

THE ECOLOGY AND BEHAVIOR OF SPRING MIGRATING INDIANA BATS
(*MYOTIS SODALIS*)

DISSERTATION

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in the
College of Agriculture, Food and Environment
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ABSTRACT OF DISSERTATION

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Migration of animals has been studied for decades and has included everything from large terrestrial and pelagic mammals traveling thousands of kilometers to many types of birds flying through several countries to insects going through multiple life cycles in a single migration. The migration of bats has been studied in broad terms to gather coarse information such as distance traveled, connecting summer and winter habitat, and a general understanding of timing. However, only recently have researchers begun to understand the specifics of bat migration including physiology and fine resolution behavior.

Using nine years of spring migration data collected on VHF radio-tagged federally endangered female Indiana bats (*Myotis sodalis*), I predicted behavior based on previous migration studies for bats that used various methods such as band recovery data, stable hydrogen isotopes, and automated telemetry. My project used aerial telemetry to collect location points while tracking individual bats throughout the migration. I describe distances traveled, how much time bats spent in migration, traveling and foraging behavior during migration, and how weather affects bat behavior. In addition, this project resulted in the location of 17 previously unknown maternity colonies for the species including the southernmost colony known to date. Next, I used temperature data collected from individual bats along with ambient temperature to determine how air temperature affects specific bat behavior. I calculated air temperature thresholds for use of torpor in Indiana bats and described how air temperature affects transition states between torpor and normothermy. Finally, I determined landscape preferences for migrating bats during travel and foraging. Indiana bats tend to migrate in a direct path from hibernaculum to summer grounds and use the habitat in the proportion that it is available. Although bats used forested cover when possible, they did travel in open areas (e.g., across agricultural fields) when necessary to continue along the intended trajectory.

This data set is the first to track individual nocturnally migrating bats via aerial telemetry for the entirety of the spring migration journey. It provides specific information about how far Indiana bats travel and how long they are migrating across the landscape, illustrates a web of connections between summer and winter habitat, describes the effect

of weather on bat behavior, and provides landscape use information that can be useful for land managers and developers.

KEYWORDS: aerial radio-telemetry, bat migration, Chiroptera, compositional analysis, landscape use, torpor-assisted migration

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DEDICATION

To my uncle, Dr. Clifford Hallam, professor of American Literature. He loved nature, he loved bats, he loved life and the pursuit of knowledge in all its forms. He was a huge supporter of my academic endeavors and I mourn the fact that he passed before he could witness the completion of my degree.

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I never intended to return to academia after 10 years following the completion of my Master of Science degree, but with the suggestion of my mentor, boss, and friend, Mark Gumbert, here I am. As one of the first employees of Copperhead Consulting, I was mentored by Mark and supported in every way, including the financial support and the time to complete my degree while also working full-time for Copperhead. Mark is an inspiration to me, and many after me, to be the hardest working, most knowledge-seeking, and most exhausted biologist I can be. It has paid off in the publication of the first chapter of this dissertation and the completion of my degree. Thanks Mark, there is no way I would be where I am today without your guidance and support. Thanks also to his wife and my friend, Dr. Amanda Gumbert, for emotional support, commiserating, and cheering me on through this process.

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CHAPTER 1. INTRODUCTION

1.1 A BRIEF HISTORY OF MIGRATION

“...to resolve this intricate issue [of migration] it is essential that many people in various places on Earth make careful observation and report them to the learned world.”

– Carlos Linnaeus (1757)

The idea of animal migration has been acknowledged by humans since the Stone Age as evidenced by primitive art (Nebel 2010). Greek philosophers interpreted the disappearance of some bird species as transmutation into other species since these birds were not present at the same time, while in the 16th century, people in the Nordic countries believed that birds hibernated underwater in lakes (Lienhard 2007). By the 18th century, naturalists were beginning to understand that animals underwent seasonal movements. However, it was not until the arrival of a white stork (*Ciconia ciconia*) in Klütz, Germany in 1822 that was impaled through the neck by a 30-inch long central African spear (Brosnan 2019) that highly influenced the understanding of bird migration. Known as the Pfeilstorch, the German word for arrow-stork, these birds were hunted in their African winter grounds but, if they survived, migrated to their European summer range. Although we understand the idea of migration much better now, the actual definition differs within and between taxa. Migration can be represented by seasonal movement dictated by weather, movement between breeding areas, along food gradients, or based on life cycle. The simplest and most direct definition is used by Baker (1978a): “the act of moving from one spatial unit to another.”

1.2 BAT MIGRATION

By the late 1800s, it was so well accepted by the scientific community that bats in temperate regions hibernated that “...an attempt to prove the contrary...is likely to be received with surprise...” (Merriam 1887). However, Merriam (1887) did establish support for migratory movements in hoary bats (*Lasiurus cinereus*, then called *Atalapha cinerea*) and strongly suggested that silver-haired bats (*Lasionycteris noctivagans*, then known as the genus *Vesperugo*) were also migratory. Miller (1897) also made migratory observations of these two species, along with that of the eastern red bat (*Lasiurus borealis*, then called *Atalapha noveboracensis*). By the early 1930s, banding (called ringing in Europe) of bats for identification upon recapture began in both Europe (Hutterer et al. 2005) and in North America (Ellison 2008). Europeans banded about 1 million bats in 73 years and Americans banded about 1.5 million bats in the United States, Canada, Mexico, and Central America over 40 years. These programs were the first to provide specific data about migration distances and some idea of timing, as well as illuminating the fact that hibernating bats may also migrate. Baker (1978b) describes seasonal movements by bats and summarizes migration results of bats worldwide, including many hibernating species. More recently, Fleming and Eby (2003) defined three categories of bat migration: 1) Sedentary bats typically move < 50 km between seasons, therefore using the same area to breed and hibernate; 2) Regional migrants move 100 – 500 km, describing the behavior of bats that hibernate and migrate, i.e., moderate migration movements between hibernacula and summer maternity habitat (McGuire 2012).; and 3) Long-distance migrants can travel > 1,000 km during migratory movements and are typically latitudinal. Altitudinal migrations have been documented in various taxa with birds being the most studied (Hsiung et al. 2018), but only recently has the phenomenon been investigated for bats (McGuire and Boyle 2013). Banding studies have been able to elucidate these migratory patterns and

remain an invaluable tool for understanding not only bat movement, but also longevity and fidelity to summer and winter roosting sites. Nevertheless, advances in understanding migration have progressed with technological advancements.

1.3 METHODS FOR STUDYING BAT MIGRATION

Banding (described above) is by far the most widely used method for relocating bats, whether it be within the same or different maternity colony or hibernaculum from which it was originally banded. Relocating a banded bat in a different season/habitat than it was banded provides only two points on a map between which a straight line can be inferred. In other words, if a bat was banded in its summer maternity area and then detected in a winter hibernaculum, the only data collected are the distance between these two habitats. A more recent method that has provided migration or movement data for a wide variety of taxa is the use of stable hydrogen isotopes (Rybczynski et al. 2008, de L. Brooke et al. 2010, Snover et al. 2010, Hallworth et al. 2018). This method has also been applied to bats (Cryan et al. 2004, Britzke et al. 2009, Britzke et al. 2012, Sullivan et al. 2012, Fraser et al. 2017), but with mixed results. Because of the predicted hydrogen isotope ratios across an area the size of North America is so broad (e.g., Pylant et al. 2014), only very general migratory movements can be estimated for long-distance migrants and the estimation for regional migrants is unreliable.

The use of GPS tags for larger animals has been a successful way to track long-distance migrants, both terrestrially and pelagically. Although there are GPS tags that can be used on some bats, the smallest GPS tag currently available is only small enough for the largest bats found in the Eastern US and have to be recovered to access the data (Weller et

al. 2016). Although remotely accessed GPS data from a migrating bat would be ideal, this technology is not currently available.

Radio-telemetry was first used on a wild animal 60 years ago when LeMunyan et al. (1959) developed a tag for woodchuck-sized (*Marmota monax*) animals, closely followed by Cochran and Lord (1963) who developed a tag that was used on rabbits (*Sylvilagus floridanus*), striped skunks (*Mephitis mephitis*), and raccoons (*Procyon lotor*). Radio-telemetry tags were then created for flying animals, i.e., birds (Lord et al. 1962) and bats (Williams and Williams 1967, 1970), but the technique has now been used on an array of animals. Within a decade, aerial tracking technology was developed (Whitehouse and Steven 1977), followed by the technological advancement of smaller transmitters to apply to smaller animals. VHF radio-signal technology has also been adapted for use in coded VHF radio-transmitters that are detected by stationary towers to record the individual's unique alphanumeric code when it passes within range. Again developed for high flying birds, this method is intended to detect long-distance migrants within a limited line-of-sight distance from the tower and can only track animals where the towers are placed. This technology has been successfully used to collect stopover behavior of some long-distance migrant bat species (McGuire et al. 2012) and can answer some questions about migration timing, but provides only a snapshot of the overall migration story. Holland et al. (2006) used aerial radio-telemetry to track big brown bats (*Eptesicus fuscus*) during homing experiments along short distances (i.e., 20 km), and Holland and Wikelski (2009) stated that 'ideally' migrating bats could be tracked via aerial telemetry but that it had not yet been attempted. Since then, fast-flying bats such as Brazilian free-tailed bats (*Tadarida brasiliensis*; McCracken et al. 2016) and gray bats (*Myotis grisescens*; Moore et al. 2017)

have been tracked via aerial telemetry during foraging, but the project reported in this dissertation is the first time that sequential location data have been collected for multi-night migrations of bats.

1.4 KNOWN MIGRATION OF MYOTIS

Banding studies (Ellison 2008) along with some aerial daytime telemetry to document migration steps (Butchkoski and Cheng 2008) have been conducted on a few *Myotis* species in the US, primarily little brown bats (*Myotis lucifugus*), gray bats, and Indiana bats. In Europe, there are migration movements known from banding data for at least 11 species of *Myotis* (Hutterer et al. 2005). These data show that bats are migrating away from hibernacula in a random pattern (Baker 1978b, Hutterer et al. 2005), but the majority of studies on little brown bats and Indiana bats that reside in the US revealed particular directional behavior (Ellison 2008). To date, the longest Indiana bat migration distance known (via banding) is 672.2 km from Pennsylvania to Kentucky (Butchkoski and Bearer 2016), but nothing else is known about that migration journey. Although vital for beginning to understand connections between winter and summer habitat and the distances these species can travel, detailed information concerning the migratory journey has been lacking. There are still questions about how long bats are migrating across the landscape, how far bats travel in a night and for how long, if bats forage during migration, if weather influences migration behavior, if bats are influenced by the landscape over which they are flying, and what types of roosts they use in the pre-maternity season.

1.5 DISSERTATION STRUCTURE

The sections above cover a summary of what is known about bat migration. Previous studies have been instrumental in answering questions about bat migration and

have resulted in useful summaries about what is known (Baker 1978b, Neuweiler 2000a, Fleming and Eby 2003, Krauel and McCracken 2013). However, these studies have answered general questions and lack information about the specifics of how individual bats migrate. This dissertation is the first study aimed at answering these specific questions for at least one bat species.

The following chapters were prepared as independent manuscripts for publication in peer-reviewed journals. Chapter 2 entitled *Nine years of Indiana bat (Myotis sodalis) spring migration behavior* has been published in the Journal of Mammalogy with Mark Gumbert and Dr. Michael Lacki as co-authors. Mark Gumbert developed the methods for tracking Indiana bats via aerial telemetry and Dr. Lacki assisted with organization and language of the manuscript. This chapter provides a summary of overall migration behavior by female Indiana bats including overall migration distances and directions from hibernacula to summer grounds as well as timing, speed, and duration of these movements and how weather affected migration behavior. This study resulted in the location of several previously unknown maternity colonies, particularly in the southeastern US. Providing basic information about migration behavior initiated follow-up questions about the specifics of changes in bat physiology based on temperature and how bats use the landscape during migration. These questions are answered in Chapters 2 and 3.

In Chapter 3, *Influence of temperature on spring migrating Indiana bats (Myotis sodalis)*, I investigate how ambient temperature affects bat temperature and bat behavior. This chapter was co-authored by Dr. Eric Vanzant who created the algorithm to determine when bats were in various physiological states and wrote part of the methods for the algorithm. After collecting anecdotal evidence that bats were not active when ambient

temperatures fell below 10°C, I compared ambient temperature data collected during migration to bat temperature collected from temperature sensitive transmitters during inactivity and while bats were active. This provided temperature threshold values for varying physiological states for bats during migration.

In Chapter 4, *Landscape and roost use by spring migrating female Indiana bats* (*Myotis sodalis*), I investigate what habitat parameters are important to bats during this time of year. This chapter was significantly enhanced by Allison Davis who wrote all the R code to prepare data and conduct compositional analysis to determine resource use by bats. Roost use and habitat requirements for Indiana bats has been well studied during the summer and winter, but very little data has been collected for this species during spring and autumn. This information can be important for land managers to provide habitat needed or to avoid impacting that habitat during these transitory seasons.

CHAPTER 2. NINE YEARS OF INDIANA BAT (*MYOTIS SODALIS*) SPRING MIGRATION BEHAVIOR

2.1 ABSTRACT

The endangered Indiana bat (*Myotis sodalis*) congregates in large hibernation groups in winter and travels after spring emergence to form summer maternity colonies, but information on migration behavior in this species remains limited to mostly band recovery observations. We tracked female Indiana bats in spring migration toward summer grounds using aerial radiotelemetry. Adult female Indiana bats were radiotagged in spring from 2009 through 2017, with 15 individuals successfully tracked to summer grounds and an additional 11 bats located in summer grounds via aerial telemetry after migration was complete. This resulted in the location of 17 previously unknown summer grounds for female Indiana bats, including adding Georgia, Alabama, and Mississippi to the summer maternity range. Two of the colonies identified in the this study were south of the previously known southernmost colony in Tennessee, expanding the summer maternity range for the species by 178 km. Time-stamped location fixes along the migration path provided information about nightly and overall distances traveled, duration of travel, migration speed, and weather-related influences on bat behavior. Bats traveled $164.6 \text{ km} \pm 26.2 (\pm SE)$ on average from hibernacula to summer grounds and were migrating for an average of 7.3 ± 1.4 calendar nights. Bats alternated between foraging and traveling throughout each night of their migration route. Nightly migration rate was $9.9 \pm 0.8 \text{ km/h}$ and bats were active on the landscape for an average of $6.1 \pm 0.4 \text{ h/night}$. Lower nighttime temperatures and lower barometric pressure correlated with use of layover areas during a migration night. Understanding bat behavior during migration can provide pertinent

information for land managers to consider in efforts to conserve potential migration corridors, foraging areas, and roosting habitats of species in decline.

2.2 INTRODUCTION

The definition of animal migration has been debated and there is no consensus of its definitive meaning (Fryxell et al. 2011). However, for bats, it is generally defined as seasonal movement between two habitats that each provide climatic advantages (Fleming and Eby 2003). Migration of bats is not well understood for many species, partly due to the difficulty in tracking them over long distances at night. Regardless, movement of bats on the landscape has been studied for decades (summarized in Voigt et al. 2017) using wing banding studies (Hall 1962, LaVal and LaVal 1980, Murray and Kurta 2002, Winhold and Kurta 2006, Ellison 2008, Rockey et al. 2013), stable hydrogen isotopes (Cryan et al. 2004, Britzke et al. 2009, Britzke et al. 2012, Sullivan et al. 2012, Fraser et al. 2017), and automated telemetry (Holland et al. 2011, McGuire 2012, Taylor et al. 2017). However, there are shortcomings for each of these methods. For example, band recovery data have been collected since the 1930s in the U. S. (Ellison 2008) and in Europe (Hutterer et al. 2005) and have provided an origin point and an end point, but with limited information on timing or behavior in between. Band recoveries provide data on minimum distance traveled (assuming a straight-line flight) and, potentially, the minimum amount of time to complete the journey (e.g., Tuttle 1976), but they are limited by low recovery rates (e.g., Griffin 1940; Ellison 2008).

The Indiana bat (*Myotis sodalis*) has been listed as federally endangered since 1967. The majority of the species congregates in large colonies (>10,000 bats) in 23 hibernacula (i.e., Priority 1 hibernacula) across seven states (USFWS 2007). This high concentration

of bats is likely to require more resources on the landscape than are available immediately around the hibernacula in the summer. Therefore, Indiana bats engage in female-biased partial migration (Fleming and Eby 2003), where females can migrate up to 673 km (Butchkoski and Bearer 2016), but males often remain near hibernacula or migrate shorter distances (USFWS 2007). The average distance estimated from band recoveries of migration by Indiana bats in the central part of the range is 401.9 ± 29.6 ($\pm SE$) km (Hall 1962, Davis 1964, LaVal and LaVal 1980, Gardner and Cook 2002, Kurta and Murray 2002, Winhold and Kurta 2006, Rockey et al. 2013, Butchkoski and Bearer 2016). Migration distances, as determined by radio-tracking, of populations near the periphery of the range in northeastern U.S. are much shorter with an average of 62.5 ± 11.9 km (Butchkoski and Bearer 2016; C. Butchkoski and G. Turner, Pennsylvania Game Commission, personal communication, July 2009). Factors influencing timing and speed while traveling these distances are likely related to regional weather differences and animal health upon spring emergence.

Bats lose heat easily, so nighttime weather conditions are likely an influence on if, when, and how far bats migrate in a night. Spring weather conditions in the southern U.S. can be unpredictable, creating a challenge for nighttime-flying animals. Bats are heterothermic mammals with high surface area-to-volume ratios (Speakman 2000). This equates to thermoregulatory challenges that can be exacerbated by weather conditions, including cold (e.g., Racey and Swift 1981, O'Shea et al. 2016) and heat (e.g., Welbergen et al. 2008, O'Shea et al. 2016). Bats emerging from hibernation are vulnerable because they have depleted fat stores over the winter (Bernard and McCracken 2017), but still must have enough in reserve to start migrating to maternity colonies. Bats likely forage while

migrating to supplement lost fat reserves (Fleming and Eby 2003, Hedenström 2009), and certain weather conditions are required to ensure prey availability along migration routes (Kunz 1988, Paige 1995). Therefore, weather is likely a contributing factor to spring migration behavior of Indiana bats.

We tracked individual female Indiana bats during spring migration using aerial telemetry to describe migration behavior in this species. We predicted that bats would migrate north from hibernacula to maternity colonies based on data from band recoveries (Winhold and Kurta 2006, USFWS 2007). We further predicted that Indiana bats would not migrate >400 km. This distance threshold was used to distinguish between long-distance and regional migration of the noctule bat (*Nyctalus noctula*) in Europe (Lehnert et al. 2018) is the average distance documented by band recoveries as stated above, and is supported by Gardner and Cook (2002) who postulated that Indiana bats would not migrate “large distances.” Lastly, we predicted migration behavior of bats would be influenced negatively by weather conditions such as lower temperatures, stronger winds, and heavier amounts of precipitation (USFWS 2007, McGuire et al. 2014, Weller et al. 2016, Pettit and O’Keefe 2017).

2.3 MATERIALS AND METHODS

2.3.1 Study Area and Use of Hibernacula

Karst topography has resulted in an abundance of caves throughout the southeastern portion of the U.S. including central parts of Indiana, Kentucky, Tennessee, and Alabama (Weary and Doctor 2014). We attached radiotransmitters to female Indiana bats from ten different cave hibernacula in three states: Tennessee ($n = 8$), Indiana ($n = 1$), and Alabama ($n = 1$). We visited five of the caves once, four caves twice, and one cave in central

Tennessee (referred hereafter as TN1) in seven consecutive years (2010 – 2016). Typically, we visited more than one cave in a year resulting in 20 bat collection events over nine years (2009 – 2017). Start dates were based on the known timeframe of natural emergence of Indiana bats from hibernation, but we chose nights forecasted with favorable weather conditions that permitted aerial tracking at night (i.e., no rain, low wind speeds, and temperatures remaining above 10°C until at least midnight). Other factors for selection of start dates included the geographic location of a cave, the number of bats hibernating inside a cave, and the acoustic activity recorded at a cave entrance in previous years. The land cover around the caves was mostly deciduous forest on public or private land with scattered residences and very little agricultural use. The number of hibernating Indiana bats in sampled caves ranged from two individuals to >60,000, with most caves housing fewer than 100 bats.

2.3.2 Bat Capture

In the spring of 2009 through 2017, we hand-collected Indiana bats from inside hibernacula ($n = 8$ caves), or bats were caught in harp traps ($n = 2$ caves) as they emerged at dusk. We identified bats to species, measured mass (g) and right forearm length (mm) and banded them with aluminum-lipped uniquely numbered bat bands (Porzana Ltd., Icklesham, East Sussex, United Kingdom). We used beeper VHF radiotransmitters from Holohil Systems Ltd. (Carp, Ontario, Canada) and coded VHF radiotransmitters from Lotek Wireless Inc. (Newmarket, Ontario, Canada) to radiotag select females by trimming hair from between the scapulae and securing transmitters with surgical cement (Perma-Type Co Inc., Plainville, Connecticut). We released bats individually near hibernacula in

coordination with aerial crews circling overhead. The mass of transmitters used ranged from 0.29 – 0.42 g, but the majority (75.8%) were <0.35 g.

All methods followed the American Society of Mammalogists guidelines for use of wild animals in research (Sikes et al. 2016) and were approved by the University of Kentucky Institutional Animals Care and Use Committee (protocol #2017-2787). All protocols were conducted under Endangered Species Act Section 10(a)(1)(A) permits for endangered species (TE070584-4 and TE94849B-0) and appropriate state permits for the years in which work was conducted.

2.3.3 Radiotelemetry

We conducted aerial tracking using a Cessna 172 Skyhawk fixed-wing aircraft fitted with Advanced Telemetry Systems (ATS, Isanti, Minnesota) aircraft strut mount assemblies and a 172-3FB 4-element ATS Yagi directional antenna on each wing. All aircraft pilots and navigator data collectors were trained bat biologists. We detected transmitter signals using an ATS receiver-datalogger (model R4500CD) while the plane maneuvered in tight circles above the bat's mobile position. We used mapping software (Delorme Topo North America 9.0) loaded to laptop computers with installed GPS (Panasonic Toughbook, Newark, New Jersey) to view the location of the plane and for the navigator to manually place location fixes (i.e., waypoints) on the map based on the signal strength from either or both antennas. We placed waypoints on the map that were automatically time-stamped with the computer's internal clock. Using three navigators and two pilots resulted in an overall location accuracy of $382.7 \text{ m} \pm 44.7$ ($n = 65$ points, range: 5.9 – 1,765 m).

For the purposes of this document, “migration” is defined as the entire process after emergence from hibernacula to the arrival at summer grounds. Summer grounds indicate the areas where female Indiana bats are congregating before 15 May to form maternity colonies (USFWS 2007). During migration, bats travel (move away from the hibernaculum toward the summer grounds), forage (engage in an erratic flight pattern), roost (inactive inside a roost for one day), or use a layover area (inactive inside a roost or using multiple roosts in the same area for >1 day). Tracking of travel and foraging were conducted during nighttime hours (i.e., approx. 19:00 – 07:00 h) on a single radiotagged bat at a time. We monitored other active bat frequencies periodically to determine if target bats were migrating with other radiotagged bats. Ground support crews tracked bats throughout the night and maintained contact with bats when the plane was temporarily unavailable for refueling during the night. Vehicles were equipped with telemetry receivers and long-range 5-element Yagi antennas to maintain contact with radiotagged bats. Contact between aerial and ground crews was maintained by two-way radios and text messaging with cellular telephones.

We placed temperature data loggers (iButton, Maxim Integrated, San Jose, California) on the roofs of field vehicles for collecting ambient temperature (T_a) data at night and on trees near roosting bats to collect T_a during days and nights. From 2013 through 2017, interpulse periods emitted by temperature sensitive transmitters were stored in an ATS receiver-datalogger to determine skin temperature of bats (T_{sk}) during post-processing.

Since multiple bats were radiotagged at each tracking event, we conducted daytime searches of known maternity colonies to document use by the remaining radiotagged bats

as well as flying predetermined transects with the intent of locating radiotagged bats at previously undocumented maternity colonies. We determined that a bat had arrived at its summer grounds when: 1) the bat did not continue to migrate in favorable weather, 2) it began roosting with other bats to form a maternity colony, and 3) it was roosting in habitat typical for summer roosting Indiana bats, e.g., dead or dying standing trees with sloughing bark typically within riparian areas or bottomland habitat surrounded by contiguous forest (USFWS 2007).

2.3.4 Data Analysis

We imported time-stamped waypoint files representing bat location fixes into ArcGIS v.10.5 (ESRI, Redlands, California) and overlaid them onto topographic and aerial maps to determine distance and direction of bat flights and to quantify behavior. We evaluated linear flight distances (between start and end points) in this study, which included distances from hibernacula to summer grounds and lengths of behavioral segments, i.e., traveling or foraging.

We used Oriana v 4.02 (Kovach Computing Services, Anglesey, Wales) software to determine the direction bats migrated. We calculated a circular-linear correlation between direction and distance traveled in Oriana. Data used in these analyses were the straight-line azimuth and distance calculated in ArcGIS from the bat's hibernaculum of origin to the first roost at the summer grounds. We used Rao's spacing goodness-of-fit test (or Rao's U) to test the prediction that bats migrate north (Bergin 1991). We conducted a one-way analysis of variance (ANOVA) to determine if the size of the hibernating population affected the distance that bats migrated. We also used a one-way ANOVA to

determine the relationship, if any, between the distance from hibernacula to summer grounds and the number of nights a bat spent migrating.

We classified flight behavior based on patterns of sequential GPS locations (Fig. 2.1). We characterized closely spaced points that did not form a linear pattern as foraging, while we characterized sequential points that moved away from an origin (i.e., hibernaculum, roost, or foraging area) as traveling. We conducted cluster analysis in the R environment (R Development Core Team 2017) to validate the manual classification of each point using X–Y coordinates, date–time stamp, and the distance from origin hibernaculum. The distance from origin hibernaculum did not add to the predictive power of the model, therefore, we only used location coordinates and the date–time information in separating foraging from migration traveling. The accuracy value describing how often the classifier is correct was 0.84 ± 0.01 (range: 0.77 – 0.98) for 18 bats.

Because the data were not normally distributed, we used separate Student's *t*-tests (Zar 1999) for unequal variances to determine differences in the amount of time bats spent traveling versus foraging, bat speed before and after the use of a layover area, and nightly distance traveled before and after the use of a layover area. The overall amount of time bats spent traveling per night was normally distributed, therefore we used Student's *t*-tests to determine differences in these activities before and after a layover event.

To determine if the number of nights migrating was affected by weather, we conducted analysis of T_a and T_{sk} to assess whether bats were torpid or normothermic on a given night. Calibration points were provided by the manufacturer for each temperature-sensitive transmitter, which we then used to create individual polynomial equations for determining T_{sk} from the collection of interpulse periods. Subsequently, we paired T_a and

T_{sk} by timestamp for further analysis. We determined torpor onset temperature for roosting bats with bat mass (BM) and T_a in the equation described by Willis (2007) using model parameters minus one standard error:

$$T_{sk-onset} - 1 SE = (0.041)*BM + (0.04)* T_a + 31.083$$

We compared individual recorded T_{sk} values to the torpor onset value to determine if the bat was normothermic ($T_{sk} > T_{sk-onset} - 1 SE$) or torpid ($T_{sk} < T_{sk-onset} - 1 SE$).

We obtained weather factors that could potentially affect bat behavior during migration from Weather Underground (www.wunderground.com). These included minimum temperature (nearest 1°C), precipitation (0.1 mm), wind speed (1.0 km/h), barometric pressure (1.0 hectopascal [hPa]), and absolute humidity (1%). We used data recorded from 19:00 – 07:00 h each night at the nearest weather station to a tracked bat. From these data, we derived Pearson correlations for 11 weather metrics using a pairwise method: low temperature, precipitation, high wind speed, average wind speed, gust wind speeds, high barometric pressure, average barometric pressure, low barometric pressure, high humidity, average humidity, and low humidity. Correlated variables (Pearson's $|r| > 0.20$) were removed and the three remaining uncorrelated variables were used in further analysis. These were low temperature, low pressure, and high humidity.

For each night of tracking, we assigned bat behavior to one of the categories defined in the Section 2.3.3 Radiotelemetry above based on the behavior that dominated throughout the night: travel ($n = 39$ nights), foraging ($n = 8$ nights), or layover ($n = 26$ nights). We conducted one-way ANOVAs to determine how nightly weather variables affected nightly bat behavior.

We assessed possible differences in mass of radiotagged bats and those not tagged using a Student's *t*-test. Both data sets were normally distributed and possessed equal variances. We used Student's *t*-test for unequal variances to determine if body mass of bats that migrated the first night after release differed from those that did not migrate the first night. Except for the cluster analysis in Program R stated earlier, we conducted remaining analyses in JMP (Version Pro 14. SAS Institute Inc., Cary, North Carolina, 1989-2007). For all statistical tests conducted, $\alpha = 0.05$.

2.4 RESULTS

2.4.1 Bat Capture

Project start dates ranged from 20 March to 17 April depending on the onset of spring from one geographic location to another. There were a total of 372 adult female Indiana bat captures at hibernacula, 272 of which were banded. A total of 260 transmitters were attached to 205 individuals: 160 bats were radiotagged once and 45 individuals were radiotagged 2 – 4 times each throughout the 9-year study period. Regardless of capture frequency, migration data were only collected on an individual once. Most bats ($n = 239$) were radiotagged from TN1 and largely outnumbered all captures combined from the other nine caves (sum = 133). Mean mass of captured bats was $6.7 \text{ g} \pm 0.03$ (range: 5.0 – 9.0 g), with radiotagged bats heavier ($\bar{x} = 6.8 \pm 0.04 \text{ g}$; range: 5.5 – 9.0 g) than bats not radiotagged ($\bar{x} = 6.3 \pm 0.06 \text{ g}$; range: 5.5 – 7.8 g; $t_{370} = 7.22$, $P < 0.01$). Mean transmitter mass was $4.8 \pm 0.04 \%$ (range: 3.7 – 6.7%) of body mass. Of the 51 recaptured bats, 46 were radiotagged multiple times and 26 were radiotagged with transmitters weighing $>5\%$ of the bat's body mass, either once or twice. Of these 26 bats, 22 were recaptured in following years after having carried a transmitter that exceeded 5% of the body mass.

2.4.2 Radiotelemetry

We collected 4,398 location fixes on 20 individual bats tracked from eight hibernacula. Of these, 3,429 location fixes were collected on 15 bats that were tracked to their summer grounds with an average of 228.6 ± 46.9 fixes per bat (range: 39 – 777 fixes). The remaining 969 fixes were collected on bats that were tracked during incomplete migration routes but which still provided behavioral information. The majority of bats (82.4%) foraged after release either before starting migration travel or during staging behavior. We defined staging as the behavior when bats foraged and roosted within 5 km of the hibernaculum, based on known distances of roosts from hibernacula used by bats after spring emergence (Gumbert et al. 2002). Some bats may have engaged in staging without being detected due to the tracking crew following a migrating bat, but those bats that were documented to remain near the hibernaculum the first night ($n = 22$ bats) did not differ in mass ($\bar{x} = 6.8 \pm 0.1$ g) from those that migrated the first night ($n = 20$ bats; $\bar{x} = 6.9 \pm 0.2$ g; $t_{34.4} = -0.6$, $P = 0.53$). There was no difference in ambient temperature on nights when bats migrated ($n = 7$ nights, $\bar{x} = 15.9 \pm 1.9^\circ\text{C}$) from nights when bats staged ($n = 6$ nights; $\bar{x} = 14.6 \pm 6.0^\circ\text{C}$; $t_{5.8} = -0.5$, $P = 0.63$). Once migration had begun, bats foraged upon emerging from a roost 58.1% of the time and then began traveling toward summer grounds. During the other 41.9% of the time, bats commenced traveling upon emergence from a roost without a detectable foraging bout. A larger majority of the time (85.7%), bats foraged before roosting for the day, whereas bats did not forage before roosting only 14.3% of the time.

Data for the entire migration route were collected on 15 individual bats that traveled 6.3 – 368.1 km between hibernacula and summer grounds or confirmed maternity colonies

($\bar{x} = 164.6 \pm 26.2$ km). Distance and direction from the hibernaculum were not correlated ($r = 0.3$, $P = 0.07$). Nightly migration distance was 59.8 ± 5.2 km (range: 2.2 – 153.3 km) and bats were active for 6.1 ± 0.4 h (range: 1.4 – 9.7 h) per night of migration. This resulted in an average nightly migration rate of 9.9 ± 0.8 km/h (range: 0.7 – 20.1 km/h). These distances are the minimums measured for bats in flight, with the total distances flown likely being much longer.

During migration, bats alternated between foraging and traveling throughout a night. The mean distance that bats traveled between foraging areas was 16.2 ± 1.5 km, but the range of these values was wide (1.3 – 69.4 km). The distribution was not normal (Shapiro-Wilk $W = 0.81$, $P < 0.01$) and it was heavily weighted to short-distance movements (Fig. 2.2). Migrating bats used 3.3 ± 0.3 foraging areas per night on average (range: 1 – 8 foraging areas) and 2.8 ± 0.3 traveling bouts per night (range: 1 – 7 traveling bouts). Bats spent more time in individual traveling bouts ($\bar{x} = 1.3 \pm 0.1$ h) than in foraging bouts ($\bar{x} = 0.6 \pm 0.1$ h; $t_{156.3} = 5.1$, $P < 0.01$) and spent more time traveling per night ($\bar{x} = 3.9 \pm 0.3$ h) than foraging ($\bar{x} = 2.2 \pm 0.2$ h; $t_{66.7} = 4.3$, $P < 0.01$). In addition, bats spent more time traveling per night after a layover event ($\bar{x} = 4.5 \pm 0.6$ h) than during the nights at the onset of migration ($\bar{x} = 2.8 \pm 0.6$ h; $t_{20.4} = -2.13$, $P = 0.046$). Although nightly flight speed was not significantly faster after a layover event ($\bar{x} = 10.7 \pm 1.0$ km/h) than before the use of a layover ($\bar{x} = 8.1 \pm 1.2$ km/h; $t_{22.8} = -1.64$, $P = 0.11$), the distance traveled in a night was longer after a layover ($\bar{x} = 68.5 \pm 9.9$ km) than before a layover ($\bar{x} = 42.9 \pm 6.1$ km; $t_{21.2} = -2.2$, $P = 0.04$).

Bats were tracked on average for 7.3 ± 1.4 nights (range: 1 – 22 nights), but they actively traveled along the migration route for 2.7 ± 0.4 nights (1 – 5 nights). The overall

linear distance a bat traveled was highly correlated with the number of migration nights ($R^2 = 0.8$; $F_{1,13} = 55.8$, $P < 0.01$).

Although 15 bats were actively tracked, we located an additional 11 bats in their summer grounds via aerial telemetry after the completion of migration. The direction from hibernacula to summer grounds of all bats located in their summer grounds ($n = 26$ connections) was not random ($U = 159.78$, $P < 0.05$) and the mean cardinal direction was west ($278.9 \pm 15.9^\circ$, 95% $CI = 247.7^\circ - 310.2^\circ$; Fig. 2.3). Population size of hibernating bats did not have an effect on migration direction ($F_{13,57} = 1.68$, $P = 0.09$). For example, the only two female Indiana bats hibernating in a cave in northwest Tennessee migrated in different directions to different summer grounds (northwest and north), and two female bats radiotagged from a hibernaculum housing 60,000 bats in Indiana also each migrated in different directions (southwest and northeast).

Bats did not travel in a straight line from hibernacula to summer grounds. Therefore, the migration path for each bat was determined by measuring the farthest deviation from a straight line connecting the hibernaculum and summer grounds. The mean migration path width from hibernacula to summer grounds was 24.8 ± 4.2 km (range: 2.7 – 55.3 km). Five bats were tracked from two hibernacula to the same summer grounds in northeastern Alabama (Fig. 2.4), effectively creating a migration corridor measuring 23.5 km wide. Although there was variability in the exact path, the collective routes of these five bats converged at a point in northwestern Georgia (Fig. 2.4, inset), before diverging to cross Weiss Lake in Alabama and again reconvene near the confirmed maternity roost in eastern Alabama.

No bat radiotagged multiple times was actively tracked in multiple years, but three were located again in their respective known maternity colonies during targeted searches. Radiotagged bats were never documented migrating together and were always documented roosting alone until they reached the summer grounds. We identified connections between eight hibernacula and 20 summer grounds across eight different states for a total of 26 connections, including some summer grounds connected to multiple hibernacula (Fig. 2.5). Of the 20 summer grounds and maternity colonies, 17 were previously undocumented including adding Alabama, Georgia, and Mississippi as new states to the known maternity range. Of these, Alabama now houses the southernmost colony known to date that extends the summer range of the species by 61 km (Redinger 2006, USFWS 2007). However, this summer record reported by Redinger (2006) is from a cave that was surveyed multiple times in 2005, and only males and non-reproductive females were captured. Prior to the current study, the southernmost maternity colony of Indiana bats known was in southern Tennessee. Therefore, our southernmost colony located in Alabama extends the maternity range by 178 km. Arrival date to summer grounds ranged from 24 March in central Tennessee to 2 May in northeastern Indiana.

2.4.3 Effects of Weather

Pearson correlation filtering resulted in three uncorrelated weather variables for evaluating bat behavior: low temperature, low pressure, and high humidity. High humidity did not affect behavior ($F_{2,70} = 0.45$, $P < 0.64$), but low temperature ($F_{2,70} = 7.63$, $P = 0.001$) and low pressure ($F_{2,70} = 18.49$, $P < 0.0001$) varied among the three behavior types. There was no difference between foraging and layover behavior for either of these variables, but migrating behavior was different from both foraging and layover behavior ($P < 0.05$ post-

hoc Tukey's HSD). Mean low temperature during a travel night ($\bar{x} = 11.3 \pm 0.8^\circ\text{C}$) was higher than during a layover ($\bar{x} = 7.1 \pm 0.8^\circ\text{C}$) and during a foraging night ($\bar{x} = 6.9 \pm 1.7^\circ\text{C}$). Mean low pressure was higher during migrating ($\bar{x} = 995.9 \pm 0.9$ hPa) than during a layover ($\bar{x} = 988.7 \pm 1.5$ hPa) or a foraging night ($\bar{x} = 983.0 \pm 2.0$ hPa). Bats typically were not active when T_a was $\leq 10^\circ\text{C}$, even if T_{sk} was normothermic. Only 9.1% of the data points revealed that bats were normothermic at temperatures below 10°C (Table 2.1). One exception was an individual that foraged for up to two hours when T_a was 9°C on two separate nights.

Precipitation events and high wind nights (i.e., >10.3 m/s as determined for safety by pilots during this study) grounded aircraft, requiring the team to rely on ground monitoring. However, ground monitoring of radiotagged bats during those nights or the following days typically recorded little bat movement. An exception was the loss of a transmitter signal the day following severe storms and the subsequent location of this bat within its summer grounds 180 km away six days later.

2.5 DISCUSSION

The migration pattern used by Indiana bats once they exit hibernacula is comprised of alternating steps of linear and concentrated flights. Some bats migrated the first night, while others remained near the hibernaculum, i.e., engaged in staging behavior. It is unknown why some bats used the staging area for ≥ 1 night while others migrated after release, but there are likely many factors. Although four of the five bats caught in harp traps during natural emergence from hibernacula migrated on the night of capture, the majority of the bats radiotagged in this study were hand-collected from within the cave. Some of the hand-collected bats migrated the first night while others remained in the

staging area the following day. There was no difference in body mass of bats that staged and those that started migrating the first night, a phenomenon also documented by Dechmann et al. (2017). However, there could still be a physiological difference that would influence timing of migration, such as physically imperceptible impairment due to white-nose syndrome (WNS), a devastating disease caused by the fungus *Pseudogymnoascus destructans* that is reducing bat populations throughout the eastern U.S. and Canada (Frick et al. 2010a). Although no physiological measurements were taken, staging bats may not retain enough fat reserves from the winter due to any number of factors (e.g., arousing too often, not enough fat during the onset of hibernation, roosting in sub-optimal temperatures, etc.). The amount of time animals remain in hibernation is regulated by “an endogenous circannual clock” (Wang and Wolowyk 1988) and females require hibernation for the storage of sperm (McNab 1974). Therefore, because bats do not all enter hibernation at the same time, neither do they emerge at the same time. Bats that staged may have entered hibernation later than ones that migrated. In addition, individuality among bats cannot be ruled out; not all bats behave the same way.

Regardless if bats staged or began migrating the night of release, they generally used a foraging bout initially. Once bats began moving away from hibernacula toward summer grounds, they alternated between migration flight and foraging flight. This alternating pattern persisted until weather became unfavorable to continue migrating (i.e., temperature dropped or storms were encountered) or until sunrise when bats often foraged before selecting a diurnal roost. Indiana bats also used layover areas consisting of a multi-night inactive period that was occasionally accompanied by foraging. This pattern of travel,

foraging, and layovers continued until bats arrived at summer grounds when only nightly foraging occurred during favorable weather.

Although the number, frequency, and duration of foraging bouts varied among bats, all individuals engaged in this behavior during migration and frequently before selecting a roost. This is in contrast to the postulation that silver-haired bats (*Lasionycteris noctivagans*) do not forage along migration routes (McGuire et al. 2014) but is in agreement with the theoretical model by Hedenström et al. (2009). Indiana bats spend up to six months in hibernation resulting in their lowest body condition in the spring (Bernard and McCracken 2017). Their fat reserves acquired in autumn are used for homeostasis and to support their arousal every 12 – 15 days during hibernation (Speakman and Thomas 2003). Consequently, prey items must be consumed upon emergence from hibernation to replenish fat stores and acquire needed calories for migration (Sapir et al. 2011).

After initial foraging in the staging area and foraging bouts in subsequent nights, bats spent more time traveling and traveled farther after using a layover than at the onset of migration. Presumably bats had acquired or conserved sufficient energy requirements during a layover and therefore were able to fly for longer traveling bouts and use fewer foraging bouts during the last leg of their journey. Arriving at summer grounds early is likely advantageous for several reasons. Bats could potentially reduce the amount of time and effort exerted during migration, would arrive in an area of familiarity for ease of foraging and roosting opportunities, and could begin establishing the maternity colony to prepare for pregnancy.

Band recovery data for Indiana bats has revealed migration pathways in a north-south direction (USFWS 2007, Rockey et al. 2013). However, in portions of the

Midwestern U.S., band recoveries document bats traveling southwest, southeast, east, and west (Gardner and Cook 2002). Spring migrating bats in Pennsylvania were actively tracked along both north-south and east-west pathways (Butchkoski and Bearer 2016; Hart and Brenner 2016; C. Butchkoski and G. Turner, Pennsylvania Game Commission, personal communication, July 2009). Indiana bats in our study favored a westerly migration path on average, rejecting our prediction of northward spring migration. This suggests that there may be variation in the general migration direction across geographic regions. This is supported by band recovery data of many species of bats (Baker 1978b). The variation in migration pathways and lack of clearly defined linear flyways also suggests that the whole range of the Indiana bat should be considered potential flyway habitat. The locations of <10% of maternity colonies of this species are known (USFWS 2007), so bats could be migrating in any direction from a given hibernaculum. Therefore, it would be unreasonable to consider any part of the range devoid of Indiana bat activity during at least some portion of the year.

Bats in our study migrated relatively short distances (i.e., <400 km). Other studies have reported band recoveries documenting longer migration distances (i.e., 575 km in Winhold and Kurta 2006; 673 km in Butchkoski and Bearer 2016), indicating that individuals of the species are capable of migration movements >400 km. We respectfully disagree with Krauel et al. (2017), who used automated radiotelemetry to conclude that Indiana bats that travel farther than 100 km are outliers. In our study based on aerial radiotelemetry tracking, 67% of the bats traveled farther than 100 km from hibernacula, suggesting that these are not outliers.

Air temperature was a significant factor determining Indiana bat behavior on a given night. Bats did not migrate at lower temperatures, and essentially no activity was recorded when air temperature was lower than 10°C. This value is generally accepted as the temperature at which bat activity during the summer months is reduced (USFWS 2019) and when bats start to enter hibernacula in the fall (Hall 1962, Myers 1964). This provides a starting point for understanding how temperature might affect bat migration activity, and further research is needed to determine different levels of torpor and the effect of transition temperatures between two behavioral states, i.e., normothermy and torpor. Low atmospheric pressure was also a significant indicator of layover use in our study, as documented in previous studies (Cryan and Brown 2007, Baerwald and Barclay 2011, Wolcott and Vulinec 2012, Bender and Hartman 2015). Even though wind speed was not a predictor of behavior, wind speeds sufficient to ground the aircraft also tended to deter bat movement. This is in agreement with McCracken et al. (2016), who found that Mexican free-tailed bats (*Tadarida brasiliensis*) adjusted their flight behavior depending on wind speed. Spring weather appears to be an important external cue for migrating bats of many species (Park et al. 2000, Smith and McWilliams 2016, Jonasson 2017) including Indiana bats.

The dates of arrival at maternity roosts in our study are within the range of earliest arrival (17 March – 15 April) and colony formation (8 April – 14 May) found by Pettit and O'Keefe (2017) at a large Indiana bat colony in central Indiana. Geographic location, distance traveled, and weather all influence this wide range of travel dates. Summer habitat used by Indiana bats from 15 May to 15 August is protected under the Endangered Species Act. However, with the use of maternity areas in the transition period between migration

and official establishment of maternity colonies, we agree with Pettit and O'Keefe (2017) that the time periods before 15 May and after 15 August are equally important for land managers to protect bat habitat. Tree clearing is allowed from 15 October to 31 March (USFWS 2019), but empirical data demonstrate that at least some Indiana bats are using trees outside of these dates.

Table 2.1—Measurements of Indiana bat (*Myotis sodalis*) skin temperatures (T_{sk}) and associated ambient air temperatures (T_a) during day and night, and energetic states, 2013 – 2017.

Day or night behavior state	Mean T_a (°C)	Range of T_a (°C)	Mean T_{sk} (°C)	Range of T_{sk} (°C)
Day				
normothermic	24.4	13.0 – 27.0	33.1	32.0 – 34.4
torpor	21.8	5.0 – 34.5	24.3	12.1 – 32.4
Night				
normothermic	16.2	4.5 – 23.0	33.0	31.5 – 35.1
torpor	12.5	4.5 – 23.0	21.9	11.9 – 32.1

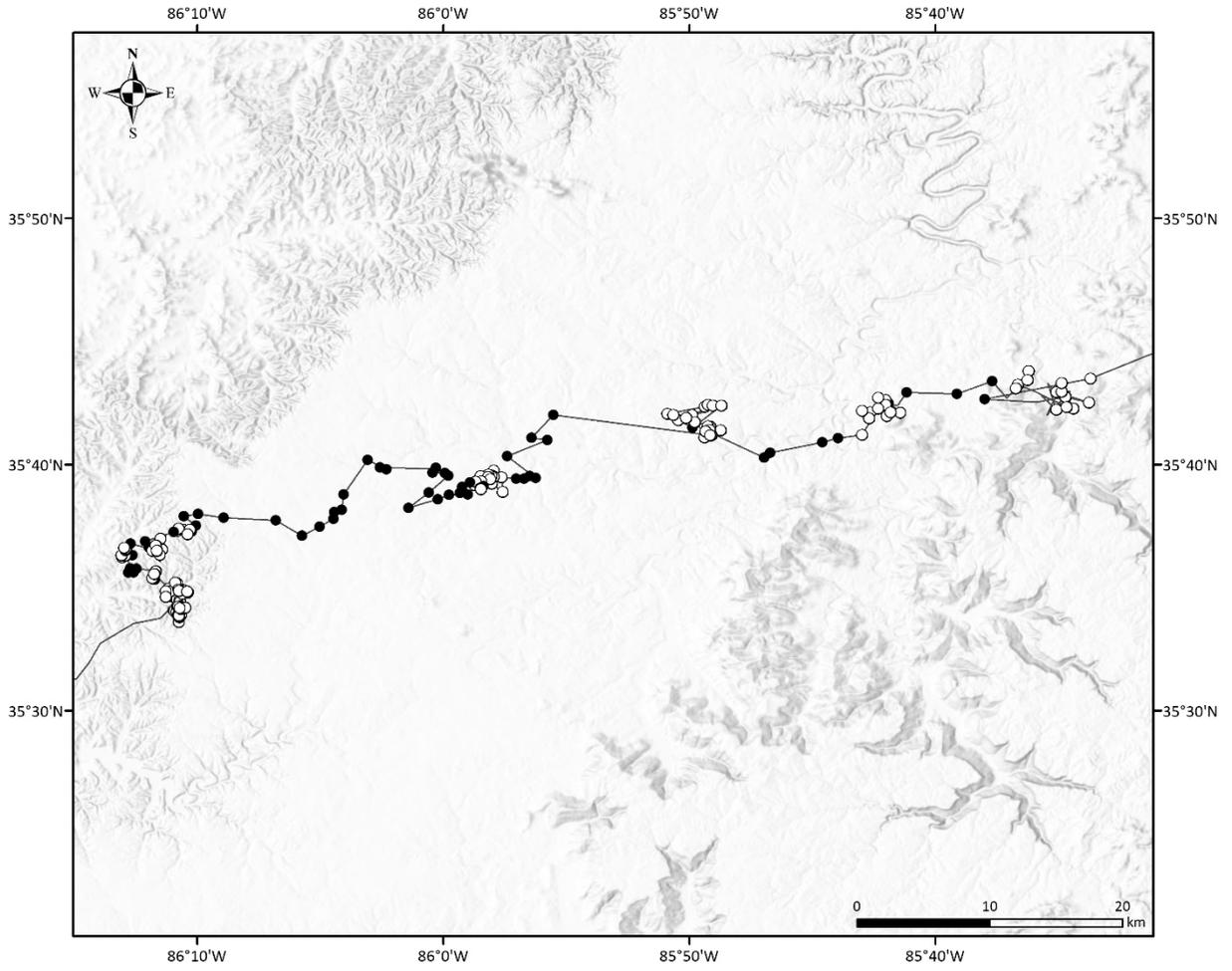


Figure 2.1—Visual representation of an Indiana bat (*Myotis sodalis*) traveling (closed circles) and foraging (open circles) during migration.

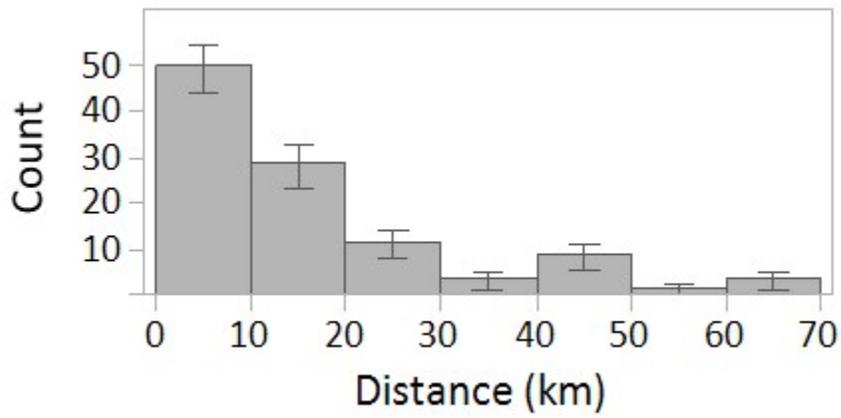


Figure 2.2—Distribution of distances traveled (km) between foraging bouts by spring migrating female Indiana bats (*Myotis sodalis*) from hibernacula to summer grounds. The majority of distances were short (<20 km).

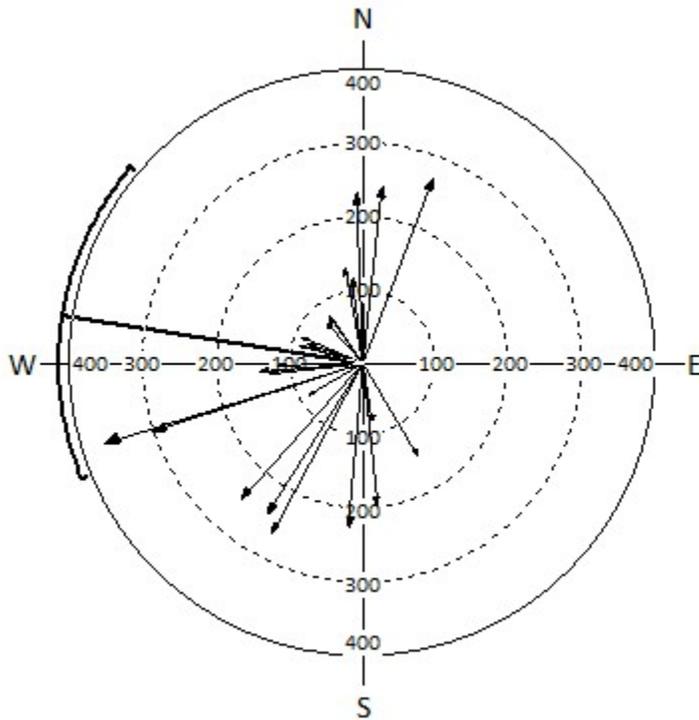


Figure 2.3.— Direction and distance traveled by 26 female Indiana bats (*Myotis sodalis*) migrating in the spring from hibernacula to summer grounds. We actively tracked 15 individuals, but 11 bats were located via aerial telemetry in summer grounds after migration was completed. Bats traveled in a westerly direction on average (dark black line). Direction values: 0 = north, 90 = east, 180 = south, 270 = west. Values within the circles represent distance in kilometers.

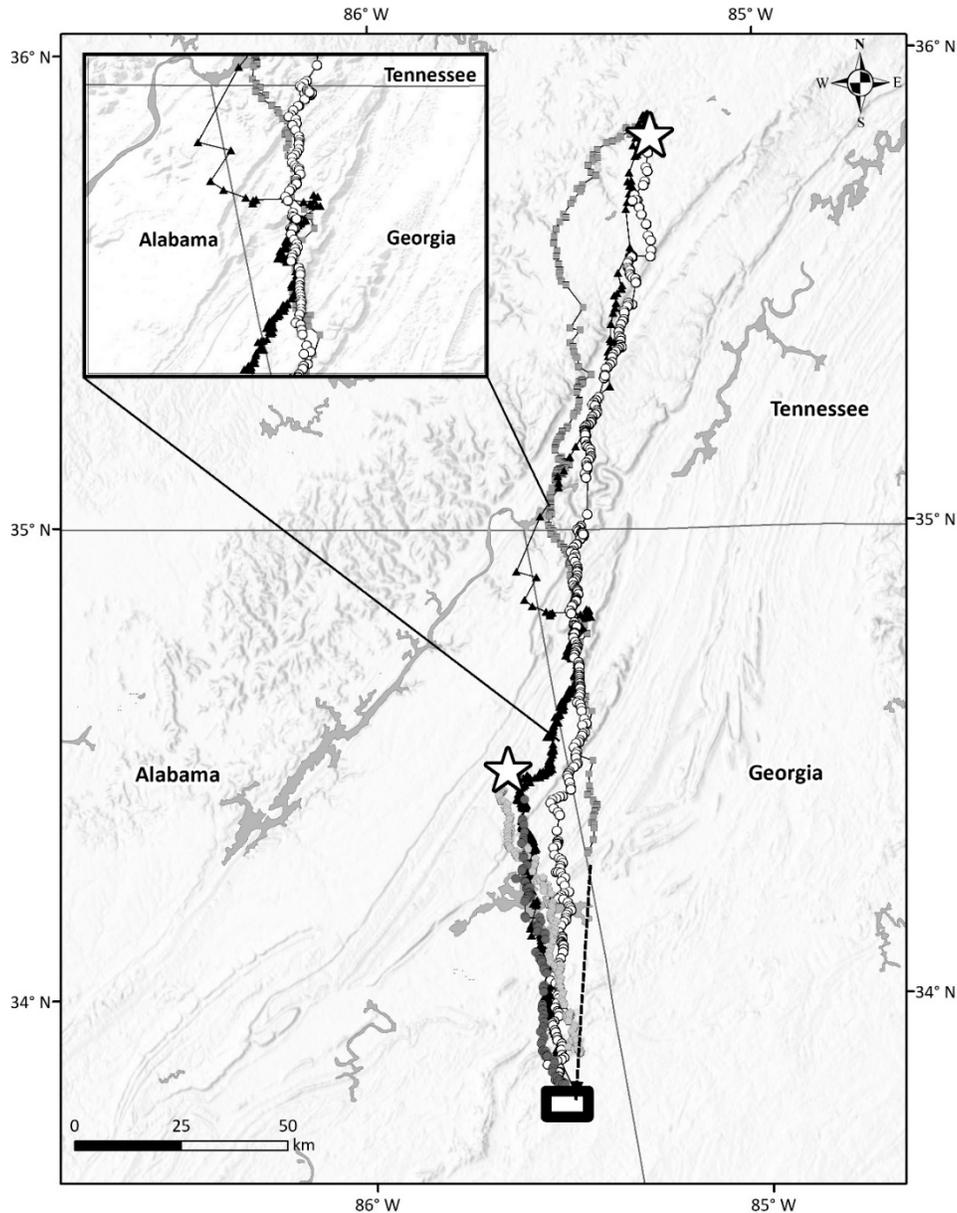


Figure 2.4.— Travel paths comprised of location fixes for individual female Indiana bats (*Myotis sodalis*) aerially radiotracked during spring migration. Each large white star is a hibernaculum and each smaller symbol represents a different individual ($n = 5$ bats). All bats traveled south from hibernacula during spring migration to their shared maternity area (rectangle at the bottom of the migration paths). Filled gray irregular polygons represent lakes. Inset: overlapping migration paths.

CHAPTER 3. INFLUENCE OF TEMPERATURE ON BEHAVIOR OF SPRING MIGRATING INDIANA BATS (*MYOTIS SODALIS*)

3.1 ABSTRACT

Many animals undergo seasonal migrations to take advantage of suitable habitat during different times of year, either by migrating long distances between winter and summer areas or by migrating shorter distances to hibernate in winter. Several temperate zone bats are either long distance or regional migrants, but both must contend with fuel acquisition and conservation for this energy-demanding endeavor. Although it was postulated that bats likely refuel along migration routes, this was only recently demonstrated for long distance migrating silver-haired bats (*Lasionycteris noctivagans*) and termed torpor-assisted migration. To determine if the regional migrant Indiana bat (*Myotis sodalis*) also engages in this behavior, we used temperature sensitive radio-transmitters to track adult females migrating in spring from hibernacula toward summer grounds and collected ambient temperature (T_a) during the migration. We created an algorithm to determine when bats were in one of four physiological states: torpor, warming, normothermy, or cooling. We then used decision tree analysis to predict physiological state based on T_a and diel condition. We also calculated warming and cooling rates at different T_a . The T_a was significantly warmer when bats were normothermic than when they were in torpor or when cooling, but there was no significant difference between any other bat temperature (T_{sk}) and T_a combinations. The nighttime T_a threshold for a change in physiological state was 9.8°C where there was an 87.7% chance bats were in torpor below this temperature. During the day, the T_a threshold was 23°C where there was a 96.3% chance of a bat being in torpor below this temperature. Lower T_a at any time increased the cooling rate of the bat, but there was no effect of T_a on warming based on these data.

Indiana bats used torpor-assisted migration. During conducive weather, bats entered torpor during the day likely to conserve the fuel they acquired the night before, emerged and foraged before migrating, alternated between traveling and foraging throughout the night, and often foraged before selecting a diurnal roost. If weather was inclement, bats warmed physiologically but did not emerge, eventually returning to a state of torpor. Understanding how weather affects migrating bats can provide information about when bats are active on the springtime landscape.

3.2 INTRODUCTION

There is a considerably more information and data on bird migration than bat migration, and hypotheses for how bats migrate often arise from patterns in bird migration studies (Hedenström 2009, Hedenström et al. 2009, McGuire and Guglielmo 2009). Even though birds and bats exhibit convergent adaptations for flight, they have different evolutionary histories resulting in differing strategies for migration. Birds migrate during the day or at night and use long layovers where they build up fuel (Hedenström and Ålerstam 1997). Bats, on the other hand, migrate and feed during nighttime hours while resting during the day, therefore deviating from the avian migration model (Hedenström et al. 2011). To offset this time constraint, silver-haired bats (*Lasiurus noctivagans*) used daytime torpor to conserve energy for nighttime activity (McGuire et al. 2014), and it is likely this strategy is used by other migrating bat species.

Bats in eastern United States are nocturnal insectivores that are either long distance migrants that stay active year-round or regional migrants that hibernate in the winter and undergo relatively short migrations to and from summer grounds in spring and autumn. During these journeys, nighttime flight must be divided between traveling and refueling

(Hedenström 2009); however, diurnal inactivity could be used for energy savings by entering torpor. Two species of long-distance migrant bats have been shown to use torpor-assisted migration where the bats “intersperse periods of migratory flight with roosting in torpor” (McGuire et al. 2012, McGuire et al. 2014). In addition, McGuire et al. (2014) found that the amount of torpor used by silver-haired bats was related to ambient temperature. Much is unknown about how bats migrate, but recent studies have started to provide answers about how bats are getting from hibernacula to summer grounds (Bergquist 2017, Roby et al. 2019, Samoray et al. 2019). Regardless, many more questions remain about how migration behavior is affected by endogenous and exogenous cues (Bauer et al. 2011).

The Indiana bat (*Myotis sodalis*) is a federally endangered species considered to be a regional migrant in the eastern United States. Indiana bats hibernate for up to 7 months during which time they ingest no food (Whitaker and Rissler 1992, 1993), and like many bat species (Ewing et al. 1970, Speakman and Rowland 1999, Kunz et al. 2016), subsist on fat stores accumulated in autumn (Hall 1962, LaVal and LaVal 1980). Upon emergence, prey is sparse (Park et al. 2000, Meyer et al. 2016) and some individuals travel hundreds of kilometers over several nights to reach summer grounds (Roby et al. 2019). Therefore, we predicted that like long distance migrants, Indiana bats use torpor-assisted migration to conserve energy during the day so that nightly refueling can be used for efficient travel. Because ambient temperature has been shown to affect bat behavior (Davis and Reite 1967, Lacki 1984, O'Donnell 2000), we also set out to describe this in more detail by investigating how ambient temperature influenced bat thermoregulatory patterns during migration. In the process, we wanted to develop a method to classify physiological state of a bat that

provides more information than two-state option provided by Willis (2007), i.e., torpor or normothermy. Torpor is defined as reduced metabolic activity (Wang and Wolowyk 1988) while normothermy is when the body temperature is at a level conducive for activity, i.e., normal body temperature.

3.3 MATERIALS AND METHODS

3.3.1 Data Collection

We radio-tracked female Indiana bats from hibernacula during spring migration using temperature sensitive radio-transmitters (model LB-2XT, Holohil Systems Ltd, Carp, ON) from 2013 – 2016. We tracked bats via aerial telemetry and ground personnel as individual bats migrated to their maternity areas. See Roby et al. (2019) for complete methods. Interpulse periods of the transmitter signal were stored in a receiver-datalogger (model R4500CD, Advanced Telemetry Systems [ATS], Isanti, MN). We calculated bat skin temperature (T_{sk}) data using calibration curves obtained from the manufacturer for each transmitter. In this study, T_{sk} is used as a measurement for body temperature (T_b , Audet and Thomas 1996, Barclay et al. 1996, McKechnie et al. 2007). In addition, we placed temperature data loggers (iButton®, Maxim Integrated, San Jose, CA) on the roofs of field vehicles and on trees near roosting bats throughout the project to collect simultaneous ambient temperatures (T_a). All temperature data were time stamped so that T_{sk} and T_a were paired for analysis.

For initial investigation of the data, we calculated a torpor onset ($T_{sk-onset}$) value using the equation in Willis (2007) with model parameters minus 1 standard error:

$$T_{b-onset} - 1 \text{ SE} = (0.041)(\text{body mass}) + (0.040)T_a + 31.083$$

where $T_{b\text{-onset}}$ in Willis (2007) is equivalent to $T_{sk\text{-onset}}$ in this document. We calculated this $T_{sk\text{-onset}}$ value for every data point collected and then compared it to each T_{sk} data point. If $T_{sk} > T_{sk\text{-onset}}$, the bat was considered normothermic. If $T_{sk} < T_{sk\text{-onset}}$, the bat was considered to be in torpor. However, it was clear by plotting the data that there were obvious transition temperatures that should not be categorized into one of these two categories. By visually evaluating the data, each point was categorized into one of four physiological states: torpor, warming, normothermic, or cooling. To automate this analysis, we created a method for identifying when a bat was in one of the four states. Data were collected at irregular intervals; therefore, all data were evaluated using averages of temperatures by 10-minute intervals to allow clear discrimination of critical events.

The Willis (2007) equation was created using mammal body masses ranging from 14.7 – 406.0 g, T_{sk} of those mammals, and associated T_a . Most of the bat species in the eastern U.S. weigh < 10 g, including the Indiana bat (range in this study: 5 – 9 g). Using this equation on Indiana bats resulted in a misclassification of data points and was not created to consider the designation of transition states, i.e., warming and cooling. Therefore, we developed an algorithm using body mass and T_{sk} of migrating Indiana bats and corresponding T_a to determine physiological states of bats. The algorithm described some quantitative criteria that could be used to generate reasonably accurate predictions. We implemented this algorithm using code written in Microsoft Excel Visual Basic for Applications (VBA; v. 7.1). In general, our approach involved empirical determination of rates of change in T_{sk} that were indicative of warming and cooling transitions. The rate value that provided the highest accuracy in classification (compared to visual examination of plotted temperature data) was 0.14°C/minute. Data points following warming transitions

were identified as ‘normothermic’ and points following cooling transitions were identified as ‘torpor’. When gaps were present in the data, such that preceding data were unavailable for categorizing state, a setpoint temperature was used. This value (30°C) was also empirically determined from the dataset to provide the greatest classification accuracy of all points in the dataset. Each point categorized by the algorithm was compared to the manual classification, resulting in $96.4 \pm 0.01\%$ accuracy (range: 90 – 100% for each bat).

3.3.2 Data Analysis

Using T_{sk} data classified into one of four physiological states, we conducted one-way analysis of variance (ANOVA) tests to determine differences among T_{sk} for each state as an additional confirmation that the algorithm accurately classified four distinct physiological states. We conducted a one-way ANOVA to determine differences among T_a for each physiological state to investigate the influence of T_a on each state. To identify the potential to predict physiological state based on external influences, we used decision tree analysis with the partition platform to split data according to a relationship between T_a values and diel condition (i.e., whether it was day or night). This provided a threshold value for T_a and the probability that a bat was either normothermic or in torpor for a given combination of T_a and diel condition. Transition values were excluded from the partition platform analysis.

We calculated the duration and rate of change for the transition states and then used a one-way ANOVA to determine if the difference between T_a and T_{sk} at the beginning of a transition state would affect the rate of that transition state. Student’s t-tests assuming unequal variances were used to determine differences between transition states for duration and for rate of change, i.e., to answer whether warming and cooling events take the same

amount of time. All analyses were conducted in SAS JMP Pro (v. 14.0). Means are reported as plus or minus standard error ($\bar{x} = SE$) and results were significant at $\alpha = 0.05$.

3.4 RESULTS

A total of 10,381 paired temperature data points were analyzed for 8 radio-tagged bats over 4 years. There was a difference in mean T_{sk} among the 4 physiological states ($F_{3,1750} = 1974.22$, $P < 0.0001$) and all states were different from each other (Tukey all $P < 0.0001$; Table 3.1), validating the algorithm's classification. There was also a difference in T_a when bats were in each of the 4 physiological states ($F_{3,1750} = 29.57$, $P < 0.0001$), but these were not all different from each other (Table 3.2). The T_a when bats were normothermic was higher than when bats were in torpor ($P < 0.0001$) and when bats were cooling ($P = 0.0393$), but there was no difference between any other combinations (all $P > 0.05$). The ranges for T_{sk} and the ranges for T_a overlapped with each other among physiological state, but not in the same pattern (Table 3.3).

Female Indiana bats used torpor daily during spring migration, arousing in the evening to emerge and continue migrating, forage at a layover site, or return to torpor (Fig. 3.1). Results of partition analysis revealed that T_a was a stronger predictor in the split criteria (0.68) than the diel condition. During the day, there was an 83.5% chance that a bat would be in torpor, where the threshold for this physiological state was $T_a = 23^\circ\text{C}$. If $T_a < 23^\circ\text{C}$, there was a 96.3% chance the bat was in torpor. However, if $T_a > 23^\circ\text{C}$, there was a 53.9% chance the bat was in torpor. At night, there was a 54.8% chance the bat was normothermic, where the threshold for this physiological state was $T_a = 9.8^\circ\text{C}$. If $T_a < 9.8^\circ\text{C}$, there was an 87.7% chance the bat was in torpor. If $T_a > 9.8^\circ\text{C}$, there was a 25.7% chance the bat was in torpor.

The duration of cooling was longer ($\bar{x} = 35.1 \pm 4.4$ min) than warming ($\bar{x} = 15.9 \pm 1.2$ min; $t_{15} = -4.17$, $P = 0.0008$); therefore, the rate of cooling was slower ($16.3 \pm 1.9^\circ\text{C h}^{-1}$) than the rate of warming ($31.0 \pm 2.8^\circ\text{C h}^{-1}$; $t_{36.9} = 4.3$, $P < 0.0001$). The value of T_a triggered when bats began cooling at the end of the night (i.e., before sunrise), but bats actively warmed themselves at dusk before nightly emergence regardless of T_a . Because cooling is a passive process, it was influenced by the difference between T_a and T_{sk} at the start of cooling ($F_{1,12} = 5.13$, $P = 0.0428$): the lower the T_a at the beginning of cooling (i.e., the larger the difference between T_a and T_{sk}) the faster rate of cooling. The start of a warming bout was not influenced by the difference between T_{sk} and T_a ($F_{1,12} = 0.11$, $P = 0.7454$).

3.5 DISCUSSION

Indiana bats used torpor-assisted migration in the spring similar to silver-haired bats (McGuire et al. 2014). Indiana bats were in torpor during the day, aroused in the evening, migrated and foraged at night, or returned to torpor without emerging if T_a was low (i.e., $< 9.8^\circ\text{C}$). Using the algorithm to classify the T_{sk} dataset provided temperature thresholds for the physiological state of bats based on diel condition and T_a . When T_a was $< 23^\circ\text{C}$ during the day, bats were in torpor. During the day, Indiana bats “abandon homeothermy” (Speakman and Thomas 2003) as evidenced by T_{sk} fluctuating with T_a , until T_a reached 23°C at which point bats became normothermic. This was also documented for silver-haired bats when $T_a > 25.7^\circ\text{C}$ (McGuire et al. 2014) and Australian long-eared bats (*Nyctophilus* sp.) at “about 25°C ” (Geiser and Brigham 2000). The metabolic rate of torpor intersects that of normothermy at these T_a for Australian long-eared bats (Geiser and Brigham 2000), for silver-haired bats (McGuire et al. 2014), and presumably Indiana bats

based on their behavior in our study, at which point it is no longer energy-saving to remain in torpor. It has been suggested that bats are able to dissipate body heat in relation with body size, a phenomenon known as heat dissipation limit (HDL) theory (Speakman and Krol 2010). Once bats are no longer in torpor, they may switch to heat dissipation in order to regulate their body temperature.

Bats exhibited passive rewarming during the day, but due to thermoconforming, T_{sk} reduced in the evening along with T_a until bats engaged in active warming at dusk. If $T_a < 9.8^\circ\text{C}$ at dusk, bats abandoned heterothermy and underwent passive cooling into torpor. If $T_a > 9.8^\circ\text{C}$ at dusk, bats emerged from the roost to forage and migrate until T_a dropped below this threshold temperature, wind or rain suspended activity, or it became daylight. If weather conditions remained unsuitable for active bats, they would use multi-day torpor, a phenomenon also documented by Geiser and Brigham (2000). In addition, Johnson et al. (*In Prep*) report that bats used torpor more extensively during lower temperature days.

Homeothermy is energetically expensive and because bats in the eastern U. S. experience extreme ambient temperatures throughout the year, they employ the energy-saving tactic of heterothermy (Neuweiler 2000b). The benefit of using torpor daily is to conserve energy and there is a tradeoff between foraging and thermoregulating at low temperatures. The prey availability is less abundant in cooler temperatures (Taylor 1980, O'Donnell 2000, Rachwald et al. 2001) resulting in bats expending proportionally more energy to feed than would be saved by entering torpor. The use of torpor is also affected by food intake (Wojciechowski et al. 2007, Matheson et al. 2010). Cooler spring temperatures result in less insect prey so spring migrating bats may also be food deprived, supporting our finding that bats use torpor daily.

The value of T_a affected whether bats were normothermic or in torpor, but it also influenced the activation and rate of transition states. Cooling is a passive process via thermal conductance (McNab 1980) and therefore requires little energy. Although active rewarming is a metabolic process that is energetically costly, rewarming quickly is energetically advantageous (Stone and Willmer 1989, McKechnie et al. 2007). Some bats actively rewarmed and then cooled back into torpor if the evening T_a was too low to warrant exiting the roost, and at least one bat did remain in the roost for several days without active rewarming when T_a was low.

Ambient conditions affect all living things, and bats are no exception. The small size and high surface-to-volume ratio make these heterothermic mammals susceptible to being negatively affected by weather. Indiana bats use torpor-assisted migration to conserve replaced energy after emerging from several months of hibernation. It is likely that Indiana bats are not pregnant during this transition between winter and summer habitat (Wimsatt 1944). Many studies have documented delayed parturition by bats that use torpor (Racey 1973, Racey and Swift 1981, Audet and Fenton 1988, Speakman 2008), so the fact that migrating Indiana bats used torpor daily supports the idea that they are not pregnant. It is advantageous for bats to use torpor daily as they undertake an energetically costly migration while also rebuilding fat stores used during hibernation. Upon arrival to maternity grounds, bats must be healthy enough to implant the previously fertilized egg for on-time parturition. Using torpor-assisted migration allows these bats to complete their migration and join maternity colonies for the summer.

Other studies have used a temperature cut-off value or a set change in temperature to determine when bats are in torpor or normothermic (Park et al. 2000, Barclay et al. 2001,

Geiser 2004, Willis 2007, Grinevitch et al. 2009, Britzke et al. 2010, Johnson et al. 2012, Dzal and Brigham 2013, Johnson and Lacki 2013, 2014, McGuire et al. 2014). We utilized information from individual bats to define not only when bats were in torpor or normothermic, but also when they were transitioning between these states, i.e., warming or cooling. Due to the variability of individuals, variability in conditions, and inevitable variations in the data, some outliers may exist. For example, the model reported that at least one bat's T_{sk} was 32.2°C while the bat was in torpor. Closer examination of this bat's temperature pattern reveals that the bat was normothermic, but then thermoconformed to the high T_a of the afternoon. The rate of cooling along with the bat's T_{sk} then closely following T_a resulted in those data points being classified as torpor. Because part of model was based on rates of temperature change and these changes were in 10-minute intervals, there are bound to be minor inaccuracies in the results. These high T_{sk} in torpor could also represent shallow torpor (Willis and Brigham 2003), a concept not discussed here but deserves investigation. Overall however, we believe that this method allows for more input resulting in more accurate output.

Table 3.1—Female Indiana bat skin temperature (T_{sk}) in four different physiological states during spring migration.

Physiologic state	N	Mean (°C)	Std Error	Lower 95% (°C)	Upper 95% (°C)
torpor	983	19.3	0.1	19.0	19.5
cooling	51	24.9	0.5	23.9	26.0
warming	42	30.9	0.6	29.7	32.1
normothermic	678	34.2	0.1	33.9	34.5

Table 3.2—Ambient temperature (T_a) when female Indiana bats were in four different physiological states during spring migration.

Physiologic state	N	Mean (°C)	Std Error	Lower 95% (°C)	Upper 95% (°C)
torpor	983	14.0	0.2	13.6	14.4
cooling	51	14.5	0.9	12.7	16.2
warming	42	16.3	1.0	14.4	18.3
normothermic	678	16.9	0.2	16.5	17.4

Table 3.3—Range of temperatures in degrees Celsius (°C) for Indiana bat skin (T_{sk}) and ambient temperature (T_a) while bats were in one of four physiological states during spring migration.

Physiological state	T_{sk} (°C)		T_a (°C)	
torpor	11.9	32.2	3.5	40.0
cooling	16.6	34.9	5.8	38.9
warming	21.2	36.1	7.0	22.8
normothermic	30.7	37.4	4.5	36.5

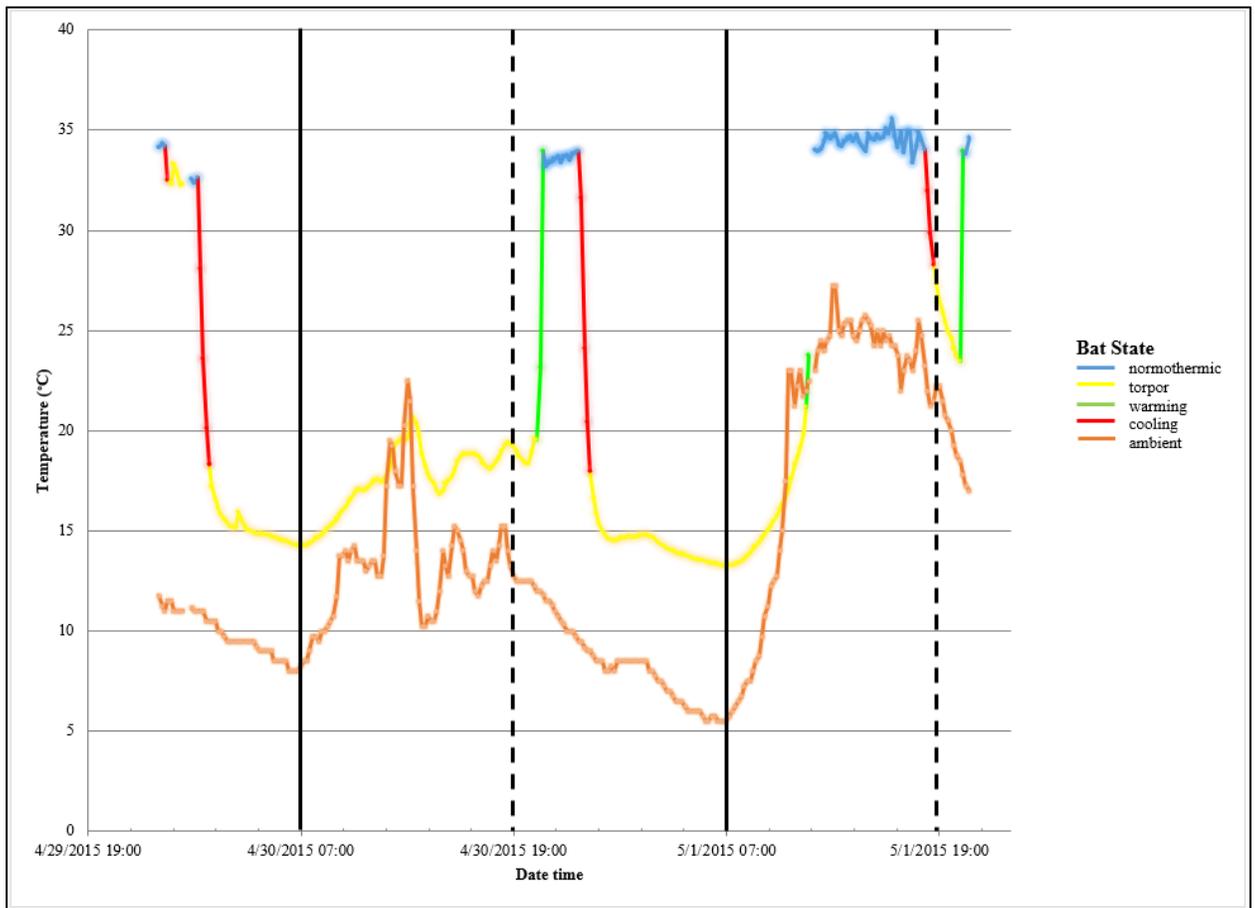


Figure 3.1—Thermoregulatory pattern of a female Indiana bat (*Myotis sodalis*) using a roost at a layover site for multiple days. Dashed vertical lines indicate sunset and solid vertical lines indicate sunrise.

CHAPTER 4. LANDSCAPE AND ROOST USE BY SPRING MIGRATING FEMALE INDIANA BATS (*MYOTIS SODALIS*)

4.1 ABSTRACT

Landscape use by wild animals is an important topic for land managers to make informed decisions with the best available science and for understanding the ecology of species. Migrating animals pose a challenge in that they are not confined to a home range, and the landscape variables available are likely more extensive than those available to a resident group of animals. The federally endangered Indiana bat (*Myotis sodalis*) is a regional migrant that inhabits the eastern United States. We radio-tracked female individuals via aerial telemetry during spring migration from hibernacula to summer maternity areas over 9 years to better understand the process and behavior of these bats during an understudied life history event. We identified diurnal roosts during pre-migration staging, along the migration routes, and within spring use of summer home ranges. Of the 137 roosts visited, 1 was a bridge and 136 were trees of 25 species within 10 genera. Four species comprised 63% of all roosts used: *Carya ovata* (n = 53), *Ulmus americana* (n = 13), *Pinus echinata* (n = 10), and *Pinus taeda* (n = 10). Roosts were categorized as staging, migration, layover, or arrival. There was no difference in tree characteristics (i.e., diameter at breast height, tree height, or roost height) among these roost categories. The majority of staging trees were live *Carya ovata* whereas arrival trees were mostly dead standing trees of various species. High amounts of useable bark (i.e., bark usable for roosting bats) were found on staging trees and layover trees, but there was no preference for usable bark on migration or arrival trees. In addition, there was no difference between migration trees and those used during summer months in other studies. We used compositional analysis to determine resource use compared to resource availability for 20 migrating bats. Bats used

forests at higher proportions than other resources evaluated during foraging, but there was no difference in resource use during traveling. Migrating bats used maximum elevation as available with no difference in elevation use between traveling and foraging. There was also no difference in distance to water between the two behaviors. Although Indiana bats require forests for foraging and roosting, overall, spring migrating bats travel in a relatively straight line from hibernacula to summer grounds with little regard to the landscape cover.

4.2 INTRODUCTION

Land management for endangered species is challenging since they are rare by definition, resulting in low detection probabilities (Thompson 2004) and insufficient data to create population models (Beissinger and Westphal 1998). Home ranges of radio-tracked individuals are often estimated and evaluated to determine resource use by a population of animals, but this assumes that those tracked use a constrained area. Evaluating landscape use by migrating animals is problematic since there is no set home range used repeatedly by the same individuals within a season. Migratory animals use different habitats during different parts of the year and move through protected and unprotected areas. While winter and summer locales may be protected from human disturbance, migratory paths are frequently interrupted by anthropogenic features (Shuter et al. 2011). The federally endangered Indiana bat (*Myotis sodalis*) is a regional migrant that overwinters in caves or mines and spends the summer reproductive period roosting primarily in trees (USFWS 2007). Many hibernacula for this species are federally protected and surveys to detect federally listed bats are required for removal or disturbance of summer or winter habitat (USFWS 2019).

Winter habitat used by the Indiana bat has been studied since at least the early 1960s (Humphrey 1978), and summer landscape use and roost use have been studied for over 40 years (Humphrey et al. 1977). The summer roosting and foraging requirements of Indiana bats are well known in most of the range of the species (Kurta et al. 2002, Britzke et al. 2003, Kurta 2004, Sparks and Whitaker 2004, Menzel et al. 2005, Sparks et al. 2005, Britzke et al. 2006, Watrous et al. 2006, Whitaker and Sparks 2008, Lacki et al. 2009, Womack et al. 2013, Jachowski et al. 2014, Kniowski and Gehrt 2014, Silvis et al. 2014, Pauli et al. 2015, Fishman 2016, Hammond et al. 2016, O'Keefe and Loeb 2017, Schroder et al. 2017, St. Germain et al. 2017). However, habitat requirements for this species are completely unknown during spring and autumn migration. Information about migration has been primarily gathered from band recoveries, providing a start and an end point between winter and summer habitat (Griffin 1945, Davis and Hitchcock 1965, Kurta and Murray 2002, Fleming and Eby 2003, Hutterer et al. 2005, Winhold and Kurta 2006, USFWS 2007, Ellison 2008, Cryan and Diehl 2009). Only recently has tracking technology progressed to allow studies of behavior and routes of bat migration (Holland et al. 2006, McGuire 2012, McGuire et al. 2012, McGuire and Boyle 2013, Dechmann et al. 2014, McGuire et al. 2014, McCracken et al. 2016, Dechmann et al. 2017, Krauel et al. 2017, Lehnert et al. 2018, Roby et al. 2019).

Decades of study have resulted in the protection of winter hibernacula and allowed for the mitigation (Whitaker and Sparks 2004), protection (USFWS 2006), and habitat enhancement of some summer maternity colonies (Adams et al. 2015). With the introduction of white-nose syndrome (WNS) to the United States in 2006 (Blehert et al. 2009), populations of cave-hibernating bats have declined precipitously (Frick et al. 2015).

If bats survive the winter, they can heal throughout the summer (Fuller et al. 2011). However, animal migration is metabolically costly (Cresswell et al. 2011), and migrating to summer grounds after spring emergence from hibernacula is a crucial survival period for cave-hibernating bats (Fleming and Eby 2003). The roosting, foraging, and traveling habitat used by bats during spring migration is unknown and, therefore, not protected. Understanding the requirements of migrating bats could result in informed protection decisions for bats that both migrate hundreds of kilometers and may be doing so while recovering from WNS infection.

Collecting specific behavioral data on small, nocturnal, volant animals is difficult. Holland and Wikelski (2009) suggested that although hypothetically possible, tracking migrating bats via aerial telemetry had not been accomplished. Roby et al. (2019) did accomplish this by tracking 20 spring migrating Indiana bats and collecting behavior information during each bat's migration. The purpose of the current study was to explore the land use and roost use of traveling, foraging, and diurnally roosting Indiana bats tracked in Roby et al. (2019).

Based on known summer habitat requirements for Indiana bats and basic migratory information, we predicted that spring migrating Indiana bats would 1) use roosts differently along the migration route, e.g., roosts used at the start of migration would be different species, size, and condition than those used at the conclusion of migration, and 2) preferentially use forested habitat for traveling and foraging. In addition, we investigated if there was a difference in distance from water for traveling versus foraging bats and the maximum elevation over which bats would travel.

4.3 MATERIALS AND METHODS

4.3.1 Study Area

We visited 10 Indiana bat hibernacula in 3 states to radio-tag female Indiana bats in the spring from 2009 – 2017: Tennessee (n = 8 caves), Indiana (n = 1 cave), and Alabama (n = 1 cave). All hibernacula were surrounded by deciduous forest. Although most of the bats migrated through the heavily forested southeastern states (KY, TN, MS, AL, and GA), one bat did migrate through the agricultural patchwork landscape of Indiana (Roby et al. 2019).

4.3.2 Bat Capture and Radiotelemetry

We radio-tagged 260 female Indiana bats in spring and tracked 20 via aerial telemetry as they migrated from winter hibernacula to summer maternity grounds. We tracked one bat at a time, but we tracked multiple bats in the same year rather than tracking one bat per year. Data collected were nightly sequential location points categorized as either traveling or foraging. Most of the points (80%) were taken ≤ 5 minutes apart. Telemetry error was 383 m and estimated by comparing the distance between aerial location points to corresponding bat roosting locations confirmed by the ground crew. This value was used as smoothing parameter σ^2 in analysis below. See Roby et al. (2019) for full capture, radio-tagging, and tracking methods.

We located Indiana bat diurnal roosts using model TRX-1000S (Wildlife Materials Inc., Carbondale, Illinois, USA) tracking receivers and 172-3FB 3- and 5-element Yagi directional antennas. Once located, we photographed the roost and obtained coordinates using a handheld GPS unit. For roosts that were in trees, we recorded tree species, diameter

at breast height (dbh; cm), tree height (m; estimated), roost height (m; estimated if known), decay stage (live, live-damaged, or snag [i.e., dead standing tree]) percent usable bark cover for roosting, percent total bark cover, tree ranking (whether a tree's crown was in the canopy, sub-canopy, or understory), and any other noteworthy observations (e.g., bat vocalization, guano). We determined basal area (an expression of tree density; Avery 1967) of the forest surrounding the roost tree with a 10-factor English prism. We characterized each tree within this plot using the same criteria as the roost tree. We placed each tree roost into 1 of 4 categories: staging, migration, layover, or arrival. Staging roosts were located within 5 km of the cave (Gumbert et al. 2002, Roby et al. 2019), migration roosts were used for 1 day along the migration route, layover roosts were used for either > 1 day or were located in the same area as a previous roost, and arrival roosts were used upon arrival to the summer grounds.

4.3.3 Data Analysis

All roost tree data were analyzed in JMP Version 14.3 (2018). We conducted a nominal logistic regression to determine differences in dbh, tree height, and roost height among the 4 roost types and to determine differences in tree condition, amount of useable bark, amount of total bark, and tree ranking among the 4 roost types. We used a likelihood ratio test or two-sided Fisher's exact test to determine differences of significant parameters. We used a multivariate analysis of variance (MANOVA) test to determine if there was a difference between measurements of roosts used during the summer reproductive period from published literature and the current springtime study with regards to roost characteristics. We used a one-way analysis of variance (ANOVA) to determine a

difference in roost condition between the published summer roosts and the roosts in the current study.

To analyze resource selection along the migration route, we conducted a compositional analysis (Aebischer et al. 1993) using the R package ‘adehabitatHS’. Compositional analysis is robust for unequal sample sizes, uses defined available habitat rather than arbitrary boundaries, and can be used at multiple scales. Separate analyses were conducted on traveling behavior, foraging behavior, and both behaviors together. Means are reported as plus or minus standard error ($\bar{x} \pm SE$) and all results were evaluated with a rejection level of $\alpha = 0.05$.

We created polygons to define areas used by and available to bats along their migration routes in the R environment (R Core Team 2019). First, we created a trajectory for each bat’s locations using the R package ‘adehabitatLT’. Each bat’s trajectory was then divided into bursts by sampling night and by behavior bout (i.e., traveling or foraging) within a sampling night. Trajectory bursts with fewer than 3 locations were deleted and not included in further analysis. For each burst, we estimated utilization distributions (UD) within a kernel Brownian bridge movement model (kernelbb) using the R package ‘adehabitatHR’. This method was used because it explicitly incorporates autocorrelation of locations and telemetry error (Horne et al. 2007). To account for variable levels of autocorrelation among successive points due to irregular sampling frequency and bat speed, we used a maximum likelihood approach to estimate the Brownian bridge smoothing parameter σ_1 for each burst, given the empirical position error σ_2 (i.e., 383 m). The resulting 95% contour represented the bat’s use area for that burst. We then created minimum bounding boxes around the vertices of the 95% UD polygon, with boxes oriented

along a straight line through the points (Wollschlaeger 2013). The resulting bounding box for each burst represented the bat's available area. We used multivariate regression analysis to determine if the area used by bats was different among individuals and among habitats.

We reclassified the 2011 National Land Cover Database (NLCD; Homer et al. 2015) into 4 landcover categories: water, open land (developed, rock, sand), forest, and low vegetation (agricultural crops, grasslands, pasture). We identified water resources by importing National Hydrography Data (NHD) from US Geological Survey (USGS 2019) into ArcMap Desktop 10.6.1 (ESRI, Redlands, CA). Then we overlaid a rasterization of the water resources layer onto the land cover map and reclassified all overlapping cells as open water. We used the Spatial Analyst tool 'Tabulate Area' in ArcMap Desktop 10.6.1 to measure the area of each land cover class within each bat's use and available area polygons.

For the compositional analysis, the R package 'compana' log-transformed the proportion of used area vs. available area covered by each land cover class for each bat. Then it conducted a one-way ANOVA on these log-ratios to determine whether there was significant habitat selection among the land cover classes. Next, for each bat, pairwise differences are calculated in log-ratios among all combinations of land cover classes, and then combine these tables to get population mean log-ratios and associated standard errors. Row-sums of the number of positive mean values were used to rank the land cover classes from most to least preferred, and t-values derived from means and standard errors were tested for significant differences among rank values.

Elevations and distances to water along bat migratory routes were analyzed separately. Summary statistics of elevation values from the National Elevation Dataset

(U.S. Geological Survey 2017) were calculated within each bat's use and available polygons using 'Zonal Statistics As Table' from the Spatial Analyst extension for ArcMap 10.6.1. We used linear regression analysis (in JMP) to determine if there was a difference in the available maximum elevation and the used maximum elevation. To examine water use more closely, distance from each bat location to the nearest water source was calculated using gDistance from the R package 'rgeos'. Then we conducted linear mixed-effects regression analysis with the R package 'lme4' to compare distance to water resources between behaviors while controlling for individual variation among bats with a random intercept. For analysis of elevation, we conducted linear regression analysis to determine the relationship between the maximum elevation available and the maximum elevation used. We then conducted Student's t-tests to determine if there was a difference in elevation for either foraging or traveling.

4.4 RESULTS

4.4.1 Roost Use

We identified 137 roosts during spring (March – May) migration from 2009 - 2017. One arrival roost was in an expansion joint underneath a concrete constructed bridge on a 2-lane state highway. The bat used this roost during the day, emerged to forage at night, returned to the bridge as a night roost or foraged nearby for 1.5 h (detected on the data recorder), and then moved away from the bridge to roost in a tree the next day. The remaining 136 roosts were in trees comprised of 10 genera, 25 species, and 3 unknowns (Table 4.1). Most of the roosts were categorized as arrival roosts ($n = 63$), 36 were staging roosts, 23 were migration roosts, and 15 were used during layovers. Shagbark hickory (*Carya ovata*) was used more than any other species (38%) followed by American elm

(*Ulmus americana*; 9%), shortleaf pine (*Pinus echinata*; 7%), and loblolly pine (*Pinus taeda*; 7%; Table 4.1). These top 4 species were distributed significantly differently among the 4 roost categories ($P < 0.0001$, Fisher's exact test). Almost all the staging trees and layover trees were *Carya ovata* (93% and 90%, respectively), along with the majority of migration trees (60%). Arrival trees were more evenly distributed among these 4 species (Table 4.2).

There was no difference in dbh, tree height, or roost height among the 4 roost categories ($\chi^2 = 19.10$, $DF = 21$, $P = 0.5787$; Table 4.3). There was a difference in tree condition, useable bark, and tree ranking ($\chi^2 = 80.40$, $DF = 24$, $P < 0.0001$). Although tree ranking appeared to be significant among the 4 categories ($\chi^2 = 14.62$, $P = 0.0234$), removal of the understory ranking that only contained 4 records in 1 category revealed that there was no difference between canopy and subcanopy trees ($\chi^2 = 3.65$, $P = 0.3022$). Trees had significantly different amounts of usable bark among the 4 categories ($\chi^2 = 27.35$, $P = 0.0001$). Staging trees primarily had high amounts of useable bark as did layover trees, but both migration and arrival trees were similar among the 3 levels of useable bark (Table 4.4). The condition of trees was significantly different among the 4 categories ($\chi^2 = 30.06$, $P < 0.0001$). The majority of staging trees were live, and the majority of arrival trees were snags. A higher percentage of migration trees were snags, but live trees and snags were used almost equally as layover roosts (Table 4.5).

Just as there was no difference in tree characteristics among roost types, there was also no difference between the roosts used in this study and those used by maternity roosting bats as compiled by Kurta (2004) ($F_{2,117} = 0.80$, $P = 0.4519$; Table 4.6). Similarly, although there was a difference in the condition of roosts along the migration route, the

proportion of live to dead roosts was not different from the literature (Callahan et al. 1997, Britzke et al. 2003, Fishman 2016, Bergeson 2017, Schroder et al. 2017)($F_{6,11} = 0.02$, $P = 1.000$; Table 4.7).

4.4.2 Resource Selection Analysis

We conducted a compositional analysis of resource selection for 20 migrating bats that traveled 165.4 ± 20.8 km (range: 6.3 – 368.1 km) on average from hibernacula to either summer grounds or to where tracking teams lost contact with a bat (Table 4.8). The number of location points taken ranged from 39 – 777 per individual, and this was highly correlated with distance traveled ($R^2 = 0.296$, $F_{1,18} = 7.57$, $P = 0.131$). The mean available area was 826.6 ± 136.4 km² (range: 16.7 – 2,180.3 km²) of which bats used $38.2 \pm 3.4\%$ (range: 12.0 – 72.0%; Table 4.8).

Overall, bats' use of the landscape consisted primarily of forest (48%) and low vegetation (38%), whereas water and open areas each covered 7% of the utilization distributions. Forest and low vegetation classes were also available in the highest proportions for both traveling and foraging behaviors (Fig. 4.1). In addition, some individual bats used habitats differently. This was especially noticeable in the difference between Bat 387's high percentage of low vegetation use and the higher percentage of forest use by all other bats (Fig. 4.2). Bat 387 migrated through most of Indiana which is dominated by agricultural fields, whereas the other bats migrated through the southeast where forests dominate (Fig. 4.3). Compositional analysis revealed that migrating Indiana bats demonstrated significant resource selection while foraging ($\Lambda = 0.6610$, $P = 0.0320$) but not while traveling ($\Lambda = 0.7537$, $P = 0.2360$). The ranking matrix comparing proportional habitat use with proportion of available habitat indicates that forests > open

areas > water > low vegetation. However, only one of these combinations was significant: forests were used in higher proportion than were available more significantly than proportional low vegetation use (Table 4.9).

The highest elevation available was 892.6 m and the highest elevation used was 856.4 m, both by the same bat. There was a significant relationship between the maximum elevation used by migrating bats and the maximum elevation available ($R^2 = 0.61$; $F_{1,285} = 441.74$, $P < 0.0001$). There was no difference in the maximum elevation used between traveling ($\bar{x} = 385.0 \pm 17.0$ m) and foraging ($\bar{x} = 357.3 \pm 13.9$ m; $t_{218,5} = 1.26$, $P = 0.2095$). Similarly, there was no difference in the distance to water when bats were traveling ($\bar{x} = 3,264.03 \pm 66.8$ m) versus when they were foraging ($\bar{x} = 2,846.6 \pm 78.0$ m; $t_{19} = -1.19$, $P = 0.2506$).

4.5 DISCUSSION

Indiana bats used a wide variety of tree species for roosting before, during, and after spring migration, and tree species use changed with geographical location and stage of migration. Consistent with other studies (Kurta 2004, USFWS 2007), the species of tree is less important than characteristics, such as the presence of a roosting area and tree size. Indiana bats primarily use exfoliating bark on relatively large trees as roosts during the maternity season (USFWS 2007), and these are also the roosts used during migration. The top 4 tree species used by bats in this study are commonly used throughout the range (USFWS 2007).

The use of a bridge for roosting by a bat in the summer grounds was unexpected and unusual. It is likely that inclement weather influenced the use of this roost on 4 April 2014; there was significant rainfall in the early morning hours of 3 April and the ambient

temperature was 9°C by 20:00 on 4 April. To date, the authors are only aware of a few other documented cases on Indiana bats using bridges as roosts (Mumford and Cope 1958, Kiser et al. 2002, Cervone and Yeager 2016, King 2017, Roby 2018). Although it is likely that Indiana bats have used bridges more often, the phenomenon is rare and therefore noteworthy.

Bats did not use roosts of different sizes (i.e., dbh or height) during different stages of migration, but the characteristics of roosts varied as migration progressed. Bats mostly used live roosts with high amounts of usable bark during staging, layover roosts used during inclement weather were also primarily live trees for protection against the environment, and snags were used as arrival trees. This is consistent with physiological needs of heterothermic bats that require more thermally stable roosts during cooler weather (i.e., staging roosts at the beginning of springtime) but use variable temperature roosts that warm quickly during the maternity season (Humphrey et al. 1977). Temperature and precipitation events are important in the parturition and survival of bats, particularly smaller species like those in the genus *Myotis* (Frick et al. 2010b). Typically, Indiana bats use dead or dying trees with high solar exposure for passive warming to reduce the amount of energy required for active warming and to promote fetal growth (Humphrey et al. 1977, Callahan et al. 1997, Menzel et al. 2001). Bats in the eastern U. S. have a relatively short amount of time to migrate to summer grounds and give birth in time for juveniles to mature for autumn migration to hibernacula. Indiana bats are likely not pregnant during migration, but the fertilization and embryo implantation occur shortly after they arrive at the summer grounds (Wimsatt 1944). Therefore, they use “typical” maternity roosts upon arrival to summer grounds at the end of migration to begin pregnancy and expedite parturition. Bats

in the south may experience a longer growing season due to earlier springs and later autumns, but this has yet to be investigated.

Information on Indiana bats in the southern U. S. is lacking and there has been little to alleviate this even after Harvey (2002) called for additional information to be gathered. As part of this study, several previously unknown maternity colonies were located, including the first colony to be discovered in Mississippi and southernmost known colony in the range located south of Birmingham, Alabama (Roby et al. 2019). These colonies are all inside the crescent-shaped Black Belt region (Barone 2005) which may act as the Southern edge of the species range. Perhaps not incidentally, all these newly discovered colonies south of Tennessee are located on U. S. Forest Service (USFS) land (Fig. 4.4). The management of these USFS lands has been conducive to Indiana bat summer habitat without the land being specifically managed for the species. Regardless, these colonies are on the extreme edge of the species range and would likely benefit from active management (Krusac and Mighton 2002), especially if southern colonies are at risk due to climate change (Loeb and Winters 2012).

Our prediction that bats would use forests preferentially during migration was partially supported. Bats used forests more than available for foraging, but not for traveling. Foraging behavior was consistent with habitat use in summer when Indiana bats forage in forested areas preferentially, even when the landscape is dominated by agriculture (Menzel et al. 2005, Sparks et al. 2005, Womack et al. 2013, Kniowski and Gehrt 2014, Pauli et al. 2015). Traveling bats are moving over the landscape quickly to reach a destination. This is in contrast to bats in summer ranges that use roosting and foraging areas repeatedly within a home range of high-quality habitat. Migrating Indiana bats fly in a relatively straight line

between hibernacula and summer grounds and this is supported by the lack of preferred habitat, water resources, or topography use along the way. Although bat flight altitude was not measured during this study, they are flying below the tracking plane that often operates at 450 m above ground level and the behavior of migrating bats indicates that they are likely flying just above treetop level. Because they are flying fast in a relatively straight line without regard to landscape types, they are probably not traveling within the forest where they would need to maneuver among trees. However, flying just above treetop could provide the option to drop down into the forest for protection from aerial predators such as owls (Rydell and Speakman 1995). Since bats stop to forage often throughout the night (Roby et al. 2019), they are likely flying low enough to detect areas for feeding, drinking, and roosting. Migrating common noctule bats (*Nyctalus noctula*) fly at a consistent altitude that follows the terrain (O'Mara et al. 2019), so migrating Indiana bats flying at treetop level would also fit this pattern of movement. Migrating is an energetically costly behavior (McGuire et al. 2013, McGuire et al. 2014, Sommers et al. 2019) and direct flight allows for efficient energy use.

Although bats did not exhibit preference for resource use while traveling, they did take advantage of landscape features when encountered and may have used waterways for navigation due to the behavior of traveling closer to water than when foraging. We tracked 3 bats from the same hibernaculum as they migrated to the same maternity colony over 3 different years. All 3 bats followed a large valley (~6 km wide) for approximately 60 km before they exited the valley to continue the trajectory to their summer grounds. Even though these bats used the same beginning and end points, their paths were not identical (Fig. 4.5), including one bat that changed direction abruptly to fly through a mountain gap.

The tracks from these bats created a migration path 25-km wide which is much greater than the 4-km-wide buffer assumed to be the “most reasonable scenario” by Erickson et al. (2016). It remains unknown whether individuals use the same paths every year, or if pathways shift due to prey availability, weather conditions, changes in landscape features, or other unknown factors. We did document individuals using the same summer grounds in consecutive years. This is consistent with the philopatry of Indiana bats to maternity colonies (Humphrey et al. 1977, Gardner et al. 1991, Callahan et al. 1997, Kurta and Murray 2002, Mellos et al. 2014) and with behavior of the migratory common noctule bat which showed little variability in migration from year to year (Lehnert et al. 2018). Another individual followed a dammed river for 80 km, and most bats avoided cities which could be associated with light avoidance (Lacoeuilhe et al. 2014, Rowse et al. 2016, Russo et al. 2017, Azam et al. 2018). Finally, the bat that migrated through Indiana appeared to fly along riparian corridors when they were available along the intended trajectory but would fly quickly across open fields to arrive at the next riparian area. This behavior was also noted by Kniowski and Gehrt (2014).

Management practices for migrating bats should be similar to that for maternity areas in terms of tree and forest characteristics. The seasonal restriction for tree clearing already covers spring (and fall) migration, i.e., tree clearing can only occur between 15 October and 31 March (USFWS 2011). Migrating Indiana bats use roosting and foraging habitat that is already understood and protected in some areas. Bats showed no preference for landscape variables during travel, but forests are still important along the migration route to provide trees for roosting, provide cover from predators, night roosts between foraging bouts, and likely for insect propagation.

Table 4.1—Female Indiana bat (*Myotis sodalis*) roosts used during spring migration. See text for definitions of each roost category.

Tree Species	Staging	Migration	Layover	Arrival	Total
<i>Acer rubrum</i>	1	1	0	1	3
<i>Acer saccharinum</i>	1	0	1	2	4
<i>Acer saccharum</i>	0	0	0	2	2
<i>Carya laciniosa</i>	0	0	0	1	1
<i>Carya ovata</i>	27	6	9	11	53
<i>Carya tomentosa</i>	1	2	0	0	3
<i>Fagus grandifolia</i>	0	0	0	1	1
<i>Fraxinus americana</i>	0	1	1	2	4
<i>Fraxinus pennsylvanica</i>	0	1	0	4	5
<i>Liriodendron tulipifera</i>	0	1	0	0	1
<i>Nyssa aquatica</i>	0	0	0	1	1
<i>Pinus echinata</i>	1	2	1	6	10
<i>Pinus sp.</i>	1	0	0	1	2
<i>Pinus strobus</i>	0	0	0	3	3
<i>Pinus taeda</i>	0	0	0	10	10
<i>Populus deltoides</i>	0	0	0	1	1
<i>Quercus alba</i>	2	2	0	1	5
<i>Quercus coccinea</i>	0	1	0	0	1
<i>Quercus falcata</i>	0	0	1	0	1
<i>Quercus lyrata</i>	0	0	1	0	1
<i>Quercus phellos</i>	0	0	0	1	1
<i>Quercus prinus</i>	0	0	1	0	1
<i>Quercus rubra</i>	0	2	0	1	3
<i>Quercus sp.</i>	1	0	0	0	1
<i>Robinia pseudoacacia</i>	0	1	0	0	1
<i>Ulmus alata</i>	0	0	0	2	2
<i>Ulmus americana</i>	1	2	0	9	12
<i>Ulmus sp.</i>	0	0	0	1	1
unknown	0	1	0	1	2
Hwy 641 Bridge	0	0	0	1	1
TOTAL	36	23	15	63	137

Table 4.2—Top 4 tree species used as roosts by spring migrating female Indiana bats (*Myotis sodalis*). # (%) = number of trees (% of trees used in that category).

Tree species	Staging	Migration	Layover	Arrival	Total
<i>Carya ovata</i>	27 (93%)	6 (60%)	9 (90%)	11 (31%)	53 (62%)
<i>Ulmus americana</i>	1 (3%)	2 (20%)	0 (0%)	9 (25%)	12 (14%)
<i>Pinus echinata</i>	1 (3%)	2 (20%)	1 (10%)	6 (17%)	10 (12%)
<i>Pinus taeda</i>	0 (0%)	0 (0%)	0 (0%)	10 (28%)	10 (12%)
TOTAL	29	10	10	36	85

Table 4.3—Roost characteristics for spring migrating female Indiana bats (*Myotis sodalis*) by roost category.

Measurement	<u>arrival</u>		<u>layover</u>		<u>migration</u>		<u>staging</u>	
	mean (N)	±SE	mean (N)	±SE	mean (N)	±SE	mean (N)	±SE
dbh (cm)	45.0 (63)	2.0	45.6 (15)	3.3	45.3 (22)	2.9	40.9 (36)	1.7
tree height (m)	18.0 (61)	0.8	18.3 (15)	1.7	19.5 (22)	2.3	18.9 (36)	1.2
roost height (m)	9.4 (52)	0.7	6.5 (11)	1.1	8.9 (18)	0.8	9.8 (31)	1.0

Table 4.4—Number and percentages of trees with low, moderate, or high amounts of usable bark suitable for roosting by Indiana bats (*Myotis sodalis*) by roost category.

Amount of bark	Staging	Migration	Layover	Arrival	Total
Low	2 (6%)	6 (27%)	4 (27%)	19 (30%)	31 (23%)
Moderate	4 (11%)	7 (32%)	2 (13%)	23 (37%)	36 (26%)
High	30 (83%)	9 (41%)	9 (60%)	21 (33%)	69 (51%)
TOTAL	36	22	15	63	136

Table 4.5—Number and percentages of trees that were live, live-damaged, or dead by roost category.

Condition	Staging	Migration	Layover	Arrival	Total
Live	22 (61%)	7 (32%)	8 (53%)	8 (13%)	45 (33%)
Live-damaged	1 (3%)	1 (5%)	0 (0%)	6 (10%)	8 (6%)
Snag	13 (36%)	14 (64%)	7 (47%)	49 (78%)	83 (61%)
TOTAL	36	22	15	63	136

Table 4.6 Comparison of roost tree characteristics in this study and maternity roost trees used by Indiana bats (*Myotis sodalis*) in the summer summarized by Kurta (2004). dbh = diameter at breast height.

Metric	This study			Kurta 2004 summary		
	Mean	SE	N	Mean	SE	N
dbh (cm)	44.0	1.2	136	45	2	359
tree height (m)	18.5	0.6	134	20	1	231
roost height (m)	9.1	0.4	112	9	1	141

Table 4.7 Comparison of roost tree condition in this study used by Indiana bats (*Myotis sodalis*) in spring and maternity roost trees used by Indiana bats as reported in summer studies.

Source	Condition	
	Live	Snag
Callahan et al. 1997	28%	72%
Britzke et al. 2003	13%	88%
Fishman 2016	31%	69%
Bergeson 2017	8%	72%
Schroder et al. 2017	21%	79%
This study	33%	67%

Table 4.8—Distances tracked and details on resource variable use for 20 female spring migrating Indiana bats (*Myotis sodalis*).

Number of location points	Distance between hibernaculum and end point (km)	Available habitat (km²)	Used habitat (km²)	Percent used of available
58	263.7	800.8	265.8	33%
203	168.6	1120.5	296.5	26%
333	148.1	521.9	271.1	52%
359	226.1	1417.2	444.0	31%
183	300.1	920.9	175.1	19%
396	368.1	2180.3	867.6	40%
191	241.0	385.1	228.5	59%
129	78.1	405.6	176.1	43%
312	226.1	777.4	312.2	40%
295	107.9	401.3	162.5	40%
777	268.4	1513.2	583.2	39%
111	85.1	347.5	97.6	28%
39	6.3	16.7	12.0	72%
246	202.9	533.4	257.6	48%
202	116.9	1635.6	188.8	12%
113	80.8	223.4	111.1	50%
76	80.8	216.4	114.1	53%
146	80.8	292.6	119.9	41%
115	116.4	988.0	223.9	23%
148	140.8	1826.5	260.3	14%
221.6 ± 37.1	165.4 ± 20.8	826.2 ± 136.4	258.4 ± 42.7	38.2 ± 3.4

Table 4.9 Ranking matrices for migrating female Indiana bats (*Myotis sodalis*) based on comparing proportional habitat used with proportion of habitat available. Signs indicate significance tests where a triple sign (+++ or ---) represents significance at $P < 0.05$

	Habitat type			
	Water	Open	Forest	Low Veg
Water	0	-	-	+
Open	+	0	-	+
Forest	+	+	0	+++
Low Veg	-	-	---	0

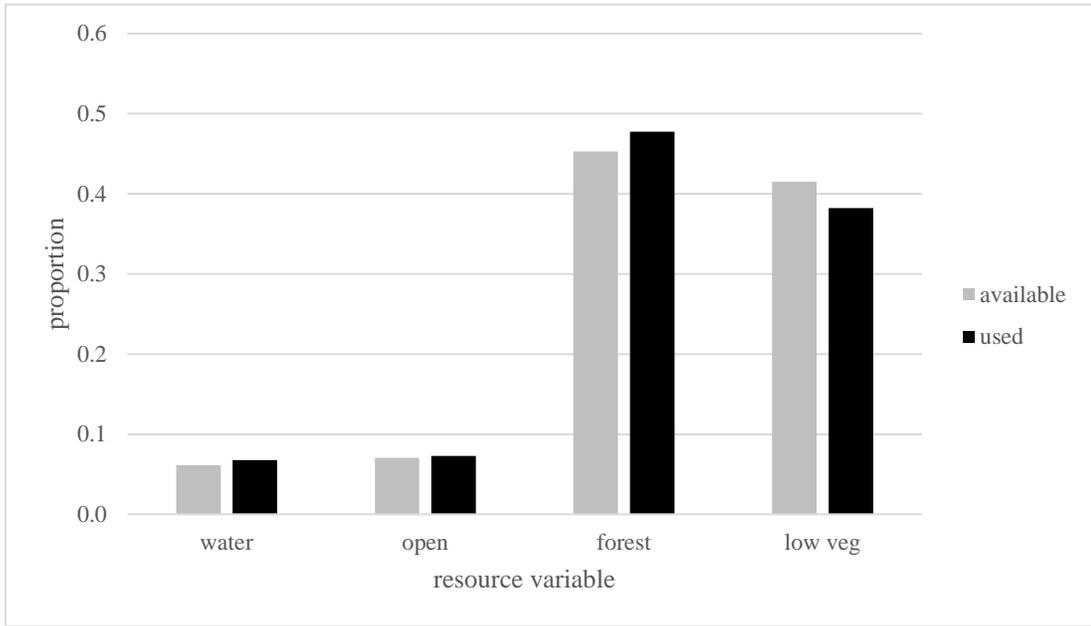


Figure 4.1— Proportion of available and used habitat for spring migrating Indiana bats (*Myotis sodalis*).

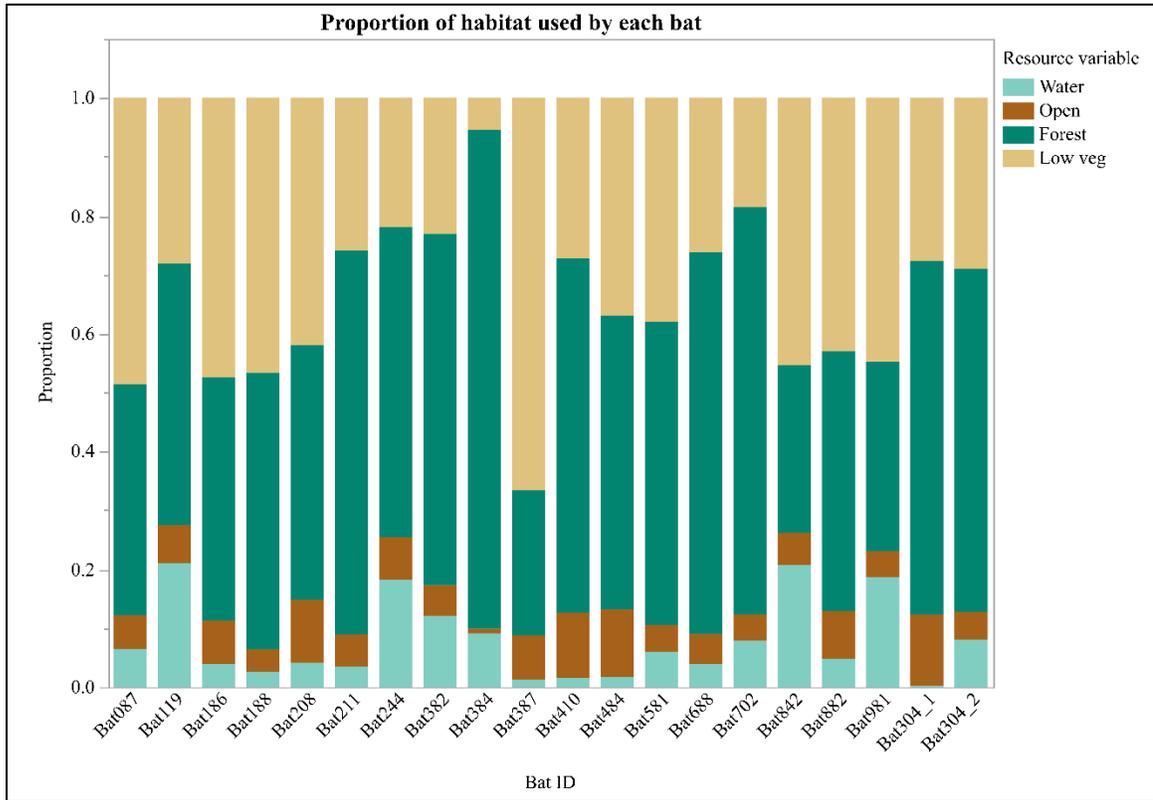


Figure 4.2—Proportion of resource use by each female Indiana bat (*Myotis sodalis*) tracked during spring migration.

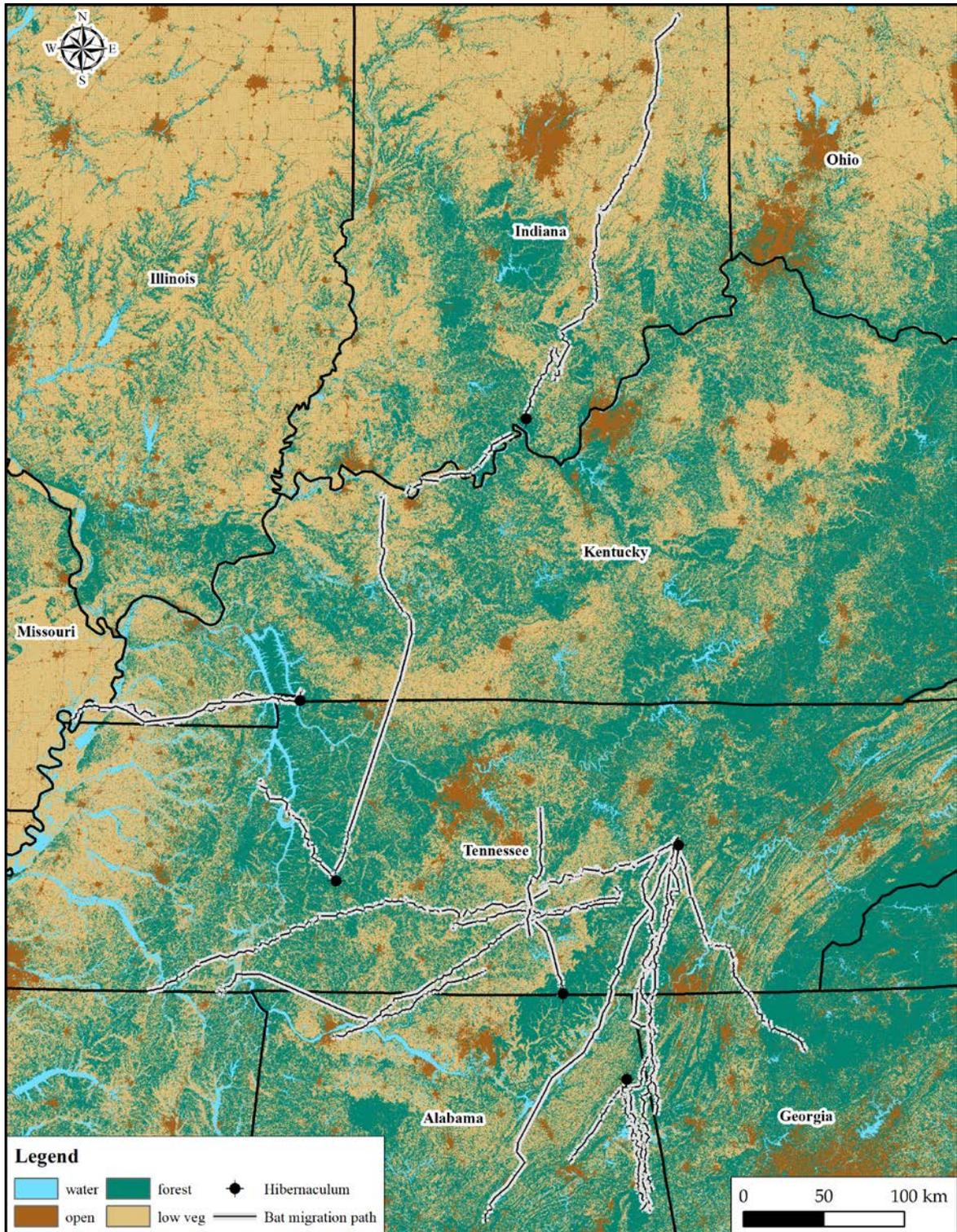


Figure 4.3—Resource variable distribution within areas used by spring migrating Indiana bats (*Myotis sodalis*).

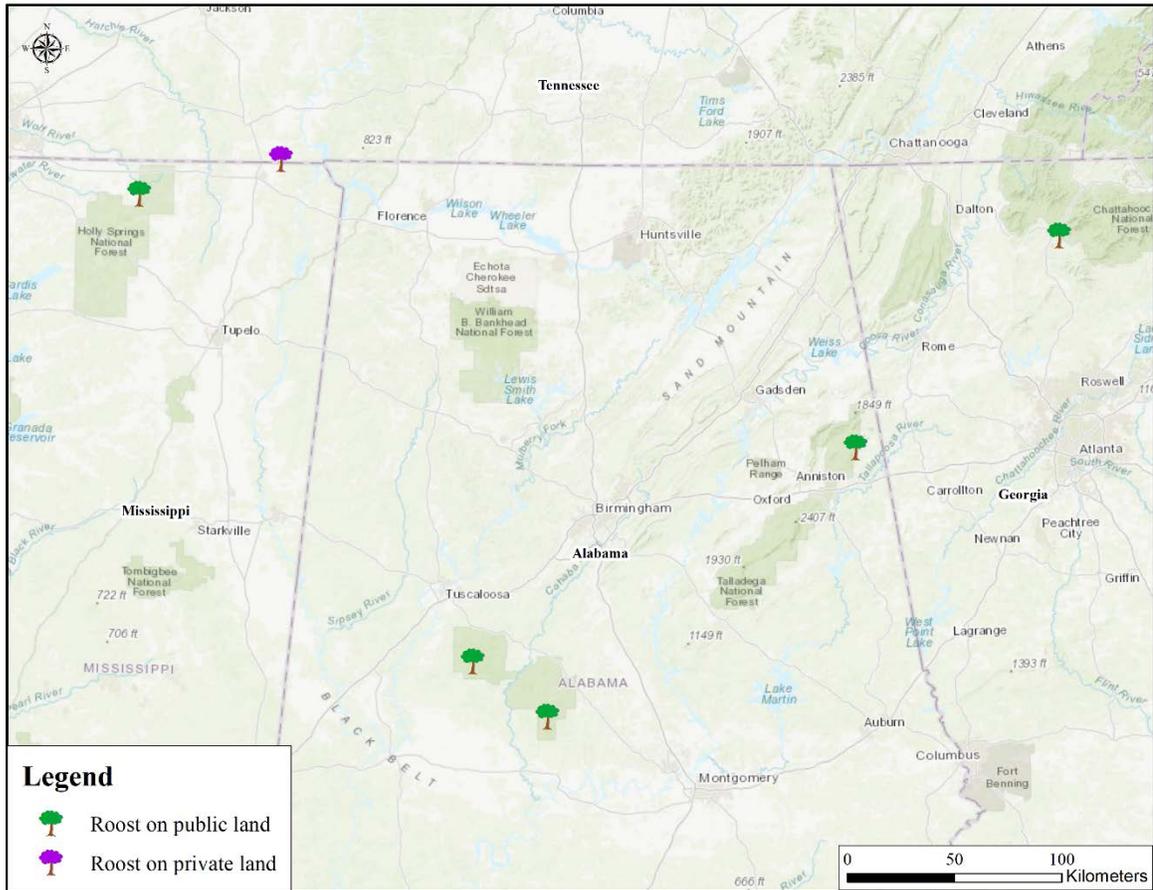


Figure 4.4—Location of summer grounds in southern states located by tracking spring migrating Indiana bats (*Myotis sodalis*).

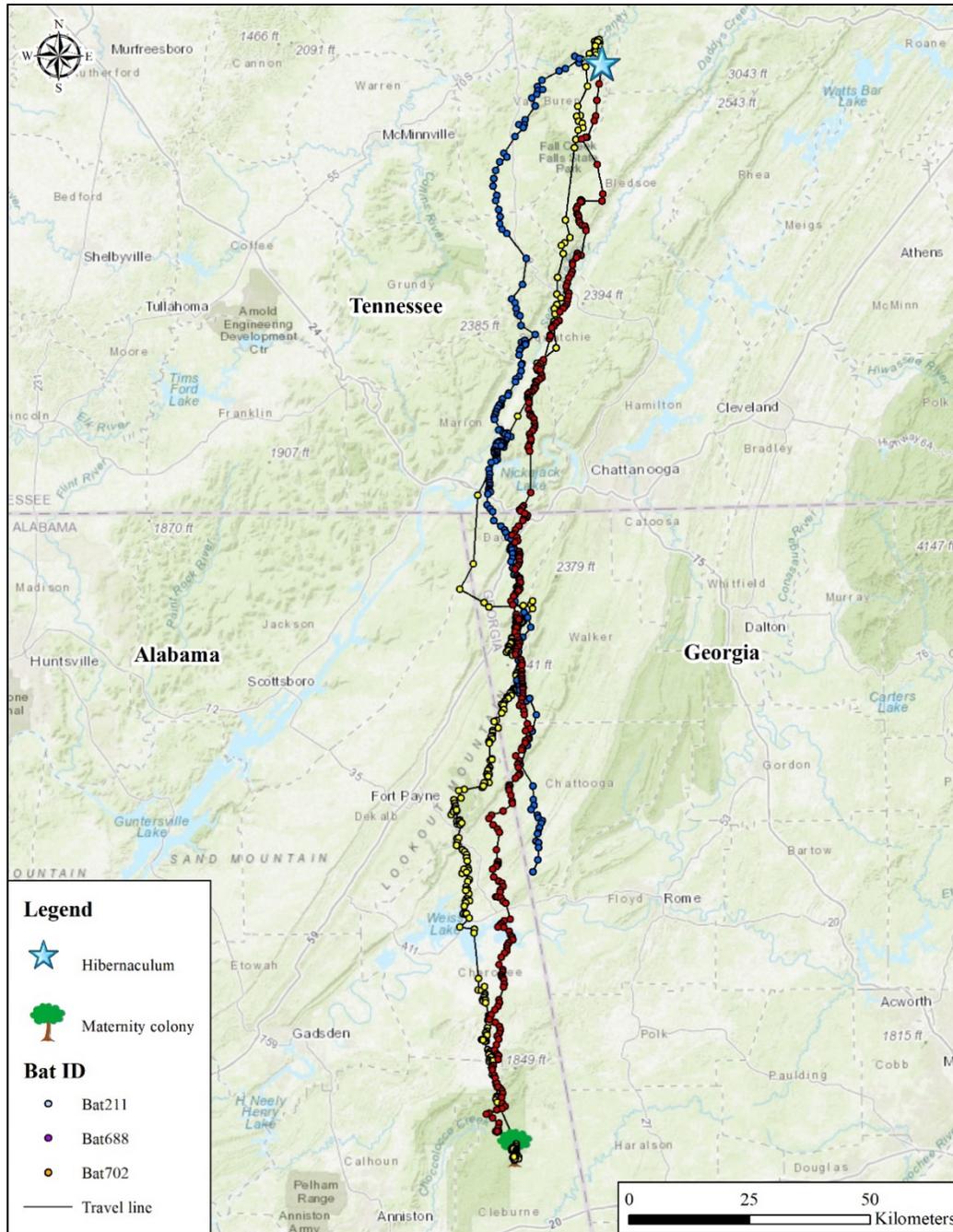


Figure 4.5—Locations of individual female spring migrating Indiana bats (*Myotis sodalis*) radio-tagged from the same hibernaculum in 3 different years that traveled to the same maternity colony. Bats are traveling from hibernacula (blue star) south to a maternity colony (green tree). Trackers lost contact with Bat211 (light blue dots) prior to tornadic activity before it arrived at the maternity colony, resulting in a truncated migration track.

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Peer Reviewed Publications:

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