for northern long-eared bats in the Park dating back to 2009 that demonstrated the species to be widely distributed (Figure 2.2), I observed adult females selecting trees within clusters, or roost areas, with no overlap among roost areas between non-reproductive females in spring and reproductively active females during the summer maternity season, further evidence for seasonal differences in habitat needs of adult female, northern long-eared bats (Broders and Forbes 2004; Garroway and Broders 2008). Use of roost areas by northern long-eared bats was anticipated, as this species is known to use roost areas (Sasse and Pekins 1996; Broders et al. 2006) and form roost networks elsewhere in its distribution (Johnson et al. 2012; Silvis et al. 2015).

Although the maximum of 40 bats exiting a roost tree that I observed was within the range of maximum values reported for the northern long-eared bat pre-WNS (Range: 26 – 100), I recorded low average numbers of northern long-eared bats exiting roost trees
during both spring staging and the summer maternity seasons, with the maximum and mean exit counts in spring staging being lower than any previously published estimates for the species. Data from other roosting studies of northern long-eared bats post-WNS in Tennessee (Lereculeur 2013) and Indiana (Badin 2014), also show average exit counts below historic values recorded elsewhere, except for the extreme northeast U.S. and Canada where average exit counts of northern long-eared bats have historically appeared to be lower than in the southern and Midwestern United States (Sasse and Pekins 1996; Broders and Forbes 2004). Regardless, my data suggests that spring and summer colony sizes of northern long-eared bats have declined due to mortalities from WNS, at least in Kentucky, which could lead to disruptions in social networks (Johnson et al. 2012; Johnson and Lacki 2013; Silvis et al. 2014; Silvis et al. 2015) and alterations to the internal thermal environments of roosts of these bats (Willis and Brigham 2007; Roby et al. 2011; Johnson and Lacki 2012). I suggest both of these scenarios could impact future rates of summer survival and reproductive success in this species range-wide, thus data are needed to evaluate these potential impacts to northern long-eared bats.

Roost tree and stand characteristics selected by male and female northern long-eared bats varied with sex and reproductive condition. Relative to pregnant and lactating females, non-reproductive females in spring selected roosts that had the highest percent canopy cover, with greater basal area, and situated at lower elevations. The importance of canopy cover to roost selection by northern long-eared bats is documented (Foster and Kurta 1999; Menzel et al. 2002); however, the association I observed for selection of stands with greater basal area was inconsistent with observations recorded elsewhere (Johnson et al. 2009). To my knowledge a relationship between roost selection and
elevational differences has not been reported previously for the species. I hypothesize that habitat patterns observed for non-reproductive females in spring, more mature forests with higher canopy cover situated at low elevations, are reflective of forest conditions that likely foster microclimates at lower temperatures inside roosts. Reduced solar radiation and decreased ambient temperatures should be expected to promote use of daytime torpor in tree roosting bats (Turbill et al. 2003; Willis et al. 2005; Ruczyński 2006), especially for non-reproductive females during the staging period when food supplies are likely scarce and weather conditions frequently inclement.

My results for roosting heights of northern long-eared bats were consistent with patterns observed for tri-colored bats which demonstrated pregnant and lactating females roosted farther beneath the forest canopy than non-reproductive females and males (Veilleux et al. 2004). A lower position in roost height could result in decreased roost temperatures, but may also shelter the colony from severe weather conditions (Veilleux et al. 2004). I hypothesize selection of roost trees by pregnant and lactating females in stands with low amounts of canopy cover at higher elevations should increase exposure to sunlight, and that these bats were more likely choosing trees with warmer roosting microclimates to reduce the cost of maintaining normothermic body temperatures that aid in more rapid development of young.

Of the habitat models compared, the model reflecting torpor use ranked as parsimonious for all sex and reproductive condition classes evaluated, and as best-fit for males and non-reproductive females. The only other model receiving support as parsimonious was the stand model and then only for pregnant and lactating bats. Snag decay class was important in model selection against random snags for all three torpor
models with northern long-eared bats choosing trees in earlier stages of decay than randomly available snags. The relative preference for cavities and crevices over sloughing bark as roosting substrates of northern long-eared bats is well known (Lacki et al. 2009a), and could be a reflection of selection for an earlier decay class of roost tree by this species.

The torpor model also indicated that non-reproductive females were more likely to roost in trees larger in diameter and with a higher percentage of canopy cover than randomly selected trees; consistent with non-reproductive females choosing roosting sites in more thermally stable conditions (Simpson and TenWolde 1999). By roosting in large diameter trees at lower elevations, bats occupying such roosts likely encounter a stable, cooler micro-environment during the day, potentially facilitating lowered body temperatures, reduced metabolic rates, and increased energy savings in these bats. Bats in this scenario, however, would also be less likely to use passive rewarming as an energy saving strategy to arouse from torpor (Lausen and Barclay 2003; Rambaldini and Brigham 2008; Johnson and Lacki 2013).

The stand model was also found to be the best-fit model for pregnant and lactating females, and indicated that these bats preferentially chose roost trees in forests with lower basal areas and live tree densities than randomly selected trees. Minimizing clutter and tree density surrounding roost trees may create open air space for newly volant young to practice flying and foraging, especially during the first few days of flight (Garroway and Broders 2008).

Other studies (Willis et al. 2006; Garroway and Broders 2008) have suggested that known roost trees are not being equally used throughout the growing season and,
therefore, should not be classified together across reproductive periods. Certain time periods are more energetically expensive than others for temperate zone bat species, especially for females during the lactation period (Racey and Swift 1981; Wilde et al. 1995; Wilde et al. 1999; Garroway and Broders 2008). The spring emergence season, in particular, remains a poorly understood period in the seasonal cycle of North American cave-roosting bats, and is likely critical to the long-term survival of species in regions affected by WNS. Seasonal differences in the pattern of roost tree selection and surrounding stand characteristics appears to reflect the costs of energetic demands by sex and reproductive status. My study shows that combining data on roost characteristics across all reproductive and sex classes would mask differences in roost choice between males and females, limiting the ability to accurately identify seasonally important roost and stand characteristics of each group across the landscape. Within-season variation in roost selection has been suggested to be an important habitat component that should be incorporated into future conservation management plans for threatened and endangered bat species (Brigham et al. 1997; Kalcounis and Brigham 1998; Garroway and Broders 2007; Garroway and Broders 2008), and my findings corroborate this recommendation along with the additional consideration of differences between sex classes.

My observed colony sizes provide further evidence for the decline in northern long-eared bat populations following WNS and are consistent with reports from other states affected by WNS (Francl et al. 2012; Moosman et al. 2013; Reynolds et al. 2016). The northern long-eared bat has declined significantly enough across its range over the past decade for the species to be added as threatened under the Endangered Species Act in spring of 2015 (U.S. Department of the Interior 2015). There is a need to consider
management of aboveground habitats of the northern long-eared bat to ensure that seasonal differences in habitat use among sexes and reproductive classes (Broders and Forbes 2004; Garroway and Broders 2008; this study) are accounted for in local and region-wide forest planning efforts. It will also be important to maintain larger stands in support of networks of trees for colony members to associate with during the growing season (O’Donnell 2000; Willis and Brigham 2004; Garroway and Broders 2008). My study demonstrated that roosting areas, i.e., clusters of roosts, of northern long-eared bats can be identified and mapped to better ensure long-term conservation of maternity habitats. However, as habitats change with succession and time, so might the locations of roost clusters across forested landscapes. The use of roost networks by northern long-eared bats (Johnson et al. 2012; Silvis et al. 2015) along with the variability in movement of these bats among roosts on the landscape resulting from fission-fusion social behaviors (Garroway and Broders 2007; Patriquin et al. 2010), suggests that periodic monitoring will be necessary to adequately manage maternity habitats of this species.

Based on model outcomes and the patterns in roost selection observed, the data presented offer compelling evidence in favor of ‘suitability for daytime torpor’ as a motivating factor behind selection of roosting sites by northern long-eared bats in this study. Models reflecting structural complexity of the habitat (stand) and proximity to available resources (landscape) were evaluated with some support for ‘importance of structural complexity’ in driving roost selection in these bats, but only for pregnant and lactating females, suggesting that habitat complexity and resource proximity may not be as limiting to roost selection in this species as previously thought (Carter and Feldhamer 2005; Lacki et al. 2009a). Because I looked only at roost features and did not directly
collect data on daytime torpor use by bats, my findings are limited in scope and inference, with results and interpretations generating new hypotheses for further testing. The seasonal differences in roost selection observed between pregnant and lactating and non-reproductive females indicated these two groupings of bats roosted under differing habitat conditions. A number of studies have demonstrated differences in thermoregulatory strategies within species, especially for non-reproductive females as they are not constrained by the demands of pregnancy and lactation (Hamilton and Barclay 1984; Cryan and Wolf 2003; Rambaldini and Brigham 2008; Johnson and Lacki 2013). I hypothesize that a comparable pattern might exist for northern long-eared bats, however, the non-reproductive females in our study were from spring staging, not the maternity season, and could possibly reflect behavior of pregnant females in early stages of gestation.

In the face of climate change, anthropogenic disturbance and disease, bat species are being challenged to survive across North America, effectively creating an unparalleled conservation hurdle. The long-term cascading effects of losing such a diverse and abundant group of species, including the northern long-eared bat, across the continent remains unknown (Jachowski et al. 2014), drawing attention to the need for increased research, monitoring, and management to better understand the life history strategies of cave-hibernating bat species affected by WNS.
CHAPTER 4: SHIFTS IN THE COMPOSITION OF BAT ASSEMBLAGES FOLLOWING ARRIVAL OF WHITE-NOSE SYNDROME TO MAMMOTH CAVE NATIONAL PARK

4.1 Abstract

The arrival of white-nose syndrome (WNS) to North America in 2006, and the subsequent decline of hibernating populations of bats, has potential long-term implications for communities of bats in heavily affected regions. Predictably, severe declines in wintering populations of bats should lead to concomitant shifts in the composition and relative abundance of bat species during the growing season in nearby forested landscapes. I used data from mist-net captures obtained from 2009 to 2016 to evaluate summer patterns in bat species abundance pre- and post-arrival of WNS in Mammoth Cave National Park (MNCP), Kentucky, USA. I examined temporal patterns of abundance across the Park and also compared changes in capture success rates for a subset of net locations sampled both before and after arrival of WNS in 2013. Data demonstrate a significant change in overall relative abundance of species captured post-WNS ($\chi^2 = 134$, df = 7, $P < 0.001$). The northern long-eared bat ($Myotis septentrionalis$; $F_{6,44} = 6.42$, $P < 0.0001$) was the most commonly captured species pre-WNS, but declined to the fourth most abundant species in mist-net captures post-WNS. The evening bat ($Nycticeius humeralis$; $F_{76,44} = 2.02$, $P < 0.0832$) demonstrated the largest increases in capture success following arrival of WNS to the Park, and was the most frequently captured species from 2014 to 2016. These data indicate that losses of cave-hibernating bats to WNS can lead to a restructuring of foraging bat assemblages on forested landscapes, with species not affected by WNS potentially exploiting niche space vacated by bats succumbing to WNS infection.
4.2 Introduction

Species are strongly influenced by environmental changes that include natural or anthropogenic disturbance events. Species are affected at different spatial scales that range from events such as climate change that act on a broad geographic scale to events like habitat destruction, deforestation and fragmentation that act on regional and local scales (Karl et al. 2009; Habel et al. 2015). Changes in land use have been the primary driver of biodiversity loss worldwide, especially in tropical regions (Meyer and Kalko 2008). The community composition of bats remaining after large-scale disturbances may be the result of specific habitat requirements of the local taxa and their ability to exploit resources (Meyer and Kalko 2008). Habitat generalists and highly mobile species are most likely to avoid extirpation after extensive environmental impacts (Habel et al. 2015).

Shifts in the assemblage of species at the community level are difficult to document due to the lack of historical data and scarcity of information on an entire community. Shifts in the faunal composition of fish communities have been documented in the U.S., and often result in the replacement of endemic species with wide-spread cosmopolitan species (Scott and Helfman 2001; Johnston and Maceina 2008). Determining the reasons behind species loss and assemblage shifts in freshwater streams are difficult, but changes in land use and increased urbanization are considered catalysts for rising water temperatures, changes in sediment load and other factors that may have large consequences for sensitive species (Sutherland et al. 2002; Johnston and Maceina 2008). Habel et al. (2015) studied species composition of burnet moths (Zygaenidae) and southeastern German butterfly (Rhopalocera) communities for two decades and found a gradual transformation of the species assemblage from numerous habitat specialists to a few habitat generalist species.
with disturbance. Many of the habitat specialists in their study had low dispersal capabilities and were heavily influenced by the decline in adequate habitat across southern Germany.

Today, many North American bat species face not only threats from anthropogenic disturbances (i.e., habitat fragmentation, development of wind power facilities, etc.), but also from white-nose syndrome (WNS). White-nose syndrome is caused by an infectious fungal disease (*Pseudogymnoascus destructans*) responsible for regional population collapse of many cave-hibernating North American bat species (Frick et al. 2010). Since WNS was introduced in 2006, millions of hibernating bats in eastern North America have been lost to the disease, with potential implications for possible restructuring of local bat assemblages (Jachowski et al. 2014). Shifts in the community composition of many species, including bats, are typically accompanied by disturbance events that create measurable changes in habitats (Scott and Helfman 2001; Johnston and Maceina 2008; Fukui et al. 2006; Habel et al. 2015). However, declines in numbers of bats on the landscape due to WNS is not associated with structural changes in forested habitats.

After the introduction of WNS to New Hampshire, Moosman et al. (2013) observed a large reduction in the overall abundance of local bat populations. Declines in capture rates in their study varied among species, with the little brown bat (*Myotis lucifugus*) and the northern long-eared bat (*M. septentrionalis*) having the largest population declines, and the big brown bat (*Eptesicus fuscus*) showing the least amount of change. Ultimately, the community of bats in New Hampshire was reduced from 7 species before the onset of WNS to effectively 4 species (Moosman et al. 2013). Similarly, in West Virginia and Virginia the trends in declining bat populations continue after the introduction of WNS,
especially for the northern long-eared bat (Francl et al. 2012; Reynolds et al 2016). Francl et al. (2012) suggest that an ecological release due to the decline in Myotis bats on the landscape in West Virginia may signal a permanent shift in the bat assemblage. The bat community composition before arrival of WNS was primarily dominated by little brown bats and northern long-eared bats, but currently shifts in the assemblage of bats now favors big brown bats (Francl et al. 2012).

With declines in population numbers of several bat species due to WNS and other human related activities, it is unclear how the recovery process will shape bat communities on forested landscapes in eastern North America. The loss of hibernating bat populations has potential for long-term implications in bat assemblages during the summer maternity season in heavily affected regions. I hypothesize that the decline of wintering bat populations in Mammoth Cave National Park, Kentucky, should lead to shifts in the composition and relative abundance of bat species during the growing season in local forested landscapes. Species with similar ecological requirements not affected by WNS should find foraging and roosting resources more readily available following the collapse of WNS-affected bat populations. I predict that composition of forest bat assemblages present after the arrival of WNS will most likely be a subset of the historical species composition present in affected areas before arrival of WNS. I used data from mist-net captures, collected before and after arrival of WNS to assess temporal changes, if any, in the assemblage of bats present.
4.3 Methods

Research was conducted at MCNP, Kentucky, USA, where recurring mist-netting surveys began in 2009 and continued through 2016. Data were obtained for 7 years on 51 calendar nights. No surveys were conducted during 2012. Data were collected from July to September in 2009, May-July in 2010 to 2013, the month of May in 2014, April to September in 2015 and April to July 2016. Bats were captured using mist-nets that measured 6-18 m in length and were stacked 6-9 m high (Avinet, Dryden, NY) at 6 different capture sites that included cave entrances, backcountry roads and ephemeral ponds (Figure 2.2). Mean sampling intensity was 2.7 ± 0.2 (SE) nets set per visit. Visits were limited to 4-5 times per season to reduce the tendency for bats to become net averse. Other capture sites were sampled on the Park from 2009 and 2016 but were not included in comparative statistical analyses.

Upon capture, body mass (g), right forearm length (mm), reproductive condition (females: pregnant, lactating or non-reproductive; males: scrotal or non-scrotal), Reichard’s wing index score (Reichard and Kunz 2009), sex, and age (Brunet-Rossinni and Wilkinson 2009) of each bat were collected. Bats were identified to species and released at the site of capture. Myotis bats were banded with 2.9 mm bands provided by the Kentucky Department of Fish and Wildlife Resources. Methods included adherence to decontamination protocols laid out by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 2016).

I used a Chi-square Test of Independence to compare relative abundance of bats by species pre- and post-WNS. I calculated capture rates (captures net\(^{-1}\) night\(^{-1}\)) for eight different species pre- and post-WNS, and examined changes in capture rates over the 7
years of sampling at the Park using single-factor ANOVAs (PROC GLM; SAS 9.4, SAS Inc., Cary, NC). When overall ANOVAs were significant, I examined differences in capture rates across years using Fisher’s least significant difference multiple comparison procedures. Historical weather data were obtained from the closest weather station to the Park (Weather Underground 2016) from 2009 to 2016. From April to September of every year, I derived mean weekly average, mean weekly maximum and mean weekly minimum temperatures and analyzed these data across years with single-factor ANOVAs to examine whether any significant change in temperature conditions took place that might account for any difference in capture success observed across years.

4.4 Results

Effects of WNS-period on species abundance was significant ($\chi^2 = 133.6, P < 0.001, df= 7; Table 4.1$). A total of 204 bats/120 net nights and 186 bats/ 121 net nights were captured during the pre-and post-WNS periods, respectively. During the pre-WNS period, the overall rate of capture was 1.7 bats net$^{-1}$ night$^{-1}$ (Table 4.2), with the overall rate of capture declining after WNS was introduced to the Park in the winter of 2013 to 1.54 bats net$^{-1}$ night$^{-1}$ (Table 4.2). The additional 19 capture sites, sampled from 2009 to 2016, produced a total of 834 bats collected over 384 net nights. The northern long-eared bat declined from the most frequently captured bat on the Park before the arrival of WNS to the fourth most captured species. After the onset of WNS, percent contributions to the Chi-square score demonstrated the evening bat (18.7%) and eastern red bat (14.5%) to be the more frequently captured species at the subset of capture sites.
General linear models of the effect of year on capture rate were significant for northern long-eared bat \( (F_{76,44} = 6.42, P < 0.0001) \), evening bat \( (F_{6,44} = 2.02, P = 0.0832) \) and Rafinesque’s big-eared bat \( (Corynorhinus rafinesquii; F_{6,44} = 5.35, P < 0.0003; \) Figure 4.1). Capture rate for the northern long-eared bat was greatest in summer 2010, but declined to lowest levels in 2015 and 2016 after arrival of WNS to cave systems in the Park \( (P < 0.05) \). Fisher’s LSD also demonstrated significantly lowest capture rates for Rafinesque’s big eared bat in post-WNS years \( (P < 0.05) \). Capture rates of evening bats were significantly higher in summers 2014 and 2016 compared with all other years of sampling \( (P < 0.05) \).

Big brown bat \( (F_{6,44} = 0.51, P = 0.794) \), eastern red bat \( (F_{6,44} = 0.72, P = 0.638) \), little brown bat \( (F_{6,44} = 0.78, P = 0.5875) \), Indiana bat \( (F_{6,44} = 1.16, P = 0.344) \), and tricolored bat \( (F_{6,44} = 0.69, P = 0.6609) \) showed no detectable change in capture rate over the 7-year period. For the big brown bat, large variations in capture success rate, i.e., wide SE bars (Figure 4.1), within years likely masked our ability to identify any temporal difference across years of sampling. I captured too few individuals of remaining species that occur on the Park (eastern small-footed bat, gray bat, hoary bat, and silver-haired bat) for robust statistical analysis.

Capture histories were further broken down into three distinct periods to illustrate the differences in the bat assemblage among pre-WNS (2009-2011), transitionary (2013; first year of WNS detection), and post-WNS (2014-2016) periods (Figure 4.2). An additional 15 capture sites were sampled at MCNP from 2009 to 2014, with a total of 467 bats captured over 228 net nights (Figure. 4.3). Overall, 25 capture sites were used at MCNP during the 2015 and 2016 season with a total of 367 bats captured over 156 net
nights (Figure 4.4). Data demonstrate precipitous declines in the capture of northern long-eared bats following arrival of WNS to the Park, with the big brown bat, evening bat, and eastern red bat becoming the most frequently captured species post-WNS across all netting sites.

Tests for possible changes in local temperature conditions showed no temporal patterns. Historical data for mean weekly average ($F_{7,183} = 0.57; P < 0.7805$), mean weakly maximum ($F_{7,183} = 1.3; P < 0.2543$) and mean weakly minimum ($F_{7,183} = 0.32; P < 0.9439$) temperatures from 2009 to 2016 did not differ across years (Figure 4.5).
Table 4.1. Number of bats captured by species in mist-nets at 6 capture sites in Mammoth Cave National Park, Kentucky from 2009 to 2016, excluding 2012, along with the percent contribution to the Chi-square score.

<table>
<thead>
<tr>
<th>Species</th>
<th>Observed Pre-WNS</th>
<th>Observed Post-WNS</th>
<th>Percent Contribution (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Corynorhinus</td>
<td>29</td>
<td>25</td>
<td>0.08</td>
</tr>
<tr>
<td>Eptesicus fuscus</td>
<td>10</td>
<td>19</td>
<td>2.24</td>
</tr>
<tr>
<td>Lasiurus borealis</td>
<td>8</td>
<td>37</td>
<td>14.5</td>
</tr>
<tr>
<td>Myotis leibii</td>
<td>3</td>
<td>17</td>
<td>7.59</td>
</tr>
<tr>
<td>Myotis lucifugus</td>
<td>4</td>
<td>13</td>
<td>3.73</td>
</tr>
<tr>
<td>Myotis septentrionalis</td>
<td>130</td>
<td>24</td>
<td>52.7</td>
</tr>
<tr>
<td>Nycticeius humeralis</td>
<td>7</td>
<td>41</td>
<td>18.7</td>
</tr>
<tr>
<td>Perimyotis subflavus</td>
<td>13</td>
<td>9</td>
<td>0.46</td>
</tr>
<tr>
<td>Total</td>
<td>204</td>
<td>186</td>
<td>100</td>
</tr>
</tbody>
</table>
Table 4.2. Capture rates by species from mist-netting efforts over 7 years at 6 different capture sites in Mammoth Cave National Park, Kentucky, USA. Capture rates for pre- and post-WNS were determined by 120 net nights and 121 net nights, respectively.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number Caught Pre-WNS</th>
<th>Capture Rate Pre-WNS</th>
<th>Number Caught Post-WNS</th>
<th>Capture Rate Post-WNS</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Corynorhinus rafinesquil</em></td>
<td>29</td>
<td>0.24</td>
<td>26</td>
<td>0.21</td>
</tr>
<tr>
<td><em>Eptesicus fuscus</em></td>
<td>10</td>
<td>0.08</td>
<td>19</td>
<td>0.16</td>
</tr>
<tr>
<td><em>Lasiurus borealis</em></td>
<td>8</td>
<td>0.07</td>
<td>37</td>
<td>0.31</td>
</tr>
<tr>
<td><em>Myotis lebei</em></td>
<td>3</td>
<td>0.03</td>
<td>17</td>
<td>0.14</td>
</tr>
<tr>
<td><em>Myotis lucifugus</em></td>
<td>4</td>
<td>0.03</td>
<td>13</td>
<td>0.11</td>
</tr>
<tr>
<td><em>Myotis septentrionalis</em></td>
<td>130</td>
<td>1.08</td>
<td>24</td>
<td>0.2</td>
</tr>
<tr>
<td><em>Nycticeius humeralis</em></td>
<td>7</td>
<td>0.06</td>
<td>41</td>
<td>0.34</td>
</tr>
<tr>
<td><em>Perimyotis subflavus</em></td>
<td>13</td>
<td>0.11</td>
<td>9</td>
<td>0.07</td>
</tr>
<tr>
<td>Total</td>
<td>204</td>
<td>1.7</td>
<td>186</td>
<td>1.54</td>
</tr>
</tbody>
</table>
\[ F_{6,44} = 5.35; \quad P < 0.0003 \]

\[ F_{6,44} = 0.51; \quad P = 0.794 \]
c. 

\[ F_{6,44} = 0.72; P = 0.638 \]

LABO/net/night

![Graph showing LABO/net/night data for years 2009 to 2016.]

d. 

\[ F_{6,44} = 0.78; P = 0.5875 \]

MYLU/net/night

![Graph showing MYLU/net/night data for years 2009 to 2016.]

44
$F_{6,44} = 6.42; P < 0.0001$

$F_{6,44} = 1.16; P = 0.344$
g. $F_{6,44} = 2.02; P = 0.0832$

h. $F_{6,44} = 0.69; P = 0.6609$
Figure 4.1. Capture rate comparisons of 8 bat species at Mammoth Cave National Park, Kentucky, USA, over 7 years: (a) Rafinesque’s big-eared bat (CORA) *Corynorhinus rafinesquii*; (b) big brown bat (EPFU) *Eptesicus fuscus*; (c) eastern red bat (LABO) *Lasiurus borealis*; (d) little brown bat (MYLU) *Myotis lucifugus*; (e) northern long-eared bat (MYSE) *M. septentrionalis*; (f) Indiana bat (MYSO) *M. sodalis*; (g) evening bat (NYHU) *Nycticeius humeralis*; and (h) tri-colored bat (PESU) *Perimyotis subflavus*. 
a. 

![Graph a](image1.png)

b. 

![Graph b](image2.png)
Figure 4.2. Totals for species captured before the arrival of WNS (a), during the first year of WNS detection (b), and after the onset of WNS (c) at Mammoth Cave National Park, Kentucky, USA. Species included: Rafinesque’s big-eared bat (CORA) Corynorhinus rafinesquii; big brown bat (EPFU) Eptesicus fuscus; eastern red bat (LABO) Lasiurus borealis; silver-haired bat (LANO) Lasionycteris noctivagans; gray bat (MYGR) Myotis grisescens; small-footed bat (MYLE) M. lebeii; little brown bat (MYLU) M. lucifugus; northern long-eared bat (MYSE) M. septentrionalis; Indiana bat (MYSO) M. sodalis; evening bat (NYHU) Nycticeius humeralis; and tri-colored bat (PESU) Perimyotis subflavus.
Figure 4.3. Cumulative totals for species captured pre-WNS from 2009-2014, excluding 2012, at 15 capture sites in Mammoth Cave National Park, Kentucky, USA. Species included: Rafinesque’s big-eared bat (CORA) *Corynorhinus rafinesquii*; big brown bat (EPFU) *Eptesicus fuscus*; eastern red bat (LABO) *Lasiurus borealis*; silver-haired bat (LANO) *Lasionycteris noctivagans*; gray bat (MYGR) *Myotis grisescens*; small-footed bat (MYLE) *M. lebeii*; little brown bat (MYLU) *M. lucifugus*; northern long-eared bat (MYSE) *M. septentrionalis*; Indiana bat (MYSO) *M. sodalis*; evening bat (NYHU) *Nycticeius humeralis*; and tri-colored bat (PESU) *Perimyotis subflavus*. 
Figure 4.4. Cumulative totals for species captured post-WNS from 2015 to 2016 at 25 capture sites in Mammoth Cave National Park, Kentucky, USA. Species included: Rafinesque’s big-eared bat (CORA) *Corynorhinus rafinesquii*; big brown bat (EPFU) *Eptesicus fuscus*; eastern red bat (LABO) *Lasiurus borealis*; silver-haired bat (LANO) *Lasionycteris noctivagans*; gray bat (MYGR) *Myotis grisescens*; small-footed bat (MYLE) *M. lebeii*; little brown bat (MYLU) *M. lucifugus*; northern long-eared bat (MYSE) *M. septentrionalis*; Indiana bat (MYSO) *M. sodalis*; evening bat (NYHU) *Nycticeius humeralis*; and tri-colored bat (PESU) *Perimyotis subflavus*. 
a. $F_{7,183} = 1.3; P = 0.2543$

b. $F_{7,183} = 0.57; P = 0.7805$
Figure 4.5. Historical daily high (a), average (b) and low (c) temperatures from a local weather station close to Mammoth Cave National Park, Kentucky, USA.

\[ F_{7,183} = 0.32; P = 0.9439 \]
4.5 Discussion

Capture rates observed during the progression of WNS in MCNP indicate that the fungal disease has led to declines in the overall abundance of some bat species on the landscape, but that severity varied by species. Both the Chi-square Test of Independence and the general linear model analysis demonstrated a decline in abundance of northern long-eared bats and an increase in capture success and relative abundance of evening bats after arrival of WNS to the Park. I suspect that an increase in evening bats combined with the decline in northern long-eared bats may signal a shift in bat assemblages and relative abundances of these two species in the region. The results of my mist-net surveys provide further evidence for the decline in northern long-eared bats following WNS exposure and is consistent with reports from other states (Francl et al. 2012; Moosman et al. 2013; Reynolds et al. 2016).

Many bat species partition niche space which maximizes resource use within a habitat, although there can be considerable overlap in habitat use among species (Patterson et al. 2003). Bats are thought to partition resources based on preferences for cluttered versus uncluttered foraging space (Law et al. 2005) and for roost preferences in trees of varying conditions of decay class (Kunz and Lumsden 2003; Barclay and Kurta 2007). A competitive exclusion release could possibly account for the shift in relative abundance observed in the bat assemblage at MCNP after the onset of WNS, especially for evening bats. I suggest that increased availability of roosting substrates is enhancing population numbers of evening bats since the onset of WNS at MCNP. During the maternity season in southwestern Missouri, female evening bats were found to roost in the cavities of trees that are in late stages of decay (Boyles and Robbins 2016). Much of the research completed
on the roosting preferences of the northern long-eared bat during the growing season suggest some overlap in preferences for roosting sites. Roosts of female northern long-eared bats are commonly under exfoliating bark or in cavities and crevices of dead or live trees (Owen et al. 2003; Broders et al. 2004; Carter and Feldhamer 2005; Lacki et al. 2009; Timpone et al. 2015). During the maternity season, roost trees used by female northern long-eared bats were more likely to be in early to mid-stages of decay compared to randomly-selected potential roost trees (Carter and Feldhamer 2005; Johnson et al. 2009; Johnson et al. 2012). With the northern long-eared bat no longer the most common species on the landscape at MCNP, the evening bat may now be able to access roosting sites during the maternity season that otherwise would have been unavailable and which are critical for recruitment into the population.

I detected no difference in yearly capture rates of big brown bats or eastern red bats, despite temporal patterns in relative abundance of these species that indicated they were relatively more common in mist net captures, except for evening bats, than all other species following arrival of WNS to the Park. Big brown bats in other geographic locations have been observed to remain common in forested landscapes during the summer maternity season following exposure to WNS (Ford et al. 2011, Francl et al. 2012, Reynolds et al. 2016). Being larger in size than other cave-hibernating bats in eastern North America, big brown bats likely possess sufficient fat stores to enhance their overwinter survival, regardless of WNS exposure, relative to smaller-sized Myotis and Perimyotis species which experience substantial drops in body mass from fall swarming to spring staging (Lacki et al. 2015). Ford and co-workers (2011) proposed that the big brown bat might also have gone through an ecological release following population decline of the little brown bat in
Fort Drum, New York. It is unknown, however, if the removal of another formerly common species, such as the northern long-eared bat, will prompt changes in habitat use for the remaining bat species in the region (Ford et al. 2011).

Our results indicated that eastern red bats were relatively more abundant in mist net captures than many other species following arrival of WNS to the Park. It is unlikely that the eastern red bat has begun to roost in spaces vacated by the northern long-eared bat, as this bat commonly roosts in the foliage of trees or in leaf litter (Hutchinson and Lacki 2000; Limpert et al. 2007; Mormann and Robbins 2007; O’Keefe et al. 2009), and not in crevices or beneath bark. Conversely, the eastern red bat may now be foraging in habitats where the species previously could not due to the abundance of northern long-eared bats pre-WNS, and may have expanded their diet to include prey that have increased in abundance following the collapse of northern long-eared bat populations. Many prey analysis studies have shown a great deal of overlap in the diets of many forest-dwelling bats in the eastern U.S., especially eastern red bats and northern long-eared bats which feed heavily on Lepidopterans, i.e., moths (Faure et al. 1993; Brack and Whitaker 2001; Carter et al. 2003; Whitaker 2004; Feldhamer et al. 2009; Dodd et al. 2012). Before the arrival of WNS, the northern long-eared bat was the most common species on the MCNP landscape (Lacki et al. 2015). Their diet in Kentucky, in particular, consists primarily of moths and to a lesser degree beetles (Dodd et al. 2012). Diet analysis in other states found eastern red bats fed primarily on moths, but also preyed upon beetles and leafhoppers (Carter et al. 2003; Feldhamer et al. 2009) further suggesting overlap in the types of insect prey consumed by these two bat species. Diet analysis of the evening bat has shown this species to be primarily a beetle strategist, with some selection of moths and leafhoppers (Whitaker and
Clem 2013), so benefits in increased foraging success from the disappearance of northern long-eared bats are less likely.

General linear model analysis indicated over the 7-year period that capture rates of Rafinesque’s big-eared bat declined, especially in 2013, 2015 and 2016. Reasons for these differences are unclear. Park officials continually monitor Rafinesque’s big-eared bat colonies and have noted no difference in colony sizes since the arrival of WNS to the Park in 2013 (S. Thomas, NPS, personal communications). Further, susceptibility of Rafinesque’s big-eared bat to WNS exposure does not appear to be strong and behavioral studies have shown this species to have overwintering strategies, i.e., shallow torpor and frequent roost switching, which likely render it less susceptible to WNS infection (Johnson et al. 2012).

The susceptibility that a species of bat has to WNS is largely dependent on whether a species is a cave-hibernator or whether it migrates to other habitats to overwinter. For Myotis bats, including the northern long-eared bat, hibernating in caves poses a large risk of exposure to WNS. With the drastic declines in populations of many cave-hibernating bats, secondary impacts such as lowered reproductive success can be amplified and lead to reduced levels of recruitment or potential for populations to recover from WNS. Because of this slowed recovery potential, species like the northern long-eared bat are likely to remain at reduced population numbers during the summer maternity season for years, if not indefinitely. Responses by other bats to this change in abundance of a formerly common species are likely and I believe the findings presented here indicate these responses are already occurring in MCNP. My inability to detect any temporal patterns of change in local weather data points to no apparent effect of climate on capture success rates.
of bats at MCNP. Thus, climate is an unlikely explanation for changes in bat species composition observed on the Park. I suggest that impacts of WNS and subsequent species responses are the most plausible mechanisms behind the shifts in the bat assemblage recorded over time. I believe these data represent empirical evidence in support of the prediction of novel restructuring of forest bat communities following WNS mortalities (Jachowski et al. 2014). It is unknown whether these trends in bat species abundance are temporary or whether they will lead to permanent and lasting shifts in relative species abundance on forested landscapes in eastern North America. Monitoring bat populations both regionally and at local scales will be imperative in helping conservation efforts for bat species affected by WNS, and to more fully understand the ecological consequences resulting from dynamic shifts in species occurrence following large-scale WNS mortalities.
CHAPTER 5: LANDSCAPE-SCALE PATTERNS IN THE DISTRIBUTION OF TREE ROOSTS OF THE NORTHERN LONG-EARED BAT (MYOTIS SEPTENTRIONALIS) AT MAMMOTH CAVE NATIONAL PARK

5.1 Abstract

Declining bat populations in North America due to white-nose syndrome (WNS) have sparked much interest in determining the importance of summer maternity roost trees in recovery efforts for forest-dwelling bat species affected by WNS. The roosting habits of many temperate zone bats have been well documented at microhabitat scales but few studies have included multi-scale assessments of landscape patterns in bat roost site selection. I used spatial point pattern analysis to quantify distributional trends for spring and early maternity season roosts of female northern long-eared bats located from 2015 to 2016 at Mammoth Cave National Park (MCNP), Kentucky, USA. A variety of spatial covariates were used to model the effect landscape pattern on locations of female bat roosts. My results indicate that in MCNP roost locations of female northern long-eared bats were within 2,000 m of known winter hibernacula, situated more often at higher elevations in mesic upland deciduous forests and were in close proximity to water sources and roads. I present hypotheses to account for the patterns observed in relation to landscape features and habitat resources. My data indicate that consideration of habitat requirements of bats at landscape scales and not just at local levels will benefit conservation efforts for forest-dwelling bats, especially species affected by WNS.
5.2 Introduction

Bats (Order: Chiroptera) are second only to rodents (Order: Rodentia) in numbers and constitute approximately one-fifth of all mammal species (Martin et al. 2011). They are broadly distributed, occupy a variety of feeding guilds, and may be the most abundant mammals on a local scale, especially in the tropics (Patterson et al. 2003; Gorresen et al. 2005). Anthropogenic forces worldwide, such as deforestation and fragmentation, are elevating the rates of species extinctions and the loss of biological diversity (Wilcox and Murphy 1985; Gorresen et al. 2005). Globally, deforestation and fragmentation represent the most abrupt form of landscape change (Millennium Ecosystem Assessment 2005; Boughey et al. 2011). Unfortunately, responses of bat species to these anthropogenic forces and other disturbances across a range of spatial scales remains largely unexplored (Gorresen et al. 2005).

Declining populations of cave-hibernating bats in North America due to white-nose syndrome (WNS) has sparked much interest in determining the importance of roost tree selection by forest-dwelling bat species, especially species heavily impacted by WNS. A majority of studies on bat roosting ecology have focused on variables comparing habitat at the scale of the roost tree or surrounding forest stand (Lacki and Baker 2003; Kalcounis-Rueppell et al. 2005; Barclay and Kurta 2007; Limpert et al. 2007). Theoretical and empirical evidence suggests that species rarely follow a linear association with gradients in habitat characteristics (Wiens 1989; Lord and Norton 1990; With and Crist 1995; Gorresen et al. 2005), and, therefore, criteria a species uses for habitat and resource selection likely varies depending on scale (Johnson 1980; Wiens 1981; Limpert et al. 2007). Use of a multi-scale analysis that includes landscape patterns could be beneficial in
discerning resource selection of a species such as the northern long-eared bat (*Myotis septentrionalis*), which likely perceives the landscape on different spatial scales, and which is in region-wide decline due to impacts from WNS.

Before the onset of WNS in temperate North America, the northern long-eared bat was considered a common forest-dwelling bat that ranged from the central and eastern United States to western Canada. Most studies conducted at the roost tree and stand scales demonstrate the importance of hardwoods for roosting by the northern long-eared bat (Carter and Feldhamer 2005; Perry and Thill 2007), but these bats also roost in conifers (Lacki and Schwierjohann 2001). It is widely accepted that the northern long-eared bat shows plasticity in choice of summer roost trees, suggesting that the structural complexity of the habitat or available resources nearby are important factors in roost selection (Carter and Feldhamer 2005; Lacki et al. 2009b). Roost tree networks of the northern long-eared bat are similar to those documented for the Indiana bat (*Myotis sodalis*), where colonies typically have one or more primary trees that provide the necessary roosting conditions for sustaining maternity colonies (Callahan et al. 1997; Carter and Feldhamer 2005). The northern long-eared bat has been shown in previous studies to roost non-randomly and to roost with conspecifics in a network of roost trees across a landscape, focusing on a central-node roost tree (Garroway and Broders 2007; Johnson et al. 2012).

Studies focused on multi-scale landscape patterns in bat roost selection in North America have demonstrated eastern red bats (*Lasiurus borealis*) to favor mature streamside management areas within an intensively managed pine plantation in Mississippi, USA (Elmore et al. 2005). Personal communications documented by
O’Keefe et al. (2009) suggest that tri-colored bats (*Perimyotis subflavus*) also exhibit the same roost exclusivity in intensively managed pine stands. O’Keefe et al. (2009) posited that the study conducted by Elmore et al. (2005) provided very little evidence for landscape-scale selection due to the homogeneity of the intensively managed landscape. However, eastern red bats have also been shown to select roosting sites near open urban land and water compared with random sites (Limpert et al. 2007). Veilleux et al. (2003) demonstrated that tri-colored bats in Indiana, USA, selected riparian and upland forests over bottomlands.

Globally, the effects of landscape patterns on bat roost selection have received more attention. Patterns in roosting behavior associated with patch size have been compared in tropical regions (Gorresen et al. 2005; Klingbeil and Willig 2009; Loayza and Loiselle 2009). The effect of patch size seems to differ among species, with those species dependent on trees as roost structures most negatively affected by the loss of adequate forested habitat (Lesinski et al. 2007). Boughey et al. (2011) showed that six bat species in the U.K. were greatly influenced by landscape composition closer to the roost, more so than the landscape composition within their home-ranges. Gorresen et al. (2005) concluded that there is no single focal scale that species respond to and that animal species are aware of resources and landscape features at a range of spatial scales. Expanding on studies such as these is important in determining the landscape-level factors that affect the roosting ecology and behavior of forest-dwelling bat species. Effective conservation plans for bats require a better understanding of macrohabitat requirements, as many forest management practices operate at these scales (O’Keefe et al. 2009).
Wildlife populations are rarely uniformly distributed across a landscape and often resemble metapopulations that are connected by varying degrees of temporary species movement (Leibold et al. 2004; Wilschut et al. 2015). The spatial structure of wildlife populations may have significant implications for the spread and persistence of infectious diseases across landscapes (Keeling and Gilligan 2000; Grenfell et al. 2001; Wilschut et al. 2015), including effects from WNS. Studying the roosting ecology of the northern long-eared bat from a landscape-scale perspective may help elucidate behavior patterns and habitat needs not identified through studies framed at local-scales.

Spatial statistics of point patterns provide a rigorous format for describing distributions and testing hypotheses about those distributions at larger spatial scales (Reiter and Anderson 2013). I employed spatial point pattern analysis to quantify patterns of spring and early maternity season roosts of female northern long-eared bats at Mammoth Cave National Park (MCNP), Kentucky, USA. My objective was to determine what landscape characteristics, if any, were important for roost selection of non-reproductive and reproductive (i.e., pregnant or lactating) females and whether landscape patterns helped determine those outcomes. Given what we already understand about roosting behavior of northern long-eared bats, I hypothesized that these bats would roost within mesic upland deciduous forests (Foster and Kurta 1999; Menzel et al. 2002; Broders and Forbes 2004; Henderson and Broders 2008) and within close proximity to flyways such as water sources and roads (Henderson and Broders 2008); the latter to enhance foraging success. I also hypothesized that topography could influence the likelihood of roosting occurrences on the landscape. Topographic features known to be important to female northern long-eared bats elsewhere include: higher elevation areas
(Lacki et al. 2009), and upper and mid-slope position (Lacki and Schwierjohann 2001; Krynak 2010). Slope aspect was also tested even though only one study on Indiana bats 
(Myotis sodalis) reported on it and found no correlation between roosting locations (Watrous et al. 2006; Lacki et al. 2009b). However, the position of roost trees by slope aspect may be important as roosts on southwest facing slopes are likely associated with warmer, drier and higher roost microclimates (Lacki et al. 2009b). Finally, I hypothesized that female northern long-eared bats would roost near known winter hibernacula, especially during spring emergence, i.e., staging, when fat reserves are reduced and availability of insect prey remain at seasonal lows. Reproductive female bats are presumably more constrained by energy demands than male bats (Cryan et al. 2000), so it would be reasonable to assume that roost selection of female bats during staging would be consistent with minimizing energy expenditures during an energetically taxing season of the year.

5.3 Methods

Research was conducted at MCNP, Kentucky, USA, during the spring and early summer of 2015 and 2016. Data were collected from April to August of 2015 and from April to July in 2016. Northern long-eared bats were captured with mist-nets that measured 6-18 m in length and were stacked 6-9 m high (Avinet, Dryden, NY) at 25 sites on the Park. Nineteen adult female northern long-eared bats and one juvenile male were fitted with LB-2XT radio-transmitters (Holohil Systems, Ltd., Ontario, Canada) with surgical glue (Perma-Type Company, Inc., Plainville, CT) between the shoulder blades. Bats were tracked daily for approximately 8-15 days or until the transmitter battery failed or fell off
the bat. A 3-element yagi antenna (Wildlife Materials, Inc., Murphysboro, IL) and an Icom IC-R20 radio-receiver (Icom America, Inc., Kirkland, WA) were used to track bats. For each roost identified, the coordinates were recorded with a Garmin GPS unit (Garmin International, Inc., Olathe, KS).

Spring and summer roost locations were geographically referenced using the UTM (Universal Transverse Mercator) coordinate system. Spatial covariates (i.e., roadways, hydrology, and land cover) were mapped and processed using a geographic information system (ArcGIS 10.4.1, Redlands, CA). I obtained digital vegetation coverage, and data for hydrology and roadways from Lillian Scoggins, MCNP, U.S. National Park Service. Locations of known bat overwintering caves were provided by Dr. Rickard Toomey, MCNP, U.S. National Park Service. I used ad quantative modeling approaches similar to the one used in Yang et al. (2007) to describe spring and summer roost locations using an inhomogeneous Poisson process. This type of modeling is a point process that records the number and the values of records associated with a sequence of independent and identically distributed random variables (Pellerey et al. 1998). Poisson process models assume that spatial patterns of roost locations resulted only from environmental heterogeneity on the landscape (i.e., nearby roosts were independent variables). A variety of spatial covariates (i.e., elevation, southwestness, distance to water/roads/winter hibernacula, and proportion of mesic upland deciduous forests) with transformations were used in the inhomogeneous Poisson model. The kernel intensity estimation and Ripley’s K function were calculated to describe spatial patterns (i.e., clustering or regularity) of roosts at the Park (Yang et al. 2007). Inhomogeneous residual analysis and Akaike information criterion (AIC) methods
were used to select variables with a stepwise model selection to find the best fit model for the data (Yang et al. 2007).

Spatial covariates were primarily selected on the basis of prior research indicating patterns of habitat selection by northern long-eared bats. For example, the digital vegetation layer contained nine different vegetation classes. The ‘mesic upland deciduous’ vegetation class was chosen based off prior studies that indicated preference for this habitat type by the northern long-eared bat (Foster and Kurta 1999; Menzel et al. 2002; Broders and Forbes 2004; Henderson and Broders 2008). A moving window analysis (30 x 30 m cell size) was used to determine the proportion of mesic upland deciduous forest within a neighborhood (i.e., the window) for every location within the Park. The purpose of using the moving window analysis was to create a GIS variable that can describe local-scale vegetation composition and transform the categorical vegetation class GIS variable into a continuous variable. The continuous vegetation variable was then used in spatial point pattern modeling to quantify vegetation effects on roosting locations. Proximities to road and water were determined by calculating the Euclidian distance from each cell (30-m resolution) to the nearest road or water source, a function provided by the ArcGIS Spatial Analyst tool. I used a digital elevation model (DEM) that was published by the Kentucky Geological Survey (Kentucky Geological Survey 1998). Slope and aspect were calculated from DEM data using the surface analysis provided by the ArcGIS Spatial Analyst tool. The calculated aspect azimuth was later transformed into southwestness using the equation (COS(aspect)-225) to change the circular aspect to a gradient (linear) in order to select for higher potential solar radiation (southwestness). The Euclidian distance function was used to determine distances from roost locations to the nearest known winter bat caves. A
lurking plot variable was used to identify non-linear or spatial trends in the point processes (Baddeley et al. 2005). The residual is plotted against a select spatial covariate. Noticeable trends in the lurking variable plot are accounted for and appropriately modified for that spatial covariate. Selected covariates were plotted in R with a polynomial function up to the power of two to model the marginal effects of the variables on roost likelihood.

5.4 Results

A wide range of alternative models were considered that included all possible combinations of the potential spatial covariates. Variables with negative coefficients had negative or likelihood of roost probability, and variables with positive coefficients had positive contributions. The full model (AIC = 2100.4) predictors included: distance to road, distance to water, distance to winter caves, elevation, southwestness, slope, and mesic upland deciduous forest. Due to most continuous variables displaying curvilinear patterns, the full model also included second order transformations for all covariates except mesic upland deciduous cover type and southwestness. The best fit model possessed an AIC score = 2091.1 (Table 5.1) The second order distance to water, first order distance to roads, and both first and second order distance to winter caves were retained in the best fit model ($P<0.01$). The second order elevation, first order slope, and first order mesic upland deciduous forest cover type were rejected ($P>0.1$). Southwestness was retained in the best fit model; however, the confidence interval included zero in the output indicating the null hypothesis cannot be rejected and there was no effect due to this covariate.

I used 69 roost locations of female northern long-eared bats at MCNP in the analyses (Figure 5.1). The non-parametric kernel density estimation (Figure 5.2) showed a
high concentration of roosts in the northwest section of the Park, indicating the roost occurrence pattern was not completely random. The nearest neighbor distance (m) calculated the distance of the closest other roost for each of the 69 roost trees (Figure 5.3). Nearest neighbor distances demonstrated clustering in some sections of the Park. The minimum distance between any two roosts was 4.24 m, with an average distance of 108.3 m ± 12.4, and a maximum distance of 381 m. The estimated $K$ function was larger than the theoretical CSR, indicating spatial clustering of roosts on the landscape (Figure 5.4). Regardless, strong spatial dependence could be due to either bat behavior, i.e., fission-fusion, or to association with clustering of environmental factors (i.e., vegetation type, elevation, etc.) on the landscape.

The inhomogeneous Poisson process model demonstrated that spatial clustering of roosts could be accounted for by environmental heterogeneity. The null model (homogeneous Poisson) assumes that roost locations are equally likely across the landscape (Figure 5.5). The cumulative Pearson residuals were plotted against the seven spatial covariates (i.e., distance to road, distance to water, distance to winter caves, slope, elevation, southwestness, and proportion of mesic upland deciduous) and the two Cartesian coordinates ($x$ and $y$) for the null model. The cumulative Pearson residuals for the predicted random values exceed the observed roost occurrence values (in red; Figure 5.5), suggesting that the null model underestimated roost likelihood at this scale.

Lurking variables plotted against the null model of roost occurrence on the Park landscape indicated clear systematic patterns (Figure 5.6). Female northern long-eared bats selected roost locations within 200 m of known roadways and water sources and within approximately 2,000 meters of known winter bat hibernacula. Female bats avoided
potential roost locations at elevations between 198 and 259 m. A lurking plot of the proportion of mesic upland deciduous forest with the 900-m moving window analysis of vegetation cover type revealed the cumulative residuals of the null hypothesis were smaller than expected for areas where the proportion of mesic upland deciduous forest was less than 0.8. This suggests that female northern long-eared bats in MCNP have a strong preference towards mesic upland deciduous forests. The last two variable plots, slope and southwestness, exhibited empirical curves of cumulative Pearson residuals within the two-standard-deviation error bounds, suggesting bats are not preferentially choosing roost sites by aspect or slope position.

The full and best fit models generated a prediction map of likely roosting locations of female northern long-eared bats at MCNP. Dark blue areas on the map indicated areas the model predicted to have the highest likelihood of roost occurrence on the landscape (Figure 5.6). Both the full and best fit models indicated that the cumulative sum of raw residuals did not fit within the two-standard-deviation error bounds in the northwest portion of the Park (in red), meaning neither models accounted for all variation in the data.

Effects of likelihood of roost occurrence within the Park were plotted against three variables: elevation, distance to water and distance to winter caves (Figure 5.7). Elevation appears to have a positive association with probability of roost location, suggesting higher elevation areas are preferred habitats of female northern long-eared bats during staging and the early maternity season. Distance to water demonstrated a monotonically decreasing pattern indicating that probability of roost location decreases as distance to the nearest water source increases. The distance to known overwintering hibernacula within the Park shows an inflection point at approximately 2,000 m. Bats appeared to select roosts farther
away from winter caves up to the inflection point. Beyond the inflection point distance, the likelihood of roosts occurring on the landscape dropped significantly.
Table 5.1. Coefficients of the predictor variables of the best fit model by stepwise model selection for female northern long-eared bats at Mammoth Cave National Park, Kentucky, USA.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>Z-test</th>
<th>C.I. 95 Low</th>
<th>C.I. 95 High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td></td>
<td>-1.75E+01</td>
<td>9.88E-01</td>
<td>1.94E+01</td>
<td>-1.55E+01</td>
<td></td>
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<tr>
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<td>2.42E-06</td>
<td>1.08E-06</td>
<td>*</td>
<td>3.15E-07</td>
<td>4.53E-06</td>
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<tr>
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<td></td>
<td>4.30E-02</td>
<td>1.95E-02</td>
<td>*</td>
<td>4.81E-03</td>
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<td>1.87E-01</td>
<td></td>
<td>-2.88E-01</td>
<td>7.06E-01</td>
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<tr>
<td>Distance to water^2</td>
<td></td>
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<td>8.97E-07</td>
<td>***</td>
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<td>6.51E-04</td>
<td>***</td>
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<td>Vegetation (Mesic Upland Deciduous)</td>
<td></td>
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<td>1.71E-07</td>
<td>***</td>
<td>-9.90E-07</td>
<td>-3.18E-07</td>
</tr>
</tbody>
</table>

*** Indicates the $z$-test is rejected at the 1% significance, ** at 5%, and * 10%.
Figure 5.1. Quadrant count map of female northern long-eared bat roosts at Mammoth Cave National Park, Kentucky, USA.
Figure 5.2. Non-parametric kernal density estimation of female northern long-eared bat roosts at Mammoth Cave National Park, Kentucky, USA.
Figure 5.3. Nearest neighbor distances of female northern long-eared bat roosts at Mammoth Cave National Park, Kentucky, USA.
Figure 5.4. Estimated $K$ function graph of female northern long-eared bat roosts at Mammoth Cave National Park, Kentucky, USA.
Figure 5.5. Null model (homogeneous Poisson) and cumulative sum of raw residuals of female northern long-eared bat roosts at Mammoth Cave National Park, Kentucky, USA.
e.
Figure 5.6. Lurking variable plots against (a) distance to road, (b) distance to water, (c) distance to winter caves, (d) elevation (DEM), (e) proportion of vegetation code 3 (mesic upland deciduous), (f) slope, and (g) southwestness (aspect) for the null model of roost occurrence on the landscape at Mammoth Cave National Park, Kentucky, USA. Solid lines indicate empirical curves of cumulative Pearson residuals. Dotted lines denote two-standard-deviation error bounds.
Figure 5.7. Fit point process model prediction maps of female northern long-eared bat roost locations at Mammoth Cave National Park, Kentucky, USA for (a) full model and (b) best fit model.
b.
Figure 5.8. Likelihood of female northern long-eared bat roost occurrence at Mammoth Cave National Park, Kentucky, USA against (a) elevation, (b) distance to water, and (c) distance to known overwintering caves.
5.5 Discussion

Prior studies have demonstrated that species responses of bats to spatial structure of habitats is highly dependent on focal scale (Gorresen et al. 2005; Perry et al. 2008; O’Keefe et al. 2009). Proximity to water sources, foraging areas, and topography (i.e., slope position, elevation, aspect) all potentially affect the roost selection process on a landscape scale (Perry et al. 2008). The roosting habits of many temperate zone bats have been well documented at the microhabitat scale but few studies have focused on landscape patterns in bat roosting behavior, especially in temperate zones. My results indicate that during the spring and early maternity seasons, roosts of female northern long-eared bats are spatially clustered on the landscape and environmental factors such as elevation, and distances to roads, water, and overwintering hibernacula are important determinants of spatial locations.

Roost locations may be influenced by topography, such as elevation, slope, and aspect (southwestness) because of associated differences in microclimate (Ormsbee and McComb 1998; Rabe et al. 1998; Baker and Lacki 2006; Perry et al. 2008). My results indicated that some female northern long-eared bats preferentially chose roosting locations higher in elevation. Female bats did not differentiate between slope or aspect (southwestness) in the models, indicating that these bats are selecting roost sites due to other factors and that slope and aspect position are largely a result of roost site availability. I hypothesize that selection of roost trees at higher elevations is because pregnant and lactating females preferentially chose warmer roosting microclimates to reduce the cost of maintaining normothermic body temperatures during the early reproductive season, facilitating parturition, lactation and the rapid development of young.
My results corroborate with Perry et al. (2008) in that female northern long-eared bats roosted closer to roads, which is often directly tied with flight corridors and improved access to suitable areas for foraging (Limpens and Kapteyn 1991; Walsh and Harris 1996; Perry et al. 2008). My finding also indicated a strong positive correlation with proximity to water. Similarly, empirical evidence has demonstrated the importance of proximity to water for other bats species (Kalcounis-Rupell et al. 2005; Perry et al. 2008). During the growing season, reproductive female bats are presumably more energetically constrained than male bats (Cryan et al. 2000), so it would be reasonable to assume that habitat selection by reproductively active, adult females would prioritize proximity to water and road ways to enhance access to drinking water, increase foraging efficiency, and minimize energy expenditures during gestation and lactation. The moving window analysis revealed female northern long-eared bats had a strong preference towards the vegetation cover type described as mesic upland deciduous forest. The lurking variable plot of the proportion of mesic upland deciduous forest combined with the moving window analysis indicated that habitats where these bats are roosting at MCNP on average had up to 80% of habitat patches in the mesic upland deciduous forest cover type. My results are consistent with other findings that demonstrate preferences towards deciduous roost trees within intact forests by northern long-eared bats (Foster and Kurta 1999; Menzel et al. 2002; Broders and Forbes 2004; Henderson and Broders 2008).

Due to Mammoth Cave National Park’s karst topography, locations of known overwintering hibernacula were added into our analyses to further understand spatial patterns of summer roost locations of female northern long-eared bats. The elevation of the water table, which is roughly the elevation of the Green River, corresponds with the
elevation at which caves occur (DiPietro 2013). As the Green River cuts downslope into the landscape, active cave formation drops to lower levels, leaving dry caves at higher elevations. The uppermost passages of Mammoth Cave are located between 174 to 210 m in elevation, with the oldest and largest cave openings occurring at ground level or 227 m (DiPietro 2013). Female bats appeared to select roost locations increasingly farther away from known overwintering caves up to 2,000 m in distance; however, no female bat chose a roost location beyond the 2,000 m distance threshold from any known winter hibernacula. I hypothesize that the close proximity to overwintering caves allows for conspecifics to regroup after the hibernation period in spring (i.e., staging behavior). Considering all the spatial covariates explored in these analyses, results presented indicate female northern long-eared bats selected roosting sites upslope at higher elevations but relatively near known overwintering caves.

Although many studies have determined the need to consider management of habitats at the stand level to foster increases in bat colony numbers during the maternity season (O’Donnell 2000; Willis and Brigham 2004; Garroway and Broders 2008), my data suggest there is also a need to consider larger spatial scales when creating management plans for forest-dwelling bats. For species that have the ability to fly and travel long distances, it is likely that bats recognize resources and landscape features at a range of spatial scales (Gorresen et al. 2005). My findings support the importance of conserving habitat diversity, especially intact and contiguous forests, for the northern long-eared bat. For at least MCNP, preferred roost locations of female northern long-eared bats are situated within 2,000 m from known winter hibernacula and include high elevation, mesic upland deciduous forests in close proximity to water sources and roads. Whether these same
conditions exist for the northern long-eared bat elsewhere across its distribution is unclear but worthy of exploration. Maintaining a buffer of at least 2,000 m surrounding known overwintering caves of this bat should ensure continued availability of suitable roosting sites for the species throughout the Park. The northern long-eared bat declined significantly enough across its range over the past decade for the species to be added as threatened under the Endangered Species Act in spring of 2015 (U.S. Department of the Interior 2015). It is presently unknown whether these trends will lead to permanent and lasting reductions in abundance. Nevertheless, considering habitat requirements at local and landscape scales is imperative to helping conservation efforts for the recovery of the northern long-eared bat throughout its distribution.
CHAPTER 6: CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Assessing the status of a species requires an understanding of the basic biology, ecology, population size and trends over time (Alberta Sustainable Resource Development and Alberta Conservation Association 2009). Ultimately, more information about the basic ecology of bats is needed to effectively conserve them; however, access to shelter, food, and water resources is necessary to secure the survival of bat populations globally (Fenton and Simmons 2015). Basic information concerning life history strategies and habitat preferences has been collected for the northern long-eared bat, allowing us to make limited inferences about the species and to fill in some knowledge gaps about their habitat use (Alberta Sustainable Resource Development and Alberta Conservation Association 2009).

My research compared variation in roost tree and stand characteristics of non-reproductive female, pregnant and lactating female, and male northern long-eared bats. Logistic regression analyses comparing habitat features of roosts with random plots indicated roost selection by bats reflected the costs of energetic demands of different sex and reproductive classes. Relative to pregnant and lactating females, non-reproductive females in spring selected roosts that had higher percent canopy cover and basal area, situated at lower elevations. These forest conditions likely foster microclimates at lower temperatures inside roosts by reducing solar radiation to promote use of daytime torpor in tree roosting bats (Turbill et al. 2003; Willis et al. 2005; Ruczyński 2006). Pregnant and lactating female bats preferentially chose roost trees at higher elevations in forests with lower basal areas and percent canopies, compared with males and non-reproductive females. These bats were more likely choosing trees with warmer roosting microclimates.
to reduce the cost of maintaining normothermic body temperatures and aid in more rapid
development of young.

In this study, the patterns in roost selection observed offer compelling evidence in
favor of ‘suitability for daytime torpor’ as a motivating factor behind selection of
roosting sites by northern long-eared bats; however, there was some support for
proximity to available resources (landscape) and structural complexity of the habitat
(stand) in driving the roost selection of pregnant and lactating female northern long-eared
bats. The seasonal differences in roost selection observed between pregnant and lactating
and non-reproductive females indicated these two groupings of bats roosted under
differing habitat conditions. My study shows that combining data on roost characteristics
across all reproductive and sex classes would mask differences in roost choice between
males and females, and among females of differing reproductive conditions, limiting the
ability to accurately identify seasonally important roost and stand characteristics of each
group across the landscape. Within-season variation is already considered necessary to
incorporate into future conservation management plans for threatened and endangered bat
species (Brigham et al. 1997; Kalcounis and Brigham 1998; Garroway and Broders 2007;
Garroway and Broders 2008), and my data corroborate this recommendation along with
the additional consideration of differences between sex classes.

My research also indicates that during the spring and early maternity seasons,
roosts of female northern long-eared bats are spatially clustered on the landscape and
environmental factors such as elevation, and distances to roads, water, and overwintering
hibernacula are important determinants of spatial locations. For at least MCNP, preferred
roost locations of female northern long-eared bats are situated within 2,000 m of known
winter hibernacula and include high elevation, mesic upland deciduous forests in close proximity to water sources and roads. Management of habitats at the stand level is necessary to foster increases in bat colony numbers during the maternity season (O’Donnell 2000; Willis and Brigham 2004; Garroway and Broders 2008). My data suggest there is also a need to consider larger spatial scales when creating management plans for forest-dwelling bats. My findings support the importance of conserving habitat diversity, especially intact and contiguous forests, for the northern long-eared bat.

Reduced colony sizes compared to historical records combined with the results of my mist-net surveys provide further evidence for the decline in northern long-eared bat populations following WNS and are consistent with reports from other states affected by WNS (Francl et al. 2012; Moosman et al. 2013; Reynolds et al. 2016). Capture rates observed during the progression of WNS in MCNP indicate that the fungal disease has led to declines in the overall abundance of several bat species on the landscape, but that severity varied by species. Both the Chi-square Test of Independence and the general linear model analysis demonstrated a decline in northern long-eared bat population numbers and an increase in capture success and relative abundance of evening bats after arrival of WNS. An increase in evening bats combined with the decline in northern long-eared bats may signal a shift in bat assemblages and relative abundances of these two species in the region. A competitive exclusion release could possibly account for the shift in relative abundance observed in the bat assemblage at MCNP after the onset of WNS, especially for evening bats.

Bat populations in the United States, regardless of species, are being threatened by several anthropogenic and ecological forces. It is presently unknown whether these
trends are temporary or will lead to permanent and lasting shifts in species abundance. Roost tree selection characteristics for differing sex and reproductive conditions at varying habitat scales (i.e., tree, stand, and landscape) should be considered when assessing habitat use of forest-dwelling bat species. Monitoring bat populations at regional and local scales will also be central in helping with the recovery of WNS affected species, such as the northern long-eared bat, throughout their distribution.
APPENDICES

Appendix 1: Means of habitat variables measured at random plots and roost trees of non-reproductive females, pregnant/lactating females, and male northern long-eared bats at Mammoth Cave National Park, Kentucky, USA.

<table>
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<th>Sex/Reproductive Condition</th>
<th>Variable</th>
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<th>Std. Dev.</th>
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<th>Max.</th>
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<th>Std. Dev.</th>
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<th>Max.</th>
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Appendix 2: Predictor variable significance for all model outcomes with logistic regression for non-reproductive females, pregnant/lactating females and male northern long-eared bats at Mammoth Cave National Park, Kentucky, USA.

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<th>Parameter</th>
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<th>Estimate</th>
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REFERENCES


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2010   High School Degree
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