

EXAMINING THE SUITABILITY OF THE LITTLE BROWN BAT (*MYOTIS*
LUCIFUGUS) AS A SURROGATE FOR THE ENDANGERED INDIANA BAT (*M.*
SODALIS).

A THESIS

SUBMITTED TO THE GRADUATE SCHOOL
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR A MASTER OF SCIENCE DEGREE

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MAY 2012

ACKNOWLEDGMENTS

This project was only able to be completed due to the help and support of the people close to me. These people are indispensable to me and without them I would surely be a manic pile of over-caffeinated graduate student today. It is thanks to these people that I am currently merely over-caffeinated. I wish to sincerely thank everyone who supported me throughout this project and throughout my life. Thank you.

I first and foremost wish to thank my entire family; without them I would not be here today. My mother, Carli Bergeson, and father, Bill Bergeson, have supported me mentally, emotionally, and financially throughout my adventurous, often mother worrying, journey. Without their unyielding support and faith I would not have been able to become the man I am today. My brother, Chris Bergeson, has supported me throughout my life with his never-ending friendship. The trips to the zoo with my grandfather, Paul Bergeson, and the accomplishments my uncle, David Bergeson, made instigated my interest in the animal world. Without them I would not have gained my love of wildlife that allows me to appreciate my test subjects, even when they do exactly the opposite of what I want. My girlfriend, Kate Ruhrold, gave me her constant love and support, even during the times when I was at my most manic and over caffeinated; a feat worthy of love and respect.

I would also like to thank the members of my thesis committee. Due to my major advisor's, Dr. Tim Carter, patience and guidance, the 2 years that I have spent on this project have been the most educational, challenging, and fulfilling years of my life. The experiences I have gained due to his guidance have allowed me to become a well-

rounded professional biologist. Drs. Gary Dodson and Kevin Turcotte have guided and challenged me throughout the completion of this project. I appreciate everything that you have done for me.

I am thankful to my colleague Michael Whitby for his help within the office and the field as well as Stephen Jacquemin for his statistical guidance. Also, this project could not have been completed without the help of the summer interns that gave us, willingly, 3 months of their lives and only got 90° heat, swamps, mosquito bites, and the chance to hold some bats in return. Thank you, Joey Weber, Ben Funk, Stephanie Rutan, Arik Wallace, Brian Lindsey, and Marie McCann.

Funding for this project was provided by the Shawnee National Forest branch of the U.S. Forest Service and the Illinois Department of Natural Resources. Additional funding was provided by the Department of Biology at Ball State University, Muncie, IN.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

The Indiana bat (*Myotis sodalis*) was listed as federally endangered in 1967 and has been declining throughout its range ever since (USFWS 2007). Conservation biologists have been working to reduce the decline of the species by managing the habitat it uses during hibernation, fall swarming, and summer maternity roosting. However, due to its endangered status it is often difficult to directly study or manage this species; political, funding, and technical barriers can stand in the way. Also, disturbance caused by direct manipulation of individuals, or populations, of the species may induce varying negative effects including behavioral alteration, mortality, and others (Aldridge and Brigham 1988; Hicks and Novak 2002; Thomas et al. 1990). While reducing disturbance completely may be an impractical task, biologists may be able to reduce disturbance and stress to threatened or endangered species by using a surrogate species in place of the Indiana bat.

The Indiana bat recovery plan calls for the use of surrogates in the research and management of Indiana bats in order to avoid causing unneeded stress to the species (USFWS 2007). The recovery plan broadly suggests the use of other *Myotis spp.* as surrogates. However, it is often suggested by bat biologists that little brown bats (*Myotis lucifugus*), in particular, would be suitable surrogates (Brack et al. 2002; Schmidt et al. 2002; Richardson et al. 2008; Jones & Nagy 2010; Romeling et al. 2010). This suggestion may be due to the 2 species' close morphological similarity; which is so similar that the 2 species were considered the same until 1928 (Miller and Allen 1928). However, biologists must be careful to not assume that morphological similarity implies similarities in other traits. For example, due to their close morphological similarities, it may be assumed that Indiana bats and little brown bats have similar foraging home ranges and select for the same types of foraging habitat. Since this relationship has yet to be examined this assumption may be potentially misleading.

In order to determine whether little brown bats are acceptable surrogates for Indiana bat summer habitat research and management the species' ecologies must be compared. Ecological characteristics important to the success and survival of Indiana bat populations during the summer season should be compared between the species. For example, characteristics such as roosting ecology, foraging ecology, and diet can all affect whether a bat species will prosper in a particular landscape (USFWS 2007). If these characteristics are similar between the species, little brown bats could be considered acceptable surrogates for research on Indiana bats during the summer season. Managers will therefore be able to use information collected on little brown bats to manage for Indiana bats within the same area.

Studies on summer roosting ecology, foraging ecology, and diet are relatively common for Indiana bats (e.g., Gardner et al. 1991a; Gardner et al. 1991b; Kurta et al. 1993; Kurta et al. 1996; Callahan et al. 1997; Kurta and Whitaker 1998; Murray and Kurta 2002; Britzke et al. 2003; Carter and Feldhamer 2005; Sparks et al. 2005). However, while little brown bats are common subjects for chiropteran research, due to their relative abundance throughout their distribution, research on the bat species' ecology and behavior is somewhat lacking (Fenton and Barclay 1980). There are a relatively numerous studies reporting data on little brown bat diet (e.g., Anthony and Kunz 1977; Lee and McCracken 2004; Feldhamer et al. 2009; Clare et al. 2011). However, there is relatively little research on little brown bat maternity roost ecology (Crampton and Barclay 1998; Psyllakis and Brigham 2006) and foraging ecology (Henry et al. 2002; Broders et al. 2006). Without additional data, reliable comparisons of ecology cannot be made between the 2 species.

LITERATURE REVIEW

Surrogates

For the past several decades the terminology in the conservation biology field concerning the surrogate tool has been in contention (Armstrong 2002). There are many uses of the surrogate tool as well as many sub-terms, all of which have their own definitions and uses (Wilcox 1984; Landres et al. 1988; Mills et al. 1993; Dietz et al. 1994; Lambeck 1997; Armstrong 2002; Caro et al. 2005). Our definition of surrogate is a species used as a substitute subject for another, more inaccessible, species in order to draw conclusions on it and/or manage for it. This is similar to the definition of “substitute” that Caro et al. (2005) examined.

Surrogates are used for a number of reasons. Species for which surrogates are sought (target species) are often threatened or endangered and are more susceptible to disturbance than surrogate species, which are abundant within study areas (Githiru et al. 2007). By using these abundant species as surrogates, researchers and conservation managers can draw conclusions on the target species while avoiding direct disturbance (Caro et al. 2005). Using surrogates for rare species can also improve the quality of the research conducted. Rare species are often hard to research due to their tendencies to be low in numbers throughout their distribution. By using a surrogate species, researcher can increase sample sizes, conduct research more efficiently and avoid the need to acquire the federal or state permits required to study threatened or endangered species (Caro et al. 2005).

The suitability of a species as a surrogate is dependent on the similarity of the surrogate to the target species. The type of similarities required is dependent on the objectives of the project in which it is used. Caro et al. (2005) examined the effectiveness of surrogates in determining the influences of environmental and anthropogenic disturbances on vulnerable species. The suitability of surrogates in their study was dependent on the similarities of traits that had the largest effect on population growth rate between the species. Caro et al. (2005) stated that by measuring the relationship between these traits and the effect of disturbance on populations of

surrogates, conservation managers could draw conclusions on how disturbance would affect vulnerable species.

The objectives of endangered species management typically focus on increasing the quality and quantity of habitat preferred by the species. With this in mind, I believe that the similarities needed for surrogates to be suitable for habitat management are all ecological, focusing on the use and selection of habitat. During the summer season, Indiana bats are typically managed for female roosting habitat and foraging habitat. Female insectivorous bats have more management implications due to their exclusive parental investment when rearing pups (Kunz and Hood 2000). Therefore, to be appropriate surrogates for Indiana bat summer maternity habitat management, female little brown bats need to have roosting and foraging ecology similar to female Indiana bats.

Diet

Diet is an important factor when comparing the ecologies of 2 species. Information on a species' diet may give insight on where it forages, when it forages, the extent of its home range, metabolic rates, nutritional requirements, or reasons for population decline (McNab 1980; Kurta and Whitaker 1998). Morphological traits are also known to be predictive of the insects that insectivorous bats are able to consume (Aldridge and Rautenbach 1987; Freeman 1998; Swartz et al. 2003). By comparing the diets of 2 species, researchers are able to gain insights into how the species differ in other ecological or morphological ways.

The diets of insectivorous bats can be examined using fecal analysis, stomach content analysis, culled item analysis, and direct observations (Whitaker et al. 2009). Direct observations require the use of specialized night-vision equipment that may not be readily available to researchers (Vaughan 1976). Culled part analysis is conducted by collecting the insect material leftover from meals that is typically found within, or around, roosts (Whitaker et al. 2009) and

attempting to identify them. While culled part analyses are reasonably accurate, they can also be biased toward insects that are not eaten whole and cannot be used to estimate the ratios of insects within a bat's diet (Whitaker et al. 2009). Stomach content analyses require the sacrifice of bats; however, it provides adequate material to effectively identify prey items (Whitaker et al. 2009). Fecal analyses are conducted within many studies (e.g., Anthony and Kunz 1977; Swift et al. 1985; Kurta and Whitaker 1998; Murray and Kurta 2002; Feldhamer et al. 2009). Fecal analyses are conducted by collecting guano from the bats themselves or from under their roosts, and sorting through individual fecal pellets to identify the remains of insect prey. While fecal analysis avoids the need to sacrifice bats, prey items can usually only be identified to taxonomic order and results are biased towards hard-bodied insects (Rabinowitz and Tuttle 1982). Following the digestive process it is typically only large pieces of chitinase exoskeleton that remain identifiable (Whitaker et al. 2009). Therefore, many soft-bodied insects are completely dissolved. Despite these problems, fecal analyses still tend to be the most common method used to examine the diet of insectivorous bats.

DNA sequencing of prey items found within fecal pellets is increasingly being used within bat studies (e.g. Vege 2000; Clare et al. 2009; Clare et al. 2011; Zeale et al. 2011). This method, while more costly, provides accurate identification of insect prey items to species (Whitaker et al. 2009).

There are numerous published literature sources that report data on the diets of both Indiana bats and little brown bats (e.g., Anthony and Kunz 1977; Kurta and Whitaker 1998; Murray and Kurta 2002; Lee and McCracken 2004; Tuttle et al. 2006; Feldhamer et al. 2009, Clare et al. 2011) that allow comparison of their similarities (see Chapter 4).

Telemetry

Before the development of radio-telemetry, most ecological bat research was conducted using observation and light tagging methods (Humphrey et al. 1977; LaVal 1977). The development of radio-transmitters and radio-telemetry allowed researchers to track organisms from a distance using radio-signals, allowing research on bat ecology to be conducted relatively efficiently (Amelon et al. 2009). However, the added weight of the transmitters could reduce flight maneuverability and alter foraging behavior in bats (Aldridge and Brigham 1988). The development of lighter weight radio transmitters in the late 1980s reduced the effect they had on the behavior of bats. Consequently, the number of ecological bat studies increased exponentially (Carter 2006; Amelon et al. 2009).

While radio-telemetry is an effective method to reduce the difficulty of conducting ecological research on bats, it has some inherent problems. Due to the added weight of transmitters, bats may be forced to adapt to a higher wing-load by choosing closer and less cluttered foraging areas, limiting the time and effort spent foraging, or other adaptations (Aldridge and Brigham 1988). Even with the advent of lighter weight transmitters some transmitters remain too bulky for certain species of bats. It is suggested that transmitters that weigh less than 5% of an animal's body weight cause minimal alterations in maneuverability and behavior (Aldridge and Brigham 1988). Obtaining transmitters small enough to avoid behavior alteration in small vespertilionid bats (Family: Vespertilionidae) of the eastern United States is relatively difficult. Bats within the genera *Myotis* and *Perimyotis* tend to be smaller than other bats within the family (4-12g; Whitaker and Hamilton 1998). These bats require exceptionally small transmitters in order to avoid altering their behavior. In order for radio-transmitters to be affixed to bats weighing approximately 4g the transmitters would have to weigh approximately 0.2g. However, only the smallest transmitters available to researchers, to date, weigh around 0.2g (e.g., Model LB-2X, Holohil Systems Ltd., Ontario, Canada; Model A2405, Advanced Telemetry Systems, Isanti, Minnesota). Therefore, bat researchers must take into account the weight of the

bat they are studying as well as the weight of the transmitters they have available before conducting research (see Chapters 2 and 3).

Another potential problem with radio-telemetry is the possibility of the data collected using the method to be interdependent. Determining successive locations of an animal over short time intervals can cause locations to be interdependent (autocorrelation) due to the limited time the animal has to move away from its previous location (Swihart and Slade 1985). By estimating the locations of organisms at a time interval long enough for specimens to traverse their entire home ranges researchers can increase the independence between them (Swihart and Slade 1985). In bat radio-telemetry studies, a 5min time interval between successive location estimates gives bats adequate time to cover their entire home range.

While radio-telemetry is a powerful tool, it can be fairly inaccurate, especially when conducted by unskilled researchers. When estimating the locations of an organism using the triangulation method (Amelon et al. 2009), an erroneous bearing can result in a location estimate to be dozens, if not hundreds, of meters away from the organisms' actual location (Fuller et al. 2005). This triangulation error can greatly affect the power of studies conducted using these location data (White and Garrott 1986). Triangulation error can be calculated in several ways in order to determine how much it will affect subsequent statistical analyses and, ultimately, the power of the study (White and Garrott 1990; Amelon et al. 2009). If triangulation error is determined to be too severe, researchers can change their methods to account for it. Triangulation error can decrease by increasing the number or elevation of telemetry stations used for estimating location points, increasing the signal strength of the transmitters used, and through other means (Amelon et al. 2009). There are also several ways to account for triangulation error during analyses; these include: modeling error distributions (Samuel and Kenow 1992) and selecting robust analyses, capable of generating confident results despite telemetry error (Euclidean distance-based habitat analysis; Conner and Plowman 2001).

Maternity Roosts

Roosting ecology is an important factor to consider when determining the suitability of little brown bats as surrogates because of the management implications of maternity roosts. Roost selection by female insectivorous bats is an important factor in determining the development rate and growth rates of pups. The temperature of roosts can determine the development rate of fetuses; colder roosts delaying fetal development and warmer roosts accelerating it (Racey 1973; Racey 1982). After parturition poorly heated roosts can reduce pup growth, due to their poor thermoregulation, ultimately resulting in deficient energy stores and reduced survival during migration and hibernation (Humphrey 1975). Because maternity roosts are limiting resources for Indiana bats, managers typically manage for suitable maternity roost habitat and roost trees (Humphrey 1975; USFWS 2007). Little brown bats must, therefore, have similar roosting ecology in order to be suitable surrogates for Indiana bat habitat management.

Due to the listing of the Indiana bat as an endangered species, there have been numerous studies and meta-studies conducted on the species' roosting ecology (See Menzel et al. 2001 for review; Britzke et al. 2003; Carter and Feldhamer 2005; Lacki et al. 2009; Carter et al. 2010; Whitby et al. 2011; Timpone et al. 2010). From these studies bat biologists have developed a typical model of Indiana bat roosts. Female Indiana bats in maternity colonies typically roost under exfoliating bark of large snags with ample solar exposure (See Menzel et al. 2001 for review; Carter and Feldhamer 2005; Carter et al. 2010; Whitby et al. 2011). However, the species have also been documented roosting, to a lesser extent, within crevice/cavity roosts as well as live trees (Callahan et al. 1997; Britzke et al. 2003; Carter and Feldhamer 2005; Carter et al. 2010; Whitby et al. 2011; Chapter 3 of this thesis). Gardner et al. (1991b) suggests that the main characteristic that Indiana bats select for in exfoliating bark roosts is the roost's ability to retain heat. This ability is dependent on several factors. The bark covering the roost and the air space beneath the

bark are heated by solar radiation (Gardner et al. 1991b). The rates in which these spaces are heated and cooled are dependent on the solar exposure, the ability of the bark to absorb radiation, the solar aspect, the bark's moisture content, and other solar and thermal factors (Gardner et al. 1991b). If a potential roost meets the required ability to retain heat then Indiana bats should roost within it regardless of the tree species, and other microhabitat characteristics.

The majority of the research available on little brown bat roosts focuses primarily on anthropogenic roosts (Fenton 1970; Humphrey and Cope 1976; Schowalter et al. 1979; Riskin and Pybus 1998). The small amount of data on little brown bat natural maternity roosts come from studies that either reported data from only a few located roosts or from studies conducted in the northern portions of the species' distribution, far from the northern edge of the Indiana bat's distribution (Barclay and Cash 1985; Crampton and Barclay 1998; Broders et al. 2006; Psyllakis and Brigham 2006). Therefore, I cannot confidently compare these data to data collected on Indiana bats in order to examine the surrogate suitability of little brown bats. The data that exist suggest that little brown bats tend to roost within crevice/cavity roosts located within snags (Barclay and Cash 1985; Crampton and Barclay 1998). However, there is also evidence that they will also roost under exfoliating bark (Psyllakis and Brigham 2006).

Home Range Analyses

Home ranges can be described as the areas that are constantly traversed by organisms for the purpose of foraging, reproduction, parental care, and other reasons (Burt 1943). Biologists can use information on home ranges to understand the daily and seasonal movements of organisms and/or to manage for vulnerable species, such as the Indiana bat (Fisher 2000; Henry et al. 2002; Springborn and Meyers 2005; Morris et al. 2011). Because of the importance of home ranges to an organism's everyday life, home ranges must be similar between Indiana bats and little brown bats in order for little brown bats to be considered suitable surrogates.

Researchers typically use radio-telemetry to study the home ranges of organisms (Turfto et al. 1996; Springborn and Meyer 2005; Morris et al. 2011; Sparks et al. 2005). However, other techniques have also been effective in the study of home ranges, including GPS-telemetry (Burt 1940; Martof 1953; Frantz 1972; Layne and Glover 1977; Girard et al. 2002). While GPS-telemetry is far more accurate, radio-telemetry is the most preferred method of studying bat home ranges due to the method's relatively low cost, and the ability to use it on smaller bat species (see telemetry section above). The format of data used within home range studies is typically a single location point. Within studies conducted using radio-telemetry, this single location point is usually the coordinates of a location estimated using triangulation (Amelon et al. 2009). Regardless of the method in which they are collected, multiple location points are required to accurately determine the home range of a single individual. It is suggested that approximately 30 location points are needed to accurately determine the home ranges of bats (Seaman et al. 1999). These location points are then processed through some type of home range estimator program to generate home range models. I used the Home Range Tools (HRT; Rodgers et al. 2007) and Hawth's Tools (Beyer 2004) home range estimator programs. However, there are other programs available (CALHOME, Kie et al. 1996; KERNELHR, Seaman et al. 1998; Geospatial Modelling Environment, Beyer 2009; etc.).

There are 2 major types of home range models that are used to study the home ranges of organisms today, Minimum Convex Polygons (MCP) and Kernels. MCPs are models that form polygons to estimate organisms' home ranges by using their peripheral location points as vertices (Amelon et al. 2009). Kernels are models that use the density of animal locations in order to estimate an animal's home range (Worton 1989, Gitzen et al. 2006). Because kernels rely on the concentrations of locations within a study area, certain details of an individual's home range can be observed, that could not be observed when using MCPs. These areas of high location densities are often referred to as "core areas" and often represent nesting areas, water supplies, or preferred

foraging areas (Samuel et al. 1985; Blundell et al. 2001). These details are important to preserve if you want to understand the true daily habits of your target organism.

Kernel models are generated using smoothing parameters, or bandwidth values, set within the home range estimator program. A smoothing parameter determines the amount a single location point contributes to the density of the location points around it (Gitzen et al. 2006). A large smoothing parameter will increase the importance of each point to the model, causing single outlying location points to be grouped with dense clusters of points. This would result in over-smoothed and overestimated home range sizes (Kernohan et al. 2001). Small smoothing parameters will have an opposite effect by decreasing the value of each point and ungrouping dense clusters of location points. Small smoothing parameters ultimately lead to underestimated home range sizes (Gitzen et al. 2006). The variability of parameter values in kernel models make it hard to compare between studies, often because kernel parameters are not reported. MCPs, on the other hand, are easily compared between studies due to the model's simplicity and lack of parameters.

The 2 types of kernel models include fixed kernels and adaptive kernels. Smoothing parameters are fixed throughout the area of estimation within fixed kernels and are varied within adaptive kernels (Worton 1989). There is some contention over which kernel type is a more accurate estimate of home range size (Worton 1989; Seaman and Powell 1996). However, due to their simplicity and conservative nature, I chose to conduct fixed kernel estimates to analyze the data I collected on both bat species. I also chose to generate MCP models to study the home ranges of both bat species in order to compare my results with other studies. A detailed description of the methods to generate both models is discussed later in this document.

Habitat Use Analyses

Habitat use, habitat selection, and habitat preference are 3 terms that define different ecological processes. The use of a habitat is defined by the amount of time/effort an organism spends utilizing that particular habitat (Johnson 1980). A habitat that is used is not necessarily selected. The selection of a particular habitat suggests that an organism uses that particular habitat more than would be expected based on its availability to the organism (Johnson 1980). The preference of a particular habitat suggests that the organism will choose that habitat over others when all habitats are equally available (Johnson 1980). Researchers can determine what habitats an organism prefers when habitat is not equally available to the organism by ranking the habitats the organism selects for. While knowing what habitats organisms use is important, the knowledge of what habitats organisms select for and prefer has many more management implications. Knowing what habitats are most important to a vulnerable species will allow conservations managers to increase the quality and quantity of such habitats in order to benefit populations of the species. In order for little brown bats to be deemed as suitable surrogates for Indiana bat summer habitat management the 2 species would have to select for the same habitat.

The selection of habitat components can be conducted by organisms at several ecosystem levels. Johnson (1980) describes 4 orders of habitat selection. These orders of selection become consecutively narrower as the order increases. Also, habitat selection is a hierarchical process; habitat types that are selected for at one order of habitat selection may be the result of selection at another level (Johnson 1980). Johnson's (1980) 1st order of selection is the selection of a geographic distribution by an entire species. His 2nd order is the orientation of home ranges within that distribution. The 3rd and 4th orders are the selection of habitat within an organism's home range and the selection of food within these habitats, respectively. While biologists are able to study the selection of habitat by organisms at each of these 4 orders, it is much more difficult to study habitat selection at broader orders (orders 1 and 2) than narrower ones (orders 3 and 4). It requires much more time and funding to obtain adequate sample sizes when studying the

orientation of home ranges within a landscape than it does when studying the selection of habitat within home ranges; in the former example the landscape is the sample unit and in the later example each home range is the sample unit. Because of this hurdle, many biologists choose to study selection at the 3rd or 4th order of selection.

Aebischer et al. (1993) identified 4 issues that occur during analyses of habitat use that can lead to bias. One issue concerns inappropriate sample size which can lead to non-independence between the units (Aebischer et al. 1993). For example, using each radio-telemetry generated location estimate as a sample unit can result in pseudo-replication and increase bias. To avoid this issue each animal should be considered a separate sample unit rather than each telemetry location estimate (Aebischer et al. 1993). Another issue suggests that when an analysis uses proportions to describe habitat composition (unit-sum constraint; e.g., Neu et al. 1974), an animal's preference for a certain habitat will automatically suggest the avoidance of others (Aebischer et al. 1993). Using habitat selection analyses that avoid the use of proportions can allow biologists to avoid this issue. The third issue suggests that different subsets of a population, such as sex or age class, may select for habitat differently, and therefore introduce unwanted variation when examining the habitat selection of the population, as a whole (Aebischer et al. 1993). Avoiding this issue involves reducing the variation within the group of animals being studied. For example, studying animals of a single gender would eliminate the effects the other gender may have on analyses. The final issue suggests that boundaries for available habitat, in habitat use analyses, are usually defined arbitrarily. Habitat boundaries are usually made in reference to the logistic boundaries of the study area and are not necessarily heeded by the animals studied. In this case, avoiding the use of anthropomorphically defined boundaries, such as park boundaries or county lines, in favor of boundaries that are defined by the animals of interest can avoid this issue. For example, by defining a study area as twice the distance of the

maximum traveling extent of a study organism, researchers would avoid defining study areas arbitrarily.

There are 2 main types of analyses widely used in habitat selection studies: classification-based analyses, such as compositional analysis (CA; Aebischer et al. 1993), and distance-based analyses, such as Euclidean distance-based analysis, (EDA; Conner et al. 2003; also see Conner and Plowman 2001). EDA has been used increasingly in recent years (e.g., Perkins and Conner 2004; Elmore et al. 2005; Cox et al. 2006; Parra 2005) due to its ability to avoid certain problems associated with habitat selection analyses, as stated above. CA uses habitat proportions to determine the selection of habitats by organisms (Aebischer et al. 1993). As stated above, using proportions can cause researchers to misinterpret habitat selection data. EDA avoids the use of proportions by directly comparing the mean observed distances (mean distance from each location estimate to the nearest patch of each habitat type) to the mean expected distances (mean distance from multiple random points to the nearest patch of each habitat type (Conner and Plowman 2001). Another problem with CA is its tendency to be greatly affected by telemetry error bias (White and Garrott 1986, Pendleton et al. 1998, Conner and Plowman 2001). CA, therefore, often requires the use of model error distributions to account for this bias (Samuel and Kenow 1992). Assuming that telemetry error is not severe, EDA does not need to model telemetry error due to its use of distances to analyze selection (Conner and Plowman 2001). Organism locations that are erroneously estimated will not cause much bias in EDA (Conner and Plowman 2001; Conner et al. 2003). As long as telemetry error is not severe, the distances from an actual location of a bat and an erroneously estimated location, of the same bat at the same time, to the nearest patch of a certain habitat will be similar. If CA was conducted in the previous example the erroneous estimate would be classified incorrectly, leading to misinterpretation. EDA also takes the size and shape of habitat patches into account through the use of distances (Aebischer et al. 1993; Conner et al. 2003). This causes EDA to be a more effective analysis

when dealing with organisms that prefer edge type habitats, reside within highly fragmented ecosystems, and/or are highly mobile.

There have been some problems voiced about EDA. Dussault et al. (2005) suggests that EDA may be ineffective in certain cases. Some organisms may select for habitat that is closely associated with habitat avoided by the same organism, resulting in both habitat types to be within close proximity. Dussault et al. (2005) suggests, in this case, the interpretation of EDA will mislead researchers and suggest a selection for a habitat type that is actually avoided by the organism. Dussault et al. (2005) also suggest that EDA can be misleading when habitat patches are dramatically different in size. When there are small patches of one habitat intermixed with very large patches of a different habitat within the same ecosystem a preference for the habitat with larger patches may misleadingly result in the interpretation of avoidance of the habitat with smaller patches. In the cases above Dussault et al. (2005) suggests it may be more effective to use CA in order to avoid misinterpretation of statistical results. Conner et al. (2005) replied that the same misinterpretations could be drawn from a CA, if not all habitat selection analyses. Since habitat selection is a hierarchical process (Johnson 1980) it can be assumed that the selection of a particular type of habitat is not an independent process (Dussault et al. 2005). Conner et al. (2005) also suggests that avoiding misinterpretation of EDA in regards to ecosystems with disjoint sized habitat patches is up to the researcher's knowledge and experience regarding the subject.

Because of its ability to avoid certain biases I chose to use EDA to analyze the data that I collected for the purposes of this thesis project. A detailed methodology on how to run EDAs is discussed later in this document.

OBJECTIVES

To fill my need for additional little brown bat data in order to compare its ecology to that of the Indiana bat, we conducted research on the both species' roosting ecologies and foraging ecologies within southern Illinois and south-central Indiana. I focused on the summer maternity roost characteristics, foraging home ranges, and foraging habitat selection of bats of both species. With these data, in combination with diet data used from available literature sources, I examined the suitability of little brown bats as surrogates for Indiana bats in summer maternity habitat management. If I find these ecological characteristics to be similar between the species, the use of little brown bats as surrogates in Indiana bat research and management may be valid. My hypothesis is that little brown bats will be similar to Indiana bats in roosting ecology, foraging ecology, and diet characteristics and, therefore, would make suitable surrogates for Indiana bat summer habitat research and management.

LITERATURE CITED

- Aebischer, D.J., P.A. Robertson, and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74: 1313-1325.
- Aldridge, H.D.J.N., and R.M. Brigham. 1988. Load carrying and maneuverability in an insectivorous bat: a test of the 5% "rule" of radio-telemetry. *Journal of Mammalogy* 69: 379-382.
- Aldridge, H.D., and J.N. Rautenbach. 1987. Morphology, echolocation, and resource partitioning in insectivorous bats. *Journal of Animal Ecology* 56: 763-778.
- Amelon, S.K, D.C. Dalton, J.J. Millspaugh, and S.A. Wolf. 2009. Radiotelemetry. Pages 57-77 in Kunz, T. H., and S. Parsons editors, *Ecological and behavioral methods for the study of bats*. Second edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.
- Anthony, E.L.P., and T.H. Kunz. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology* 58: 775-786.

- Armstrong, D. 2002. Focal and surrogate species: getting the language right. *Conservation Biology* 16: 285-287.
- Barclay, R.M.R., and K.J. Cash. 1985. A non-commensal maternity roost of the little brown bat (*Myotis lucifugus*). *Journal of Mammalogy* 66:782-783.
- Beyer, H.L. 2004. Hawth's analysis tools for ArcGIS. <<http://spatial ecology.com/htools>>. Accessed 10 Oct 2010.
- Beyer, H.L. 2009. Geospatial modelling environment. <spatial ecology.com/gme>. Accessed 13 March 2012.
- Blundell, G.M., J.A.K. Maier, E.M. Debevec. 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecological Monographs* 71:469-489.
- Brack, V.Jr., C.W. Stihler, R.J. Reynolds, C.M. Butchkoski, and C.S. Hobson. 2002. Effect of climate and elevation on distribution and abundance in the mideastern United States. Pages 21-28 in A. Kurta and J. Kennedy, editors. *The Indiana bat: biology and management of an endangered species*. Bat Conservation International, Austin, USA.
- Britzke, E.R., M.J. Harvey, and S.C. Loeb. 2003. Indiana bat, *Myotis sodalis*, maternity roosts in the southern United States. *Southeastern Naturalist* 2:235-242.
- Broders, H.G., G.J. Forbes, S. Woodley, and I.D. Thompson. 2006. Range extend and stand selection for roosting and foraging in forest-dwelling northern long-eared bats and little brown bats in the Greater Fundy Ecosystem, New Brunswick. *The Journal of Wildlife Management* 70:1174-1180.
- Burt, W.H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. *Miscellaneous Publications University of Michigan Museum of Zoology* 45: 1-58.

- Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346-352.
- Callahan, E.V., R.D. Drobney, and R.L. Clawson. 1997. Selection of summer roosting sites by Indiana bats (*Myotis sodalis*) in Missouri. *Journal of Mammalogy* 78:818-825.
- Caro, T., J. Eadie, and A. Sih. 2005. Use of substitute species in conservation biology. *Conservation Biology* 19:1821-1826.
- Carter, T.C. and G.A. Feldhamer. 2005. Roost trees used by maternity colonies of Indiana bats and northern long-eared bats in southern Illinois. *Forest Ecology and Management* 219: 259-268.
- Carter, T.C. 2006. Indiana bats in the Midwest: the importance of hydric habitats. *Journal of Wildlife Management* 70:1185-1190.
- Carter, T.C., M.L. Michaels, and A.M. Schultz. 2009. Monitoring Indiana bat maternity colonies in southern Illinois. Annual Report, US Forest Service, Shawnee National Forest, Illinois.
- Carter, T.C., S.M. Bergeson, and M.D. Whitby. 2010. Monitoring Indiana bat maternity colonies in southern Illinois. US Forest Service-Shawnee National Forest, Project: Project Number: 08-PA-11090800-023. Annual Report.
- Clare, E.L., E.E. Fraser, H.E. Braid, M.B. Fenton, P.D.N. Hebert. 2009. Species on the menu of a generalist predator, the eastern red bat (*Lasiurus borealis*): using a molecular approach to detect arthropod prey. *Molecular Ecology* 18: 2532-2542.
- Clare, E.L., B.R. Barber, B. Sweeney, P.D. N. Hebert, and M.B. Fenton. 2011. Eating local: influences of habitat on the diet of little brown bats (*Myotis lucifugus*). *Molecular Ecology* 20: 1772-1780.
- Conner, L.M., and B.W. Plowman. 2001. Using Euclidean distances to assess nonrandom habitat use. Pages 275-290 in J. Millsaugh and J.M. Marzluff, editors. *Radio Tracking and Animal Populations*. Academic Press, London, UK.

- Conner, L.M., M.D. Smith, and L.W. Burger. 2003. A comparison of distance-based and classification-based analyses of habitat use. *Ecology* 84: 526-531.
- Conner, L.M., M.D. Smith, and L.W. Burger. 2005. A comparison of distance-based and classification based analyses of habitat use: reply. *Ecology* 86: 3125-3129.
- Cox, J.J., D.S. Maehr, and J.L. Larkin. 2006. Florida panther habitat use: new approach to an old problem. *The Journal of Wildlife Management* 70: 1778-1785.
- Crampton, L.H., and R.M.R. Barclay. 1998. Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. *Conservation Biology* 12:1347-1358.
- Dussault, C., J. Ouellet, and R. Courtois. 2005. A comparison of distance-based and classification-based analyses of habitat use: comment. *Ecology* 86:3119-3125.
- Dietz, J.M., L.A. Dietz, and E.Y. Nagagata. 1994. The effective use of flagship species for conservation of biodiversity: the example of lion tamarins in Brazil. Pages 32-49 in P.J.S. Olney, G.M. Mace, and A.T.C. Feistner, editors. *Creative Conservation: Interactive Management of Wild and Captive Animals*. Chapman and Hall, London.
- Elmore, L.W., D.A. Miller, and F.J. Viella. 2005. Foraging area size and habitat use by red bats (*Lasiurus borealis*) in an intensively managed pine landscape in Mississippi. *American Midland Naturalist* 153: 405-417.
- Feldhamer, G.A., T.C. Carter, and J.O. Whitaker, Jr. 2009. Prey consumed by eight species of insectivorous bats from Southern Illinois. *American Midland Naturalist* 162: 43-51.
- Fenton, M.B. 1970. Population studies of *Myotis lucifugus* (Chiroptera: Vespertilionidae) in Ontario. Royal Ontario Museum, Toronto.
- Fenton, M.B., and R.M.R. Barclay. 1980. *Myotis lucifugus*. Mammalian Species Account No. 142. The American Society of Mammalogists. New York. pp. 1-8.
- Fisher, D.O. 2000. Effects of vegetation structure, food and shelter on the home range and habitat use of an endangered wallaby. *Journal of Applied Ecology* 37: 660-671.

- Frantz, S.C. 1972. Fluorescent pigments for studying movements and home ranges of small mammals. *Journal of Mammalogy* 53: 219-223.
- Freeman, P.W. 1998. Form, function, and evolution in skulls and teeth of bats. Pages 140-156 in T.H. Kunz and P.A. Racey, editors. *Bat Biology and Conservation*. Smithsonian Institution Press, Washington, D.C.
- Fuller, M.R., J.J. Millspaugh, K.E. Church, and R.E. Kenward. 2005. Wildlife radiotelemetry. Pages 377-417 in T.A. Bookhout, editor. *Research and Management Techniques for Wildlife and Habitats*. The Wildlife Society, Bethesda, Maryland.
- Gardner, J.E., J.D. Garner, and J.E. Hofmann. 1991a. Summary of *Myotis sodalis* summer habitat studies in Illinois: with recommendations for impact assessment. Illinois Natural History Survey/Illinois Department of Conservation, Champaign, Illinois.
- Gardner, J.E., J.D. Garner, and J.E. Hofmann. 1991b. Summer roost selection and roosting behavior of *Myotis sodalis* (Indiana bat) in Illinois. Illinois Natural History Survey/Illinois Department of Conservation, Champaign, Illinois.
- Girard, I., J.P. Ouellet, R. Courtois, C. Dussault, and L. Breton. 2002. Effects of sampling effort based on GPS telemetry on home-range size estimations. *Journal of Wildlife Management* 66: 1290-1300.
- Githiru, M., L. Lens, L.A. Bennun, and E. Matthysen. 2007. Can a common bird species be used as a surrogate to draw insights for the conservation of a rare species? A case study from the fragmented Taita Hills, Kenya. *Oryx* 41: 239-246.
- Gitzen, R.A., J.J. Millspaugh, and B.J. Kernohan. 2006. Bandwidth selection for fixed-kernel analysis of animal utilization distributions. *Journal of Wildlife Management* 70: 1334-1344.

- Henry, M., D.W. Thomas, R. Vaudry, and M. Carrier. 2002. Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*). *Journal of Mammalogy* 83: 767-774.
- Hicks, A.C., Novak, P.G. 2002. History, status, and behavior of hibernating populations in the northeast, Pages 160-164 in A. Kurta and J. Kennedy, editors. *The Indiana bat: biology and management of an endangered species*. Bat Conservation International, Austin, USA.
- Humphrey, S.R. 1975. Nursery roosts and community diversity of Nearctic bats. *Journal of Mammalogy* 56: 321-346.
- Humphrey, S.R., and J.B. Cope. 1976. Population ecology of the little brown bat, *Myotis lucifugus*, in Indiana and north-central Kentucky. American Society of Mammalogists, Stillwater, Oklahoma.
- Humphrey, S.R., A.R. Richter, and J.B. Cope. 1977. Summer habitat and ecology of the endangered Indiana bat, *Myotis sodalis*. *Journal of Mammalogy* 58:334-346.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 765-771.
- Jones, J., and L. Nagy. 2010. The use of surrogate species in predicting wildlife impacts from wind development. Poster Presentation, AWEA WindPower Conference, Dallas, Texas.
- Kernohan, B.J., R.A. Gitzen, and J.J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125-166 in J.J. Millspaugh and J.M. Marzluff, editors. *Radiotracking and Animal Populations*. Academic, San Diego, California, USA.
- Kie, J.G., J.A. Baldwin, and C.J. Evans. 1996. CALHOME: a program for estimating animal home ranges. *Wildlife Society Bulletin* 24: 342-344.
- Kunz, T.H., and W.R. Hood. 2000. Parental care and postnatal growth in the Chiroptera. Pages 415-468

- in E.G. Crichton and R.H. Krutzsh, editors. Reproductive Biology of Bats. Academic Press, London, pp. 415-468.
- Kurta, A., D. King, J.A. Teramino, J.M. Stribley, and K.J. Williams. 1993. Summer roosts of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range. American Midland Naturalist 129:132-138.
- Kurta, A., K.J. Williams, and R. Mies. 1996. Ecological, behavioural, and thermal observations of a peripheral population of Indiana bats (*Myotis sodalis*). Pages 102-117 in R.M.R. Barclay and R.M. Brigham, editors. Bats and forests. Research Branch, Ministry of Forests Victoria, British Columbia, Canada.
- Kurta, A., and J.O. Whitaker, Jr.. 1998. Diet of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range. American Midland Naturalist 140: 280-286.
- Lacki, M.J., D.R. Cox, and M.B. Dickinson. 2009. Meta-analysis of summer roosting characteristics of two species of *Myotis* bats. American Midland Naturalist 162:318-326.
- Lambeck, R.J. 1997. Focal species: a multi-species umbrella for nature conservation. Conservation Biology 11: 849-856.
- Landres, P.B., J. Verner, J.W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. Conservation Biology 2: 316-328.
- LaVal, R.K., R.L. Clawson, M.L. LaVal, W. Caire. 1977. Foraging behavior and nocturnal activity patterns of Missouri bats, with emphasis on the endangered species *Myotis grisescens* and *Myotis sodalis*. Journal of Mammalogy 58: 592-599.
- Layne, J.N., and D. Glover. 1977. Home range of the armadillo in Florida. Journal of Mammalogy 58: 411-413.
- Lee, Y.F., and G.F. McCracken. 2004. Flight activity and food habits of three species of *Myotis* bats (Chiroptera : Vespertilionidae) in sympatry. Zoological Studies 43: 589-597.

- Martof, B. 1953. Home range and movements of the green frog, *Rana clamitans*. Ecology 34: 529-543.
- McNab, B.K. 1980. Food habits, energetics, and the population biology of mammals. The American Naturalist 116: 106-124.
- Menzel, M.A., J.M. Menzel, T.C. Carter, W.M. Ford, and J.W. Edwards. 2001. Review of the forest habitat relationships of the Indiana bat (*Myotis sodalis*). USDA Forest Service, Newtown Square, Pennsylvania.
- Miller, N.E., and G.M. Allen. 1928. The American bats of the genera *Myotis* and *Pizonyx*. Bulletin of the U.S. National Museum 144: 130-135.
- Mills, L.S., M.E. Soule, and D.F. Doak. 1993. The keystone-species concept in ecology and conservation. Bioscience 43: 219-224.
- Morris, A.D., D.A. Miller, and L.M. Conner. 2011. Home-range size of evening bats (*Nycticeius humeralis*) in Southwestern Georgia. Southeastern Naturalist 10:85-94.
- Murray, S.W., and A. Kurta. 2002. Spatial and temporal variation in diet. Pages 182-192 in A. Kurta and J. Kennedy, editors. The Indiana bat: biology and management of an endangered species. Bat Conservation International, Austin, USA.
- Neu, C.W., C.R. Byers, and J.M. Peek. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Management 38: 541-545.
- Parra, G.J. 2006. Resource partitioning in sympatric delphinids: space use and habitat preferences of Australian snubfin and indo-pacific humpback dolphins. Journal of Animal Ecology 75: 862-874.
- Pendleton, G.W., K. Titus, E. DeGayner, C.J. Flatten, and R.E. Lowell. 1998. Compositional analysis and GIS for study of habitat selection by goshawks in southeast Alaska. Journal of Agricultural, Biological, and Environmental Statistics 3:280-295.

- Perkins, M.W., and L.M. Conner. 2004. Habitat use of fox squirrels in southwestern Georgia. *Journal of Wildlife Management* 68: 509-513.
- Psyllakis, J.M., and R.M. Brigham. 2006. Characteristics of diurnal roosts used by female *Myotis* bats in sub-boreal forests. *Forest Ecology and Management* 223:93-102.
- Rabinowitz, A.R., and M.D. Tuttle. 1982. A test of the validity of two currently used methods of determining bat prey preferences. *Acta Theriologica* 27: 283-293.
- Racey, P.A. 1973. Environmental factors affecting the length of gestation in heterothermic bats. *Journal of Reproductive Fertility Supplements* 19:175-189.
- Racey, P.A. 1982. Ecology of bat reproduction. Pages 57-104 *in* Ecology of Bats (T.H. Kunz ed.). Plenum Press, New York, New York.
- Richardson, C.S., E.P. Widmaier, M. Hohmann, T.H. Kunz. 2008. Using fecal cortisol assays to assess stress in an endangered bat. Poster Presentation, Society for Integrative and Comparative Biology, San Antonio, Texas.
- Riskin, D.K. and M.J. Pybus. 1998. The use of exposed diurnal roosts in Alberta by the little brown bat, *Myotis lucifugus*. *Canadian Journal of Zoology* 76:767-772.
- Rodgers, A.R., A.P. Carr, H.L. Beyer, L. Smith, and J.G. Kie. 2007. HRT: home range tools for ArcGIS. Version 1.1. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.
- Romeling, S., L.W. Robbins, and C.R. Allen. 2010. Analysis of the effects of take on the Indiana bat (*Myotis sodalis*) population at a proposed wind energy facility. Wind Wildlife Research Meeting VIII, Lakewood, Colorado.
- Samuel, M.D., D.J. Pierce, and E.O. Garton. 1985. Identifying areas of concentrated use within the home range. *Journal of Animal Ecology* 54: 711-719.
- Samuel, M.D. and K.P. Kenow. 1992. Evaluating habitat selection with radiotelemetry triangulation error. *Journal of Wildlife Management* 56: 725-734.

- Schmidt, A.C., K. Tyrell, and T. Glueck. 2002. Environmental contaminants in bats collected from Missouri. Pages 228-236 in A. Kurta and J. Kennedy, editors. The Indiana bat: biology and management of an endangered species. Bat Conservation International, Austin, USA.
- Schowalter, D.B., J.R. Gunson, and L.D. Harder. 1979. Life history characteristics of little brown bats (*Myotis lucifugus*) in Alberta. Canadian Field-Naturalist 93:243-251.
- Seaman, D.E., and R.A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home ranges analysis. Ecology 77:2075-2085.
- Seaman, D.E., B. Griffith, and R.A. Powell. 1998. KERNELHR: a program for estimating animal home ranges. Wildlife Society Bulletin 26: 95-100.
- Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J., & Gitzen, R.A. (1999). Effect of sample size on kernel home range estimates. *Journal of Wildlife Management*, 63, 739-747.
- Sparks, D.W., C.M. Ritzi, J.E. Duchamp, and J.O. Whitaker, Jr. 2005. Foraging habitat of the Indiana bat (*Myotis sodalis*) at an urban-rural interface. Journal of Mammalogy 86: 713-718.
- Springborn, E.G., and J.M. Meyers. 2005. Home range and survival of breeding painted buntings on Sapelo Island, Georgia. Wildlife Society Bulletin 33:1432-1439.
- Swartz, S.M., P.W. Freeman, and E.F. Stockwell. 2003. Ecomorphology of bats: comparative and experimental approaches relating structural design to ecology. Pages 257-300 in T.H. Kunz and M.B. Fenton, editors. Bat Ecology. University of Chicago Press, Chicago.
- Swift, S.M., P.A. Racey, and M.I. Avery. 1985. Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. II. diet. Journal of Animal Ecology 54: 217-225.

- Swihart, R.K., and S.A. Slade. 1985. Testing for independence of observations in animal movements. *Ecology* 66: 1176-1184.
- Thomas, D.W., M. Dorais, and J.M. Bergeron. 1990. Winter energy budgets and cost of arousals for hibernating little brown bats, *Myotis lucifugus*. *Journal of Mammalogy* 71:475-479.
- Timpone, J.C. J.G. Boyles, K.L. Murray, D.P. Aubrey, and L.W. Robbins. 2010. Overlap in roosting habits of Indiana bats (*Myotis sodalis*) and Northern bats (*Myotis septentrionalis*). *American Midland Naturalist* 163:115-123.
- Tufto, J., R. Andersen, and J. Linnell. 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. *Journal of Animal Ecology* 65: 715-724.
- Tuttle, N.M., D.P. Benson, and D.W. Sparks. 2006. Diet of the *Myotis sodalis* (Indiana bat) at an urban/rural interface. *Northeastern Naturalist* 13: 435-442.
- U.S. Fish and Wildlife Service. 2007. Indiana bat (*Myotis sodalis*) draft recovery plan: first revision. U.S. Fish and Wildlife Service, Fort Snelling, Minnesota USA.
- Vaughan, T.A. 1976. Nocturnal behavior of the African false vampire bat (*Cardioderma cor*). *Journal of Mammalogy* 57: 227-248.
- Vege, S. 2000. Molecular analysis of big brown bat (*Eptesicus fuscus*) feces: genotyping and diet. Thesis, University of Tennessee, Knoxville, Tennessee.
- Wegner, S.J. 2008. Use of surrogates to predict the stressor response of imperiled species. *Conservation Biology* 22:1564-1571.
- Whitaker, J.O., Jr., and W.J. Hamilton. 1998. Mammals of the Eastern United States. Cornell University Press, Ithaca, New York.
- Whitaker, J.O., Jr., G.F. McCracken, and B.M. Siemers. 2009. Food habits analysis of insectivorous bats. Pages 567-592 in Kunz, T. H., and S. Parsons editors, *Ecological and behavioral methods for the study of bats*. Second edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.

- Whitby, M.D., S.M. Bergeson, S.A. Rutan, and T.C. Carter. 2011. Monitoring Indiana bat maternity colonies in southern Illinois. US Forest Service-Shawnee National Forest, Project: Project Number: 08-PA-11090800-023. Annual Report.
- White, G.C., and R.A. Garrott. 1986. Effects of biotelemetry triangulation error on detecting habitat selection. *Journal of Wildlife Management* 50:509-513.
- White, G.C., and R.A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, New York.
- Wilcox, B.A. 1984. In situ conservation of genetic resources: determinants of minimum area requirements. Pages 18-30 in J.A. McNeely, K.R. Miller, editors. *National Parks, Conservation, and Development: the Role of Protected Areas in Sustaining Society*. Smithsonian Institution Press, Washington, D.C.
- Wood, B.A., L. Cao, and M.D. Dearing. 2010. Deer Mouse (*Peromyscus maniculatus*) home-range size and fidelity in sage-steppe habitat. *Western North American Naturalist* 70:345-354.
- Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164-168.
- Zeale, M.R., R.K. Butlin, G.L.A. Barker, D.C. Lees, and G. Jones. 2011. Taxon-specific PCR for DNA barcoding arthropod prey in bat faeces. *Molecular Ecology* 11: 236-244.

CHAPTER 2

AN EXAMINATION OF THE CHARACTERISTICS OF LITTLE BROWN BAT (*MYOTIS LUCIFUGUS*) NATURAL TREE ROOSTS WITHIN THE CENTRAL PORTION OF THE SPECIES' RANGE.

Bergeson, S.M., T.C. Carter, and M.D. Whitby. To be submitted to Forest Ecology and
Management.

Abstract

Despite its intensive study, large distribution, and high abundance, there is a lack of knowledge in little brown bat (*Myotis lucifugus*) roosting ecology. While it is known that little brown bats frequently roost within anthropogenic roosts during the summer season, there is a paucity of information on their use of natural tree roosts. The few studies on little brown bats' use of natural roosts were either conducted in the northern portions of its distribution or they report only a few roost trees. In order to fill this void in information we conducted research on the roost characteristics of the little brown bat within the central portion of its distribution. We also compared the roost characteristics of little brown bat natural roosts to those of the Indiana bat (*Myotis sodalis*), which is known to use primarily natural roosts. Data were collected from 2 two study sites in south central Indiana, during the summer of 2007, and 2two study sites within southern Illinois, during the summers of 2009-2011. Radio-telemetry was used to track adult female little brown bats and Indiana bats back to their maternity roosts. Little brown bats used crevice/cavity roosts more often than Indiana bats, which primarily used exfoliating bark roosts. Specifically, little brown bats frequently roosted within the splinters of storm damaged trees. This frequent use of crevice/cavity roosts may suggest a preference for this roost type. This may explain the frequent use of anthropogenic roosts by little brown bats since anthropogenic roosts best mimic the roost characteristics of crevice/cavity roosts. This could also suggest a potential reason for the success of little brown bats and the decline of Indiana bats.

Keywords

Myotis, lucifugus, sodalis, maternity roost, natural roost, snag, anthropogenic, bat box

1.0 Introduction

The little brown bat (*Myotis lucifugus*) is one of the most widely distributed bat species in North America, where it is found across the majority of the continent (Fenton and Barclay 1980). The species has been studied intensively due to its wide distribution and high abundance (Fenton 1970; Humphrey and Cope 1976; Schowalter et al. 1979). Despite this attention, there remains a lack of knowledge in certain aspects of little brown bat roosting ecology.

The majority of research conducted on the species' summer roosting habits is on its use of anthropogenic roosts; such as attics, unoccupied buildings, barns, churches, bat boxes, etc. (Davis and Hitchcock 1965; Fenton 1970; Humphrey and Cope 1976; Schowalter et al. 1979; Riskin and Pybus 1998). This species is so closely associated with anthropogenic roosts that it has been described as being a "house bat" (Barclay and Cash 1985). While anthropogenic roosts are widely used by little brown bats, there have also been records of this species roosting within natural roosts, primarily within dead trees. However, these reports primarily originate from studies that report relatively few natural roosts (Barclay and Cash 1985; Schowalter et al. 1979) or are conducted within study areas located in the northern portion of the species' distribution (Crampton and Barclay 1998; Psyllakis and Brigham 2006). Therefore, while there is some research available, there is paucity of research focusing on the species' summer natural roost characteristics within the majority of its distribution. This is disconcerting because information on this topic has important management implications (Kunz and Lumsden 2003); especially due to the threat white-nose syndrome imposes on the species (Frick et al. 2010). To fill this void we examined the characteristics of little brown bat natural roosts within the central portion of its distribution. We also compared these roost characteristics to those of the Indiana bat (*Myotis sodalis*), a species that primarily uses natural roosts.

2.0 Materials and Methods

2.1 Study Area

Data were collected at 2 study sites in southern Illinois and 2 study sites in south-central Indiana. Study sites in Illinois were oriented around areas of high little brown bat and Indiana bat activity within the Mississippi Floodplain region of the Shawnee National Forest (Carter et al. 2010; Carter et al. 2009; Whitby et al. 2011). One study site was incorporated Oakwood Bottoms Greentree Reservoir (Oakwood Bottoms), a waterfowl management area in Jackson County near the town of Grand Tower. Oakwood Bottoms is 809ha of primarily bottomland hardwood forests surrounded by upland forests, wetlands, agricultural fields, and several bodies of water. The Big Muddy River flows through the study site and the Mississippi River is within 6.5km. Due to regular flooding, snag recruitment in the area stays at a consistently high level; causing potential bat roosts to be abundant within the area. Another Illinois study site incorporated a known Indiana bat maternity colony located within the area of Bluff Lake and Union County Conservation Area (Bluff Lake). Bluff Lake is located in Union County near the town of Mill Creek, IL. The area is approximately 2510ha in size. Habitats within the site consist primarily of bottomland hardwoods, open water, wetlands, and agricultural fields. A large patch of upland forest was adjacent to the eastern boarder of the study site. Several bodies of water, including a large creek and several lakes, are located within the area. The Mississippi River is also located 3km to the west of the area. Bluff Lake is also flooded on a regular basis. Both study areas consist primarily of pin oaks (*Quercus palustris*) and hickories (*Carya spp.*). However, maples (*Acer spp.*) and elms (*Ulmus spp.*) are also common within the areas.

The two study sites in Indiana were located in Camp Atterbury and Muscatatuck National Wildlife Refuge (Muscatatuck). Muscatatuck is 3,157ha and is located in Jackson County near Seymour, IN. The area is a conglomerate of bottomland hardwood forests, upland forests, wetlands, early successional forests, and grasslands. Parts of the study site are flooded annually in order to provide habitat for waterfowl during migration. Camp Atterbury is a U.S. Army installation consisting of 13,484ha of active military training grounds within south-central

Indiana. The installation is located primarily within Bartholomew County, IN, with some portions within Brown and Johnson Counties, IN. The closest town to the installation is Edinburgh, IN. Primary habitats within the area include forests, shrublands, and grasslands. Wetland, bottomland hardwood, and open water habitat is also present, but in less abundant and relatively smaller patches. The installation also has several creeks, streams, and man-made lakes within it. Approximately 10,700ha of forests within the area are managed for timber harvesting, wildlife habitat protection, recreation, and other purposes (Watson 1997). Bats of both species were previously recorded in both of these Indiana study sites (Sichmeller 2010; Ulrey et al. 2005).

2.2 Methodology

Data were collected for both species within Camp Atterbury and Muscatatuck during the summer of 2007 and within Oakwood Bottoms and Bluff Lake during the summers of 2009-2011. At each study site bats of both species were captured using high mist-net systems as described by Gardner et al. (1989). Adult female little brown bats and Indiana bats of varying reproductive statuses were fitted with radio transmitters (models LB-2 and LB-2X Holohil Systems, Ltd., Ontario, Canada; model SOM-2007 Wildlife Materials, Inc., Murphysboro, Illinois) with a mean weight of $\leq 0.5\text{g}$, representing $\leq 5\%$ of the body mass of each bat (Aldridge and Brigham 1988). Transmitters were attached to the skin between the scapula of each bat using SkinBond (Smith & Nephew, Inc., Largo, Florida) or Perma-Type brand surgical adhesive (Perma-Type Company, INC., Plainville, Connecticut). Radio-tagged bats of both species were then tracked back to their roosts using radio-telemetry. Roosts were located for each bat every day possible following capture of the bat until the transmitter fell off or its battery failed.

Roosts were marked, their coordinates were recorded with a handheld GPS, and roost height, tree height, tree species, tree diameter at breast height (DBH), tree condition (dead, alive), and roost type (exfoliating bark, crevice/cavity) were recorded. Emergence count surveys (Kunz et al. 2009) were conducted at roosts of both species to estimate the average number of bats

within them. Emergence counts were initiated just before sunset and continued until either no bats were observed exiting the roost after 10 minutes, or it became too dark to see. Emergence counts of anthropogenic roosts were only conducted during the summer of 2011.

Data were also collected on the number of roost changes per bat and the number of consecutive nights each bat spent within a single roost (residency). Roost tree coordinates were input into a geographic information system (GIS; Arc Info vers.10.0, ERSI, Redlands, CA) and the ArcGIS Point Distance geoprocessing tool was used to determine the average and maximum distance traveled between subsequent roosts and the maximum distance between all roosts for each bat.

2.3 Statistical Analyses

Due to small sample sizes, comparisons of roost characteristics between populations were unable to be conducted, therefore, the data from all populations were combined for each species at each site. Two-tailed, 2-sample t-tests and Mann-Whitney U-tests with 95% confidence intervals, $\alpha=0.05$, were used to compare the roost characteristics between the species from all study sites. We compared categorical data between the species by conducting Fisher's Exact tests.

3.0 Results

A total of 39 Indiana bats and 32 little brown bats were tracked during the duration of this study. Bats of both species were tracked for an average of 8.5 days (range 0-20days) per individual. A total of 96 natural maternity roosts ($n_{\text{sodalis}}=76$; $n_{\text{lucifugus}}=20$) were located throughout all of the study sites. Little brown bats were also tracked to 7 anthropogenic roosts within the 2 Illinois sites. Nineteen out of the 96 natural roosts were determined to be primary roosts as described by Callahan et al. (1997; $n_{\text{sodalis}}=13$; $n_{\text{lucifugus}}=6$). However, emergence counts were not conducted at every roost so the actual number of primary roosts may be greater.

Within the two Illinois study sites, all roosts of both species were found solely within bottomland hardwoods. However, bottomland hardwoods only accounted for 10% of the landscape's available habitat. The majority of the habitat within the landscape consisted of upland forests (53%) and agriculture/open fields (27%). Other available habitats include wetlands, open water, and urban habitat. However, these habitats each consisted of $\leq 5\%$ of the landscape. This may suggest a preference for bottomland hardwoods as roosting habitat for both species. Within the Indiana study sites, bottomland hardwoods, wetlands, and open water each accounted for $\leq 1\%$ of available habitat within this landscape. Within these study sites 97% of the Indiana bat roosts and 70% of little brown bat roosts were discovered within upland forest habitat and close to rivers and streams. The remaining roosts were located within bottomland hardwoods. Agriculture/open fields, upland forests, and urban areas accounted for the majority of habitat within the Indiana study sites' landscape (53%, 36%, and 10%, respectively). Within all 4 study sites, roosts of both species tended to be intermixed.

Both species roosted primarily in oak species (*Quercus spp.*; 34% Indiana bats; 37% little brown bats) and maple species (*Acer spp.*; 23% Indiana bat; 21% little brown bat). Indiana bat roosts were typically found in pin oaks (*Quercus palustris*), which accounted for 25.6% of all identified roosts for the species. Other tree species used by Indiana bats included red oak (*Q. rubra*; 10.3%), white oak (*Q. alba*; 7.7%) shagbark hickory (*Carya ovata*; 10.3%), red maple (*Acer rubrum*; 7.7%), and silver maple (*A. saccharinum*; 7.7%). Little brown bat roosts were found in pin oaks (*Quercus palustris*; 22.2%), red oaks (*Q. rubra*; 22.2%), and red maples (*Acer rubrum*; 22.2%) in equal percentages. Other tree species used by little brown bats included: sugar maple (*A. saccharum*; 11.1%), shagbark hickory (*Carya ovata*; 11.1%), and red elm (*Ulmus rubra*; 11.1%). An additional 20 roost trees were not identified to genus ($n_{\text{sodalis}}=14$; $n_{\text{lucifugus}}=6$).

Natural roosts of both bat species were primarily located in dead trees (78.3% Indiana bat; 80% little brown bat). Live trees (10.1% Indiana bats; 5% little brown bats) and partially

dead trees (11.6% Indiana bats; 15% little brown bats) were used relatively infrequently. All roosts within live trees occurred in *Carya spp.*, primarily shagbark hickories, except for one Indiana bat that roosted in the cavity of a live sugar maple. While both bat species tended to roost within snags, they used different types of roosts within those snags ($p=0.001$). Indiana bats roosted primarily under exfoliating bark (87.7% of all Indiana bat roosts), while little brown bat roosted in higher frequencies (58%) of crevice/cavity roosts in addition to exfoliating bark roosts. Both species also roosted at different heights as well as within different sizes of trees. Indiana bats roosted higher and tended to roost within trees that were taller than little brown bats (Table 1; $t=-2.37$, $p=0.022$; $t=-3.39$, $p=0.001$). Average roost DBH did not differ between the species despite this disparity in tree height (Table 1; $t=0.57$, $p=0.573$). The mean emergence counts for roosts of either species suggests that Indiana bat roosts had fewer bats within them per night than little brown bat roosts (Table 1; $t=3.23$, $p=0.008$).

Female little brown bats consistently roosted in anthropogenic roosts within our Illinois study sites. Within Oakwood Bottoms we found little brown bats roosting in 3-5 bat boxes during the throughout the duration of the study. Tracked bats also used a pavilion and a light fixture on a utility pole as alternative roosts (Callahan et al. 1997). Bluff Lake had 1 bat box used by little brown bats throughout the study, except during 2011 when flooding occurred. Bat boxes within both study sites were crevice/cavity roosts 5m in height. Emergence count surveys conducted on bat boxes in 2011 within the Oakwood Bottoms study site averaged 51 bats per night. However, certain bat boxes could have as many as 211 bats within them in a single night. These bats were assumed to be little brown bats due to the presence of a tracked little brown bat within the roost when emergence count surveys were conducted and the almost exclusive captures of little brown bats when boxes were trapped. Indiana bats were very rarely recorded roosting in anthropogenic roosts. In the 2 instances of Indiana bats roosting in bat boxes, only a few Indiana bats were intermixed with large numbers of little brown bats.

The movements of bats among roosts were somewhat different between the species (Table 2). Indiana bats switched roosts more often than little brown bats ($p=0.035$). However, there was no difference in average residency between the species ($p=0.208$). Both species traveled approximately the same distance between consecutive roosts (mean distance $p=0.22$, max distance $p=0.54$). Also, both species covered approximately the same maximum distance between roosts ($p=0.66$). However, in the summer of 2010 a single lactating little brown bat was located roosting within another state (Missouri) approximately 29.5km from its original roost, after it had not been observed for 9 days straight.

During the summers of 2010 and 2011 little brown bats were observed to regularly roost within large trees in which the top portion of the tree had broken off approximately halfway up the main bole during severe storms. Bats roosted in the crevices of the splintered top of the remaining bole. Seven out of 8 (88%) natural little brown bat roosts, located in 2010 and 2011, were within these storm damaged trees. This frequent use of storm damaged trees was not observed in the Indiana bats tracked during the same years, where only 13% of Indiana bat roosts were within storm damaged trees. Little brown bats also seemed to congregate within these trees in greater numbers than Indiana bats. Emergence count surveys counted more little brown bats exiting storm damaged trees than Indiana bats ($\bar{x}=121$; $\bar{x}=38$; respectively). While, the Indiana bat roosts located within storm damaged trees were a mixture of primary and alternative roosts, little brown bat roosts within these trees tended to be primary roosts. The only little brown bat roost located within a tree that was not storm damaged was an alternative roost.

4.0 Discussion

The results of our study are dissimilar to the few other studies conducted on little brown bat natural roost characteristics. Psyllakis and Brigham (2006) found that little brown bats roosted in a mixture of coniferous and deciduous trees, whereas bats within our study roosted solely

within deciduous trees. Bats within other studies also tended to roost within taller trees than the bats within our study sites, however, the DBHs and roost heights found in these studies were approximately the same to our own (Crampton and Barclay 1998; Psyllakis and Brigham 2006). Crampton and Barclay (1998) also reported smaller emergence count numbers for little brown bat roosts within their study site ($\bar{x} = 15$, max=60), six times fewer per night than within our study. However, emergence counts conducted by Psyllakis and Brigham (2006) were similar to our own ($\bar{x} = 86$, max=388; $\bar{x} = 1.3$, max=4; crevice/cavity roosts and exfoliating bark roosts, respectively). This variation in roost characteristics is potentially due to the differences in geographic location. The earlier studies were conducted within the northern portion of the little brown bat's distribution and, as such, the study sites have different habitats and tree species within them than our mid-western study sites. Little brown bats within the northern study sites roost within what is available to them, which is primarily tall lodgepole pine (*Pinus contorta*) and trembling aspen (*Populus tremuloides*) snags (Crampton and Barclay 1998; Psyllakis and Brigham 2006).

While there are some dissimilarities in little brown bat roost characteristics between our study and others, there is a common trait between them. Little brown bats tend to roost within crevice/cavity roosts more than exfoliating bark roosts. Crampton and Barclay (1998) determined that little brown bats prefer deep cavity roosts even when there are more exfoliating bark roosts available to them. And while little brown bats roosted within a larger number of exfoliating bark roosts than crevice/cavity roosts in the Psyllakis and Brigham (2006) study, these exfoliating bark roosts were all alternative roosts, averaging 1.3 (range 1-4) bats per night. Little brown bat crevice/cavity roosts located by Psyllakis and Brigham (2006) averaged 86 bats per night (range 2-388); suggesting that crevice/cavity roosts are typically used as primary roosts. Our own results show a higher number little brown bat primary crevice/cavity roosts than primary exfoliating bark roosts. This frequent use of crevice/cavity roosts as primary roosts may suggest a preference for

the roost type by little brown bats. Also, while there may be some exceptions, most anthropogenic little brown bat roosts are crevice/cavity type roosts. Therefore, the frequent use of anthropogenic roosts by little brown bats may be due to the species overall preference for crevice/cavity roosts.

5.0 Conclusions

Little brown bats tend to form large colonies and, therefore, may prefer natural crevice/cavity roosts because they often are able to accommodate more bats and remain habitable for longer periods of time than ephemeral exfoliating bark roosts (Davis and Whitaker 2002; Kunz and Lumsden 2003; Psyllakis and Brigham 2006). Perhaps because anthropogenic roosts often mimic the characteristics of natural crevice/cavity roosts, little brown bats use them more often than Indiana bats, which historically prefer exfoliating bark roosts. It is possible that one of the reasons that the little brown bat is more successful than the endangered Indiana bat is its ability to take advantage of anthropogenic roosts, which are becoming more available throughout its distribution (Barclay and Cash 1985). Fenton (1970) suggested that this ability caused little brown bat populations, within Ontario, to grow to the large numbers we see today. Because Indiana bats select for roost characteristics that are not typically found in anthropogenic roosts, they are less likely to take advantage of the resource. Therefore, Indiana bats are less well adapted to the loss of habitat and other negative effects that are associated with the continued development of potential roosting habitat across its distribution.

6.0 Acknowledgments

We would like to thank the Shawnee National Forest Division of U.S. Forest Service, specifically R. McClanahan, and the Illinois Department of Natural Resources, specifically J. Kath, for their help funding the project. We would also like to thank M. Michaels, B. Funk, J.

Weber, S. Rutan, A. Shultz, B. Lindsey, A. Wallace, and M. McCann for their contributions in the field.

7.0 Literature Cited

- Aldridge, H.D.J.N., Brigham, R.M., 1988. Load carrying and maneuverability in an insectivorous bat: a test of the 5% “rule” of radio-telemetry. *J. Mammal.* 69, 379-382.
- Barclay, R.M.R., Cash, K.J. 1985. A non-commensal maternity roost of the little brown bat (*Myotis lucifugus*). *J. Mammal.* 66, 782-783.
- Callahan, E.V., Drobney, R.D., Clawson, R.L. 1997. Selection of summer roosting sites by Indiana bats (*Myotis sodalis*) in Missouri. *J. Mammal.* 78, 818-825.
- Carter, T.C., Michaels, M.L., Schultz, A.M. 2009. Monitoring Indiana bat maternity colonies in southern Illinois. Annual Report, US Forest Service, Shawnee National Forest, Illinois.
- Carter, T.C., Bergeson, S.M., Whitby, M.D. 2010. Monitoring Indiana bat maternity colonies in southern Illinois. Annual Report, US Forest Service, Shawnee National Forest, Illinois.
- Crampton, L.H., Barclay, R.M.R. 1998. Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. *Conserv. Biol.* 12, 1347-1358.
- Davis, R.W., Whitaker, J.O., Jr. 2002. Population studies on a maternity colony of little brown bats in west-central Indiana. *Pro. Indiana Acad. Sci.* 111, 215-220.
- Davis, W.H., Hitchcock, H.B. 1965. Biology and migration of the bat, *Myotis lucifugus*, in New England. *J. Mammal.* 46, 296-313.
- Fenton, M.B. 1970. Population studies of *Myotis lucifugus* (Chiroptera: Vespertilionidae) in Ontario, Royal Ontario Museum, Toronto.
- Fenton, M.B., Barclay, R.M.R., 1980. *Myotis lucifugus*. *Mamm. Species*, 1-8.

- Frick, W.F., Pollock, J.F., Hicks, A.C., Langwig, K.E., Reynolds, D.S., Turner, G.G., Butchkoski, C.M., Kunz, T.H. 2010. An emerging disease causes regional population collapse of a common North American bat species. *Science* 329, 679-682.
- Gardner, J.E., Garner, J.D., Hofmann, J.E. 1989. A portable mist netting system for capturing bats with emphasis on *Myotis sodalis* (Indiana bat). *Bat Res. News* 30, 1-8.
- Gumbert, M.W., O'Keefe, J.M., MacGregor, J.R. 2002. Roost fidelity in Kentucky, in: Kurta, A., Kennedy, J. (Eds.), *The Indiana bat: biology and management of an endangered species*. Bat Conservation International, Austin, Texas, pp. 143-152.
- Hicks, A.C., Novak, P.G. 2002. History, status, and behavior of hibernating populations in the northeast, in: Kurta, A., Kennedy, J. (Eds.), *The Indiana bat: biology and management of an endangered species*. Bat Conservation International, Austin, Texas, pp. 160-164.
- Humphrey, S.R., Cope, J.B. 1976. Population ecology of the little brown bat, *Myotis lucifugus*, in Indiana and north-central Kentucky. American Society of Mammalogists, Stillwater, Oklahoma.
- Kerth, G., König, B. 1999. Fission, fusion and nonrandom associations in female Bechstein's bats (*Myotis bechsteinii*). *Behaviour* 136, 1187-1202.
- Kunz, T.H., Betke, M., Hristov, N.I., Vonnhoff, M.J. 2009. Methods for assessing colony size, population size, and relative abundance of bats, in: Kunz, T.H., Parsons, S. (Eds.), *Ecological and Behavioral Methods for the Study of Bats*, 2nd edition. The John Hopkins University Press, Baltimore, Maryland.
- Kunz, T.H., Hood, W.R. 2000. Parental care and postnatal growth in the Chiroptera, in: Crichton, E.G., Krutzsch, R.H. (Eds.), *Reproductive Biology of Bats*. Academic Press, London, pp. 415-468.
- Kunz, T.H., Lumsden, L.M. 2003. Ecology of cavity and foliage roosting bats Kunz, in: T.H., Fenton, M.B. (Eds.). *Bat Ecology*. The Chicago University Press, Chicago, pp. 3-89.

- Psyllakis, J.M., Brigham, R.M. 2006. Characteristics of diurnal roosts used by female *Myotis* bats in sub-boreal forests. *For. Ecol. Manage.* 223, 93-102.
- Riskin, D.K., Pybus, M.J. 1998. The use of exposed diurnal roosts in Alberta by the little brown bat, *Myotis lucifugus*. *Can. J. Zool.* 76, 767-772.
- Sichmeller, T. 2010. Determining energy conservation during torpor for three *Myotis* species and response of *Myotis* species to human disturbance while day roosting. M.S. Thesis. Ball State University, Muncie, IN.
- Schowalter, D.B., Gunson, J.R., Harder, L.D. 1979. Life history characteristics of little brown bats (*Myotis lucifugus*) in Alberta. *Can. Field Nat.* 93, 243-251.
- Ulrey, W.A., Sparks, D.W., Ritzi, C.M. 2005. Bat communities in highly impacted areas: comparing Camp Atterbury to the Indianapolis Airport. *Proc. Indiana Acad. Sci.* 114, 73-76.
- Watson, M. 1997. Survey of bat species: Atterbury Reserve Forces Training Area, Edinburgh, Indiana. Military Department of Indiana Technical Report.
- Whitby, M.D., Bergeson, S.M., Rutan, S.A., Carter, T.C. 2011. Monitoring Indiana bat maternity colonies in southern Illinois. Annual Report, US Forest Service, Shawnee National Forest, Illinois.

Table 1: Comparison of little brown bat (*Myotis lucifugus*) and Indiana bat (*M. sodalis*) natural roost characteristics from populations located in southern Illinois, studied during 2009-2011, and within south-central Indiana, studied during 2007.

Roost Characteristic	Indiana bat (n=76)	Little brown bat (n=20)	Test statistic	
	$\bar{x} \pm \text{S.E. (range)}$	$\bar{x} \pm \text{S.E. (range)}$	t	p
Roost height (m)	10.6 \pm 0.60 (3.0-28.0)	8.4 \pm 0.7 (2.0-14.0)	-2.37	0.022
Tree height (m)	15.5 \pm 0.7 (5.0-30.0)	10.7 \pm 1.1 (5.0-22.0)	-3.39	0.0010
DBH (cm)	53.6 \pm 2.8 (11.0-129.0)	56.9 \pm 4.6 (24.7-97.0)	0.57	0.57
Mean emergence count (# of bats)	40 \pm 11 (1-260)	87 \pm 21 (11-165)	3.23	0.0080

Table 2: Comparison of little brown bat (*Myotis lucifugus*) and Indiana bat (*M. sodalis*) roost movements within 2 study sites in southern Illinois during 2009-2011 and 2 study sites within south-central Indiana during 2007.

Roost Movement ^a	Indiana bat	Little brown bat	Test statistic ^b	
	$\bar{x} \pm \text{S.E. (range)}$	$\bar{x} \pm \text{S.E. (range)}$	t ^c	p
Mean # of roost changes ^d	3.8 \pm 0.5 (0-11.0)	2.2 \pm 0.4 (0-7.0)	-	0.035
Mean residency ^e (days)	1.7 \pm 0.1 (1.0-7.0)	2.8 \pm 0.7 (1.0-15.0)	-	0.21
Mean dist. between consecutive roosts (m)	1079 \pm 393 (63-5575)	815 \pm 283 (4-2960)	-1.28	0.22
Max dist. between consecutive roosts (m)	1574 \pm 585 (21-8213)	1100 \pm 331 (5-2960)	-	0.54
Max distance between roosts (m)	1468 \pm 515 (21-8213)	2964 \pm 1917 (5-29500)	-0.45	0.66

^a Movements between roosts were calculated taking both natural tree roosts and anthropogenic roosts into account.

^b Two-sample *t*-test or Mann-Whitney U-tests were conducted to compare the roost characteristics between the species.

^c A dash symbol (-) is used in place of a t-value when a Mann-Whitney U-test was performed.

^d A roost change is defined as a bat changing the roost it uses from the one it used during the previous day.

^e Residency is defined by the number of consecutive days a bat spends within a single roost.

CHAPTER 3

**HORIZONTAL RESOURCE PARTITIONING BETWEEN SYMPATRIC
POPULATIONS OF THE ENDANGERED INDIANA BAT (*MYOTIS SODALIS*)
AND THE LITTLE BROWN BAT (*M. LUCIFUGUS*).**

Bergeson, S.M., T.C. Carter, and M.D. Whitby. To be submitted to The Journal Animal Ecology.

SUMMARY

1. Resource partitioning is a common mechanism adopted as a result of pressure from inter-specific competition. Variations in ecomorphological characteristics between sympatric species are closely associated with the way resources are partitioned within that community. These variations are, therefore, often used by researchers to determine the structures of communities. However, when sympatric species are ecomorphologically similar, it is difficult to determine whether they partition resources and, therefore, how they are able to coexist without one species out-competing the other.
2. Communities containing the endangered Indiana bat, *Myotis sodalis* (Miller and Allen 1928), and the little brown bat, *M. lucifugus* (LeConte 1831), are effective models of this phenomenon. These species are morphologically similar and are both abundant in certain areas within their shared distribution. We examined sympatric populations of these species in order to determine whether they partitioned their resources through the selection of foraging habitat.
3. Using radio-telemetry, the foraging home ranges and habitat selection of both species were examined. Location estimates were used to estimate home ranges of bats, using both minimum convex polygon and 95% fixed kernel home range models. Euclidean distance-based habitat selection analyses (Conner et al. 2003) were conducted to determine if either species selected for habitat at either the landscape or home range levels.
4. *Myotis sodalis* had an average home range of $375 \pm 39\text{ha}$ while *M. lucifugus* had an average of $2739 \pm 456\text{ha}$. While both species selected for similar hydric habitats at the landscape level, *M. lucifugus* selected for additional habitats within their expansive home ranges and *M. sodalis* did not select for any habitat within their smaller home ranges.

5. Separate foraging strategies were adopted by the morphologically similar species within sympatry. This adoption may be the result of pressure from inter-specific competition to partition resources horizontally.

KEYWORDS

Resource partitioning, niche differentiation, *Myotis lucifugus*, *Myotis sodalis*, sibling species, distance-based analysis, home range, habitat selection.

INTRODUCTION

The relationship between morphology and ecology is commonly used to determine the structures of communities (Gatz 1979; Losos 1990). Ecomorphological characteristics are known to be associated with the diet and feeding strategies of organisms and, therefore, the dietary niches they fill within the community (Zaret 1980; Grant 1986; Spencer 1995). Insectivorous bat communities are excellent models of this phenomenon because they are commonly made up of morphologically similar species that partition dietary resources based on the ecomorphologically dependent feeding strategies they adopt (Aldridge & Rautenbach 1987).

Variation in characteristics such as wing morphology and echolocation calls are known to have major effects on the resource partitioning of sympatric species of insectivorous bats (Fenton 1982; Aldridge & Rautenbach 1987; Norberg & Rayner 1987; Heller & Helversen 1989; Arlettaz 1999). Variations in wing morphology (such as aspect ratio, wing loading, and wing span) can determine the flight speed, flight height, and maneuverability of bats; which, in turn, can affect the habitats they are able to forage within. Variations in echolocation call structure can also affect the areas in which bat species can forage (Aldridge & Rautenbach 1987; Broders, Findlay, & Zheng 2004). Making different bat species better suited for more cluttered habitats based on the duration and the bandwidth of their calls (Griffin 1971; Simmons & Stein 1980; Schnitzler &

Kalko 2001). However, when species with similar ecomorphological characteristics are present within a community, it becomes difficult to determine how, or if, they partition resources. However, the competitive exclusion principle suggests that species with completely identical niches should not exist in sympatry (Hardin 1960). If ecomorphologically similar species exist within sympatric situations there must be another way resources are partitioned or differences between the species in another niche characteristic.

The endangered Indiana bat, *Myotis sodalis* (Miller and Allen 1928), and the little brown bat, *M. lucifugus* (LeConte 1831), are sympatric throughout the distribution of the *Myotis sodalis*. The species are very similar morphologically; to such an extent that they were considered to be the same species until 1928 (Miller and Allen 1928). The structure of the species' echolocation calls is also similar causing echolocation calls between the species to be easily confused and a source of dispute in literature (O'Farrell 1999; Britzke et al. 2002; Britzke 2003). Both species are known to use aerial hawking foraging strategies (Fenton & Bogdanowicz 2002).

Previous studies have been conducted on the partitioning of resources between these sympatric species. Lee & McCracken (2004) found that the inter-specific competition may pressure these species to partition resources through temporal variation as well as variation in foraging heights. Several studies have been conducted on the possibility of these bats partitioning resources through variation in diet, all with varying results (Belwood 1979; Brack 1983; Lee & McCracken 2004; Feldhamer, Carter, & Whitaker 2009). However, there have been no studies that have examined a possible adaptation of a difference in habitat selection between the species as a mechanism of resource partitioning. It is possible inter-specific competition caused these species to vary the habitat they select when they are within sympatric populations (horizontal resource partitioning).

The objective of this study is to compare the home range and habitat use of *M. sodalis* and *M. lucifugus* within the same study sites in order to determine how, or if, the species horizontally partition resources.

METHODS

Study Area

This study was conducted in 2 study sites in the Mississippi River floodplains of Illinois: Oakwood Bottoms Greentree Reservoir (Oakwood) and Bluff Lake/Union County Conservation Area (Bluff Lake). There are well-known colonies of *M. sodalis* as well as large numbers of *M. lucifugus* recorded within both study sites (Carter & Feldhamer 2005; Carter, Michael, & Schultz 2009; Carter, Bergeson, & Whitby 2010; Whitby et al. 2011).

Oakwood is a bottomland hardwood forest, approximately 809ha in area, located in Jackson County near the town of Grand Tower. The area is adjacent to the Big Muddy River, is within 6.5km of the Mississippi River, contains several temporally flooded lakes, and is abutted by agricultural fields. The area around Oakwood is flooded annually due to its proximity to the Big Muddy River, a major tributary of the Mississippi River. However, flooding in the area itself is regulated by a system of levees. These flooding events can cause high tree mortality and typically result in the increased recruitment of potential snags that can be exploited by bats.

Bluff Lake consists of approximately 2510ha set aside for waterfowl hunting and management in Union County near the town of Millcreek, IL. There are numerous bodies of water in and around the area including: Upper and Lower Bluff Lake, Lyerle Lake, Clear Creek Ditch, the Mississippi River (3.2km away), numerous wetlands, and several temporal lakes and pools. Other habitat in the area includes bottomland hardwoods, agricultural fields, and upland bluffs. The wetlands and bottomland hardwoods are flooded annually and the agricultural fields remain partially harvested, or un-harvested, as part of waterfowl management.

Methodology

Data were collected from both study sites during the summers of 2003, 2009, 2010 and 2011. All bats were captured using high net mist-net systems (Gardner, Garner, & Hofmann 1989). Transmitters (models LB-2 and LB-2X, Holohil Systems, Ltd., Ontario, Canada; model SOM-2007 Wildlife Materials, Inc., Murphysboro, Illinois) were attached to healthy adult females of both species. All bats tracked were in varying reproductive stages depending on capture date. Transmitters weighed ≤ 0.5 g, less than 5% of the average bat's body mass (Aldridge & Brigham 1988). SkinBond (Smith & Nephew, Inc., Largo, Florida) or Perma-Type brand surgical adhesive (Perma-Type Company, INC., Plainville, Connecticut) was used to attach transmitters to the dorsal surface between the scapulae of each bat. Up to 5 transmitters were active at a time, depending on capture rate.

Radio-tagged bats were tracked, using radio-telemetry, the day after transmitter activation until the transmitter fell off, failed, or the season ended. Tracking started 30 min after sunset and, depending on the activity of the bat and weather conditions, lasted as late as 4:00am. Radio-tagged bats were located, during nightly activity and bearings of the animals were estimated for each bat using either simultaneous multi-azimuth triangulation (Amelon et al. 2009) or single azimuth distance estimate methods. The single azimuth distance estimate method consisted of estimating the azimuth and distance of a bat based on the direction and strength of the strongest telemetry signal. Distance estimates were based on trials conducted on transmitters placed at known distances throughout the study area. Distance estimate values included: 1.6km, 1.2km, 0.8km, and 0.4km (1mi, 0.75mi, 0.5mi, and 0.25mi, respectively). This method was implemented due to the high mobility of some animals and the impracticality of other estimate methods for these animals. Both stationary and mobile mounted telemetry systems (Amelon et al. 2009) were used depending on the landscape of the area and the activity of the bat being tracked. Location

estimates were made every 5min in order to account for non-independence (autocorrelation; Swihart & Slade 1985).

Data Analysis

Locate III (Nams 2006) was used to generate location estimates for each simultaneous multi-azimuth triangulation estimate. Azimuths collected using the single azimuth distance estimate method were converted to location estimates in ArcMap®GIS (ESRI, Redlands, CA) by plotting the location of each telemetry station and using the map measurement tool and the recorded azimuth to determine the coordinates of each location estimate. Coordinates of all location estimates, generated using both methods, were then imported into ArcMap for use in home range and habitat selection analyses.

Two analyses were conducted to determine the differences in home range size between the species. One analysis was conducted on home ranges estimated using a minimum convex polygon (MCP) method and another was conducted on home ranges estimated using a 95% fixed kernel (FK) method (Amelon et al. 2009). Within ArcMap the Hawth's Tools program (Beyer 2004) was used to generate 100% MCPs while the Home Range Tools program (HRT; Rodgers et al. 2007) was used to generate FK estimates for all bats. All FK estimates used the least-square cross-validation (LSCV) smoothing parameter and output kernels with cell sizes of 30 X 30m. All bat home ranges were calculated from ≥ 30 location estimates (Seaman et al. 1999). The home ranges of the species were compared using 2-sample t-tests run on both the MCPs and FK.

The relationships between the time (date) and the home range sizes of bats were examined for both species to determine if they changed as the season progressed. The relationship between home range size and the Julian date in which tracking was commenced was tested for both species using linear regression tests conducted on both MCP and FK estimates. These

analyses were conducted solely on data collected on during 2010 and 2011 because these were the only years in which *M. lucifugus* were tracked.

Habitat selection was analyzed at 2 ecosystem levels, Johnson's (1980) 2nd and 3rd orders of habitat selection, for both species. Johnson's (1980) 2nd order of habitat selection (i.e., landscape level) is an organism's, or a population's, orientation of its home range within a landscape. The 3rd order of selection (i.e., home range level) is defined as an organism's selection of habitat within its home range. Analyses were conducted on both species to determine whether they selected for habitat at random and if their use of habitat differed at either the landscape level or the home range level of habitat selection. Only bats that had approximately ≥ 50 location estimates were used in these analyses (Alldredge & Ratti 1986; Amelon et al. 2009). For these analyses, habitat within the study sites were categorized into wetland, open water, urban, road/railroad, upland forest, bottomland hardwood, or agriculture/grassland habitat types. These habitat categories were chosen due to previous knowledge of *M. sodalis* habitat preferences and the basic habitats that were available within the study sites (Carter & Feldhamer 2005; Carter, Michaels, & Schultz 2009; Carter, Bergeson, & Whitby 2010; Whitby et al. 2011).

Two Euclidean distance-based analyses (EDA), as described by Conner, Smith, & Burger (2003; also see Conner & Plowman 2001) were conducted to determine whether either of the species selected for habitat at the landscape level. We generated 2500 random points (using the "create random points" in ArcToolbox tool), within two 80.5km (50mi: double the maximum travel distance observed while conducting this study) circles placed in the center of both study sites. We then measured the distance from each of these random points to the nearest patch of each habitat type. The average of these distances (r_i) represented the expected distance each bat would be from a habitat type if it selected for habitat at random. We then generated 2500 random points within the MCP home range of every bat. The average distance from all of these random points to the nearest patch of each habitat type was calculated (u_i) and represented the observed

distance of each bat. Distance ratios (d_i) were created for each animal by dividing the observed distances by the expected distances (u_i/r_i). Multivariate analysis of variance (MANOVA) tests were used to test the null hypotheses that landscape level selection did not differ from random for both species by comparing the observed distances to the expected distances for each habitat type. If habitat selection differed significantly from random we used paired t-tests or non-parametric sign tests on the observed and expected distances of each habitat type to determine which habitats were used disproportionately by the species.

To examine habitat selection at the home range level for both species 2 additional EDA analyses were conducted similar to the previous analyses. However, we used the distances from random points generated within each bat's home range as expected values and the observed distances were measured from actual bat location estimates used to generate the bats' foraging home ranges. These analyses examined the distribution of bat locations within home ranges in order to determine habitat selection within the home range.

Finally, in order to compare the use of habitat between the species, we compared the average observed distances to each habitat type between the species at both the landscape and home range levels. For landscape level habitat use, MANOVAs were used to test whether the mean distances to habitat types from random points generated within each bats home range were similar between the species. For home range level habitat use, MANOVAs were used to test whether the mean distances to habitat types from actual location estimates were similar between the species. If there was a significant difference between the species, in at either level, we compared the mean distances to each habitat between the species using 2-sample t-tests or Mann-Whitney U-tests to determine if and how the species differed in their use of that habitat.

RESULTS

The home range sizes of the 2 species were significantly different when compared using both MCP and FK home range estimates (Fig. 1; Fig. 2; $T=5.16$, $p<0.001$; $T=2.73$, $p=0.017$; respectively). On average, *M. lucifugus* home ranges were larger than those of *M. sodalis* within the same landscape. The mean \pm S.E. size of *M. lucifugus* home ranges, estimated by MCP, was 2739 ± 456 ha (range: 650-5931). However, it was only 375 ± 39 ha for *M. sodalis* (range: 27-854). FK estimates resulted in a mean home range size of 515 ± 78 ha (range: 107-994) for *M. lucifugus* and 285 ± 32 ha (range: 22-650) for *M. sodalis*. Home ranges of both species overlapped within the study areas. However, *M. lucifugus* home ranges typically extended over more of the landscape, covering multiple habitat types. *M. sodalis* home ranges typically contained a smaller portion of the habitat types available in the landscape. Frequently, *M. sodalis* home ranges were contained within a single patch of habitat. Additionally, a majority (86%) of the *M. lucifugus* tracked had portions of their home range over the Mississippi River while none of the *M. sodalis* were tracked to those areas.

We found that the within the summers of 2010 and 2011 the date in which bats were tracked had a relationship with the size of the bat's home range for both species. There were relationships between the date in which tracking was commenced and *M. sodalis* home range size for both MCP and FK estimates ($R^2=0.48$, $p=0.038$; $R^2=0.73$, $p=0.007$; respectively). As the summer season progressed, the size of *M. sodalis* home ranges decreased (Fig. 3). Contrarily, *M. lucifugus* home ranges increased in size as the summer progressed (MCP; $R^2=0.50$, $p=0.007$; Fig. 1). There was no relationship between date and *M. lucifugus* home range size, as estimated by FK ($R^2=0.17$, $p=0.207$).

The results of our foraging habitat selection analyses show that *M. sodalis* orient their home ranges over specific habitats within a landscape (landscape level selection; $F=719.64$, $p<0.001$); selecting for areas with hydric habitats and open water while avoiding anthropogenically disturbed habitats (Table 1; Fig. 4). Other habitats were neither selected nor

avoided at the landscape level. At the home range level, *M. sodalis* did not select for specific habitats. Within the home ranges the observed distances to each habitat were not significantly different from expected distances ($F=0.433$, $p=0.876$).

M. lucifugus selected for habitat at both the landscape level and home range level of habitat selection ($F=201.126$, $p<0.001$; $F=4.339$, $p=0.009$; respectively). *M. lucifugus* typically orient their home ranges on the landscape to select for hydric habitats and open water and avoid habitats with open canopies (Table 2; Fig. 4). Within their home ranges, *M. lucifugus* specifically selected for closed canopy hydric habitats and open water (Fig. 4). All other habitats within their home ranges were neither selected nor avoided by *M. lucifugus* at the home range level.

Regardless of their selection of habitat, *M. sodalis* used habitat types in different amounts than *M. lucifugus* at the landscape level ($F=16.859$, $p<0.001$), orienting their home ranges closer to hydric habitats and open water than *M. lucifugus* (Table 3). However, *M. lucifugus* oriented their home ranges closer to urban habitat than *M. sodalis* ($p<0.001$). All other habitat types were used in similar amounts by the 2 species at the landscape level. The 2 species used habitat types in different amounts at the home range level of selection as well ($F=12.64$, $p<0.001$). *M. sodalis* used hydric habitats and roads more than *M. lucifugus* at the home range level (Table 3). However, *M. lucifugus* tended to forage within anthropogenic habitats more than *M. sodalis*. All other habitat types were used in similar amounts by the 2 species at the home range level.

DISCUSSION

M. sodalis and *M. lucifugus* partitioned resources within the study sites by varying their horizontal distribution (horizontal resource partitioning). This was accomplished by adopting different foraging strategies that horizontally separated the species from each other. By possessing foraging home ranges of different sizes and orienting them in different ways, the 2 bat species avoided foraging within the same habitats for prolonged periods of time. *M. lucifugus*

maintained large home ranges and selected for specific habitats within them. Alternately, *M. sodalis* oriented their smaller home ranges within large patches of preferred foraging habitat and, therefore, had no need to select for habitat within them. Both species had equal opportunity to forage within all habitats; both species roosted within the same patches of bottomland hardwood. However, *M. lucifugus* traveled large distances to forage within other patches of habitat. The immediate factor that may have caused this adoption of separate foraging strategies may be associated with the large colonies of *M. sodalis* and *M. lucifugus* within our study sites. It is possible that the 2 species adopted these different foraging strategies due to pressure from inter-specific competition caused by the large numbers of bats that have continually been within these colonies. However, we do not have sufficient evidence to adequately support this claim. We cannot rule out the possibility of other factors having effects on the foraging behavior of these species. It is possible that intra-specific competition may play a role in the increased dispersal of the large colonies of little brown bats from the roost each night. The minute morphological differences between the species may have an unforeseen impact on their foraging ecologies as well (Fenton & Barclay 1980; Fenton & Bell 1981; Thomson 1982; O'Farrell 1999). We are also unsure as to whether or not *M. lucifugus* use the same foraging strategy when they are allopatric to *M. sodalis* and, therefore, whether their foraging strategy was actually adopted due to the presence of *M. sodalis*.

M. lucifugus within both study sites had mean home ranges that were vastly larger than those of *M. sodalis*; they were 7 times larger than that of *M. sodalis* when estimated with MCPs (2739ha and 375ha respectively) and 2 times larger when estimated with FK (515ha and 285ha respectively). While our findings for *M. sodalis* were consistent with other studies (Gardner, Garner, & Hofmann 1991; Menzel et al. 2005; Sparks et al. 2005), our results on *M. lucifugus* were not consistent with other studies' results. Both Henry et al. (2002) and Broders et al. (2006) reported mean *M. lucifugus* home ranges of ≤ 52 ha. However, these studies may not be

representative of reproductively active females across the species' distribution since Henry et al. (2002) studied a population of *M. lucifugus* within a small island, 200ha, in the St. Lawrence River estuary and Broders et al. (2006) reported home range results solely for male *M. lucifugus*.

Our findings on *M. sodalis* habitat selection are consistent with other studies conducted within the northern section of the species' range (Humphrey, Richter, & Cope 1977; Gardner, Garner, Hofmann 1991; Sparks et al. 2005). When available, *M. sodalis* will forage within hydric habitats specifically. Because there was enough hydric habitat available within our study sites, *M. sodalis* were able to forage exclusively within it. This was observed in our study by the frequent use of bottomland hardwood by *M. sodalis* at both levels of selection. Our findings on *M. lucifugus* habitat selection were consistent with other studies on *M. lucifugus* foraging habits, which document the species frequently foraging over open water (LaVal et al. 1977; Saunders & Barclay 1992; Broders et al. 2006). However, this is the first study to examine the selection of foraging habitat by female *M. lucifugus*.

Both species selected for the same hydric habitats at the landscape level of habitat selection. However, *M. sodalis* oriented their home ranges much closer to these habitats than *M. lucifugus*. This is likely due to the large area of *M. lucifugus* home ranges which caused the small patches of hydric habitats to be less available to them than they were to *M. sodalis*, which oriented their home ranges over these habitats. The larger home ranges of *M. lucifugus* also explain the more frequent use of urban habitat by the species. *M. lucifugus* frequently traveled within close proximity of small towns when dispersing to distant foraging locations.

M. sodalis did not select for habitat within their home ranges (home range level). Even though they foraged at an average distance of 41m away from bottomland hardwood, *M. sodalis* did not use the habitat type more than what was expected. The *M. sodalis* we tracked not only selected for bottomland hardwood at the landscape level, they almost exclusively confined their home ranges within them. Typically, *M. sodalis* constrained their home ranges around 1 to 2

patches of bottomland hardwood, seldom deviating to stretch over open water or agriculture. However, several of the *M. sodalis* that we tracked arranged their home ranges completely within a single patch of bottomland hardwood in the Oakwood study site. Because of this, the availability of bottomland hardwood habitat within these individuals' home ranges was high, which caused the frequent use of the habitat by *M. sodalis* to be expected. *M. sodalis* oriented their home ranges in a way that allowed them to avoid traveling far distances in order to forage in preferred habitat. *M. lucifugus* on the other hand, had extensive home ranges that encompassed multiple habitat types. Within these home ranges *M. lucifugus* selected for open water and bottomland hardwood. The observation of significantly less use of these habitats by *M. lucifugus* than by *M. sodalis* can be explained by the *M. sodalis*' orientation of their home ranges within close proximity to these habitats.

We also found a difference between the 2 species' strategies of managing the increase of energy requirements caused by reproduction. Female insectivorous bats in the later stages of reproduction require larger amounts of energy for fetal and pup development (Kurta et al. 1989; Mclean & Speakman 1999). Females must therefore adopt foraging or physiological strategies in order to deal with this increased energy requirement. Both female *M. sodalis* and female *M. lucifugus* are known to alter their foraging habits as they progress through reproductive stages, developing more selective diets as the summer season progresses (Anthony & Kunz 1977; Belwood 1979; Kurta & Whitaker 1998). We can assume that this increase in dietary selectivity by both species is associated with a variation in habitat use. While we found that *M. sodalis* decreased the size of their home ranges as the summer season progressed, we found an inverse relationship for the *M. lucifugus* we tracked. It is possible that as *M. sodalis* begin to specialize in certain orders of insects as the summer progresses, they constrict their home ranges within an area that has a high abundance of these desirable insects. Female *M. lucifugus* may have increased the size of their home ranges in order to forage within specific habitats that have higher abundances

of beneficial insects. The fact that we only found a significant increase in the sizes of *M. lucifugus* home ranges estimated by MCP methods, and not in home ranges estimated by FK methods, may also support this hypothesis. Because FK takes the density of locations into account when estimating home ranges, it produces a much more accurate estimate of the bat's specific area of use than MCP estimates. MCPs represent the extent across the landscape a bat travels without regard to the density of bat locations within those areas. While this causes MCPs to be poor estimates of home range area, due to the potential of outliers and the misrepresentation of areas unused by the bats, they do provide researchers with a confident estimate of the extent of dispersal each bat traveled while foraging. Therefore, our results suggest that *M. lucifugus* may increase the distance they disperse, rather than the area they specifically use for foraging. Another possibility is that the increase in home range size (dispersal) by *M. lucifugus* over the summer season may be due to an increase in avoidance of competition. Female *M. lucifugus* in later stages of reproduction may disperse farther in order to forage within habitat that is less used by *M. sodalis* in order to avoid competing within them.

ACKNOWLEDGMENTS

We would like to thank the R. McClanahan of the Shawnee National Forest Division of U.S. Forest Service, and J. Kath of the Illinois Department of Natural Resources for their help funding the project. We would also like to thank M. Michaels, B. Funk, J. Weber, S. Rutan, A. Shultz, B. Lindsay, A. Wallace, and M. McCann for their contributions in the field.

REFERENCES

Aldridge, H.D., & Rautenbach, J.N. (1987) Morphology, echolocation, and resource partitioning in insectivorous bats. *Journal of Animal Ecology*, 56, 763-778.

- Aldridge, H.D.J.N., & Brigham, R.M. (1988). Load carrying and maneuverability in an insectivorous bat: a test of the 5% “rule” of radio-telemetry. *Journal of Mammalogy*, 69, 379-382.
- Allredge, R., & Ratti, J.T. (1986). Comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management*, 50, 157-165.
- Amelon, S.K, Dalton, D.C., Millspaugh, J.J., & Wolf, S.A. (2009). Radiotelemetry. *Ecological and behavioral methods for the study of bats*, 2nd edn (eds T.H. Kunz & S. Parsons), pp. 57-77. The Johns Hopkins University Press, Baltimore.
- Anthony, E.L.P., & Kunz, T.H. (1977). Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology*, 58, 775-786.
- Arlettaz, R. (1999). Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. *Journal of Animal Ecology*, 68, 460-471.
- Belwood, J.J. (1979). *Feeding ecology of an Indiana bat community with emphasis on the endangered Indiana bat, Myotis sodalis*. MS Thesis, University of Florida, Gainesville, Florida.
- Beyer, H.L. (2004). Hawth’s analysis tools for ArcGIS. <<http://spatial ecology.com/htools>>. Accessed 10 Oct 2010.
- Brack, V.W. (1983). *The nonhibernating ecology of bats in Indiana with emphasis on the endangered Indiana bat, Myotis sodalis*. PhD Thesis, Purdue University, West Lafayette, Indiana.
- Britzke, E.R., Murray, K.L., Heywood, J.S., & Robbins, L.W. (2002). Acoustic Identification. *The Indiana bat: biology and management of an endangered species* (eds A. Kurta and J. Kennedy), pp. 221-225. Bat Conservation International, Austin, Texas.

- Britzke, E.R. (2003). *Use of ultrasonic detectors for acoustic identification and study of bat ecology in the eastern united states*. PhD Thesis, Tennessee Technological University, Cookeville, TN.
- Broders, H.G., Findlay, C.S., & Zheng, L. (2004). Effects of clutter on echolocation call structure of *Myotis septentrionalis* and *M. lucifugus*. *Journal of Mammalogy*, 85, 273-281.
- Broders, H.G., Forbes, G.J., Woodley, S., & Thompson, I.D. (2006). Range extent and stand selection for roosting and foraging in forest-dwelling northern long-eared bats and little brown bats in The Greater Fundy Ecosystem, New Brunswick. *Journal of Wildlife Management*, 70, 1174-1184.
- Carter, T.C. & Feldhamer G.A. (2005). Roost trees used by maternity colonies of Indiana bats and northern *Myotis* in southern Illinois. *Forest Ecology and Management*, 219, 259-268.
- Carter, T.C., Michaels, M.L., & Schultz, A.M. (2009). *Monitoring Indiana bat maternity colonies in southern Illinois*. Annual Report, US Forest Service, Shawnee National Forest, Illinois.
- Carter, T.C., Bergeson, S.M., & Whitby, M.D. (2010). *Monitoring Indiana bat maternity colonies in southern Illinois*. Annual Report, US Forest Service, Shawnee National Forest, Illinois.
- Conner, L.M., & Plowman B.W. (2001). Using Euclidean distances to assess nonrandom habitat use. *Radio Tracking and Animal Populations*, (eds J. Millspaugh & J.M. Marzluff), pp. 275-290. Academic Press, London.
- Conner, L.M., Smith, M.D., & Burger, L.W. (2003). A comparison of distance-based and classification-based analyses of habitat use. *Ecology*, 84, 526-531.
- Feldhamer, G.A., Carter, T.C., & Whitaker, J.O., Jr. (2009). Prey consumed by eight species of insectivorous bats from Southern Illinois. *American Midland Naturalist*, 162, 43-51.
- Fenton, M.B., & Barclay, R.M.R. (1980). *Myotis lucifugus*. *Mammalian Species*, 142, 1-8.

- Fenton, M.B., & Bell, G.P. (1981). Recognition of species of insectivorous bats by their echolocation calls. *Journal of Mammalogy*, 62, 233-243.
- Fenton, M.B. (1982). Echolocation calls and patterns of hunting and habitat use of bats (Microchiroptera) from Chillagoe, North Queensland. *Australian Journal of Zoology*, 30, 417-425.
- Fenton, M.B., & Bogdanowicz, W. (2002). Relationships between external morphology and foraging behaviour: bats in the genus *Myotis*. *Canadian Journal of Zoology*, 80, 1004-1013.
- Gardner, J.E., Garner, J.D., & Hofmann, J.E. (1989). A portable mist netting system for capturing bats with emphasis on *Myotis sodalis* (Indiana bat). *Bat Research News*, 30, 1-8.
- Gardner, J.E., Garner, J.D., & Hofmann, J.E. (1991). *Summary of Myotis sodalis summer habitat studies in Illinois: with recommendations for impact assessment*. Illinois Natural History Survey/Illinois Department of Conservation, Champaign, Illinois.
- Gatz, A.J. (1979). Community organization in fishes as indicated by morphological features. *Ecology*, 60, 711-718.
- Grant, P.R. (1986). *Ecology and evolution of Darwin's finches*. Princeton University Press, Princeton, New Jersey.
- Griffin, D.R. (1971). The importance of atmospheric attenuation for the echolocation of bats (Chiroptera). *Animal Behaviour*, 19, 55-61.
- Hardin, G. (1960). The competitive exclusion principle. *Science*, 131, 1292-1297.
- Heller, K.G., & von Helverson, O. (1989). Resource partitioning of sonar frequency bands in rhinolophoid bats. *Oecologia*, 80, 178-186.
- Henry, M., Thomas, D.W., Vaudry, R., & Carrier, M. (2002). Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*). *Journal of Mammalogy*, 83, 767-774.

- Humphrey, S.R., Richter, A.R., & Cope, J.B. (1977). Summer habitat and ecology of the endangered Indiana bat, *Myotis sodalis*. *Journal of Mammalogy*, 58, 334-346.
- Johnson, D.H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61, 765-771.
- Kurta, A., Bell, G.P., Nagy, K.A., & Kunz, T.H. (1989). Energetics of pregnancy and lactation in free-ranging little brown bats (*Myotis lucifugus*). *Physiological Zoology*, 62, 804-818.
- Kurta, A., & Whitaker, J.O., Jr. (1998). Diet of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range. *American Midland Naturalist*, 140, 280-286.
- LaVal, R.K., Clawson, R.L., LaVal, M.L., & Caire, W. (1977). Foraging behavior and nocturnal activity patterns of Missouri bats, with emphasis on the endangered species *Myotis grisescens* and *Myotis sodalis*. *Journal of Mammalogy*, 58, 592-599.
- Lee, Y.F., & McCracken, G.F. (2004). Flight activity and food habits of three species of *Myotis* bats (Chiroptera: Vespertilionidae) in sympatry. *Zoological Studies*, 43, 589-597.
- Losos, J.B. (1990). Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecological Monographs*, 60, 369-388.
- Mclean, J.A., & Speakman, J.R. (1999). Energy budgets of lactating and non-reproductive brown long-eared bats (*Plecotus auritus*) suggest females use compensation in lactation. *Functional Ecology*, 13, 360-372.
- Menzel, J.M., Ford, W.M., Menzel, M.A., Carter, T.C., Gardner, J.E., Gardner, J.D., & Hofmann, J.E. (2005). Summer habitat use and home-range analysis of the endangered Indiana bat. *Journal of Wildlife Management*, 69, 430-436.
- Miller, N.E., & Allen, G.M. (1928). The American bats of the genera *Myotis* and *Pizonyx*. *Bulletin of the U.S. National Museum*, 144, 130-135.
- Nams, V.O. (2006). *Locate III User's Guide*. Pacer Computer Software, Tatamagouche, Nova Scotia.

- Norberg, U.M., & Rayner, J.M.V. (1987). Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London, Series B*, 316, 335-427.
- O'Farrell, M.J. (1999). Blind test for ability to discriminate vocal signatures of the little brown bat *Myotis lucifugus* and the Indiana bat *Myotis sodalis*. *Bat Research News*, 40, 44-48.
- Rodgers, A.R., Carr, A.P., Beyer, H.L., Smith, L., & Kie, J.G. (2007). *HRT: home range tools for ArcGIS. Version 1.1*. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario.
- Saunders, M.B., & Barclay, R.M.R. (1992). Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. *Ecology*, 73, 1335-1345.
- Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J., & Gitzen, R.A. (1999). Effect of sample size on kernel home range estimates. *Journal of Wildlife Management*, 63, 739-747.
- Schnitzler, H.-U., & Kalko, E.K.V. (2004). Echolocation by insect-eating bats. *BioScience*, 51, 557-569.
- Simmons, J.A., & Stein, R.A. (1980). Acoustic imaging in bat sonar: echolocation signals and the evolution of echolocation. *Journal of Comparative Physiology*, 155, 61-84.
- Sparks, D.W., Ritzi, C.M., Duchamp, J.E., & Whitaker, J.O., Jr. (2005). Foraging habitat of the Indiana bat (*Myotis sodalis*) at an urban-rural interface. *Journal of Mammalogy*, 86, 713-718.
- Spencer, L.M. (1995). Morphological correlates of dietary resource partitioning in the African Bovidae. *Journal of Mammalogy*, 76, 448-471.
- Swihart, R.K., & Slade, S.A. (1985). Testing for independence of observations in animal movements. *Ecology*, 66, 1176-1184.
- Thomson, C.E. (1982). *Myotis sodalis*. *Mammalian Species*, 163, 1-5.

Whitby, M.D., Bergeson, S.M., Rutan, S.A., & Carter, T.C. (2011). *Monitoring Indiana bat maternity colonies in southern Illinois*. Annual Report, US Forest Service, Shawnee National Forest, Illinois.

Zaret, T.M. (1980). *Predation and freshwater communities*. Yale University Press, New Haven, Connecticut.

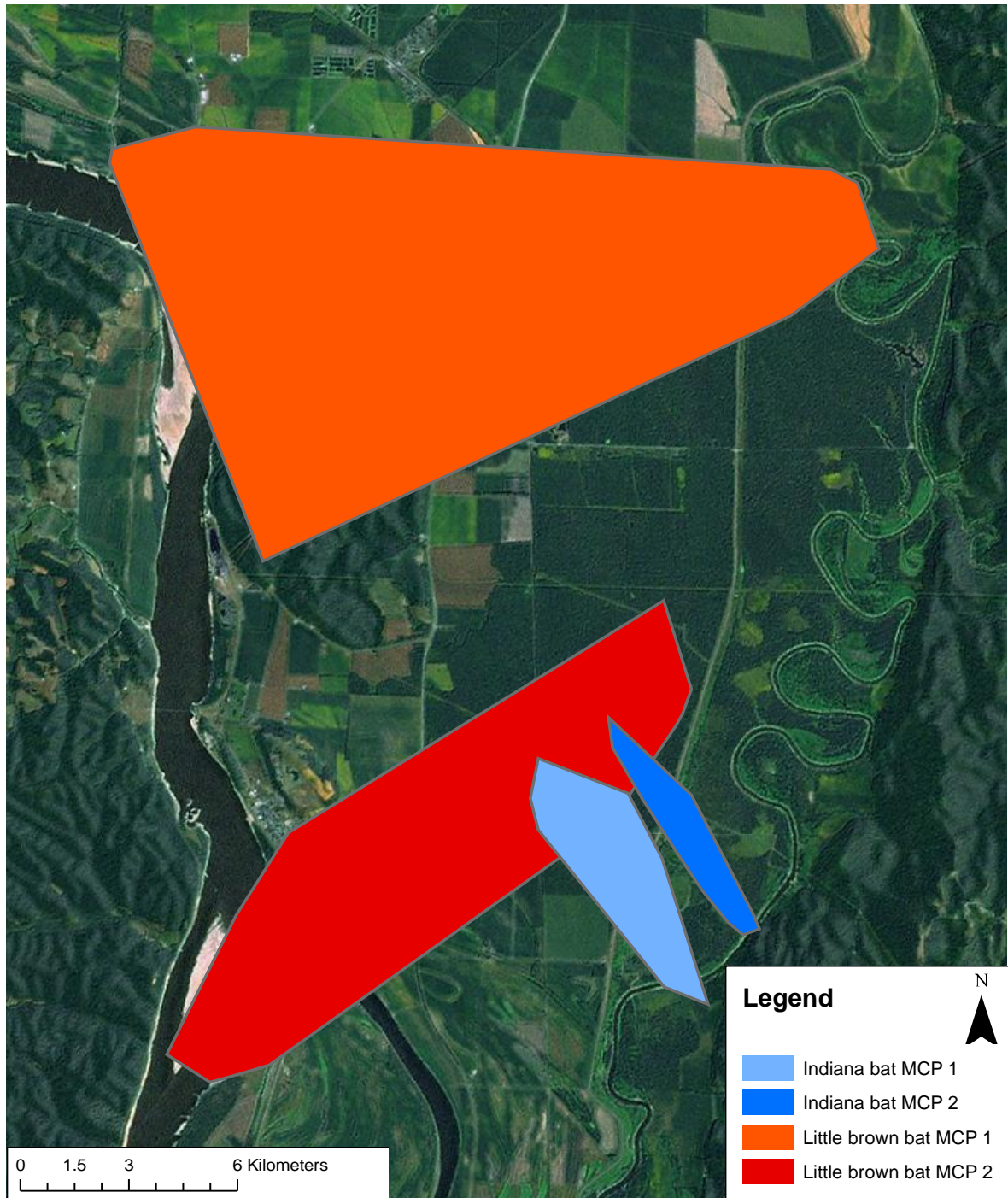


Figure 1: Minimum convex polygon (MCP) foraging home ranges of 2 *Myotis sodalis* (Indiana bat) and 2 *M. lucifugus* (little brown bat) located near Oakwood Bottoms Greentree Reservoir, Jackson County, IL.

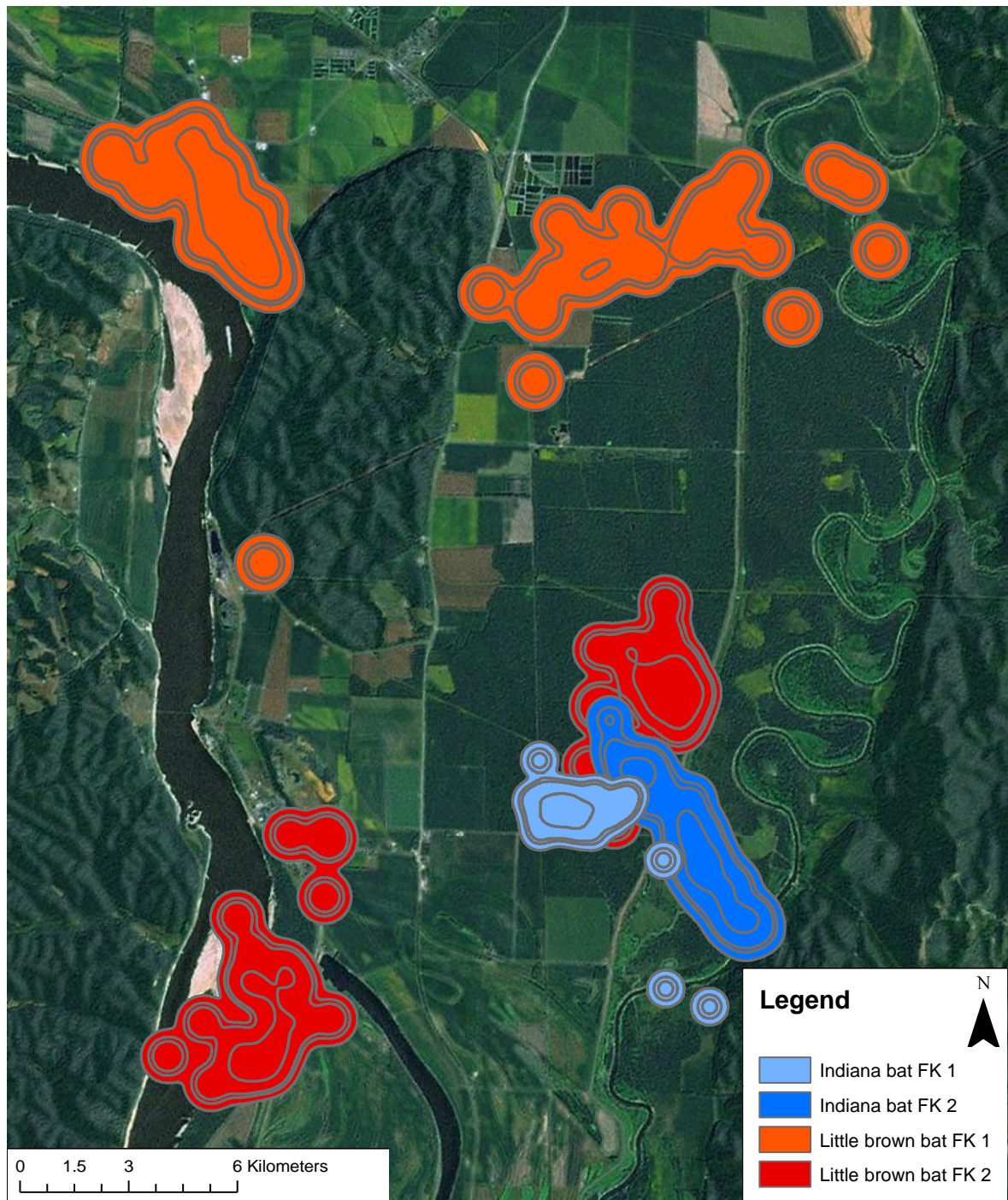


Figure 2: 95% fixed kernel (FK) foraging home ranges of 2 *Myotis sodalis* (Indiana bat) and 2 *M. lucifugus* (little brown bat) located near Oakwood Bottoms Greentree Reservoir, Jackson County, IL.

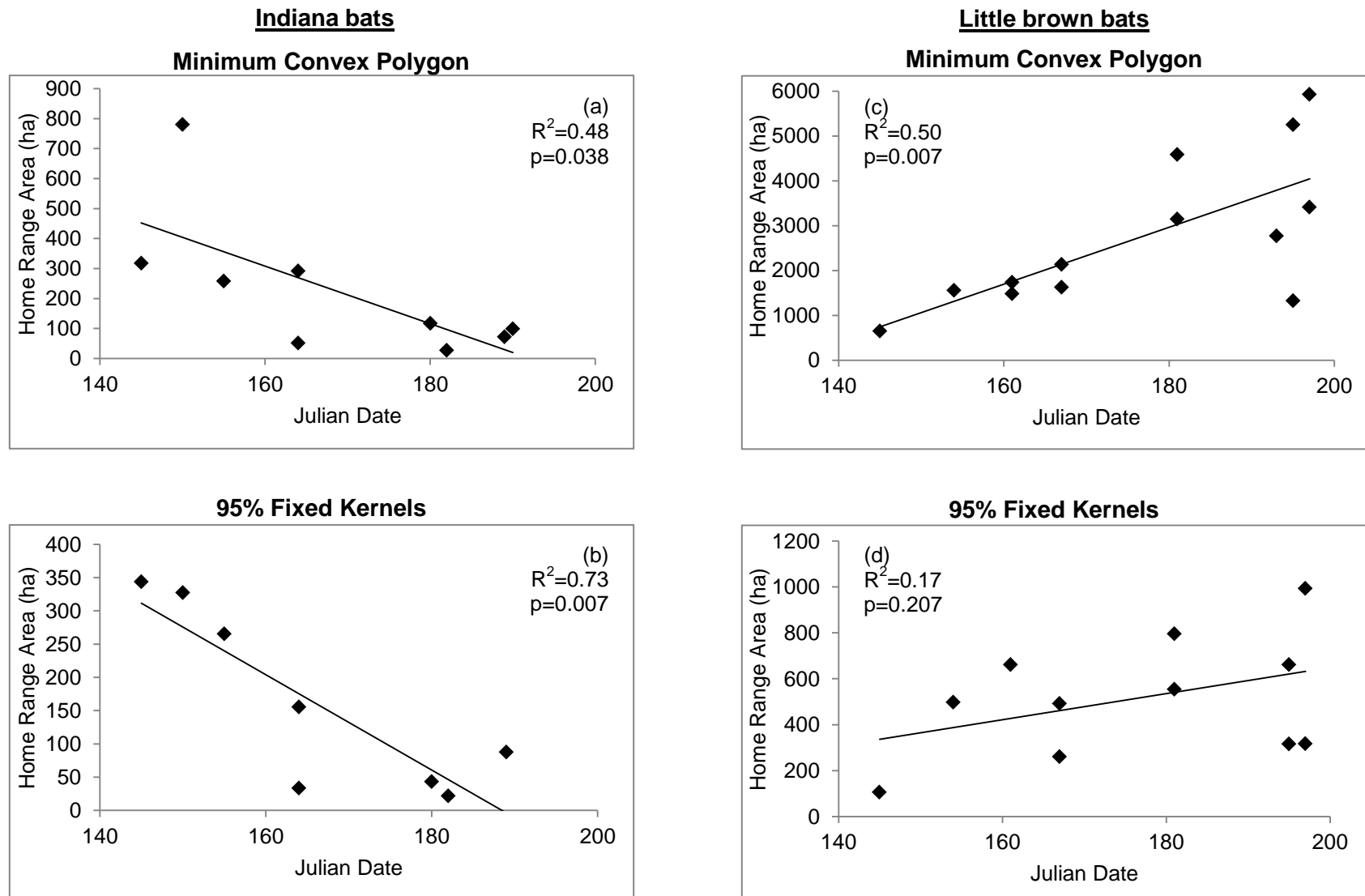


Figure 3: The relationship between home range area and Julian date of transmitter affixation in little brown bats and Indiana bats tracked within 2 study sites in southern Illinois. This relationship was tested with linear regressions conducted on Indiana bat home ranges generated by minimum convex polygons (a) and 95% fixed kernel estimates (b), as well as, little brown bat home ranges generated by minimum convex polygon (c) and 95% fixed kernel estimates (d).

Table 1: Statistical tests of disproportion between the mean distances from random and actual location points of both Indiana bats and little brown bats to the nearest patch of 7 habitat types.

Habitat Type	Indiana bat				
	Distance from random points (m; n=25)	Distance from actual points (m; n=25)	Mean Distance Ratio	Test statistic	
	$\bar{x} \pm \text{S.E. (range)}$	$\bar{x} \pm \text{S.E. (range)}$		<i>t</i>	p-value
Landscape Level Habitat Selection (2nd order)					
Wetland	4207 ± 38 (3917-4407)	513 ± 51 (130-1137)	0.12	77.61	p<0.001
Open Water	1006 ± 11 (946-1088)	468 ± 54 (91-1199)	0.46	8.36	p<0.001
Urban	750 ± 13 (699-838)	1564 ± 103 (590-2765)	2.09	-7.15	p<0.001
Road/railroad	300 ± 0.6 (296-304)	316 ± 25 (99-593)	1.05	-	p=1.00
Forest	203 ± 10 (166-268)	260 ± 41 (26-728)	1.28	-	p=1.00
Bottomland Hardwood	1898 ± 31 (1672-2037)	50 ± 11 (0-220)	0.03	45.57	p<0.001
Agriculture/grassland	110 ± 0.1 (110-111)	349 ± 40 (86-796)	3.16	-	p<0.001
Individual Level Habitat Selection (3rd Order)^a					
Wetland	513 ± 51 (130-1137)	478 ± 49 (135-1144)	0.93		
Open Water	468 ± 54 (91-1199)	422 ± 52 (81-1132)	0.90		
Urban	1564 ± 103 (590-2765)	1565 ± 98 (564-2694)	1.00		
Road/railroad	316 ± 25 (99-593)	295 ± 27 (79-558)	0.93		
Forest	260 ± 41 (26-728)	290 ± 52 (13-804)	1.12		
Bottomland Hardwood	50 ± 11 (0-220)	41 ± 11 (0-236)	0.82		
Agriculture/grassland	349 ± 40 (86-796)	357 ± 39 (88-800)	1.02		

^a Indiana bats were found to not select for habitat at the 3rd order of selection. Therefore, no statistics were run to test the disproportion between random and actual distances.

Table 2: Statistical tests of disproportion between the mean distances from random and actual location points of little brown bats to the nearest patch of 7 habitat types.

Habitat Type	Little brown bat				
	Distance from random points (m; n=25)	Distance from actual points (m; n=25)	Mean Distance Ratio	Test statistic	
	$\bar{x} \pm \text{S.E. (range)}$	$\bar{x} \pm \text{S.E. (range)}$		<i>t</i>	p-value
Landscape Level Habitat Selection (2nd order)					
Wetland	4222 \pm 9 (4135-4231)	1283 \pm 108 (640-1655)	0.30	-	p=0.001
Open Water	956 \pm 10 (946-1055)	654 \pm 52 (283-900)	0.68	-	p=0.001
Urban	710 \pm 11 (699-821)	842 \pm 86 (573-1423)	1.19	-	p=0.55
Road/railroad	302 \pm 0.1 (302-304)	377 \pm 18 (281-464)	1.25	-4.05	p=0.002
Forest	178 \pm 8 (170-257)	268 \pm 41 (107-573)	1.51	-	p=0.065
Bottomland Hardwood	2007 \pm 29 (1714-2037)	407 \pm 64 (2-808)	0.20	-	p=0.001
Agriculture/grassland	111 \pm 0.05 (110-111)	292 \pm 33 (107-502)	2.64	-	p=0.012
Individual Level Habitat Selection (3rd Order)					
Wetland	1283 \pm 108 (640-1655)	1189 \pm 159 (568-1972)	0.92	0.82	p=0.432
Open Water	654 \pm 52 (283-900)	427 \pm 75 (137-884)	0.66	3.31	p=0.008
Urban	842 \pm 86 (573-1423)	1061 \pm 124 (561-1774)	1.31	-	p=0.23
Road/railroad	377 \pm 18 (281-464)	408 \pm 36 (265-575)	1.10	-0.87	p=0.40
Forest	268 \pm 41 (107-573)	185 \pm 20 (123-349)	0.82	-	p=0.23
Bottomland Hardwood	407 \pm 64 (2-808)	224 \pm 33 (6-378)	0.81	3.56	p=0.005
Agriculture/grassland	292 \pm 33 (107-502)	236 \pm 23 (106-349)	0.90	1.68	p=0.125

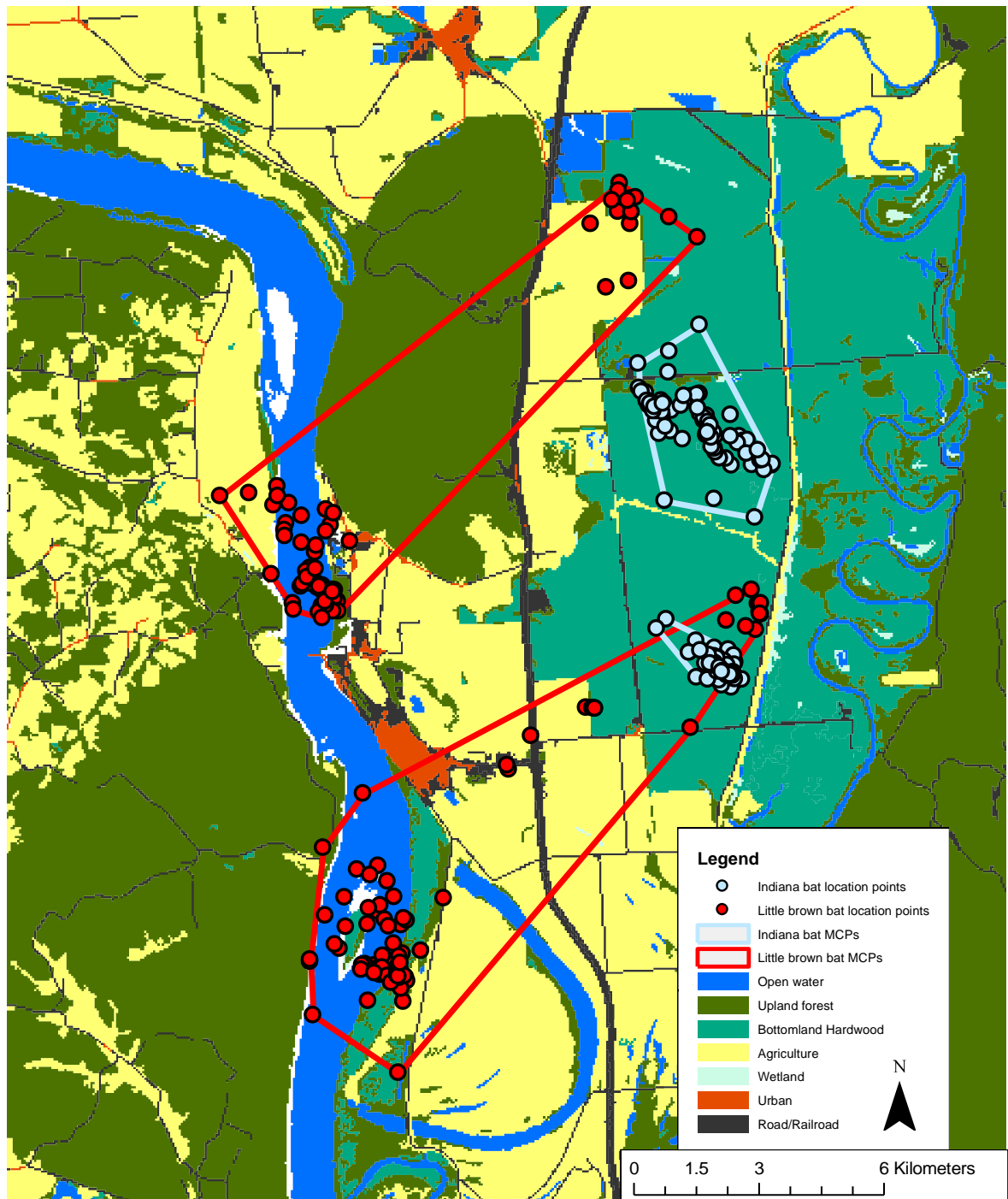


Figure 4: Map of the minimum convex polygon (MCP) home ranges and location points of 2 *Myotis sodalis* (Indiana bat) and 2 *M. lucifugus* (little brown bat) individuals foraging around Oakwood Bottoms Greentree Reservoir, Jackson county, IL; representing the landscape level and home range level foraging habitat selection of either species. Foraging habitat selection was determined for 7 habitat types within 2 study sties.

Table 3: Statistical tests of disproportion between habitat use of Indiana bats and little brown bats based on the average distances from actual location estimates from 7 habitats for both species.

Habitat Type	Indiana Bat	Little Brown Bat	Test statistic	
	Distance from actual points (m; n=25)	Distance from actual points (m; n=25)		
	$\bar{x} \pm \text{S.E. (range)}$	$\bar{x} \pm \text{S.E. (range)}$	<i>t</i>	p-value
Landscape Level Habitat Use (2nd order)				
Wetland	513 \pm 51 (130-1137)	1283 \pm 108 (640-1655)	-7.17	p<0.001
Open Water	468 \pm 54 (91-1199)	654 \pm 52 (283-900)	-	p=0.021
Urban	1564 \pm 103 (590-2765)	842 \pm 86 (573-1423)	-	p<0.001
Road/railroad	316 \pm 25 (99-593)	377 \pm 18 (281-464)	-1.95	p=0.06
Forest	260 \pm 41 (26-728)	268 \pm 41 (107-573)	-	p=0.43
Bottomland Hardwood	50 \pm 11 (0-220)	407 \pm 64 (2-808)	-	p<0.001
Agriculture/grassland	349 \pm 40 (86-796)	292 \pm 33 (107-502)	1.10	p=0.28
Individual Level Habitat Use (3rd Order)				
Wetland	478 \pm 49 (135-1144)	1189 \pm 159 (568-1972)	-4.27	p=0.001
Open Water	422 \pm 52 (81-1132)	427 \pm 75 (137-884)	-	p=0.89
Urban	1565 \pm 98 (564-2694)	1061 \pm 124 (561-1774)	2.98	p=0.005
Road/railroad	295 \pm 27 (79-558)	408 \pm 36 (265-575)	-2.43	p=0.021
Forest	290 \pm 52 (13-804)	185 \pm 20 (123-349)	-	p=0.86
Bottomland Hardwood	41 \pm 11 (0-236)	225 \pm 33 (19-378)	-	p<0.001
Agriculture/grassland	357 \pm 39 (88-800)	236 \pm 23 (106-349)	2.68	p=0.011

CHAPTER 4

**SUITABILITY OF LITTLE BROWN BATS (*MYOTIS LUCIFUGUS*) AS
SURROGATES FOR INDIANA BAT (*MYOTIS SODALIS*) SUMMER RESEARCH
AND MANAGEMENT.**

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ABSTRACT

The endangered Indiana bat (*Myotis sodalis*) has been declining throughout its distribution for the past several decades. Researchers and managers working with the species often find it hard to avoid causing the endangered Indiana bat inadvertent harm through their activities. In order to avoid these inadvertent stressors, biologists can potentially use surrogate subjects in their projects. In order for these surrogates to be suitable they must have similar characteristics to the original target species. The types of similarities required are dependent on the objectives of the project the surrogate is used in. Little brown bats are often suggested as suitable surrogates for Indiana bats. However, their suitability has never been intensively examined. Therefore, this study was conducted in order to examine the suitability of little brown bats as surrogates for Indiana bat summer habitat research and management. In order to do this, a meta-analysis was conducted on data collected from multiple published literature sources to compare the roosting ecologies, foraging ecologies, and diets of the species. While there were some similarities between the 2 species' roosting ecologies and diets, there were other characteristics that were different. The differences in the species' foraging ecologies as well as the tendency for little brown bats to use anthropogenic roosts when available reduces the suitability of little brown bats as surrogates for Indiana bat summer habitat research and management. With this in mind, conducting holistic Indiana bat summer habitat research and management using little brown bats as a surrogate is unadvised.

KEYWORDS

Surrogate, substitute, endangered, habitat management, *Myotis sodalis*, *Myotis lucifugus*

INTRODUCTION

Since its addition to the endangered species list in 1967, the Indiana bat (*Myotis sodalis*) has been a target of conservation management and concern throughout its distribution (USFWS 2007). Due to this endangered status, researchers and managers may find working with the species difficult. A major concern is the inadvertent negative effects to the species that research and management activities may produce. Activities such as hibernaculum surveys, attaching transmitters, roost surveys, habitat management, and many others can affect bat behavior, ecology, and physiology (Aldridge & Brigham 1988; Thomas et al. 1990; Gardner et al. 1991b; Hicks & Novak 2002). Also, studies that require the conscious infliction of take, such as those that require sacrificing bats to conduct research, are typically unable to be conducted on endangered species due to the effect they have on their populations. Researchers and managers also need to address legal issues dealing with the species. For example, without obtaining a federal permit, biologists are not able to legally work with the species. Additionally, studies on the species may suffer from small sample sizes due to the rarity of the species. As a result of these concerns, and others, many biologists may choose to use a surrogate when conducting research or management on endangered or hard to work with species, including the Indiana bat.

There are multiple definitions of the term “surrogate” as well as numerous uses of the surrogate tool (Wilcox 1984; Landres et al. 1988; Mills et al. 1993; Dietz et al. 1994; Lambeck 1997; Armstrong 2002; Caro et al. 2005). However, we will define a surrogate as a species used as a substitute subject for another, more inaccessible, species in order to draw conclusions on it and/or manage for it. This definition is similar to the definition of a “substitute” that Caro et al. (2005) examined. We will, therefore, use the terms interchangeably.

Caro et al.’s (2005) work focuses on determining the suitability of surrogates in ecosystem level conservation management; using surrogates to identify ecosystems potentially at risk of disturbance and to determine which disturbance factors cause the most harm to endangered species. Understandably, Caro et al. (2005) puts forth a series of stringent assumptions of

similarity that must be met before a surrogate can be deemed suitable for use in conservation management. However, these assumptions may be inappropriate for projects with other objectives. Endangered species managers are often concerned with increasing the quality and quantity of preferred habitats available to the endangered species. Therefore, there is a different, but no less stringent, set of assumptions of similarity to be met for managers to use surrogate species in this manner. The specific assumptions of similarity needed to be met for each project will be dependent on the project's objectives. For instance, a project focusing on increasing the quality/quantity of the overall summer maternity habitat for a population of Indiana bats will require a surrogate species that has similar roosting ecology and foraging ecology. If these characteristics are not similar between the species, data collected on the unacceptable surrogate may cause biologists to draw misleading conclusions, on the species of interest, and make poor management decisions.

The Indiana bat recovery plan suggests the use of surrogate species when conducting Indiana bat research and management (USFWS 2007). While the recovery plan does not specify a particular species as being a more suitable surrogate than others, many biologists suggest, or have used, little brown bats as surrogates (*Myotis lucifugus*; Brack et al. 2002; Schmidt et al. 2002; Richardson et al. 2008; Jones & Nagy 2010; Romeling et al. 2010). This suggestion may be based on the perception of ecological and behavioral similarity between the species because of their close morphological similarities. This assumption of similar ecological and behavioral characteristics has never been intensively examined; causing any interpretation of little brown bat data directed towards the Indiana bat to be potentially misleading.

The objective of this study was to examine the suitability of little brown bats as a surrogate for Indiana bats in summer habitat management by comparing their roosting ecologies and foraging ecologies. We hypothesize that little brown bats are similar enough to Indiana bats

to deem the species suitable for use as a surrogate in future Indiana bat summer habitat management.

METHODS

For the purposes of this study we compiled data from multiple existing published literature sources focused on the roosting and foraging ecologies of Indiana and little brown bats (Table 1). We focused on maternity colonies due to their importance to the survival of the species (USFWS 2007). We attempted to review studies conducted solely within the Indiana bat's range. Unfortunately, there are few studies conducted on little brown bats within the distribution of the Indiana bat. We were therefore forced to include data from studies conducted outside of the distribution in several of our analyses.

We compiled data on natural maternity roost characteristics including: roosting habitat, roost tree species, roost type, roost height, roost tree condition (dead or live), diameter of roost trees at breast height (DBH), roost tree height, the number of times bats changed roosts, the number of consecutive nights spent within the same roost (residency), the distance between consecutive roosts, and the max distance traveled between all used roosts. While we did collect published literature sources on anthropogenic roost use, we did not compile these data with the natural roost data.

We compiled and compared the mean home range sizes of bats of both species. Due to the ease of its comparison, we only used minimum convex polygon home range models, generated from data collected by radio-telemetry, for this meta-analysis. We also compared the results of studies conducted on the habitat selection of the 2 species at the landscape and home range levels, Johnson (1980)'s 2nd and 3rd order habitat selection.

We compared the diets reported in the literature of both species, as determined by fecal analysis or DNA sequencing of prey item remains (Whitaker et al. 2009).

RESULTS

Roosting Ecology

Roosting characteristics were compared between the species using data from 11 sources (Table 1). We could only find 2 published studies conducted on little brown bats, however, these were conducted outside of the Indiana bat's distribution. We examined data from a total of 381 Indiana bat roosts and 61 little brown bat roosts.

The 2 bat species were fairly similar in roosting ecology at broader ecosystem levels (stand and landscape levels). The 2 species tended to both roost within hydric habitats (bottomland hardwoods, riparian habitat) as well as upland forests throughout the Indiana bat's distribution. The 2 species also tended to use the same variety of tree species.

The roosting ecologies were different between Indiana bats and little brown bats at the microhabitat level. There were some similarities in their roosting characteristics (e.g., DBH, tree condition, and distance between consecutive roosts). However, these similarities are not as biologically important as the differences that we found. Foremost, the 2 species used different roost types. Indiana bats roosts were primarily exfoliating bark roosts (91%) while little brown bat roosts tended to be crevice/cavity roosts (58%).

Foraging Ecology

Foraging home ranges were compared between the species using data compiled from 6 sources (Table 1). While data were compiled from 1 study conducted on both species, the majority of the home range data we compiled on little brown bats was from 2 studies conducted on little brown bats outside of the Indiana bats' distribution. Foraging habitat selection data were compiled from 5 sources (Table 1). Data were used from 1 study conducted on little brown bats outside of the Indiana bat's distribution. Data from 3 and 4 studies were used to compare foraging

habitat selection at the landscape level and the home range level between the species, respectively.

Indiana bats and little brown bats select for similar foraging habitat at the landscape level, orienting their home ranges specifically over hydric habitats (wetlands, bottomland hardwood, open water, etc.) and avoiding agriculture at the landscape level within the sympatric portion of their distributions (Gardner et al. 1991a; Bergeson et al.'s Pending-b). While the selection of habitat at the landscape level is similar between the species, the sizes of their home ranges tend to be different. The average mean home range size of Indiana bats and little brown bats were 283ha and 2739ha, respectively. Bergeson et al. (Pending-b) found that the expansive home ranges of little brown bats were spread across multiple patches of varying habitats and therefore had more habitats available within them than the home ranges of Indiana bats.

The 2 species do not select for habitat similarly within their home ranges (home range level habitat selection). By reviewing multiple studies we found that Indiana bats either selected for varying habitat types (e.g., upland forest, bottomland hardwoods) or did not select for habitat at all. The species also tended to avoid agriculture, pastures, and high density residential habitat. However, Sparks et al. (2005) found that Indiana bats will select for woodlands and agriculture at the home range level when in an urban and agriculturally dominated landscape. Bergeson et al. (Pending-b) found that Indiana bats did not select for or avoid any habitats while foraging within the Shawnee National Forest, IL; stating that the bats had preferentially positioned their small home ranges within large patches of their preferred foraging habitat, bottomland hardwoods, eliminating the need to further select for habitat at a finer scale. The data we compiled on little brown bat home range level habitat selection suggests that the species selects for open water and bottomland hardwoods within their extensive home ranges while consciously avoiding nothing (Broders et al. 2006; Bergeson et al. Pending-b).

Diet

In order to compare the diets of each species we reviewed 5 sources (Table 1). The results of these sources suggest that both species primarily consumed insects 3-10mm of the same 4 orders (Diptera, Lepidoptera, Trichoptera, and Coleoptera) throughout the Indiana bat's distribution. Studies on the diet of Indiana bats suggest that they consume high percentages of either flies (Diptera) and caddis flies (Trichoptera) or moths (Lepidoptera), depending on their geographic location (Kurta & Whitaker 1998; Murray & Kurta 2002; Lee & McCracken 2004; Feldhamer et al. 2009). The results of our meta-analysis supports the theory that the Indiana bat's diet changes with latitude, consisting of more aquatic-based insects (flies and caddis flies) in the northern portion of its distribution and terrestrial-based insects (moths) in its southern portion (Murray & Kurta 2002). Little brown bats had a more varied diet than Indiana bats, typically predated relatively equal amounts of moths, beetles (Coleoptera), and caddis flies throughout the eastern portion of its distribution (Anthony & Kunz 1977; Lee & McCracken 2004; Feldhamer et al. 2009). Little brown bats also consumed other groups of arthropods, such as May flies (Ephemeroptera) and spiders (Araneae), at relatively high proportions (Anthony & Kunz 1977; Feldhamer et al. 2009). These arthropod taxa were rarely recorded in the diets of Indiana bats. Also, little brown bats did not have a clear differentiation between the diets of northern populations and southern populations, as did Indiana bats. While little brown bat diets did change throughout the species' distribution, it was not a dramatic change. Additionally, Lee and McCracken (2004) found that Indiana bats had a greater preference for lepidopterans and little brown bats had a greater preference for insects with a medium-hard exoskeleton (caddis flies, flies, and May flies) when both species were studied in Indiana, in sympatry. They also found that when the species were syntopic, little brown bats predated more flies and less moths than they did when the species were allotopic.

DISCUSSION

Using little brown bats as a surrogate for holistic Indiana bat summer maternity habitat research or management is risky. While there are several summer ecological characteristics that are similar between the species there are other characteristics that are dissimilar enough to question the suitability of little brown bats as a surrogate.

Several fine scale roost characteristics were dissimilar between the species. However, larger scale characteristics were similar between the species. Similarities in large scale roost characteristics are more pertinent to the suitability of little brown bats as surrogates because managers typically manage for bat habitat at larger scales. Since the species roost within similar habitats and within similar tree species, managers may be able to manage for known little brown bat roosting habitat and natural roosts in order to potentially increase roosting habitat for Indiana bats. However, little brown bats typically roost within anthropogenic roosts more than Indiana bats (Barclay & Cash 1985). Additionally, there are more reports of little brown bats using anthropogenic roosts (e.g., Fenton 1970; Humphrey & Cope 1976; Schowalter et al. 1979; Bergeson et al. Pending-a) than there are of Indiana bats (Butchkoski & Hassinger 2002; Bergeson et al. Pending-a). Anthropogenic roosts can be located in urban habitats that are devoid of potential natural roost trees, potentially causing this suitable habitat for little brown bats to be uninhabitable by Indiana bats (Bergeson et al. Pending-a). In this case, little brown bats would not be an acceptable surrogate for Indiana bats.

While bats of both species orient their home ranges over similar habitat (i.e. they select for similar habitat at the landscape level) they have very different home ranges. Little brown bats tend to spread their home ranges over the landscape in order to reach preferred foraging habitats. This generalist strategy is inherently different from that of Indiana bats which tend to focus their home ranges around, and select for, a few particular habitats (Bergeson et al. Pending-b). The diets of either species supports this difference in feeding strategy; little brown bats having a more

varied diet, typically consisting of a majority of aquatic-based insects, while Indiana bats specialize in the predation of only a few particular insect orders. This difference in feeding strategy further reduces the suitability of little brown bats as surrogates for Indiana bat summer habitat research and management. While, managing for little brown bat foraging habitat may indirectly increase potential Indiana bat foraging habitat due to both species' tendencies to forage within hydric habitats, managers are more likely to spend valuable time and resources conserving multiple habitats, some of which Indiana bats may never use.

Managers may be able to confidently manage for Indiana bat roosting habitat using little brown bats as surrogates, depending on the presence of anthropogenic roosts. However, managers must target more than a single resource in order for management projects to be effective. The Indiana bat recovery plan calls for the management of roosting and foraging habitat (USFWS 2007). Managers must, therefore, manage for these multiple habitats in order to effectively conserve the endangered species. In order for managers to be confident in their use of little brown bats as surrogates for this holistic management strategy, the 2 species must be similar in both roosting and foraging ecology. Because of the established dissimilarities in foraging ecology, little brown bats are an unacceptable surrogate for Indiana bats for holistic summer maternity habitat management.

More research needs to be conducted on little brown bat roosting ecology and foraging ecology in order to support these theories. While the studies on Indiana bats reviewed for this meta-analysis cover a large portion of the species' distribution, only a few studies reported data on little brown bats within the distribution of the Indiana bat. Additional research needs to be conducted on little brown bats within the Indiana bats distribution in order to reliably compare the species ecologies. Also, research on additional roost micro-climate characteristics is needed in order to determine if any microhabitat scale differences occur between the species, that this study was not been able to address. By increasing the research on little brown bats across the Indiana

bat's distribution as well as in these subjects, researchers will be able to get a better understanding on how ecologically similar the 2 species are. This will, therefore, give researchers a better idea on whether little brown bats are a suitable surrogate for Indiana bats.

It is possible that there are other species of bats within the Indiana bat's distribution that would make more suitable surrogates than little brown bats. Studies conducted on the northern bat (*Myotis septentrionalis*), which is relatively common within the Indiana bat's distribution, suggest that the species may have a closer similarity to Indiana bats in roosting ecology than little brown bats do (Foster & Kurta 1999; Carter & Feldhamer 2005; Lacki et al. 2009; Timpone et al. 2010). However, northern bats are also known to forage within highly cluttered habitats and exhibit very different foraging strategies than Indiana bats (Norberg & Rayner 1987; Faure et al. 1993; Broders 2003). Because of this it is questionable as to whether the species would be a suitable surrogate for holistic Indiana bat summer habitat research and management. More research needs to be conducted on the northern bat, as well as other potential surrogate species, in order to determine which, if any, would be suitable surrogates.

LITERATURE CITED

- Aldridge, H.D.J.N., and R.M. Brigham. 1988. Load carrying and maneuverability in an insectivorous bat: a test of the 5% "rule" of radio-telemetry. *Journal of Mammalogy* **69**: 379-382.
- Anthony, E.L.P., and T.H. Kunz. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology* **58**: 775-786.
- Armstrong, D. 2002. Focal and surrogate species: getting the language right. *Conservation Biology* **16**: 285-287.
- Barclay, R.M.R., and K.J. Cash. 1985. A non-commensal maternity roost of the little brown bat (*Myotis lucifugus*). *Journal of Mammalogy* **66**: 782-783.

- Bergeson, S.M., M.W. Whitby, and T.C. Carter. Pending_a. Summer maternity roost comparisons between Indiana bats and little brown bats.
- Bergeson, S.M., M.W. Whitby, and T.C. Carter. Pending_b. Spatial resource partitioning between sympatric populations of Indiana bats and little brown bats in southern Illinois.
- Brack, V.Jr., C.W. Stihler, R.J. Reynolds, C.M. Butchkoski, and C.S. Hobson. 2002. Effect of climate and elevation on distribution and abundance in the mideastern United States. Pages 21-28 in A. Kurta and J. Kennedy, editors. The Indiana bat: biology and management of an endangered species. Bat Conservation International, Austin, USA.
- Britzke, E.R., M.J. Harvey, and S.C. Loeb. 2003. Indiana bat, *Myotis sodalis*, maternity roosts in the southern United States. Southeastern Naturalist **2**: 235-242.
- Broders, H.G. 2003. Summer roosting and foraging behaviour of sympatric *Myotis septentrionalis* and *M. lucifugus*. PhD dissertation, Department of Biology, University of New Brunswick, Fredericton, Canada.
- Broders, H.G., G.J. Forbes, S. Woodley, and I.D. Thompson. 2006. Range extend and stand selection for roosting and foraging in forest-dwelling northern long-eared bats and little brown bats in the Greater Fundy Ecosystem, New Brunswick. The Journal of Wildlife Management **70**:1174-1180.
- Butchkoski, C.M., and J.D. Hassinger. 2002. Ecology of a maternity colony roosting in a building. Pages 130-142 in A. Kurta and J. Kennedy, editors. The Indiana bat: biology and management of an endangered species. Bat Conservation International, Austin, USA.
- Callahan, E.V., R.D. Drobney, and R.L. Clawson. 1997. Selection of summer roosting sites by Indiana bats (*Myotis sodalis*) in Missouri. Journal of Mammalogy **78**: 818-825.
- Caro, T., J. Eadie, and A. Sih. 2005. Use of substitute species in conservation biology. Conservation Biology **19**:1821-1826.

- Carter, T.C. 2006. Indiana bats in the Midwest: the importance of hydric habitats. *The Journal of Wildlife Management* **70**: 1185-1190.
- Carter, T.C., and G.A. Feldhamer. 2005. Roost tree use by maternity colonies of Indiana bats and northern long-eared bats in southern Illinois. *Forest Ecology and Management* **219**: 259-268.
- Clare, E.L., B.R. Barber, B.W. Sweeney, P.D.N. Herbet, and M.B. Fenton. 2011. Eating local: influences of habitat on the diet of little brown bats (*Myotis lucifugus*). *Molecular Ecology* **20**: 1772-1780.
- Crampton, L.H., R.M.R. Barclay. 1998. Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. *Conservation Biology* **12**: 1347-1358.
- Dietz, J.M., L.A. Dietz, and E. Y. Nagagata. 1994. The effective use of flagship species for conservation of biodiversity: the example of lion tamarins in Brazil. Pages 32-49 in P.J.S. Olney, G.M. Mace, and A.T.C. Feistner, editors. *Creative Conservation: Interactive Management of Wild and Captive Animals*. Chapman and Hall, London.
- Faure, P.A., J.H., Fullard, and J.W. Dawson. 1993. The gleaning attacks of the northern long-eared bat, *Myotis septentrionalis*, are relatively inaudible to moths. *Journal of Experimental Biology* **178**: 173-189.
- Fenton, M.B. 1970. Population studies of *Myotis lucifugus* (Chiroptera: Vespertilionidae) in Ontario. Royal Ontario Museum, Toronto.
- Feldhamer, G.A., T.C. Carter, and J.O. Whitaker, Jr. 2009. Prey consumed by eight species of insectivorous bats from Southern Illinois. *American Midland Naturalist* **162**: 43-51.
- Foster, R.W., and A. Kurta. 1999. Roosting ecology of the northern bat (*Myotis septentrionalis*) and comparisons with the endangered Indiana bat (*Myotis sodalis*). *Journal of Mammalogy* **80**: 659-672.

- Gardner, J.E., J.D. Garner, and J.E. Hofmann. 1991a. Summary of *Myotis sodalis* summer habitat studies in Illinois: with recommendations for impact assessment. Illinois Natural History Survey/Illinois Department of Conservation, Champaign, Illinois.
- Gardner, J.E., J.D. Garner, and J.E. Hofmann. 1991b. Summer roost selection and roosting behavior of *Myotis sodalis* (Indiana bat) in Illinois. Illinois Natural History Survey/Illinois Department of Conservation, Champaign, Illinois.
- Henry, M., D.W. Thomas, R. Vaudry, and M. Carrier. 2002. Foraging distances and home range of pregnant and lactating little brown bats (*Myotis lucifugus*). *Journal of Mammalogy* **83**: 767-774.
- Hicks, A.C., Novak, P.G. 2002. History, status, and behavior of hibernating populations in the northeast, Pages 160-164 in A. Kurta and J. Kennedy, editors. The Indiana bat: biology and management of an endangered species. Bat Conservation International, Austin, USA.
- Humphrey, S.R., and J.B. Cope. 1976. Population ecology of the little brown bat, *Myotis lucifugus*, in Indiana and north-central Kentucky. American Society of Mammalogists, Stillwater, Oklahoma.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**: 765-771.
- Jones, J., and L. Nagy. 2010. The use of surrogate species in predicting wildlife impacts from wind development. Poster Presentation, AWEA WindPower Conference, Dallas, Texas.
- Kurta, A., D. King, J.A. Teramino, J.M. Stribley, and K.J. Williams. 1993. Summer roosts of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range. *American Midland Naturalist* **129**: 132-138.
- Kurta, A., K.J. Williams, and R. Mies. 1996. Ecological, behavioural, and thermal observations of a peripheral population of Indiana bats (*Myotis sodalis*). Pages 102-117 in R.M.R.

- Barclay and R.M. Brigham, editors. Bats and forests. Research Branch, Ministry of Forests
Victoria, British Columbia, Canada.
- Kurta, A., and J.O. Whitaker, Jr.. 1998. Diet of the endangered Indiana bat (*Myotis sodalis*) on
the northern edge of its range. *American Midland Naturalist* **140**: 280-286.
- Kurta, A., S.W. Murray, and D.H. Miller. 2002. Roost selection and movements across the
summer landscape. Pages 118-129 in A. Kurta and J. Kennedy, editors. *The Indiana bat:
biology and management of an endangered species*. Bat Conservation International,
Austin, USA.
- Lacki, M.J., D.R. Cox, and M.B. Dickinson. 2009. Meta-analysis of summer roosting
characteristics of two species of *Myotis* bats. *American Midland Naturalist* **162**:318-326.
- Lambeck, R.J. 1997. Focal species: a multi-species umbrella for nature conservation.
Conservation Biology **11**: 849-856.
- Landres, P.B., J. Verner, J.W. Thomas. 1988. Ecological uses of vertebrate indicator species: a
critique. *Conservation Biology* **2**: 316-328.
- Lee, Y.F., and G.F. McCracken. 2004. Flight activity and food habits of three species of *Myotis*
bats (Chiroptera : Vespertilionidae) in sympatry. *Zoological Studies* **43**: 589-597.
- Menzel, J.M., W.N. Ford, M.A. Menzel, T.C. Carter, J.E. Gardner, J.D. Gardner, and J.E.
Hofmann. 2005. Summer habitat use and home-range analysis of the endangered Indiana
bat. *Journal of Wildlife Management* **69**: 430-436.
- Mills, L.S., M.E. Soule, and D.F. Doak. 1993. The keystone-species concept in ecology and
conservation. *Bioscience* **43**: 219-224.
- Murray, S.W., and A. Kurta. 2002. Spatial and temporal variation in diet. Pages 182-192 in A.
Kurta and J. Kennedy, editors. *The Indiana bat: biology and management of an
endangered species*. Bat Conservation International, Austin, USA.

- Norberg, U.M., and J.M.V. Rayner. 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London, Series B* **316**: 335-427.
- Psyllakis, J.M., and R.M. Brigham. 2006. Characteristics of diurnal roosts used by female *Myotis* bats in sub-boreal forests. *Forest Ecology and Management* **223**: 93-102.
- Richardson, C.S., E.P. Widmaier, M. Hohmann, T.H. Kunz. 2008. Using fecal cortisol assays to assess stress in an endangered bat. Poster Presentation, Society for Integrative and Comparative Biology, San Antonio, Texas.
- Romeling, S., L.W. Robbins, and C.R. Allen. 2010. Analysis of the effects of take on the Indiana bat (*Myotis sodalis*) population at a proposed wind energy facility. Wind Wildlife Research Meeting VIII, Lakewood, Colorado.
- Schmidt, A.C., K. Tyrell, and T. Glueck. 2002. Environmental contaminants in bats collected from Missouri. Pages 228-236 in A. Kurta and J. Kennedy, editors. The Indiana bat: biology and management of an endangered species. Bat Conservation International, Austin, USA.
- Schowalter, D.B., J.R. Gunson, and L.D. Harder. 1979. Life history characteristics of little brown bats (*Myotis lucifugus*) in Alberta. *Canadian Field-Naturalist* **96**: 243-251.
- Sparks, D.W., C.M. Ritzi, J.E. Duchamp, and J.O. Whitaker, Jr. 2005. Foraging habitat of the Indiana bat (*Myotis sodalis*) at an urban-rural interface. *Journal of Mammalogy* **86**: 713-718.
- Thomas, D.W., M. Dorais, and J.M. Bergeron. 1990. Winter energy budgets and cost of arousals for hibernating little brown bats, *Myotis lucifugus*. *Journal of Mammalogy* **71**:475-479.
- Timpone, J.C., J.G. Boyles, K.L. Murray, D.G. Aubrey, and L.W. Robbins. Overlap in roosting habits of Indiana bats (*Myotis sodalis*) and Northern bats (*Myotis septentrionalis*). *American Midland Naturalist* **163**:115-123.

- U.S. Fish and Wildlife Service. 2007. Indiana bat (*Myotis sodalis*) draft recovery plan: first revision. U.S. Fish and Wildlife Service, Fort Snelling, Minnesota USA.
- Wilcox, B.A. 1984. In situ conservation of genetic resources: determinants of minimum area requirements. Pages 18-30 in J.A. McNeely, K.R. Miller, editors. National Parks, Conservation, and Development: the Role of Protected Areas in Sustaining Society. Smithsonian Institution Press, Washington, D.C.
- Whitaker, J.O., Jr., G.F. McCracken, and B.M. Siemers. 2009. Food habits analysis of insectivorous bats. Pages 567-592 in Kunz, T. H., and S. Parsons editors. Ecological and behavioral methods for the study of bats. Second edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Table 1: Literature sources from which data were compiled in order to compare the 4 characteristics being studied to determine whether little brown bats are suitable surrogates for Indiana bats.

Reference	State/Province	Characteristic ^a
<i>Indiana bat</i>		
Carter and Feldhamer 2005	Illinois	R
Gardner et al. 1991b	Illinois	R
Gardner et al. 1991a	Illinois	HR,F1
Menzel et al. 2005	Illinois	HR,F2
Sparks et al. 2005	Indiana	HR,F1,F2
Kurta et al. 1993	Michigan	R
Kurta et al. 1996	Michigan	R
Kurta et al. 2001	Michigan	R
Kurta and Whitaker 1998	Michigan	D
Murray and Kurta 2002	Michigan	D
Callahan et al. 1997	Missouri	R
Timpone et al. 2010	Missouri	R
Britzke et al. 2003	North Carolina/ Tennessee	R
<i>Little brown bat</i>		
Anthony and Kunz 1977	New Hampshire	D
<i>Both Species</i>		
Bergeson et al. Pending-a	Illinois	R
Bergeson et al. Pending-b	Illinois	HR,F1,F2
Feldhamer et al. 2009	Illinois	D
Lee and McCracken 2004	Indiana	D
<i>Reports on little brown bats outside of the Indiana bat's distribution</i>		
Crampton and Barclay 1998	Alberta	R
Psyllakis and Brigham 2006	British Columbia	R
Broders et al. 2006	New Brunswick	HR, F2
Clare et al. 2011	Ontario	D
Henry et al. 2002	Quebec	HR

^a Data from these articles will be used to compare the summer roosting (R), foraging home range (HR), foraging habitat selection at the 2nd order (F1), foraging habitat selection at the 3rd order (F2), and diet (D) characteristics between Indiana bats and little brown bats.