HABITAT USE AND FORAGING ECOLOGY OF BATS IN NORTH DAKOTA

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Title

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The Supervisory Committee certifies that this ***disquisition*** complies with North Dakota State University's regulations and meets the accepted standards for the degree of

DOCTOR OF PHILOSOPHY

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ABSTRACT

Habitat use is a key component to understanding the conservation needs of species. While an array of quantitative analyses for studying fine-scale habitat use and selection have been developed, such methods have rarely been applied to bat species, with most work focused at a broad scale or using qualitative methods. Insectivorous bat communities face major threats from habitat conversion, exploitation of natural resources, and the impending spread of white-nose syndrome. Hence, detailed knowledge of their habitat needs is critical for developing effective management plans. In North Dakota, little was known about local bat populations prior to 2009, with essentially no knowledge of habitat associations and preferences of bat species. The overall objective of this research was to survey habitats across North Dakota to document species occurrences within key ecological regions and to assess the influence of fine-scale habitat characteristics on community diversity and foraging patterns. We further aimed to assess the foraging habitat selection of little brown bats, Myotis lucifugus, a species of conservation concern. Our specific objectives were to: 1) assess species' occurrence and distributions within North Dakota; 2) assess the influence of habitat and the availability of water resources on species diversity and community-level foraging activity; 3) identify habitats associated with areas of high foraging activity; 4) identify indicator species that characterize key habitats; 5) assess foraging habitat selection of female *M. lucifugus*; 6) and assess individual variation in habitat selection of *M. lucifugus*. From 2009 to 2012, mist netting and acoustic surveys were conducted to document species occurrence at 68 sites. From 2012 to 2015, targeted acoustic surveys were conducted at 37 sites to assess foraging activity levels in variable habitats. In 2014 and 2015, data-logging telemetry receivers were used to assess foraging habitat selection of *M. lucifugus*. The presence of 11 species was confirmed in the state. We found that bat community diversity and foraging activity were influenced by fine-scale habitat characteristics. *M. lucifugus* selected for edge habitats and nearby water sources. These results will be valuable for the conservation and management of bats and provide baseline information for future research on habitat use of bats.

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Finally, I’d like to thank my friends and family for their continued support.

DEDICATION

To Jacki, for putting up with me.

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LIST OF ABBREVIATIONS

Coto; COTO	*Corynorhinus townsendii*
Epu; EPFU	*Eptesicus fuscus*
Lano; LANO	*Lasionycteris noctivagans*
Labo; LABO	*Lasiurus borealis*
Laci; LACI	*Lasiurus cinereus*
Myci; MYCI	*Myotis ciliolabrum*
Myev; MYEV	*Myotis evotis*
Mylu; MYLU	*Myotis lucifugus*
Myse; MYSE	*Myotis septentrionalis*
Myth; MYTH	*Myotis thysanodes*
Myvo; MYVO	*Myotis volans*

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INTRODUCTION

Bats (order Chiroptera) are specially adapted to access a wide diversity of habitats, occupying most terrestrial land types and climatic zones (Schnitzler and Kalko 2001). Insectivorous bats comprise more than 70% of bat species throughout the world; bat communities are diverse assemblages in which different species exploit a variety of insect resources and rely on heterogeneous habitats of variable structural complexity (Johnson et al. 2010; Razgour et al. 2010). Understanding the habitat and resource needs of these bat communities is critical for effective management and conservation efforts, of which many bats have become the focus of in recent years.

Echolocation is the key link between foraging bats and the habitats in which they hunt. Bats use echolocation for spatial orientation and to detect, identify, and localize insect prey (Schnitzler et al. 2003). They use a wide variety of species-specific echolocation signal types that differ in frequency structure, duration, and sound pressure level that are adapted for specific tasks; and further, signal structure varies depending on the echolocation task confronting the bat (Schnitzler and Kalko 2001). Circumstances such as the structural complexity of habitat the bat must navigate through, foraging mode, and diet favor different signal types (Schnitzler and Kalko 2001). Foraging bats must detect, classify, and localize prey and discriminate between prey and echoes of unwanted “clutter” such as branches, foliage, or the ground. Echolocation calls can be grouped into narrowband (constant frequency or quasi-constant frequency), signals with the most prominent harmonic sweeps over less than half an octave, or broadband (frequency-modulated) where the most prominent harmonic covers more than half an octave (Schnitzler and Kalko 2001). Narrowband calls are well suited for detection of echoes and especially those of long duration, can also be used for target classification but are less suited for precisely locating a target when bats must accurately judge range as well as angles (Schnitzler and Kalko 2001). Broadband calls are less suited for the detection of weak echoes but are well suited for localizing an exact target where the range and angles must be measured precisely (Schnitzler and Kalko 2001).

Foraging Habitat Use

Characterizing the habitat use of a species is a fundamental component to understanding the niche, ecological interactions, and evolutionary implications of species' behavior. Habitat is particularly important to understanding bat foraging, as echolocation in bats may have first evolved for spatial orientation and was later refined for prey acquisition (Schnitzler et al. 2003). The composition and structure of habitats are important components resource partitioning and foraging modes of bats (Arlettaz 1999; Sattler et al. 2007). Here, we define habitat composition as categorical land cover attributes (e.g. forest, grassland, river) and habitat structure as the arrangement and density of vegetative cover (e.g. cluttered forest, edge/gap, or open habitat) or canopy cover. Both terrestrial and aquatic microhabitat characteristics affect the distribution and availability of resources, which ultimately shapes fine-scale species distributions of bats (Biscardi et al. 2007; Johnson et al. 2010; Razgour et al. 2010; Jung et al. 2012; Charbonnier et al. 2016).

Habitat composition can also play a key role in the distribution of insect prey and foraging strategies of bats, as well as the partitioning of resources by sympatric bat species. Bats may spatially segregate foraging habitats based on differing habitat requirements of specific prey or partition foraging habitats behaviorally through microhabitat selection (Arlettaz 1999; Bergeson et al. 2013). Habitats over or near open water resources are associated with relatively high levels of bat foraging activity, as they provide drinking water and abundant insects (Grindal et al. 1999; Seidman and Zabel 2001; Ciechanowski 2002; Johnson et al. 2010). The size, type, and characteristics of water sources also influences foraging activity and bat community composition (Seidman and Zabel 2001; Ciechanowski 2002; Razgour et al. 2010). However, bat use of water resources is also influenced by the composition and structure of the surrounding terrestrial habitat. Water sources within forests or that are bordered by well-developed vegetation are often selected for over water in open habitats (Zahn and Maier 1997; Warren et al. 2000; Biscardi et al. 2007).

Finally, habitat structure has been shown to influence bat foraging strategies and community composition (Aldridge and Rautenbach 1987; Kalcounis and Brigham 1995; Schnitzler and Kalko 2001; Jung et al. 2012). Habitat structure has often been studied with a strong focus on understanding how morphological features and physiological states of individual species impact the structural complexity of the habitat in which they are primarily found (Kalcounis and Brigham 1995; Adams 1996). Habitat structure also influences bat communities; habitat structural heterogeneity has been found to be correlated with higher levels of bat species activity and species occurrence (Jung et al. 2012). Further, some studies have focused on classifying bats into functional groups based on echolocation call signal structure, wing morphology and flight behavior as it relates to habitat structure (Aldridge and Rautenbach 1987; Schnitzler and Kalko 2001).

Current State of Knowledge

As described above, studies of habitat use by bats are abundant in the ecological literature, yet detailed habitat characterizations are often limited, and a basic understanding of bat foraging habitat preferences is often lacking for many species beyond anecdotal observations and partial quantitative analyses (Ford et al. 2005). Inconsistencies in study protocols combined with intra- and interspecific variation in bat foraging behaviors has made identifying patterns of foraging habitat use problematic (Kalcounis-Ruppell et al. 2005). Many studies focus on a limited number of broad habitat classes based on management practices or disturbance (e.g. deforestation or fragmentation). Holistic habitat use assessments are lacking, and the influence of fine-scale habitat characteristics on bat communities and foraging activity remains largely unexplored (Charbonnier et al. 2016).

Our work focused on bat communities in North Dakota. Prior to 2009, minimal research had been done on bat species in the state. Distribution and occurrence information was primarily based on 40+ year old occurrence records (Hall 1981). Eleven species were thought to be summer residents: *Corynorhinus townsendii*, *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Lasiurus borealis*, *Lasiurus cinereus*, *Myotis ciliolabrum*, *Myotis evotis*, *Myotis lucifugus*, *Myotis septentrionalis*, *Myotis thysanodes*, and *Myotis volans*. Despite limited documentation of these species in the state, detailed information about species distributions were severely lacking, and occurrences of *Corynorhinus townsendii* and *Myotis thysanodes* had not been confirmed outside of grey literature. Further, habitat associations for bats in North Dakota were almost completely undocumented.

Objectives

The primary objectives of this research were to survey habitats across the state to document species occurrences within key ecological regions and to assess the influence of fine-scale habitat characteristics on the intensity of bat foraging activity at both the species and community level. Further, we aimed to assess the foraging habitat selection of the little brown bat, Myotis lucifugus, a species of special conservation concern. Specific objectives included: 1) assess bat species' occurrence and distributions within North Dakota; 2) assess the influence of habitat and the availability of water resources on bat species diversity and community-level foraging activity; 3) identify habitats associated with areas of high foraging activity; 4) identify indicator species that characterize key habitats; 5) assess foraging habitat selection of female *M. lucifugus* in terms of habitat composition and structure in tandem; 6) and assess individual variation in habitat selection of *M. lucifugus*.

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CHAPTER 1. DISTRIBUTION AND OCCURRENCE OF BAT SPECIES IN NORTH DAKOTA[1]

Introduction

Knowledge of the distribution and habitat use of species is essential for successful conservation efforts. While the natural history of bats has been extensively studied in most of the United States, a few states still lack detailed information about the ecology of local bat populations. North Dakota is such a state; prior to 2009, little was known beyond that 9 bat species were known to be summer residents. This information was primarily based on 40+ year old occurrence records (Hall 1981). Bailey (1926) noted anecdotal sightings and scattered museum specimens of *Lasiurus cinereus*, *L. borealis*, *Eptesicus fuscus*, *Myotis septentrionalis* (incorrectly identified as *M. ciliolabrum*; Genoways and Jones Jr. 1972), *M. evotis* and *M. lucifugus*. Museum records of bats from southwestern North Dakota include *M. ciliolabrum*, *M. evotis, M. lucifugus, M. volans* and *E. fuscus* (Jones and Stanley 1962; Jones and Genoways 1966; Genoways 1967). More recently, separate surveys along the Little Missouri River in western North Dakota reported captures of *Corynorhinus townsendii, E. fuscus*, *Lasionycteris noctivagans*, *L. cinereus*, *M. ciliolabrum*, *M. evotis*, *M. lucifugus*, *M. septentrionalis*, and *M. volans*, as well as acoustical detection of *M. thysanodes* (Tigner 2006; Lenard 2010). For a thorough summarization of these occurrences, see Hall (1981) or Seabloom (2011). Despite documentation of these bat species in North Dakota, detailed information about distributions within the state are lacking.

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[1] The material in this chapter was co-authored by Dr. Paul Barnhart. Dr. Barnhart and Josiah Nelson shared in the responsibility of data collection. Josiah Nelson was the primary developer of the conclusions, tables, and figures advanced here. Josiah Nelson also drafted and revised all versions of this chapter.

Several factors are currently affecting bat populations throughout the United States, including ongoing habitat loss/modification, development of wind energy, and the impending spread of white-nose syndrome, a fungal disease of hibernating bats (Alves et al. 2014; Zukal et al. 2014), to the Great Plains. As bat populations decline nationally due to these factors, it is imperative to verify species' distributions and document key habitat requirements so that effective conservation plans can be established. Such information is especially needed in areas like North Dakota, where baseline information is scant, if available at all. The overall objective of this study was to obtain baseline information about bats in North Dakota. Specifically, we aimed to: 1) confirm the presence/absence of bat species that have previously been recorded in North Dakota, 2) use our data to generate current occurrence maps of each bat species in the state, and 3) compare our maps to currently accepted distributions of these species in North Dakota (Hall 1981, IUCN 2014).

Methods

Study Area

Sampling focused on five ecologically distinct regions within the state: the badlands, the Missouri River Valley, the Turtle Mountains, Pembina Gorge, and the Red River Valley (Fig. 1.1). We did not sample areas dominated by agriculture or anthropogenic development due to the lack of natural roosting resources available for bats. Within these five regions, 68 sites were sampled across the state (Fig. 1.1, Appendix A).

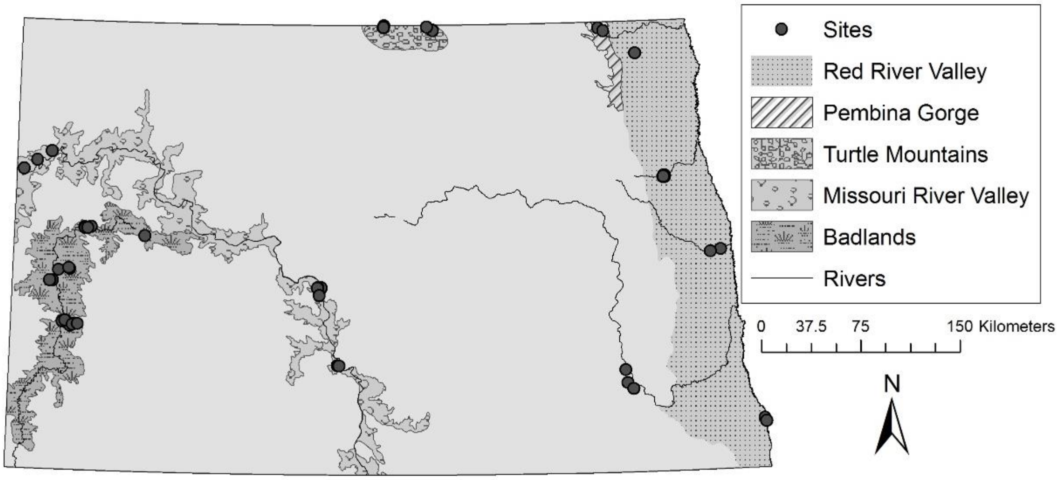

Figure 1.1. Ecological Regions and Study Sites
Map showing the five ecological regions where sampling was focused in this study. Dots represent the 68 sampling sites. Note: given map scale, a single dot often represents multiple sites.

Study Regions

The Badlands of North Dakota are characterized by heavily eroded, rugged terrain with layers of exposed rock and soil strata, mixed grass prairie, and stands of Rocky Mountain Juniper (*Juniperus scopulorum*; Gonzalez 2001). Exposed slopes have abundant rock and soil crevices, and subsurface erosion forms many sinkholes and cave-like formations (Torri et al. 2000). These features potentially provide roosting habitat for crevice-dwelling bat species. Within the badlands, we surveyed sites in the Little Missouri National Grasslands, Theodore Roosevelt National Park, and Little Missouri State Park. Theodore Roosevelt National Park is comprised of three park units. The South Unit of the park is located along Interstate 94 near Medora. The North Unit is located about 130 km north of the South Unit, 24 km south of Watford City. The Elkhorn Ranch Unit is located between the North and South units, approximately 32 km west of

Fairfield. The Little Missouri River flows north and east through all three units of the park until it meets the Missouri River at Lake Sakakawea.

The Missouri River is the largest river system in North Dakota, flowing through the western part of the state from Montana and south into South Dakota. The riparian vegetation is comprised of cottonwood forests, grasslands, and wetland habitat (Johnson et al. 1976). Along the Missouri River, areas surveyed included Cross Ranch State Park, Lewis and Clark Wildlife Management Area (WMA), Neu WMA, Oahe WMA, Painted Woods WMA, Smith Grove WMA, and Trenton WMA.

The Turtle Mountains is an area in north-central North Dakota and a southwestern portion of the Canadian province of Manitoba. It is a plateau approximately 600 m above sea level, and 183 m above the surrounding flat, agriculturally dominated landscape (Potter and Moir 1961). Extending some 22.5 km from north to south and 64 km from east to west, the area is covered by deciduous forest, wetlands, and numerous lakes, including Lake Metigoshe, which straddles the international border. The relatively dense woodlands are dominated by quaking aspen (*Populus tremuloides*) but also include green ash (*Fraxinus pennsylvanica*), box elder (*Acer negundo*), American elm (*Ulmus americana*), paper birch (*Betula papyrifera*), bur oak (*Quercus macrocarpa*), and balsam poplar (*P. balsamifera*; Potter and Moir 1961). Within the Turtle Mountains, we surveyed Lake Metigoshe State Park and Wakopa WMA.

The Pembina Gorge consists of the most extensive oak woodland in North Dakota and is also one of the largest uninterrupted blocks of woodlands in the state (Faanes and Andrew 1983). The Pembina River has carved one of the deepest and steepest river valleys in North Dakota. Areas surveyed in this region included multiple sites associated with the Pembina Gorge State

Recreation Area and Icelandic State Park. Icelandic State Park is located along the Tongue River, a tributary of the Pembina River.

The Red River Valley lies in the flat lakebed of ancient glacial Lake Agassiz, an enormous glacial lake created at the end of the Wisconsin glaciation (Stoner et al. 1993). While the Red River of the North drains the region, the actual Red River Valley is only ~100 m wide, while the floodplain is much wider. The riparian zone of the Red River consists of tracts of deciduous forest bordered by agriculture (Stoner et al. 1993). Along the Red River, we surveyed two sites near Wahpeton, as well as multiple sites along three tributaries: the Sheyenne River, Turtle River, and Goose River. These sites included Fort Ransom State Park, Little Yellowstone Park, and Sheyenne State Forest along the Sheyenne River and Turtle River State Park on the Turtle River.

Survey Methods

Surveys were conducted between mid-May and mid-August in 2009–2012. We sampled a total of 68 sites, with repeated sampling at many sites across years. We sampled using two methods: direct capture of bats via mist netting and ultrasonic recording of echolocation calls from free-flying bats. All research protocols were approved by the Institutional Animal Care and Use Committee (Protocol #s A0941 and A12040) at North Dakota State University.

We captured bats using mist nets and standard mist netting techniques (Kunz et al. 2009; Nelson et al. 2012); two to five mist-nets were deployed at each sampling site each night. Mist nets were opened each night just before sunset and closed shortly before sunrise, or 120 minutes after the last capture of a bat. Bats were identified to species using van Zyll de Jong (1985) supplemented with a regional key developed for identifying bats in South Dakota (South Dakota

Bat Working Group 2004). A subset of captured bats were light tagged and recorded during free flight (see below).

Active acoustic monitoring was conducted at mist netting sites using two broadband D240X Pettersson bat detectors (Pettersson Elektronik, Uppsala, Sweden). This time expansion bat detection system records for a short period of time (1.7 or 3.4 sec) and then plays back the recorded calls at one-tenth the original speed (i.e., time-expanded). Time-expanded calls were stored as an MP3 file on an Iriver player (Model iFP-890, Iriver Inc., Irvine, CA, USA) attached to the detector. Recordings were manually initiated when bats were detected in the area by the observer, who was listening to a heterodyne detector.

Passive acoustic monitoring used the same D240X detector and Iriver recorder setup as described above. The system was housed in a protective casing and placed within 4 km of a netting site at a location of similar habitat, typically near vegetation and water. The bat detector was manually activated before sunset and automatically recorded sounds when an amplitude threshold was crossed. In 2011, Pettersson D500X detectors were substituted for the D240X model. These real-time, full-spectrum detectors are set to detect and record echolocation in .wav format without the need for a separate recording device.

Recordings of the echolocation calls of captured bats, which had been identified in the hand to the species level, were used to build a call library for analysis of unknown calls and to verify the accuracy of automated classification software. Bats were tagged with a 1.5-inch chemoluminescent stick attached between the scapulae of the bat using non-toxic washable craft glue to make observations of activity and aid in recording echolocation calls (Brigham et al. 1992; Fellers and Pierson 2002). To obtain these calls, select captured bats were housed in cloth bags and transported to an open release site within a short distance of the capture site. The release site was continually monitored for bat activity to ensure no bats were foraging in the vicinity; after ~60 sec of no bat detections in the area, one individual, light-tagged bat was released. Echolocation calls from the released bat were manually recorded with the same Pettersson D240X and Iriver recording system described above. Calls from the first 5 sec after release were excluded from analysis, as we presumed that immediately after release bats are orienting to their environment and potentially emitting atypical search phase echolocation calls.

Recorded echolocation calls were analyzed using SonoBat 3 (SonoBat, Arcata, CA). This software uses a decision engine, based on the quantitative analysis of approximately 10,000 known recordings from species across North America, to identify each recording to the species level. Because variation in call structure between geographic locations is a possibility, we also included our recordings from light-tagged bats in the reference database. For each call in a sequence, SonoBat measures 72 call parameters, including highest frequency, lowest frequency, and duration, and feeds this information into a series of algorithms that combine information from multiple calls to ultimately identify a call sequence to a particular species.

Results

During the summers of 2009–2012, we sampled 68 sites, captured 333 individuals, recorded 6,629 high-quality echolocation call sequences, and confirmed the presence of 11 bat species (Tables 1.1, 1.2). We physically captured individuals of all 11 species and acoustically documented 10 species, including *C. townsendii* and *M. thysanodes* (Figures 1.2-1.4). Species richness varied across the state; we physically captured 10 bat species in the badlands region, 4 species along the Missouri River, 3 species in the Turtle Mountains, 2 species in the Red River Valley, and 1 in the Pembina Gorge (Table 1.1). Across species, bat captures in mist nets were biased towards females (80.8%; 269 individuals; Appendix B). Echolocation call sequences for the call library were collected from 107 individuals of the six most commonly captured species.

Table 1.1. Bat Species Captures by Region in North Dakota, 2009-2012

	Species										
Region	COTO	EPFU	LANO	LABO	LACI	MYCI	MYEV	MYLU	MYSE	MYTH	MYVO	Total
Badlands	1	26	1	0	2	17	13	75	5	1	2	143
Missouri River Valley	0	23	11	0	0	0	0	88	18	0	0	140
Turtle Mountains	0	0	1	3	0	0	0	6	0	0	0	10
Pembina Gorge	0	0	2	0	0	0	0	0	0	0	0	2
Red River Valley	0	0	36	2	0	0	0	0	0	0	0	38
Total	1	49	51	5	2	17	13	169	23	1	2	333

Numbers of bats captured by region in North Dakota, 2009-2012. See Appendix A for a detailed listing of all capture sites. COTO= Corynorhinus townsendii, EPFU= Eptesicus fuscus, LANO= Lasionycteris noctivagans, LABO= Lasiurus borealis, LACI= L. cinereus, MYCI=Myotis ciliolabrum, MYEV= M. evotis, MYLU= M. lucifugus, MYSE= M. septentrionalis, MYTH= M. thysanodes, MYVO= M. volans.

Table 1.2. Numbers of Bat Species Echolocation Call Sequences by Region in North Dakota, 2009-2012

	Species										
Region	COTO	EPFU	LANO	LABO	LACI	MYCI	MYEV	MYLU	MYSE	MYTH	MYVO	Totals
Badlands	12	255	383	7	83	302	72	149	0	1	2	1,266
Missouri River Valley	4	308	1,437	4	186	2	73	1,557	0	0	2	3,573
Turtle Mountains	0	2	308	0	29	0	0	30	0	0	0	369
Pembina Gorge	0	1	60	0	9	0	0	0	0	0	0	70
Red River Valley	3	36	1,082	36	194	0	0	0	0	0	0	1,351
Totals	19	602	3,270	47	501	304	145	1,736	0	1	4	6,629

Numbers of echolocation call sequences by region classified to species using automated classification in North Dakota, 2009-2012. COTO= Corynorhinus townsendii, EPFU= Eptesicus fuscus, LANO= Lasionycteris noctivagans, LABO= Lasiurus borealis, LACI= L. cinereus, MYCI=Myotis ciliolabrum, MYEV= M. evotis, MYLU= M. lucifugus, MYSE= M. septentrionalis, MYTH= M. thysanodes, MYVO= M. volans.

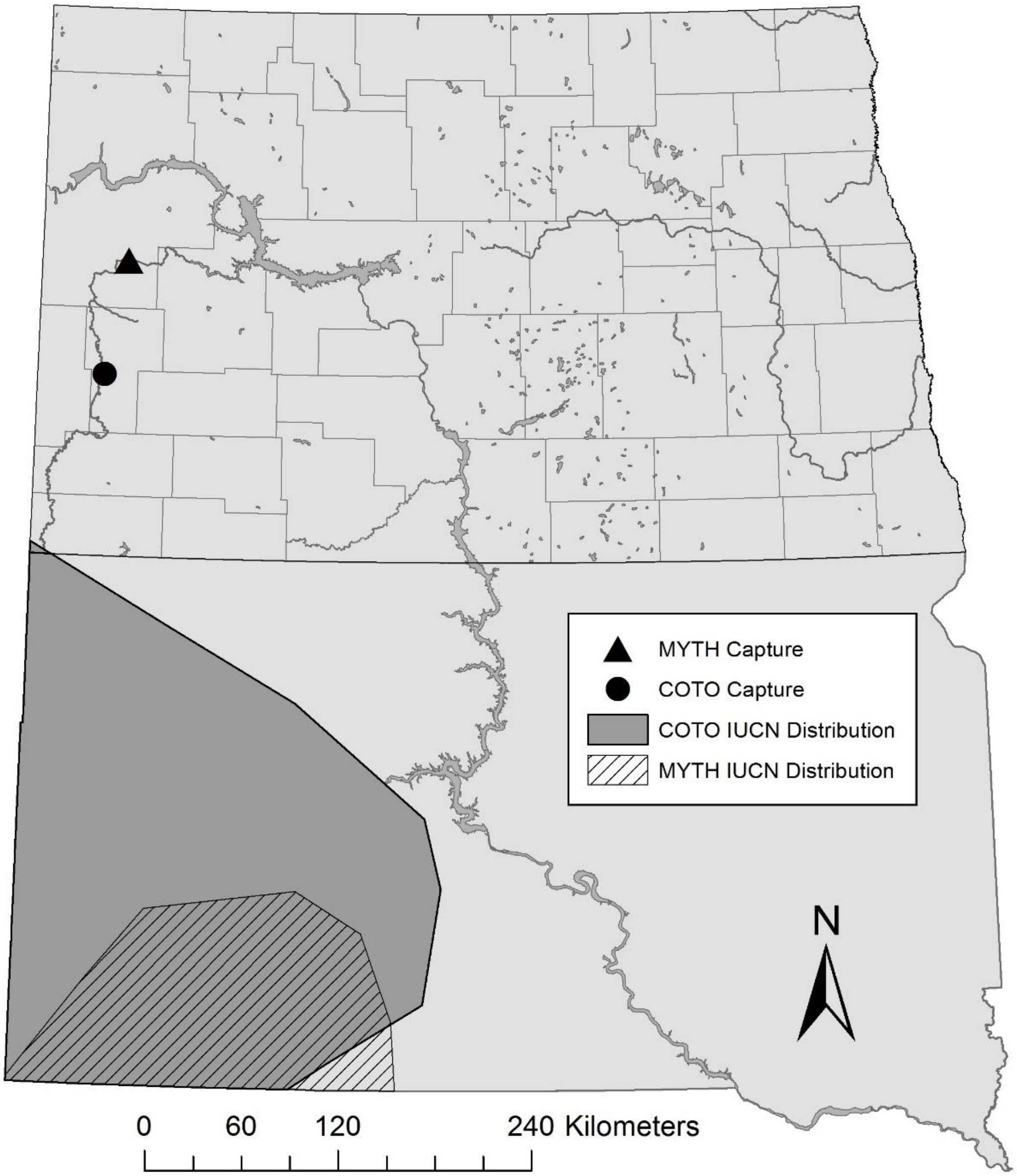

Figure 1.2. Capture Sites and Known Distributions of *M. thysanodes* and *C. townsendii* Map of North Dakota and South Dakota displaying capture sites of *M. thysanodes* (black triangle) and *C. townsendii* (black dot) and IUCN Red List Distributions for each species.

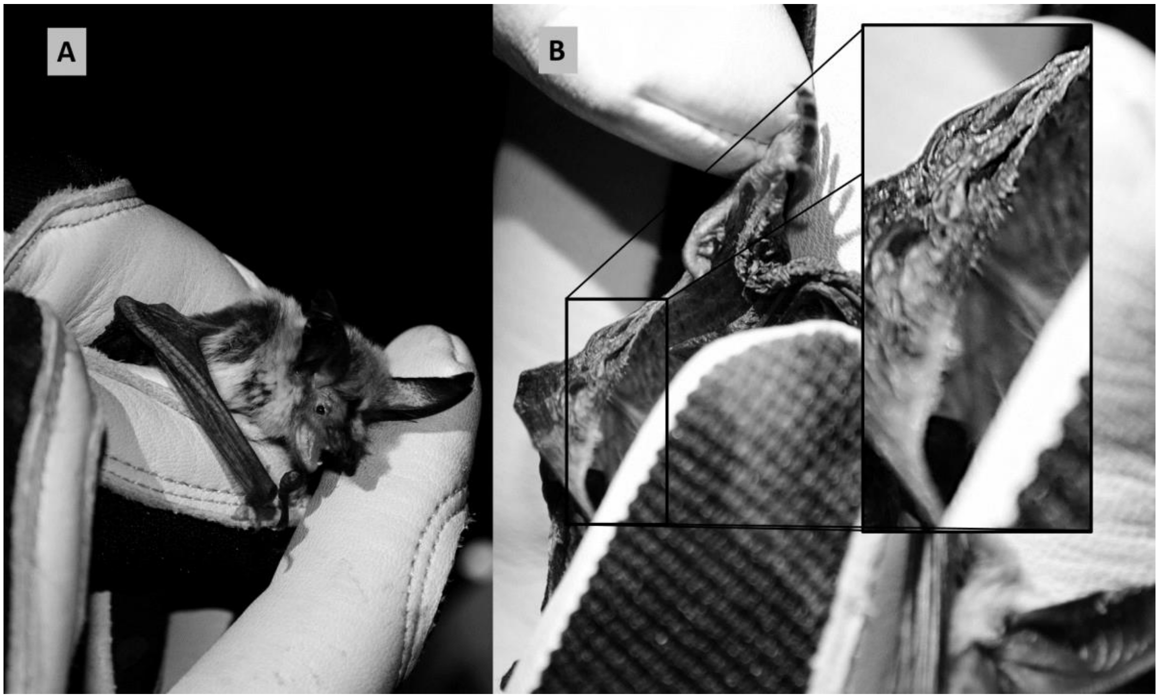

Figure 1.3. Voucher Photographs of *M. thysanodes*
(A) Voucher photograph of *M. thysanodes*. (B) Photograph of interfemoral membrane with magnified portion where distinctive fringe hairs of this species are visible.

Figure 1.4. Voucher Photograph of C. townsendii.

Discussion

This study provides the first detailed picture of the bat communities inhabiting natural areas of North Dakota. Our efforts substantially increase the areas of North Dakota in which detailed bat surveys have been conducted, and can serve as a baseline for comparison in the face of changing climate and land use. Species richness appears to follow a high to low gradient from southwest to northeast, with the most species documented in the badlands and the fewest documented in the Pembina region. The large number of species found in western North Dakota is likely due to the varied roosting and foraging habitats available in the badlands ecosystem. The Missouri River Valley, Turtle Mountains, Pembina Gorge, and Red River Valley all provide crucial forested habitat needed to support foliage and tree roosting bats in North Dakota's agriculturally dominated landscape.

Prior to 2006, *M. thysanodes* and *C. townsendii* had not been documented in North Dakota. The results of this study confirm the presence of these species in the state. *Myotis thysanodes* was first acoustically documented in North Dakota in 2006 (Tigner 2006) and again in 2009 (Lenard 2010); here, we confirm the presence of this bat with the first physical capture of *M. thysanodes* in the state. Although bats were identified through careful inspection in the field, we acknowledge that our photographs may not be sufficient to validate species identification (Fig. 1.3). The key characteristic for differentiation of *M. thysanodes* from *M. evotis* is the presence of conspicuous fringe hairs along the interfemoral membrane of *M. thysanodes*, which is in contrast to the inconspicuous and sparse hairs that may be found on *M. evotis* (Hall 1981; van Zyll deJong 1985). More detailed photographs, morphological measurements, and tissue samples should be taken of future captures to stand as vouchers for *M. thysanodes* in the state. While captures of *C. townsendii* had previously been reported in North

Dakota, our accompanied voucher photograph (Fig. 1.4) clearly provides evidence for the occurrence of this species. Given these new/confirmed findings, we have generated a map comparing our reported occurrences with current IUCN distributions (Fig. 1.2). We also captured *M. ciliolabrum* (Appendix C) and *M. septentrionalis* outside of their respective IUCN distributions, however, these occurrences are congruent with historical occurrences in the state.

We found a sex bias toward females for most of the bat species in this study, which is in contrast to patterns observed for those same species in South Dakota (Bogan et al. 1996; Mattson et al. 1996; Choate and Anderson 1997; Cryan et al. 2000; Swier 2003). However, this bias in South Dakota was not observed in the winter months (Cryan et al. 2000). The apparent sex biases observed throughout the region may be due to differences in seasonal distributions between sexes; future studies examining sex biases among captured bats in the region would be valuable for better understanding this pattern.

While we captured multiple *M. septentrionalis*, automated classification of recorded echolocation calls failed to identify this species in the state. Species within the genus Myotis are notoriously difficult to separate based solely on echolocation calls (Thomas et al. 1987). While call libraries and identification algorithms have vastly improved in recent years, our results reveal that such issues can still exist when attempting to identify select species. Specifically, *M. septentrionalis* and *M. evotis* exhibit similar echolocation call structures, which likely led to misclassification in our study, as *M. septentrionalis* was physically captured multiple times, but never identified via automated classification of acoustic recordings. Even *M. septentrionalis* calls recorded from light-tagged individuals were misclassified as *M. evotis* by the analysis software. However, additional call data from 2014 that was not included in this study, positively identified *M. septentrionalis* calls from the Missouri River region. Overall, confirmation of species occurrence must come from physical captures, as documented in our study. *M. septentrionalis* was recently listed as threatened by the U.S. Fish and Wildlife Service (U.S.F.W.S. 2015), therefore special consideration should be given to sampling methods and validation of automated classification of echolocation calls when conducting surveys to assess the presence of this species.

While acoustic sampling has known challenges, it is a useful tool for documenting bat occurrences. For example, in our study, *C. townsendii* was first acoustically detected in the badlands in 2010, but despite extensive sampling was not physically captured until 2012. Mist netting is not without biases, as some species may be underrepresented if researchers rely only on this method (Kuenzi and Morrison 1998). While our acoustic data indicates species presence in areas where they have not been captured, further sampling may result in physical captures and extensions of known species distributions. This highlights the importance of using multiple sampling methods when surveying for bats, as differing sampling biases may impact conclusions about species distributions and habitat preferences (Barnhart and Gillam 2014).

The North Dakota Game and Fish Department currently lists *C. townsendii*, *E. fuscus*, *M. lucifugus*, and *M. septentrionalis* as Species of Conservation Priority Level I (highest priority), and *M. ciliolabrum*, *M. evotis*, and *M. volans* as Level III (moderate priority, populations assumed to be peripheral or nonbreeding in North Dakota). All of these species can be found in the badlands region of the state and four of these species have been captured exclusively in the badlands. Since the development of extensive oil and natural gas production in the Bakken Formation, landscape modification has invariably altered the habitat, although no research has attempted to quantify the effect on bats. Although Theodore Roosevelt National Park is afforded some protection from such development, the Little Missouri National Grasslands and other private lands of the region, which include high quality bat habitat essential to support the diverse bat community of the badlands, are not protected from oil exploration. Management efforts should focus on preservation of critical habitats, such as the badlands, Turtle Mountains, Pembina Gorge, and forested riparian zones, and work to reduce the environmental effects of oil and natural gas development in the region.

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CHAPTER 2. INFLUENCE OF HABITAT ON COMMUNITY COMPOSITION AND FORAGING ACTIVITY OF BATS

Introduction

The study of habitat characteristics and resource availability is essential for the conservation and management of complex ecological communities. Bat communities are diverse assemblages in which different species exploit dynamic resources in heterogeneous habitats of variable physical complexity and structure (Johnson et al. 2010; Razgour et al. 2010). However, foraging habitat use studies of insectivorous bats often focus on a limited number of components describing the physical structure of the habitat or available water resources. Most studies focus on individual species use of different broad habitat classes that are based on management practices or disturbance (e.g. deforestation or fragmentation). Holistic habitat use assessments are lacking, and the influence of fine-scale habitat structure combined with the availability of varying water resources on bat community composition, diversity, and foraging activity remains largely unexplored (Charbonnier et al. 2016).

It is well known that habitats over or near open water resources are associated with relatively higher amounts of bat foraging activity, as they provide drinking water and abundant insects (Grindal et al. 1999; Seidman and Zabel 2001; Ciechanowski 2002; Johnson et al. 2010). Some studies have found bat activity to be ten times greater or more over water sources than the surrounding habitat (Lunde and Harestad 1986; Thomas 1988) and the size, type, and characteristics of water sources influences the bat community composition and foraging activity (Seidman and Zabel 2001; Ciechanowski 2002; Razgour et al. 2010). However, the quality of aquatic habitats to bats is not independent of the surrounding habitat. Bats often select for water sources within forests or that are bordered by well-developed vegetation over water in open habitats (Zahn and Maier 1997; Warren et al. 2000; Biscardi et al. 2007).

Habitat structure, defined here as the arrangement and density of vegetative cover, has been shown to be an important factor influencing bat foraging strategies and community composition (Aldridge and Rautenbach 1987; Kalcounis and Brigham 1995; Schnitzler and Kalko 2001; Schnitzler et al. 2003; Jung et al. 2012). Typically, habitat structure has been studied with a strong focus on understanding how morphological features and physiological states of a given bat species impact the vegetative complexity of the habitat in which they are primarily found (Kalcounis and Brigham 1995; Adams 1996). Many studies have focused on classifying bats into functional groups based on echolocation call structure, morphology and flight behavior as it relates to habitat structure and habitat use (Aldridge and Rautenbach 1987; Schnitzler and Kalko 2001; Schnitzler et al. 2003). However, habitat use may not be predictable by echolocation or morphology alone (Arlettaz 1999; Davidson-Watts et al. 2006). Jung et al. (2012) found that increased structural heterogeneity of habitat was correlated with higher levels of bat species activity and species occurrence. Yet, few studies have investigated the effects of structural heterogeneity on bat communities, and most studies investigating the effects of habitat structure on bat foraging do not consider the availability and characteristics of water resources in conjunction with terrestrial habitat types.

Both terrestrial and aquatic microhabitat characteristics can affect the distribution and availability of resources, which ultimately impacts foraging habitat quality and shapes fine-scale species distributions and community composition of bats (Biscardi et al. 2007; Johnson et al. 2010; Razgour et al. 2010; Jung et al. 2012; Charbonnier et al. 2016). Despite the abundance of habitat use and bat community studies in the ecological literature, a basic understanding of bat foraging habitat preferences is often lacking for many species beyond anecdotal observations and partial quantitative analyses (Ford et al. 2005). Further, inconsistencies in study protocols combined with intra- and interspecific variation in bat foraging behaviors makes identifying general patterns of foraging habitat use problematic (Kalcounis-Ruppell et al. 2005). Habitat relationships are typically assessed at the species level through univariate methods, and multivariate approaches that evaluate holistic community responses have been underused (Jaberg and Guisan 2001). As management decisions often must consider ecological communities instead of focusing on a select species, studies using multivariate approaches to investigate the influence of fine-scale habitat characteristics on bat communities should be beneficial for conservation and management.

The objectives of this study were to: 1) assess the influence of habitat and the availability of water resources on bat species diversity and community-level foraging activity, 2) identify habitats associated with areas of high foraging activity, and 3) identify indicator species that characterize key habitats. Our work focused on bat communities in North Dakota. Prior to 2009, minimal research had been done on bat species in the state. Since then, a total of 11 species have been documented in the state, with species diversity peaking in the western Badlands region (Nelson et al. 2015). These species include: *Corynorhinus townsendii*, *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Lasiurus borealis*, *Lasiurus cinereus*, *Myotis ciliolabrum*, *Myotis evotis*, *Myotis lucifugus*, *Myotis septentrionalis*, *Myotis thysanodes*, and *Myotis volans*. Barnhart and Gillam (2016) modeled habitat suitability for seven species (*C. townsendii, L. borealis, M. ciliolabrum, M. evotis, M. septentrionalis*, *M. thysanodes*, and *M. volans*) within the state and identified potential environmental variables and land cover attributes driving habitat preferences. However, these models did not incorporate fine-scale microhabitat factors that may have major influences on patterns of habitat use.

Methods

Surveys were conducted between mid-May and mid-August from 2012–2015. We sampled a total of 37 sites in 6 study areas across North Dakota (Figure 2.1): Theodore Roosevelt National Park (North and South Units), Cross Ranch State Park, Lake Metigoshe State Park, Turtle River State Park, and Mirror Pool Wildlife Management Area (Sheyenne Grasslands). These areas were chosen based upon the ecological significance of the available habitats to bats (Nelson et al. 2015). All research protocols were approved by the Institutional Animal Care and Use Committee (Protocol # A0941 and A12040) at North Dakota State University.

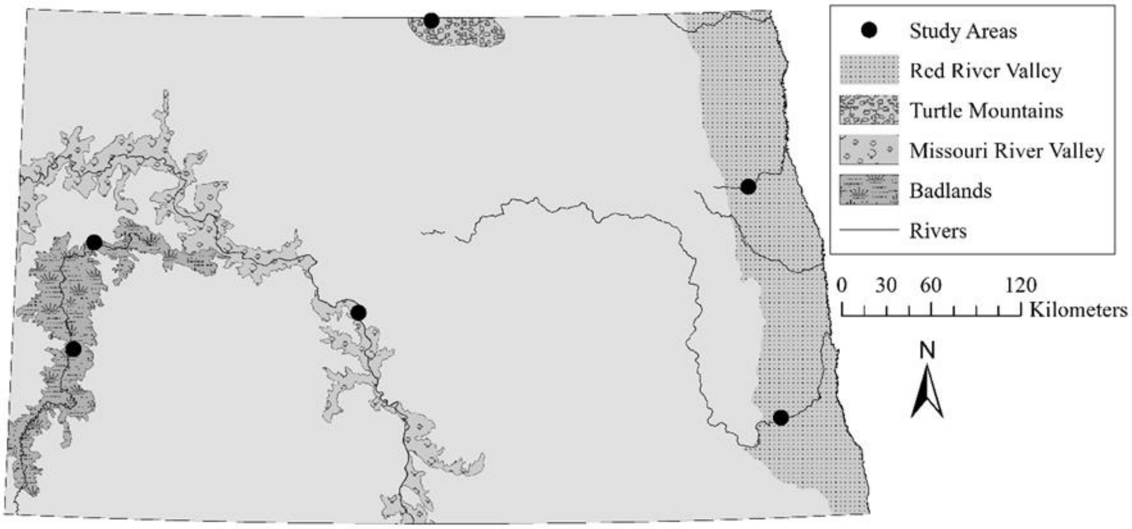

Figure 2.1. Map of Acoustic Study Areas
Map of North Dakota depicting six study areas (black dots) within the Red River Valley, Turtle Mountains, Missouri River Valley, and badlands regions.

Study Areas

The six study areas spanned a diversity of ecosystems in North Dakota. Theodore Roosevelt National Park (TRNP) is comprised of three geographically separated areas of badlands in western North Dakota. We sampled within two units of TRNP, the South Unit and the North Unit. The badlands are characterized by rugged terrain with heavily eroded layers of exposed soil strata, mixed grass prairie, stands of Rocky Mountain juniper (*Juniperus scopulorum*), and stands of cottonwood (*Populus deltoides*) trees along the Little Missouri River (Gonzalez 2001). Cross Ranch State Park (CRSP) is located along the Missouri River in central North Dakota. The Missouri River riparian corridor is characterized by cottonwood dominated forests, grasslands, and wetlands (Johnson et al. 1976). Lake Metigoshe State Park (LMSP) is located along Lake Metigoshe in the Turtle Mountains of north-central North Dakota. This area is characterized by numerous lakes, wetlands, and dense deciduous forest (Potter and Moir 1961). Turtle River State Park (TRSP) is located along the Turtle River, a tributary of the Red River of the North, within the Red River basin. While more that 70% of the basin has been converted to agriculture, the riparian corridor of Turtle River State Park contains tracts of deciduous forest with oak, cottonwood, elm, willow, and ash trees (Stoner et al. 1993). Mirror Pool Wildlife Management Area is a state managed protected area dominated by deciduous forest along the Sheyenne River in southeastern North Dakota, adjacent to the Sheyenne National Grasslands.

Acoustic Monitoring

Bat activity was passively sampled at each site using Pettersson D500 bat detectors (Pettersson Elektronik, Uppsala, Sweden), for a minimum of 6 nights at each site to reduce biased activity estimates from temporal variation in bat activity (Hayes 1997). Detectors were set to record from sunset to sunrise each night. Numbers of search-phase echolocation calls or bat passes were counted as basic units of bat activity (Seidman and Zabel 2001; Avila-Flores and Fenton 2005). A bat pass is defined as a sequence of one or more echolocation pulses with less than one second between pulses (Hayes, 1997). Because individual bats may pass a detector multiple times, bat passes cannot be used as an absolute count of bats, however, this bias can be assumed to be similar for all survey sites, providing relative estimates of bat activity (Seidman and Zabel 2001). We made no effort to distinguish between commuting and foraging activity, as commuting bats may opportunistically forage and higher quality foraging habitats should produce relatively higher levels of bat activity. Therefore, we consider bat activity at all sites to be relative measures of foraging habitat use. Recorded echolocation calls were identified to species using SonoBat 3 echolocation analysis software (SonoBat, Arcata, CA) and only echolocation call sequences identified to species with a 95% classification quality value or higher were used for analysis.

Habitat Characterization

For each site, habitat characteristics were recorded for a 20 m radius centered on the bat detector. These characteristics included: percent canopy cover, habitat structure, type of nearest water, and distance to water. The geographic coordinates and elevation were also recorded for each site. Canopy cover was assessed by recording the presence/absence of canopy at the center of the plot (directly above the acoustic detector) and at 10 and 20 meters in the 8 cardinal directions, for a total of 17 measurements. The counts of canopy present were then divided by the total for an index of percent canopy cover. Habitat structure was qualitatively categorized as open, edge, corridor, or cluttered based on the spatial distribution of vegetation. Water resources were categorized as river, lake, stream, pond, or marsh. Rivers, lakes, and streams were categorized based upon local legal designations. Water sources inundated with vegetation (>50% of surface area) were characterized as marsh while those with open water were designated as ponds. Distance to the nearest water resource was recorded in meters.

Analysis

To assess the distribution of bat diversity across North Dakota and investigate the influence of habitat on bat community diversity, we examined ordination of sampling sites according to bat species assemblages with nonmetric multidimensional scaling (NMDS). Ultimately, NMDS provides a simplified graphical representation of multivariate species and site data that allows for the recognition and interpretation of patterns that reflect the underlying relationships between species and habitats. This method is often regarded as the most robust unconstrained ordination method in community ecology (McCune and Grace 2002; Estrada-Villegas et al. 2010). This analysis was conducted using the metaMDS function in the R vegan package (Estrada-Villegas et al. 2010; Johnson et al. 2010; Oksanen et al. 2013; R Core Team 2013) applied to the data, which was compiled in a matrix with bat species (presence/absence), latitude, longitude, elevation, nearest water type, distance to water, habitat structure category, and percent canopy cover as columns and sites in rows. For the bat species portion of the data, Bray-Curtis dissimilarity distances among sites were determined. In NMDS, sites are ordered hierarchically by their Bray-Curtis distances, and then the optimum position of n entities in k-dimensional space is sought out. NMDS optimizes the position of entities to reduce stress, or the magnitude entities must be moved in k-dimensional space to preserve the original hierarchical ordering of sites. We iteratively inspected stress levels of 1-6 dimensional ordinations with 10 iterations for each dimension and chose to use the dimension (k=3) that produced the best compromise between stress (<.20) and interpretability (Clarke 1993; Johnson et al. 2010). Prior to analysis, elevation was found to be correlated with longitude (Spearman's coefficient -0.76) so it was not included in further analysis. To determine if longitude, latitude, habitat variables, and the availability of water resources were correlated with the bat community diversity, we used the envfit function in the R vegan package (Oksanen et al. 2013; R Core Team 2013). Longitude, latitude, distance to water, and percent canopy cover were fitted to the ordination as vectors based on 1000 permutations of the data. Vectors are represented as arrows, where the arrow points in the direction of the gradient and the length is proportional to the correlation. The vector output includes the squared correlation coefficient (r^2) and p-values based on random permutations of the data. Nearest water and habitat structure were fitted to the ordination as factors (class centroids of sites) based on 1,000 permutations of the data.

We also used NMDS to investigate relationships between habitat characteristics and bat foraging activity using methods as previously described above. For this analysis, the data was compiled in a matrix with bat species (proportion of total number of call sequences per site for each species), nearest water type, distance to water, habitat structure category, and percent canopy cover as columns and sites in rows. For the bat species data, the number of call sequences of each species at each site was divided by the total call sequences for each species. In this manner, each species was equally weighted within the data set. As before, we iteratively inspected stress levels of 1-6 dimensional ordinations with 10 iterations for each dimension and chose the dimension (k=3) that produced a compromise between stress and interpretability. To determine if habitat structural characteristics and the availability of water resources were correlated with the NMDS ordination axes of proportional bat species activity, we used the envfit function in the R vegan package (Oksanen et al. 2013; R Core Team 2013). Distance to water and percent canopy cover were fitted to the ordination as vectors based on 1000 permutations of the data. Nearest water and habitat structure were fitted to the ordination as factors based on 1000 permutations of the data.

To identify sets of habitat variables associated with higher levels of bat foraging activity, we used a multivariate regression tree (MRT) analysis (De'ath 2002; McCune and Grace 2002; Larsen and Speckman 2004) using the mvpart extension of the R rpart package (Therneau et al. 2012; De'ath 2013; R Core Team 2013). MRT is an extension of univariate regression trees that allows for the exploration of relationships between multispecies data and habitat or environmental characteristics (De'ath 2002; Larsen and Speckman 2004). MRT clusters sites by repeatedly splitting the data based on the habitat characteristics. Splits are chosen to minimize the dissimilarity within clusters, and the clusters with their dependence on the habitat characteristics are graphically represented by a tree. On the tree, each leaf represents a species assemblage and the variables associated with each node leading to a resulting leaf define the habitat associations of the leaf. The analysis was conducted using the proportional bat call data and habitat variables. For better interpretability of results, canopy cover was categorized into classes as high (> 66%), medium (33-66%), or low (< 33%), and distance to water was categorized as near (< 75 m) or far based upon natural breaks in the data. We ran 5 iterations of the analysis with 50 multiple cross validations on 10 random subsets of the data for each iteration to ensure stability of our results in terms of the tree size and cross-validation error rate. Tree size was determined by selecting the largest tree with a cross-validation error within one standard error of the minimum (Johnson et al. 2010).

Not all bat species within a community will be impacted equally by any given habitat characteristic. Therefore, community measures such as absolute species richness or total bat activity may not be sufficient to fully understand the importance of a given habitat or water resources on bat community diversity or foraging activity. Alternatively, it is recommended that the activity of each species be used as an indicator of the quality of specific habitats (Korine et al. 2014). To identify indicator species or species assemblages that characterize the habitats associated with each leaf of the MRT, we performed an indicator species analysis (Dufrene and Legendre 1997; De'ath 2002; Castro-Luna et al. 2007) using R functions in the labdsv package (R Core Team 2013; Roberts 2013). Indicator species analysis identifies species that characterize each group using an indicator species index, or indicator value, based on relative frequency or abundance in a given habitat or group (specificity) and relative frequency of occurrence (fidelity) (Dufrene and Legendre 1997; Castro-Luna et al. 2007). The indicator value, defined as the product of relative abundance and relative frequency of occurrence of the species within a group, can be calculated for each species–group combination, and species with high indicator values for a group are indicator species for that group (De'ath 2002). To test for significance, a Monte Carlo test of the observed maximum indicator value was performed for each species based on 1000 randomizations. The p-value is based on the proportion of randomized trials with an indicator value equal to or greater than the observed indicator value.

Results

Acoustic Monitoring

We surveyed bat activity at 37 sites in 6 study areas in summers 2012-2015. We recorded over 200,000 echolocation passes, of which 14,766 were positively identified to species. All 11 species known to occur in North Dakota were detected, however, *M. septentrionalis*, *M. thysanodes* and *M. volans* were detected infrequently.

Statistical Analysis

Solutions for NMDS ordinations of bat species presence in 3 dimensions were achieved within 4 runs of the data. The stress value stabilized at 0.06 (linear fit $r^2 = 0.98$). Longitude, latitude, percent canopy cover, and habitat structure were all significantly correlated ($p < 0.05$) with the ordination (Table 2.1). Longitude explained the most variation in the ordination ($r^2 = 0.68$) followed by percent canopy cover ($r^2 = 0.34$). Distance to water was also correlated with the ordination ($p = 0.06$). The type of nearest water was not correlated with the ordination ($p = 0.2$) indicating that the bat community diversity is not influenced by water type. Longitude, latitude, and percent canopy cover were negatively associated with the first NMDS axis (Figure 2). Latitude and distance to water were negatively associated with the second NMDS axis. While sites were not clearly separated in ordination space based upon habitat structure, those classified as open habitat were nearly separated on the second NMDS axis, indicating differences in species composition from cluttered, edge, and corridor sites (Figure 2.2). Of the 11 bat species, all but *L. cinereus* and *L. noctivagans* were positively associated with the first NMDS axis. *C. townsendii*, *L. noctivagans*, *M. ciliolabrum*, and *M. lucifugus* were negatively associated with the second NMDS axis (Figure 2.2).

Table 2.1. Habitat Variables and Results of NMDS Ordination

	Variable	Definition	NMDS Axis 1	NMDS Axis 2	r^2	*P*
A	Latitude	Latitudinal coordinate at site	-0.823	-0.568	0.268	**0.011**
	Longitude	Longitudinal coordinate at site	-0.909	0.416	0.687	**<0.001**
	Distance to Water	Distance of nearest water source	0.665	-0.746	0.143	0.063
	Canopy Cover	Percent canopy cover at site	-0.706	0.708	0.336	**0.002**
	Nearest Water	River, lake, stream, pond, or marsh	-	-	0.150	0.202
	Structure	Open, edge, cluttered, or corridor	-	-	0.191	**0.024**
B	Distance to Water	Distance of nearest water source	-0.431	-0.902	0.168	**0.048**
	Canopy Cover	Percent canopy cover at site	0.296	0.955	0.381	**<0.001**
	Nearest Water	River, lake, stream, pond, or marsh	-	-	0.381	**<0.001**
	Structure	Open, edge, cluttered, or corridor	-	-	0.160	0.070

Habitat variables for (A) NMDS ordination of bats species occurrence and (B) proportional species activity. Bolded are significant $P < 0.05$.

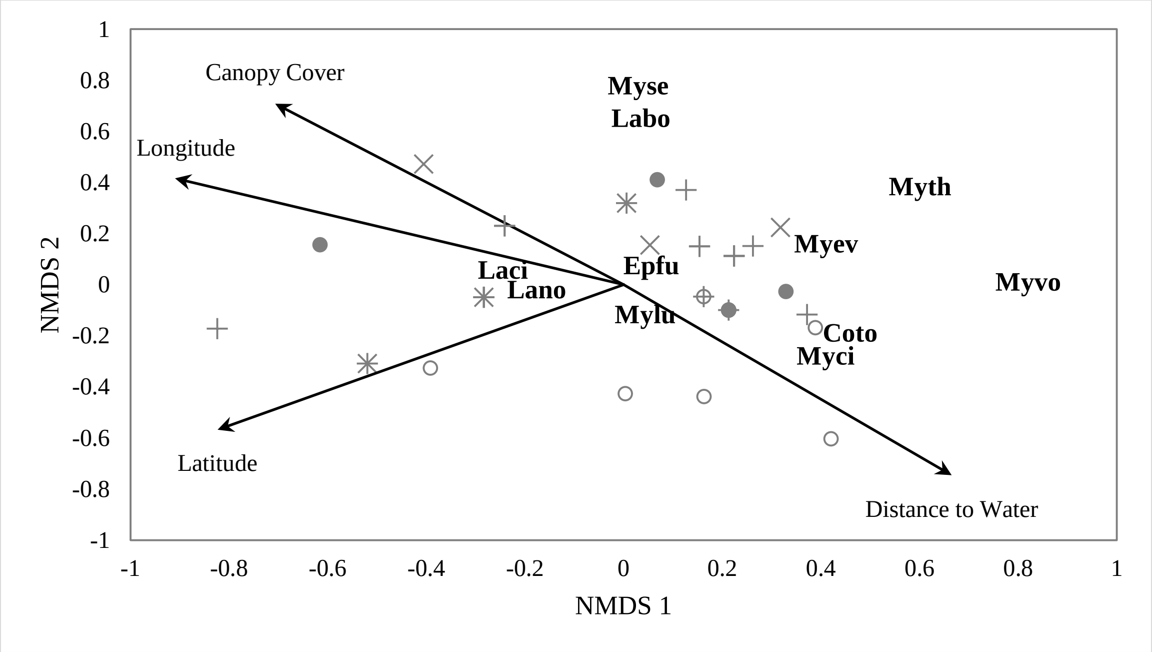

Figure 2.2. Non-metric Multidimensional Scaling of Bat Species Occurrence
Non-metric multidimensional scaling (NMDS) of bat species occurrence data with fitted habitat variable vectors. Sites are denoted with habitat structure (● = cluttered, + = edge; × = corridor; ○ = open) shown in ordination space. Bat species: Coto = *Corynorhinus townsendii*, Epfu = *Eptesicus fuscus*, Labo = *Lasiurus borealis*, Laci = *Lasiurus cinereus*, Lano = *Lasionycteris noctivagans*, Myci = *Myotis ciliolabrum*, Myev = *Myotis evotis*, Mylu = *Myotis lucifugus*, Myse = *Myotis septentrionalis*, Myth = *Myotis thysanodes*, Myvo = *Myotis volans*.

Solutions for NMDS ordinations of proportional bat activity in 3 dimensions were achieved within 5 runs of the data. The stress value stabilized at 0.10 (linear fit r2 = 0.93). Canopy cover, water type, and distance to water were significantly correlated ($p < 0.05$) with the ordination (Table 2.1). Habitat structure was also correlated with the species space axes ($p = 0.07$). Individually, all variables explained notable proportions (r2 > 15%) of variation in the ordination space. Overall, sites lacked clear separation in ordination space based upon habitat structure or nearest water; however, open stream habitat showed clear separation and was negatively associated with the first NMDS axis (Figure 2.3). Canopy cover was positively associated with both NMDS axes and distance to water was negatively associated with both NMDS axes. With the exception of *M. ciliolabrum* and *M. volans*, all bat species were positively associated with the first NMDS axis.

Due to the infrequency of detections and small sample sizes, *M. septentrionalis*, *M. thysanodes* and *M. volans* were not included in the multivariate regression tree analysis or subsequent indicator species analysis. Regression tree analysis resulted in up to 7 leaves within 1 cross-validation error of the minimum with meaningful interpretation of the contribution of habitat variables to bat activity (Figure 2.4). The model error was 0.622, indicating that 37.8% of the variation in bat activity was explained by the tree, which is comparable to similar studies (model error: 0.83; Johnson et al. 2010). High levels of bat activity were most associated with three habitats: edge, corridor, or cluttered habitats of moderate canopy cover near (< 75m) rivers; ponds; and to a lesser extent open riparian habitats (Figure 2.4).

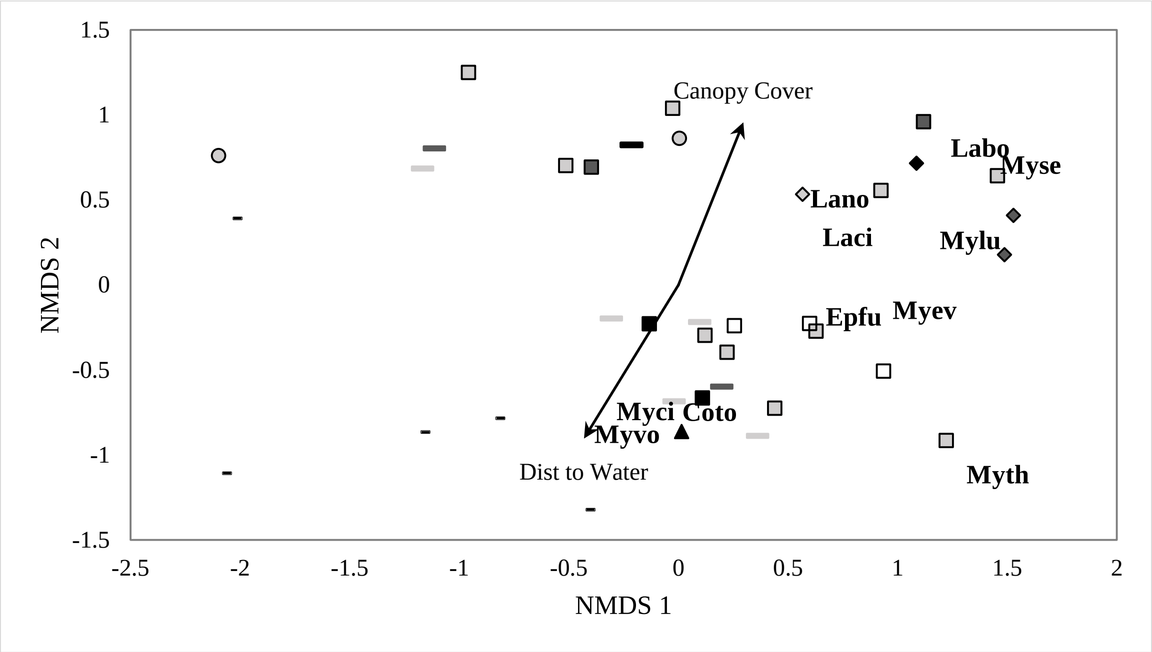

Figure 2.3. Non-metric Multidimensional Scaling of Proportional Bat Species Activity
Non-metric multidimensional scaling (NMDS) of proportional bat species activity with fitted habitat variable vectors. Sites are denoted with habitat structure and nearest water type factors are shown in ordination space. Sites nearest rivers (□), lakes (□), ponds (□), and marsh (□) are filled with black for cluttered, dark grey for corridor, light grey for edge, and white for open habitats. Sites nearest streams are denoted by dash marks: black = clutter; dark grey = corridor; light grey = edge; short black = open. Bat species: Coto = *Corynorhinus townsendii*, Epfu = *Eptesicus fuscus*, Labo = *Lasiurus borealis*, Laci = *Lasiurus cinereus*, Lano = *Lasionycteris noctivagans*, Myci = *Myotis ciliolabrum*, Myev = *Myotis evotis*, Mylu = *Myotis lucifugus*, Myse = *Myotis septentrionalis*, Myth = *Myotis thysanodes*, Myvo = *Myotis volans*.

Indicator species analysis revealed five of the eight species included in the MRT to be indicator species. *M. lucifugus* and *E. fuscus* were the most significant indicators ($p < 0.05$) while *L. cinereus*, *L. noctivagans*, and *M. evotis* were also significant at the 0.1 significance level (Table 2.2). *M. lucifugus* and *M. evotis* were found to be indicators of pond habitat; *E. fuscus* for open riparian habitat; *L. cinereus* and *L. noctivagans* for cluttered, corridor, and edge habitat of moderate canopy cover near rivers.

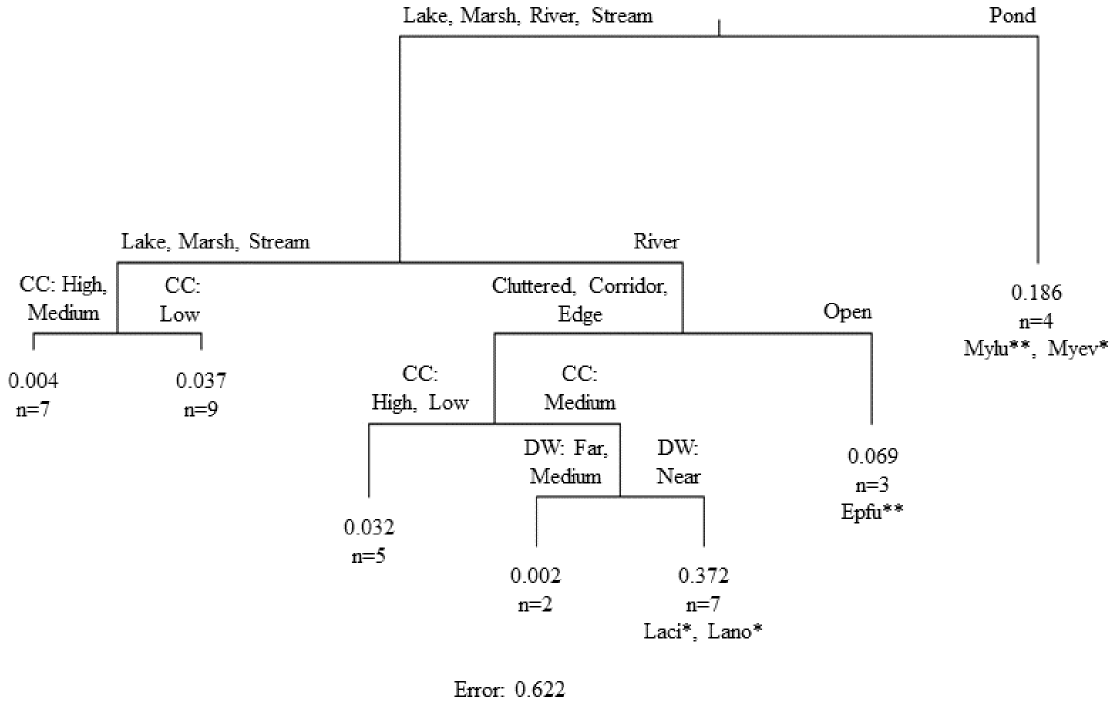

Figure 2.4. Multivariate Regression Tree for Proportional Bat Species Activity
Multivariate regression tree for proportional bat activity data. Proportional bat activity predicted by habitat variables at acoustic monitoring sites (n = 37) in North Dakota, 2012-2015. Indicator species are denoted at tree leaves. Bat species: Epfu = *Eptesicus fuscus*, Laci = *Lasiurus cinereus*, Lano = *Lasionycteris noctivagans*, Myev = *Myotis evotis*, Mylu = *Myotis lucifugus*. CC= Canopy Cover, DW= Distance to water. Indicator species significance levels: $p < 0.05$ (**), $p < 0.1$ (*).

Table 2.2. Indicator Values and Significance

	Epfu	Laci	Lano	Myev	Mylu
P	0.021	0.052	0.069	0.093	0.006
Indval	0.640	0.414	0.374	0.469	0.822

Indicator values (Indval) and significance for five indicator species. Bat species: Epfu = *Eptesicus fuscus*, Laci = *Lasiurus cinereus*, Lano = *Lasionycteris noctivagans*, Myev = *Myotis evotis*, Mylu = *Myotis lucifugus*.

Discussion

We found the NMDS ordination of bat community diversity to be significantly correlated with longitude, latitude, percent canopy cover, and habitat structure. Longitude and latitude were negatively correlated with the majority of species, indicating that bat diversity increases with decreasing longitude to the west and with decreasing latitude to the south. The availability of high quality foraging habitat may be at least partially responsible for this phenomenon. The landscape east of the Missouri River is more heavily dominated by agriculture, and agricultural practices limit the diversity and abundance of insect prey through monocultures and pesticide treatments. Canopy cover was negatively associated with *C. townsendii*, *M. ciliolabrum, M. evotis, M. thysanodes,* and *M. volans,* all species only definitively known to occur in the badlands region. While the badlands certainly have habitats with highly cluttered vegetation, these habitats often have sparse canopy cover. Riparian cottonwood stands in the badlands often have relatively low tree density, and stands of Rocky Mountain juniper are typically relatively short (< 10m tall) with the bulk of the vegetative mass near the bottoms of the trees. *C. townsendii*, *M. ciliolabrum*, *M. evotis, M. thysanodes*, and *M. volans* were also more positively associated with distance to water, indicating that these species may be less reliant on riparian forests. While cluttered, corridor, and edge habitats did not clearly separate in the ordination space, open habitats appear least associated with ordination of bat species, indicating that bat species occurrence is influenced by the presence of at least partially forested habitat.

We also found both habitat structure and the availability of water resources to be significantly correlated with NMDS ordination of proportional bat activity. *L. borealis* and *M. septentrionalis* were associated with habitats of relatively high canopy cover near rivers and ponds. *L. cinereus* and *L. noctivagans* were associated with edge habitat with moderate canopy cover near water. *M. lucifugus* were associated with corridors near pond habitats with moderate canopy cover. *E. fuscus* were associated with open and edge habitats of relatively low levels of canopy cover near rivers. *M. evotis* were associated with habitats of relatively low levels of canopy cover near rivers and ponds. *C. townsendii*, *M. ciliolabrum*, and *M. volans* were associated with cluttered, corridor, and edge habitats of little to no canopy cover relatively further from water. *M. thysanodes* was associated with riparian edge habitat of little to no canopy cover; however, results for *M. thysanodes*, *M. volans*, and *M. septentrionalis* should not be considered robust due to low sample sizes and *M. thysanodes* was only detected at one site.

Regression tree analysis revealed that high levels of bat activity were most associated with riparian edge, corridor, and cluttered habitats of moderate canopy cover near water (Figure 4). Ponds, and to a lesser extent open riparian habitats, were also found to be associated with relatively high levels of bat activity. Indicator species analysis revealed significant indicator species for each of these corresponding habitat clusters of the MRT. *L. cinereus* and *L. noctivagans* were found to be indicators of riparian edge, corridor, and cluttered habitats of moderate canopy cover near water; *M. lucifugus* and *M. evotis* are indicators of pond habitats; and *E. fuscus* are indicators of open riparian habitat. These results are consistent with the patterns observed in the NMDS ordination of proportional bat activity.

The little brown bat, *M. lucifugus*, was the most significant indicator species (p = 0.003; indicator value = 0.82). Little brown bats are of special conservation concern, as they have experienced severe population declines in the eastern United States and Canada due to white-nose syndrome (Alves et al. 2014; Vonhof et al. 2015). The indicator value is at maximum when all individuals of a species are found within a single group of sites or habitat type and when the species occurs in at all sites within the group or habitat type (Dufrene and Legendre 1997). The high indicator value for *M. lucifugus* at sites nearest ponds highlights the importance of conserving this specific habitat type. Modern agricultural practices have resulted in high rates of pond and wetland drainage for conversion to cropland in North Dakota and throughout the Great Plains, resulting in dramatic declines in waterbird productivity (Higgins et al. 2016). While conservation of ponds has been considered for desert-dwelling bat species (Razgour et al. 2010), the implications of such habitat losses on bats in the Great Plains have not been considered.

Our results highlight the importance of riparian zones to bat foraging and support previous findings (Grindal et al. 1999). However, these results also draw attention to the importance of habitat heterogeneity. Bat communities are able to efficiently exploit a diversity of habitat conditions by spatially segregating habitats and using differing foraging strategies (Schnitzler and Kalko 2001; Schnitzler et al. 2003). Therefore, heterogeneous habitats should support the highest diversity of bat species due to differences in selection of foraging habitat among species that spatially partition habitat to reduce resource competition (Kunz 1973; Johnson et al. 2010). Our results suggest that heterogeneous habitats of both varying structural habitat characteristics and water resources are best for maintaining bat species diversity and provide high quality foraging habitat for an abundance of species. Our study takes a holistic approach to studying bat habitat use which helps provide relevant insights for conservation and management. Further we have identified ponds as a key habitat with significant conservation implications for *M. lucifugus*, a species of conservation concern.

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CHAPTER 3. SELECTION OF FORAGING HABITAT BY FEMALE LITTLE BROWN BATS, *MYOTIS LUCIFUGUS*

Introduction

For effective conservation and management of wildlife populations, detailed information is needed about habitat use of a species. This information is also key for understanding ecological interactions and evolutionary implications of species' behavior. Habitat composition and structure are important factors of ecological niches and foraging behavior (Arlettaz, 1999; Sattler, Bontadina, Hirzel, and Arlettaz, 2007). Here, we define habitat composition as categorical land cover attributes (e.g. evergreen forest, grassland) and habitat structure as a description of vegetation density (e.g. cluttered forest, edge/gap, or open habitat) or canopy cover. Measures of habitat use in terms of composition or structure are particularly valuable for assessing the importance of specific habitat types or conditions.

Habitat composition plays a key role in the distribution of insect prey and foraging strategies of bats, as well as the partitioning of resources by sympatric bats species (Arlettaz 1999; Bergeson et al. 2013). For example, Arlettaz (1999) found that sympatric sister species, *Myotis myotis* and *Myotis blythii*, spatially segregate when foraging based on differences in habitat requirements of prey. Similarly, Bergeson et al. (2013) found that sympatric *Myotis sodalis* and *Myotis lucifugus* partition foraging resources behaviorally and through variation in selection of land cover.

In addition to habitat composition, habitat structure has also been studied in bats, with a strong focus on understanding how morphological features and physiological states of a given species impact the type of habitat structure in which they are primarily found. For example, Kalcounis and Brigham (1995) found that heavier *M. lucifugus* with greater wing loading foraged in lower clutter habitat. Similarly, Adams (1996) found that juvenile *M. lucifugus* with higher wing aspect ratios and lower wing loading exploit more diverse and cluttered habitat than their still growing cohorts. Further, a large body of work has focused on classifying bats into functional groups based on echolocation call structure, morphology and flight behavior as it correlates with habitat structure and habitat use (Aldridge and Rautenbach 1987; Schnitzler and Kalko 2001; Schnitzler et al. 2003). However, resource use may not be predictable by echolocation or morphology alone (Arlettaz 1999; Davidson-Watts et al. 2006), and combining data for such functional groups, guilds, or even sexes may yield ambiguous or spurious results in selection studies (Broders et al. 2006). Overall, studies of habitat use by bats are abundant in the ecological literature, yet detailed habitat characterizations are often limited, and knowledge of foraging habitat selection of many bat species is lacking.

Habitat selection is the decision making process through which animals choose resources relative to their availability or accessibility (Johnson 1980; Garshelis 2000). It is presumed that species should select for habitats that best meet their ecological and behavioral needs. A variety of study designs have been developed to investigate habitat selection (Garshelis 2000; Manly et al. 2002). The use-availability design identifies habitat selection as occurring when habitats are used disproportionately to their availability (Garshelis 2000; Manly et al. 2002). A significant challenge in habitat selection studies is defining habitats so that they are ecologically relevant and appropriately partitioned so that selection can be measured for a given species (Garshelis 2000).

The volant, nocturnal nature and relatively small size of bats make them particularly problematic for assessing habitat selection (Henry et al. 2002; Gannon et al. 2003). With recent advances in spatial analysis of habitat via Geographic Information Systems (GIS), habitat selection studies have progressed. However, the majority of such research on bats includes limited habitat characterizations, using only land cover attributes available in GIS datasets, which are not necessarily reflective of habitat structures that are important to foraging bats. Also, such GIS land cover datasets typically represent coarse landscape features which may lack the detail required for ecologically meaningful assessments of habitat use (Brambilla et al. 2009). Fewer studies have incorporated habitat structure, with those studies generally separating analysis of habitat structure from composition (Napal et al. 2010, 2013; Buckley et al. 2013; Arrizabalaga-Escudero et al. 2014; Ripperger et al. 2015). Further, most studies do not evaluate individual variation in habitat selection (Hillen et al. 2011), and therefore selection may not be detectable at the population level if individuals or sexes exhibit alternative selection strategies (Garshelis 2000).

The goal of this study was to assess foraging habitat selection of the little brown bat, *M. lucifugus*. We radio-tracked bats using autonomous telemetry data logging receivers, which allow for simultaneous, long term data collection on multiple bats with minimal researcher input. While this type of autonomous telemetry has been used to assess bat migration (McGuire et al. 2012) and various aspects of spatial ecology in other taxa (Bridger et al. 2001; Drewe et al. 2012; Ryder et al. 2012), it has not previously been used to study habitat selection in bats. Our specific objectives were to: (1) assess female *M. lucifugus* foraging habitat selection in terms of habitat composition and structure in tandem; (2) and assess individual variation in habitat selection of female *M. lucifugus*.

Methods

Study Species

The little brown bat is an insectivorous bat (6-11 g; van Zyll deJong 1985) widely distributed throughout most of North America (Fenton and Barclay 1980). *M. lucifugus* feed on a variety of small insects (3-10 mm long; Anthony and Thomas H. Kunz 1977), often in cluttered habitats near or over water (Fenton and Bell 1979; Fenton and Barclay 1980; Kalcounis and Brigham 1995; Adams 1996; Adams and Thibault 2006). Maternity colonies vary in size, ranging from a few to over a thousand individuals. Roosts are often found in man-made structures, such as old buildings (Fenton and Barclay 1980; Anthony et al. 1981), and are usually near bodies of water (Kunz et al. 1995).

Study Sites

Data was collected at two nursery colonies of *M. lucifugus*: (1) a picnic shelter in the North Unit of Theodore Roosevelt National Park (TRNP) containing ~50 adult female bats, and (2) a bat house at Cross Ranch State Park (CRSP) containing ~40 adult female bats. The TRNP site consists of cottonwood (Populus deltoides) dominated riparian forest surrounded by badlands. The CRSP site consists of cottonwood-dominated riparian forest surrounded by upland prairie, pasture, and agricultural fields. The habitat of both sites is relatively similar in composition and structure at the scale of sampling in this study. Sites were selected based on previous work identifying these areas as sites of higher abundance of *M. lucifugus* in North Dakota (Nelson et al. 2015).

Telemetry

Bats were captured using mist nets (Kunz and Parsons, 2009) placed at roost entrances. The species, sex, age, mass, and forearm length were assessed for all captured animals. Trapping and tracking of bats was avoided during parturition, which occurs mid-late June to early July (Farrrell and Studier 1973; Barclay 1982; Kunz et al. 1983). Bats selected for radio-tracking were fitted with digitally encoded transmitters (Lotek NTQB-1 Nano Tags, Lotek Wireless Inc., Newmarket, ON, Canada) attached to trimmed mid-dorsal hair over the scapulae using surgical skin adhesive. Each transmitter has a unique digital ID signature, although all transmitters emit the same frequency; this allows for simultaneous monitoring of multiple transmitters, which is not possible with traditional radio telemetry systems. Transmitters weighed 0.29 g (<5% of the bat's body mass; Aldridge and Brigham 1988), and had a pulse rate of 2s, resulting in a battery life of approximately 12 days.

Upon release, bats were tracked using a telemetry array of three automated receiving towers. The towers each consisted of a data logging receiver (SRX DL, Lotek Wireless Inc., Newmarket, ON, Canada) connected to an antenna tower affixed with a pair of five-element Yagi antennas raised ~5m in the air. Antennas were monitored on alternating 4s cycles, which ensures detection if transmitters are within detectable range. The data loggers continuously recorded all transmitter detections and logged the transmitter ID, date and time of detection, antenna number, and signal strength. Calibration tests of line-of-sight detection gave a maximum detection range of approximately 400m in the direction an individual antenna was oriented, and 150m to the side and rear. Telemetry arrays were strategically positioned so that the sampling range encompassed as much of the available area near the roost as possible. Each antenna was oriented to monitor a separate portion of the sampling area, although some overlap occurred (Figures 1 and 2). To ensure continuous monitoring, the operational status of each data logger was regularly checked and data from periods of time when batteries failed was excluded from analysis.

Habitat Selection

In GIS (ArcMap, ArcGIS version 10.3), the data logger locations and antenna detection ranges were mapped. Habitat types were designated using 20 categories based on habitat composition and structure (Table 3.1). Habitat within detection range was manually digitized as a set of polygons using georeferenced aerial imagery corroborated by manual inspection of habitats done during sampling (Figures 3.1 and 3.2). From this data, the proportional area of each habitat type within each antenna's sampling range could be determined. Telemetry data was filtered to only include detections during a window of two hours after sunset, as this corresponds with the primary peak in foraging activity of *M. lucifugus* (Anthony and Thomas H. Kunz 1977; Anthony et al. 1981; Henry et al. 2002). It is assumed that animals were selected independently with equal probability from a single population. Therefore, the animals can provide the needed replication to make inferences at the population level without concern for autocorrelation of location estimates (Otis and White 1999).

Table 3.1. Classifications and Descriptions of Habitat Types

Habitat Type	Description
Mixed Forest	Mixed species forest; highly cluttered understory
Cottonwood Forest	Cottonwood dominated forest; more sparsely distributed than mixed forest; medium clutter
Grass/Herb	Open grassland and herbaceous vegetation
Crops	Open areas of agriculturally converted land cover
Mowed	Open areas of mowed grass; predominately in campground areas
Barren	Open ground areas; characteristic of river sandbars and banks or badland bluff faces
Shrubs	Highly vegetated but lacking canopy cover
Marsh	Seasonal wetlands associated with drainages or streams
Grass/Herb Edge	Edge habitats formed from distinct boundaries between forest and associated open habitats; Water edge (water) is predominately associated with river habitat
Water Edge	
Crop Edge	
Developed/Mowed Edge	
Corridor	
Marsh Edge	
River	Aquatic habitats assigned by appropriate definitions
Pond	
Stream	
Buildings	Including picnic shelters
Roadway	Either paved or gravel roads
Developed Other	Miscellaneous anthropogenic structures

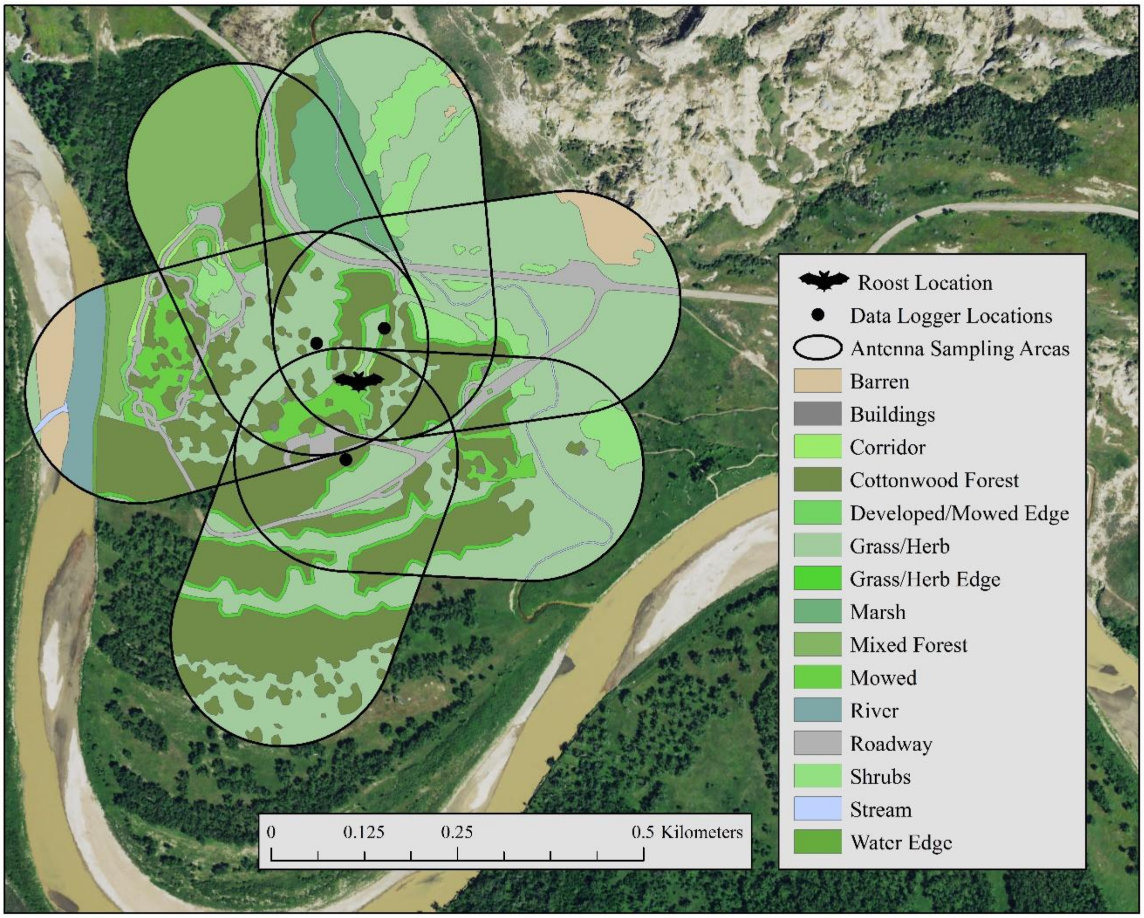

Figure 3.1. Map of Theodore Roosevelt National Park (North Unit)
Map of TRNP showing locations of roost, data loggers, and sampling areas overlaid on digitized habitat types.

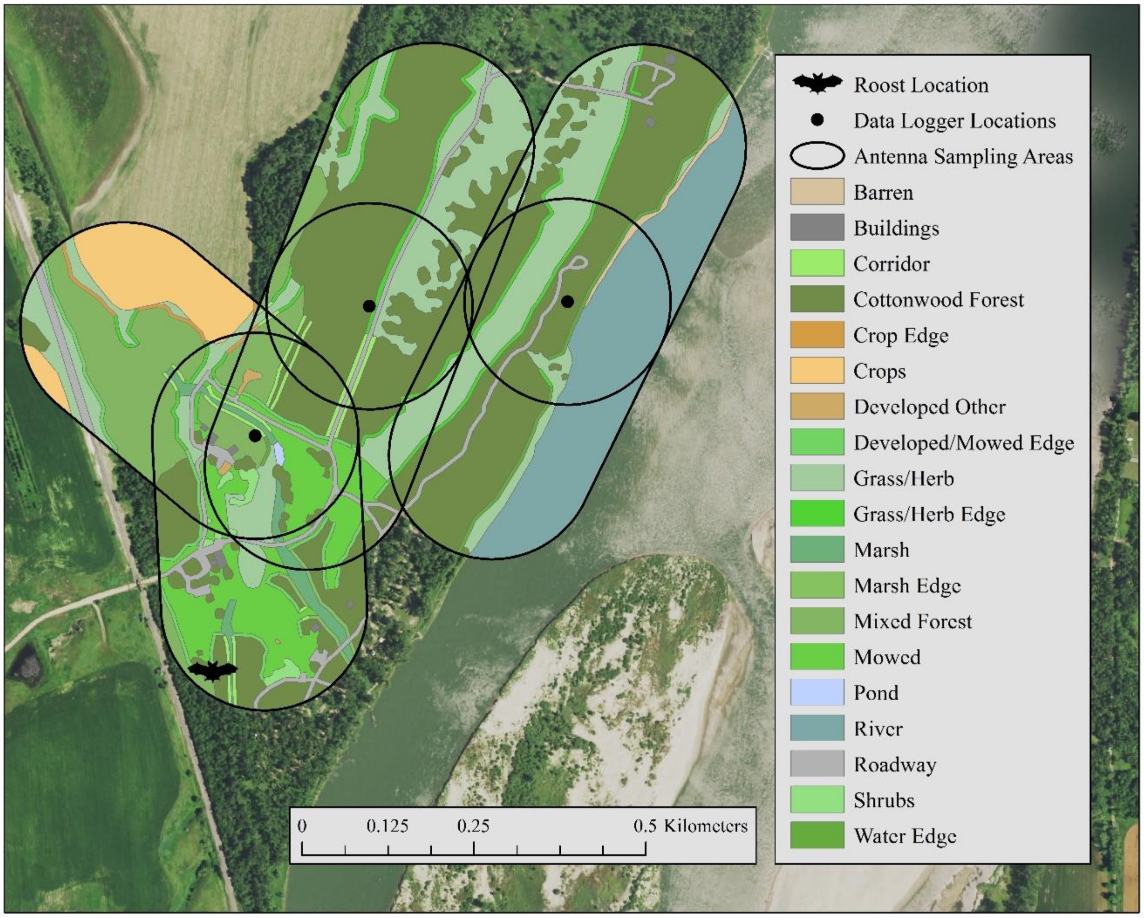

Figure 3.2. Map of Cross Ranch State Park
Map of CRSP showing locations of roost, data loggers, and sampling areas overlaid on digitized habitat types.

Because the exact location of a bat within an antenna's sampling range cannot be accurately determined, habitat use was assigned by dividing the number of detections for an antenna proportionally among the habitats available within that sampling range. The counts per habitat were then summarized across all of the antennas as a representation of habitat use for that bat. The drawback of this method is that the strength of relative selection for/against any particular habitat type is diminished because habitat use is inevitably assigned to habitat types that may not actually be used, but are co-located with habitat types for which there is positive selection. Despite this feature, selection is still detectable as long as the proportions of habitat are not uniform across all antenna sampling ranges. An additional complicating factor is that the antenna sampling ranges had some level of overlap, especially antennas attached to the same data logger. The nature of the detection system means that bats cannot be simultaneously detected on shared antennas, as the data logger systematically switches between monitoring each of the antennas individually. Hence, a bat's location cannot be confidently narrowed down to the overlapped habitat, and habitat use can only be assigned to each antenna individually. To address this issue, we used the proportions of habitat within each individual antenna's sampling range, summarized across all antennas, as the available habitat for analysis.

To assess habitat selection, selection ratios (*wi*) of used versus available habitat were calculated (Manly et al. 2002). In the absence of selection, a ratio equaling 1 is expected, while selection ratios greater than 1 reflect positive selection for that habitat. Habitats are subsequently ranked according to their selection ratio. There are three types of use-availability designs for assessing habitat selection: design I = animals are pooled and habitat use and availability are measured at the population level; design II = habitat use is measured for each animal and habitat availability is measured at the population level; design III = habitat use and availability are measured for each animal (Manly et al. 2002). Since bats at each site shared a roost and could potentially share foraging sites, analysis of study design II or III could be applied to our data by simply using the same habitat availability for all animals under the design III framework. We conducted both analyses on our data so that nonrandom habitat use could be tested at both the population and individual level. Following Manly et al. (2002), χ^2 goodness of fit tests were used to test for identical use of habitat by all animals, habitat selection by individuals, and independence of habitat use and availability (overall habitat selection). To assess selection of individual habitats, Bonferroni confidence intervals were constructed for individually estimated proportions of habitat use and availability. Pairwise comparisons between selection ratios were then evaluated for statistical significance based on Bonferroni confidence intervals. For all tests, alpha was set to 0.05, and the confidence intervals were computed at the 95% level. To run all habitat selection analyses, we used the package "adehabitat" for R software (Calenge 2006) with R Studio Version 0.98.1028 (RStudio Team 2015).

Because all animals may not exhibit the same patterns of habitat selection, we also analyzed our data at the individual level. To evaluate individual variation in habitat selection, we conducted eigenanalysis of selection ratios (Calenge and Dufour 2006), which is useful for this purpose when there is a high number of animals and habitat types. This analysis undertakes an additive linear partitioning of the White and Garrott statistic, maximizing the difference between habitat use and availability on the first factorial axis (Calenge and Dufour 2006). If all animals select the same habitat types, then the majority of variation in selection is explained on the first axis. However, when there is high variability in selection, the explained variation is distributed across multiple axes (Calenge and Dufour 2006). Therefore, variation on one factorial axis may reveal differing intensities of selection for the same habitat types, while variation on two or more axes may reveal separate modes of selection or that selection strategies differ across animals.

Results

Bat Captures

At TRNP, we captured bats on 24 July 2014 and tagged 11 adult female *M. lucifugus*. We were able to gather sufficient data for analysis of 7 individuals over the subsequent 11 nights. At CRSP, we captured bats on 4 June 2015 and tagged 18 adult female *M. lucifugus*, with sufficient data being gathered from 17 of these animals over an 11-night period. Given the capture dates combined with visual inspection of the bats and roosts, sampling corresponded with mid-gestation in CRSP and mid- to late-lactation in TRNP.

Habitat Selection

Tests of overall habitat selection were highly significant under both design II and III frameworks. For simplicity, we report results under design II for the test of overall habitat selection. At both sites, bats did not use habitat in equal proportion to availability (TRNP: $\chi^2 = 1115.5$, df = 98, $p < 0.001$; CRSP: $\chi^2 = 20189.5$, df = 306, $p < 0.001$) and there were significant differences in selection between habitat types (Appendix D). Only 1 of 24 bats in our study did not exhibit statistically significant habitat selection (Bat ML173 from TRNP; $\chi^2 = 4.6$, df = 14, $p = 0.09$).

In TRNP, bats selected for marsh, mixed forest, shrubs, and stream habitat, as well as edge habitat bordering roadways and mowed grass (Figure 3.3). In CRSP, bats showed strong selection for edge habitat bordering un-mowed grass/herb habitat (Fig. 3.4). Barren habitat was also selected for at both sites but this habitat type likely lacks ecological relevance to bats (see Discussion). Despite trends in selection at each site, bats did not exhibit identical use of habitat (TRNP: $\chi^2 = 305.4$, df = 84, $p < 0.001$; CRSP: $\chi^2 = 6584.3$, df = 288, $p < 0.001$). Most notably, there was an overall trend toward selection for river and river edge habitat at both TRNP and CRSP, but selection for these habitats was highly variable (Figures 3.3 and 3.4). Results of eigenanalysis revealed that the majority of individual habitat selection variation was accounted for on the first factorial axis (79.3% at TRNP and 84.3% at CRSP). Adding a second factor increased the variance explained to 97.6% at TRNP and 99.5% at CRSP.

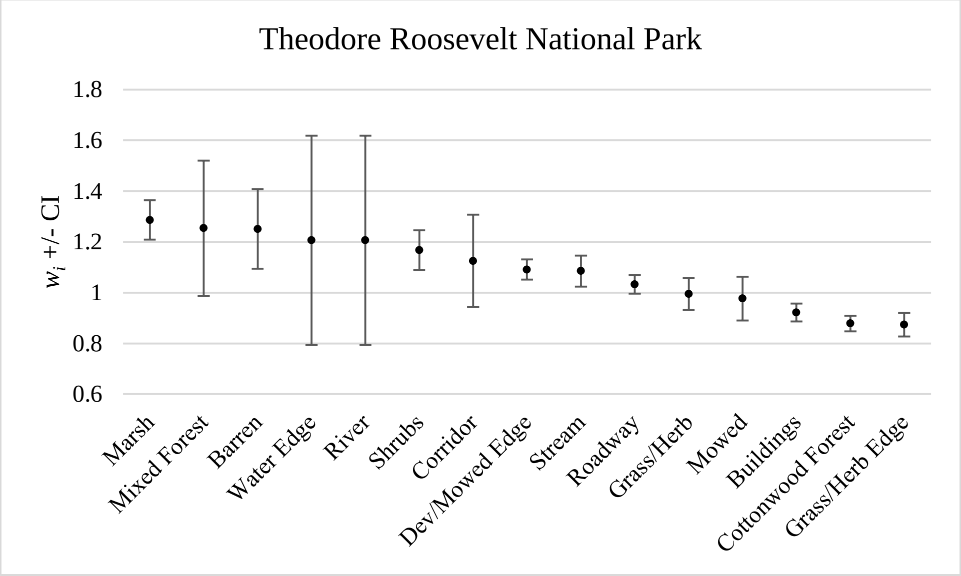

Figure 3.3. Selection Ratios for Theodore Roosevelt National Park
Selection ratios (*wi*) for habitats with Bonferroni confidence intervals for each habitat. Habitats are ranked by selection ratio.

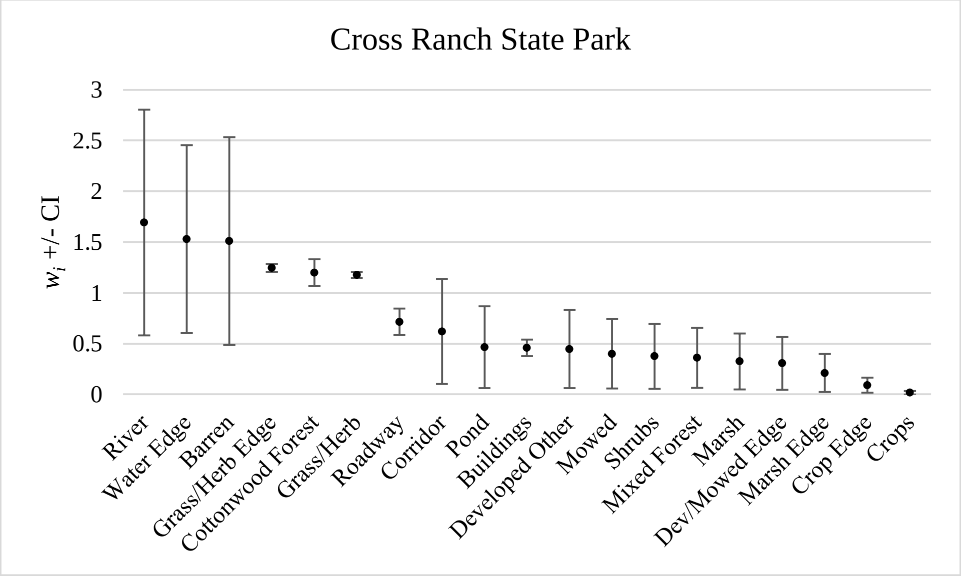

Figure 3.4. Selection Ratios for Cross Ranch State Park
Selection ratios (wi) for habitats with Bonferroni confidence intervals for each habitat. Habitats are ranked by selection ratio.

For TRNP, eigenanalysis confirms the overall trends in habitat selection found in the analysis of selection ratios. All but one individual bat exhibited similar patterns of habitat selection. However, as previously noted, this individual (bat ML173) exhibited nonsignificant habitat selection (Fig. 3.5). As confirmed by individual selection ratios (Fig. 3.6), eigenanalysis shows that the remaining bats exhibited varying intensities of selection between river, water edge, corridor, and stream habitats. Specifically, two individuals selected for stream habitat as opposed to the river and corridor.

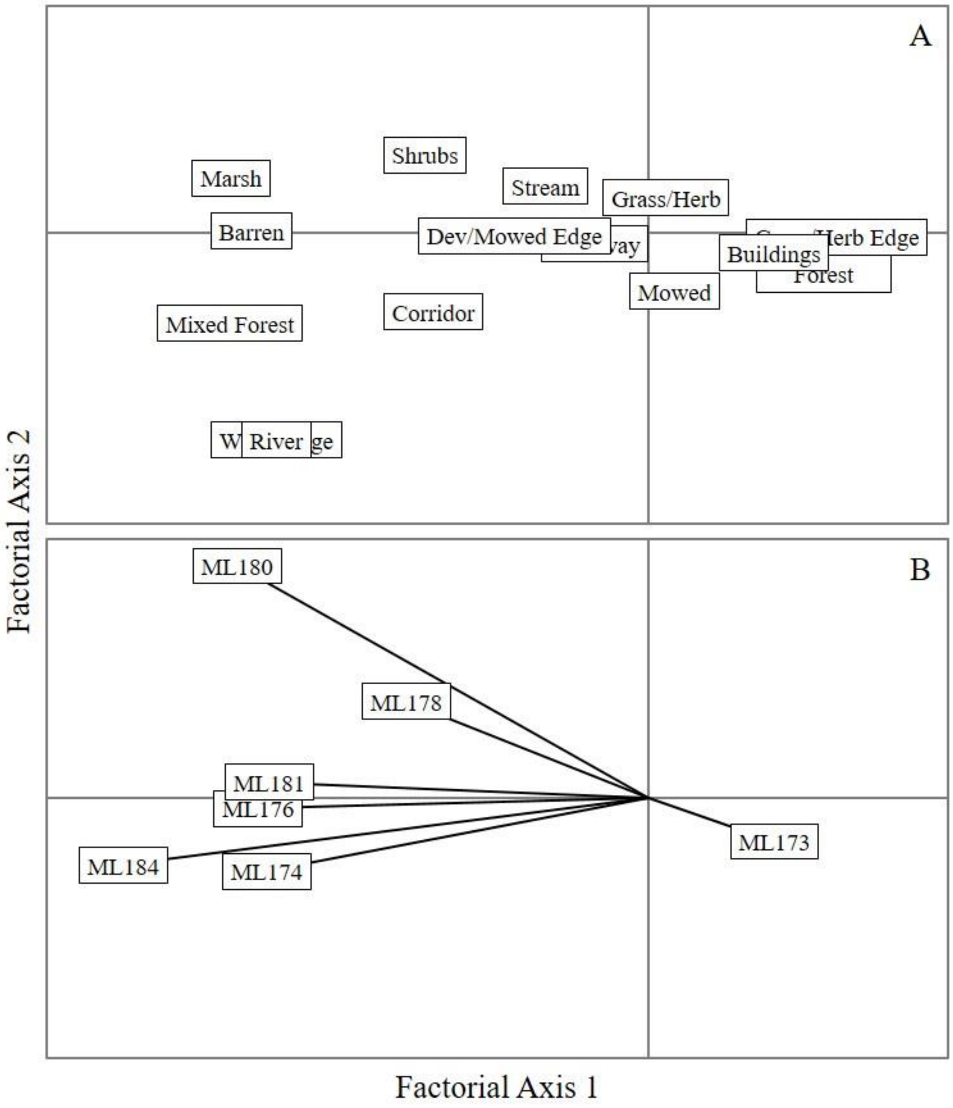

Figure 3.5. Eigenanalysis of Selection Ratios for Bats in Theodore Roosevelt National Park

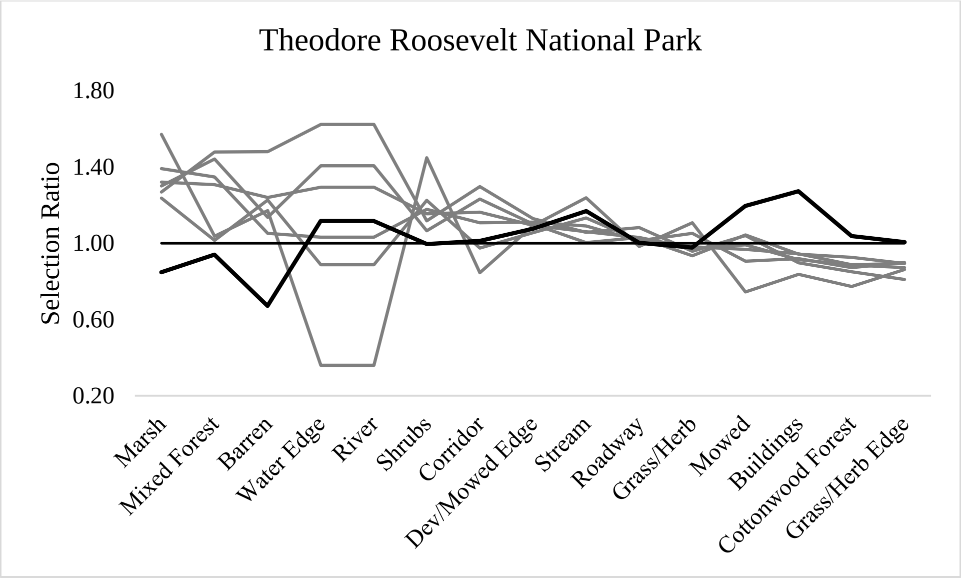

Figure 3.6. Selection Ratios of Individual Bats, Theodore Roosevelt National Park
Bat ML173 represented by bold black line. All other individuals represented by grey lines.

Similarly, for CRSP, eigenanalysis confirmed the overall trends in selection found in the analysis of selection ratios, and reveals variation among individuals in selection for river, water edge, and corridor habitat (Figure 3.7). All bats selected for grass/herb edge habitat. The majority of bats (14 individuals) selected for the river and its associated edge habitat. However, as confirmed by individual selection ratios (Figure 3.8), three individuals selected for strongly for corridor and used the river and water edge in lesser proportion than available, resulting in the division across axes seen in the eigenanalysis (Fig. 3.7).

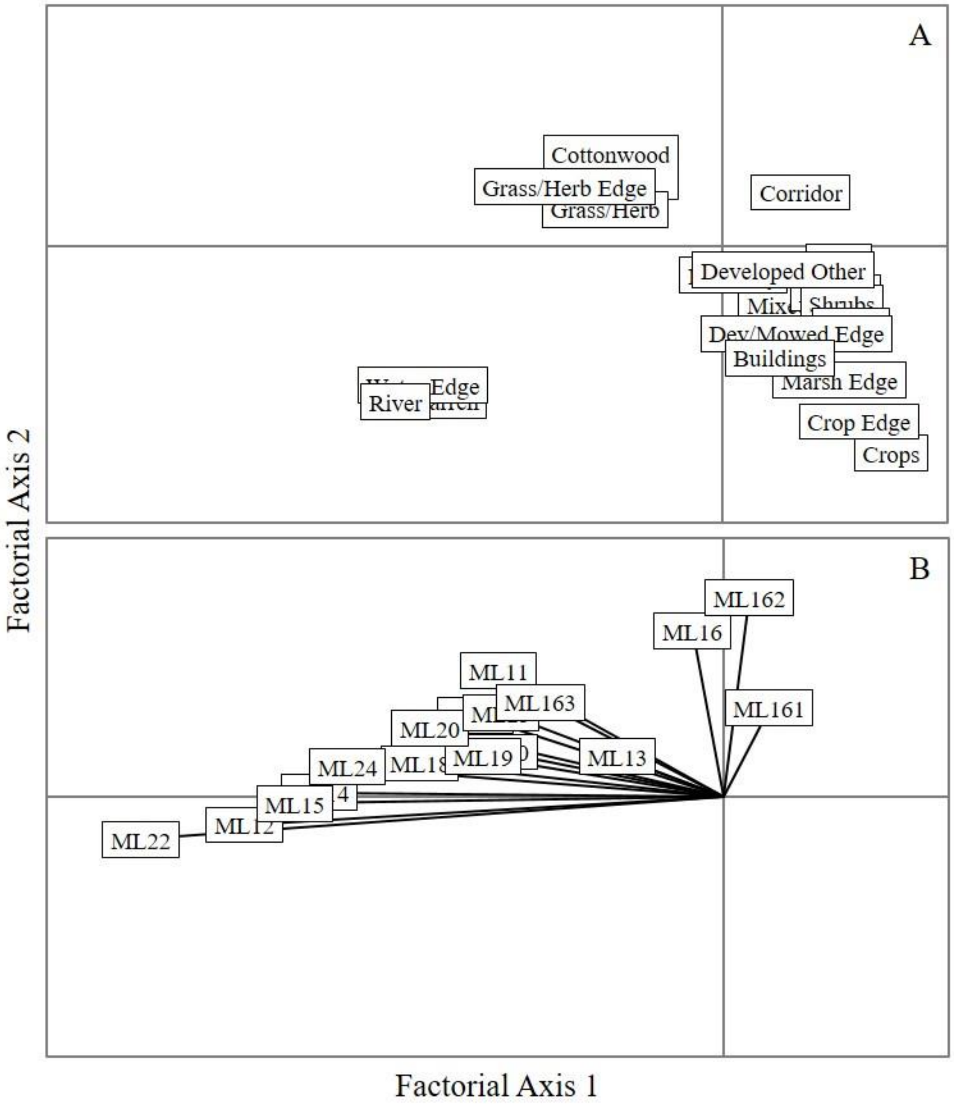

Figure 3.7. Eigenanalysis of Selection Ratios for Bats in Cross Ranch State Park

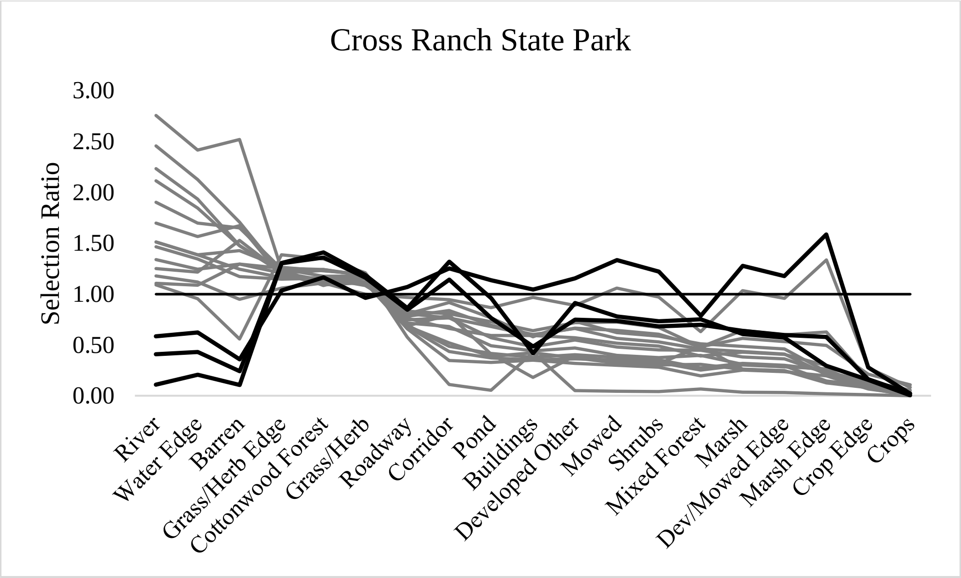

Figure 3.8. Selection Ratios of Individual Bats, Cross Ranch State Park
Bats ML16, ML161, and ML162 represented by bold black lines. All other individuals represented by grey lines.

Discussion

Bats at both TRNP and CRSP exhibited selection for edge habitats as well as selection, with significant variation, for the river and its associated edge habitat. Barren habitat was also positively selected; however, in TRNP this habitat was spatially limited and roughly equally distributed between portions of the river embankment/sand bars, and bluff faces (Figure 3.1) while in CRSP this habitat was limited solely to small portions of the river embankment (Figure 3.2). Therefore, selection for barren habitat is likely attributed to its association with other positively selected habitats, such as the river.

In TRNP, selection for marsh and shrub habitat seemed initially counter-intuitive, but inspection of the spatial distribution of these habitat types provides insight into this pattern. The majority of these habitats were spatially associated with a portion of the stream. Together, the marsh and stream habitats represent the closest water source to the roost in TRNP. The relatively weaker selection for stream habitat may also be explained by its spatial distribution. Specifically, the primary stream passes through roughly half of the sampling area, so measurable selection for this habitat type may have been limited by its relative abundance across less used portions of the sampling area.

Patterns of selection at TRNP may be at least partially attributed to the reproductive condition of bats at the time of study. During sampling, ~2 week old pups were captured at the roost, and the sampling date corresponds to mid-to-late lactation (Farrrell and Studier 1973; Fenton and Barclay 1980; Anthony et al. 1981; Henry et al. 2002). Energy demands are highest during lactation for *M. lucifugus* (Fenton and Barclay 1980; Kurta et al. 1989a; Kunz et al. 1995) and lactation represents a substantial strain on maintaining water balance (Kurta et al. 1989b; Kunz et al. 1995). Also, *M. lucifugus* exhibit a substantial decrease in home range size during lactation (~50%), making frequent trips back to the roost to nurse (Barclay 1982; Henry et al. 2002). Given that aquatic habitats provide not only drinking water but a high abundance of insect prey that *M. lucifugus* regularly exploit (Anthony and Thomas H. Kunz 1977; Fenton and Bell 1979; Fenton and Barclay 1980), it is not surprising that lactating *M. lucifugus* in our study selected for such habitat in close proximity to the maternity roost.

In contrast with CRSP, bats in TRNP selected for edge bordering roads or mowed grass. In TRNP, the campground roads and mowed camp sites have formed notably more edge habitat (of this type), relative to CRSP, in close proximity to the roost. One factor potentially contributing to these selection differences stems from prey availability. Insect control measures are typically conducted in campground areas of CRSP but not in TRNP. This could potentially drive foraging away from campground areas in CRSP, at a time when prey is a limited factor for pregnant *M. lucifugus* (Anthony and Thomas H. Kunz 1977; Anthony et al. 1981; Henry et al. 2002). Despite these differences, bats in TRNP and CRSP clearly exhibited strong selection for edge habitats. Also, bats at both sites selected for their respective rivers and associated edge habitats, although individuals exhibited a great deal of variation in selection for these habitats.

Previous studies have investigated variation in habitat use/selection between groups of individuals classified by factors such as age, sex, reproductive condition, or morphology (Aldridge and Rautenbach 1987; Kalcounis and Brigham 1995; Adams 1996; Hillen et al. 2011). However, little attention has been paid to variation among individuals (Hillen et al. 2011). We assessed variation in habitat selection among individual bats via eigenanalysis of selection ratios. We found that inconsistencies in overall habitat selection can be accounted for by differing intensities of selection for specific habitats. In these cases, differing selection among individuals can be explained by bats using different subsets of ecologically similar habitat. Edge habitats and water resources were strongly selected for by *M. lucifugus*, with variation at the microhabitat scale delineating potential individual preferences for specific edge compositions and water habitats. For example, all bats in CRSP selected for grass/herb edge, yet only 3 individuals selected for corridor habitat. Also, all bats in TRNP selected for water resources, yet 2 individuals selected for stream over river while their cohorts used both habitats.

Overall, we found that female *M. lucifugus* selected for edge habitats and water resources, which is consistent with previous observations and findings (Fenton and Bell 1979; Kalcounis and Brigham 1995; Bergeson et al. 2013). We found that bats exhibited habitat selection on a microhabitat scale when habitats are characterized by both habitat composition and structure in tandem; specifically, not all edge habitats or water resources were selected equally, with the composition of edge habitat influencing patterns of selection. Future habitat selection studies of bats should consider the relationship between habitat composition and structure to avoid overlooking important microhabitat associations.

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CHAPTER 4. CONCLUSIONS

Summary

The research presented here provides the first detailed picture of the bat communities inhabiting natural areas of North Dakota and can serve as a baseline for future comparisons in the face of changing climate and land use. Eleven bat species were documented and confirmed with physical captures. Species diversity was highest in the badlands region (all eleven species found) compared to other areas of the state. This is likely due to the abundance of variable roosting and foraging habitats available in the badlands ecosystem. The remaining areas of North Dakota have predominately been converted to agriculture. However, the Missouri River Valley, Turtle Mountains, Pembina Gorge, and Red River Valley also provide high quality forested habitat needed to support foliage and tree roosting bats. The presence of *M. thysanodes* and *C. townsendii* were each confirmed with physical captures; the distributions of these species were not previously thought to extend into North Dakota.

Analysis of the influence of habitat on bat community diversity and foraging activity confirmed not only the significance of riparian habitats but highlight the importance of habitat heterogeneity. Heterogeneous habitats should support relatively higher diversity of bat species due to differences in foraging modes/behavior and differences in foraging habitat selection among species that spatially partition habitat to reduce resource competition (Kunz 1973; Johnson et al. 2010; Jung et al. 2012). Our results suggest that bat species diversity is best maintained with heterogeneous habitats of both varying structural habitat characteristics and water resources. Heterogeneous habitats provide high quality foraging habitat for an abundance of species. The holistic assessment of not only the bat communities but the habitat as well provides relevant insights for conservation and management. Further, ponds were identified as a key habitat; this has significant conservation implications for little brown bats, *M. lucifugus*, a species that has suffered devastating population losses in the eastern U.S. and Canada due to white-nose syndrome.

Habitat selection analysis revealed that, in general, female *M. lucifugus* selected for edge habitats and water resources. These results are consistent with previous observations and findings (Fenton and Bell 1979; Kalcounis and Brigham 1995; Bergeson et al. 2013). However, we found that bats exhibited microhabitat selection when habitats are characterized by both habitat composition and structure in tandem. The composition of edge habitat influenced patterns of selection, and not all edge habitats or water resources were selected equally. Further, individual bats exhibited variation in habitat selection. More specifically, individuals showed varying levels of selection for edges of differing composition and for different types of water sources.

Synthesis

Overall, the combined works presented in this dissertation show that heterogeneous habitats are not only key to maintaining bat community diversity, but these habitats are associated with higher levels of foraging for many species. Edge habitats, which are characteristic of heterogeneous habitat, were selected by *M. lucifugus* and were also correlated with higher levels of foraging at the community level along with cluttered and corridor habitats. Habitats nearest rivers were found to be correlated with high levels of bat foraging at the community level, and rivers were selected for by most individual *M. lucifugus* in the telemetry study. In contrast to the community-level acoustic study, habitat selection analysis of *M. lucifugus* did not reveal selection for pond habitats. However, ponds were not highly available in the sampling areas where the telemetry study was conducted. The lack of selection for ponds may also be due to a sampling bias with telemetry. In this case, ponds may be selected for but individual bats may spend only a limited amount of time using these habitats, which would skew analysis of habitat selection against ponds (Garshelis 2000).

Future Work

Landscape modification has invariably altered the habitat of the badlands since the development of extensive oil and natural gas production in the Bakken Formation, although no research has attempted to quantify the effect on bats. While Theodore Roosevelt National Park is afforded some protection from such disturbances, the Little Missouri National Grasslands and other private lands of the region are not protected from oil exploration. These areas include high quality bat habitat essential to support the diverse bat community of the region. The North Dakota Game and Fish Department currently lists six of the species found in western ND as Species of Conservation Priority. *C. townsendii*, *E. fuscus*, *M. lucifugus*, and *M. septentrionalis* are listed as Species of Conservation Priority Level I (highest priority), and *M. ciliolabrum*, *M. evotis*, and *M. volans* as Level III (moderate priority, populations assumed to be peripheral or nonbreeding in North Dakota). Four of these species have been captured exclusively in the badlands. Future investigations should aim to assess the effects of oil and natural gas development on bats. Management efforts should focus on preservation of critical habitats, particularly the badlands, and work to reduce the environmental impacts of oil and natural gas development in the region.

The northern long-eared bat, M. septentrionalis was recently listed as threatened by the U.S. Fish and Wildlife Service (U.S.F.W.S. 2015). Special consideration should be given to this species for future bat research in North Dakota. Along with *M. lucifugus*, *M. septentrionalis* has suffered significant population declines due to white-nose syndrome. Future studies should assess roosting and foraging habitat selection of *M. septentrionalis* in North Dakota. It is currently unknown whether ND supports an over-wintering population of *M. septentrionalis*, or where any summer residents migrate to during the winter months. Further, the status of all over-wintering bat species populations in North Dakota is unclear. Future work is needed to identify hibernacula within the state as well as to assess migration corridors. The understanding of bat migration in the region is critical for making predictions about the potential spread of white-nose syndrome and the looming impacts to regional bat populations.

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APPENDIX A. BAT CAPTURE LOCATIONS BY SPECIES

Table A1. Capture locations of *Corynorhinus townsendii*

Region	County	Latitude	Longitude	Number Captured
Badlands	Billings	46.95845	-103.50604	1

Capture locations of *Corynorhinus townsendii* with study region, county, North latitude, West longitude, and numbers captured at each location.

Table A2. Capture locations of *Eptesicus fuscus*

Region	County	Latitude	Longitude	Number Captured
Badlands	Billings	47.30053	-103.58954	1
Badlands	Billings	47.31607	-103.48592	4
Badlands	Billings	46.94951	-103.53457	1
Badlands	Billings	46.95200	-103.49492	2
Badlands	Billings	46.92205	-103.45566	1
Badlands	Billings	46.95929	-103.50129	5
Badlands	Billings	46.93840	-103.38145	1
Badlands	McKenzie	47.60198	-103.27851	1
Badlands	McKenzie	47.59476	-103.31741	2
Badlands	McKenzie	47.59422	-103.31570	6
Badlands	McKenzie	47.59409	-103.33324	2
Missouri River Valley	McLean	47.21537	-100.96681	6
Missouri River Valley	McLean	47.21215	-100.96753	5
Missouri River Valley	McLean	47.21534	-100.96617	2
Missouri River Valley	Oliver	47.21504	-100.99831	10

Capture locations of *Eptesicus fuscus* with study region, county, North latitude, West longitude, and numbers captured at each location.

Table A3. Capture locations of *Lasionycteris noctivagans*

Region	County	Latitude	Longitude	Number Captured
Badlands	Billings	46.95929	-103.50129	1
Missouri River Valley	McKenzie	47.98080	-103.97305	1
Missouri River Valley	McLean	47.21215	-100.96753	1
Missouri River Valley	Oliver	47.21504	-100.99831	8
Missouri River Valley	Oliver	47.16420	-100.98298	1
Pembina Gorge	Cavalier	48.93917	-98.07454	2
Red River Valley	Bames	46.63182	-97.95002	1
Red River Valley	Grand Forks	47.94654	-97.50694	4
Red River Valley	Grand Forks	47.93742	-97.50542	1
Red River Valley	Grand Forks	47.93985	-97.49814	3
Red River Valley	Grand Forks	47.94646	-97.49587	1
Red River Valley	Grand Forks	47.93683	-97.49923	1
Red River Valley	Grand Forks	47.93683	-97.49923	17
Red River Valley	Grand Forks	47.94124	-97.50078	2
Red River Valley	Grand Forks	47.93597	-97.51567	6
Turtle Mountains	Bottineau	48.98541	-100.33795	1

Capture locations of *Lasionycteris noctivagans* with study region, county, North latitude, West longitude, and numbers captured at each location.

Table A4. Capture locations of *Lasiurus borealis*

Region	County	Latitude	Longitude	Number Captured
Red River Valley	Grand Forks	47.93985	-97.49814	1
Red River Valley	Grand Forks	47.94124	-97.50078	1
Turtle Mountains	Bottineau	48.98541	-100.33795	1
Turtle Mountains	Bottineau	48.98665	-100.33560	2

Capture locations of *Lasiurus borealis* with study region, county, North latitude, West longitude, and numbers captured at each location.

Table A5. Capture locations of *Lasiurus cinereus*

Region	County	Latitude	Longitude	Number Captured
Badlands	Billings	46.95200	-103.49492	1
Badlands	McKenzie	47.60198	-103.27851	1

Capture locations of *Lasiurus cinereus* with study region, county, North latitude, West longitude, and numbers captured at each location.

Table A6. Capture locations of *Myotis ciliolabrum*

Region	County	Latitude	Longitude	Number Captured
Badlands	Billings	47.30053	-103.58954	1
Badlands	Billings	47.31607	-103.48592	2
Badlands	Billings	46.95200	-103.49492	3
Badlands	Billings	46.92205	-103.45566	1
Badlands	Billings	46.93645	-103.42641	1
Badlands	Billings	46.95929	-103.50129	1
Badlands	Dunn	47.54946	-102.73499	4
Badlands	McKenzie	47.60198	-103.27851	2
Badlands	McKenzie	47.59422	-103.31570	1
Badlands	McKenzie	47.59938	-103.34322	1

Capture locations of *Myotis ciliolabrum* with study region, county, North latitude, West longitude, and numbers captured at each location.

Table A7. Capture locations of *Myotis evotis*

Region	County	Latitude	Longitude	Number Captured
Badlands	Billings	47.30053	-103.58954	3
Badlands	Billings	46.95200	-103.49492	1
Badlands	Billings	46.92205	-103.45566	1
Badlands	Billings	46.95929	-103.50129	3
Badlands	Golden Valley	47.22910	-103.67386	1
Badlands	McKenzie	47.60198	-103.27851	1
Badlands	McKenzie	47.59476	-103.31741	3

Capture locations of *Myotis evotis* with study region, county, North latitude, West longitude, and numbers captured at each location.

Table A8. Capture locations of *Myotis lucifugus*

Region	County	Latitude	Longitude	Number Captured
Badlands	Billings	46.95200	-103.49492	2
Badlands	Billings	46.95929	-103.50129	1
Badlands	Billings	46.93840	-103.38145	1
Badlands	McKenzie	47.60198	-103.27851	3
Badlands	McKenzie	47.59461	-103.33757	54
Badlands	McKenzie	47.59476	-103.31741	2
Badlands	McKenzie	47.59422	-103.31570	12
Missouri River Valley	McLean	47.21537	-100.96681	17
Missouri River Valley	McLean	47.21534	-100.96617	2
Missouri River Valley	Oliver	47.21504	-100.99831	16
Missouri River Valley	Oliver	47.21224	-100.99941	44
Missouri River Valley	Oliver	47.16420	-100.98298	9
Turtle Mountains	Bottineau	48.98541	-100.33795	3
Turtle Mountains	Rollette	48.96189	-99.83408	3

Capture locations of *Myotis lucifugus* with study region, county, North latitude, West longitude, and numbers captured at each location.

Table A9. Capture locations of *Myotis septentrionalis*

Region	County	Latitude	Longitude	Number Captured
Badlands	McKenzie	47.60198	-103.27851	2
Badlands	McKenzie	47.59476	-103.31741	2
Badlands	McKenzie	47.59422	-103.31570	1
Missouri River Valley	Oliver	47.21504	-100.99831	10
Missouri River Valley	Oliver	47.21224	-100.99941	2
Missouri River Valley	Oliver	47.16420	-100.98298	6

Capture locations of *Myotis septentrionalis* with study region, county, North latitude, West longitude, and numbers captured at each location.

Table A10. Capture locations of *Myotis thysanodes*

Region	County	Latitude	Longitude	Number Captured
Badlands	McKenzie	47.59409	-103.33324	1

Capture locations of *Myotis thysanodes* with study region, county, North latitude, West longitude, and numbers captured at each location.

Table A11. Capture locations of *Myotis volans*

Region	County	Latitude	Longitude	Number Captured
Badlands	McKenzie	47.59409	-103.33324	1

Capture locations of *Myotis volans* with study region, county, North latitude, West longitude, and numbers captured at each location.

APPENDIX B. BAT CAPTURES BY SEX

Table B1. Bat Captures by Sex 2009-2012

	Male	Female	%Male	%Female
COTO	1	0	100.00	0.00
EPFU	15	34	30.61	69.39
LANO	3	48	5.88	94.12
LABO	1	4	20.00	80.00
LACI	2	0	100.00	0.00
MYCI	7	10	41.18	58.82
MYEV	7	6	53.85	46.15
MYLU	20	149	11.83	88.17
MYSE	6	17	26.09	73.91
MYTH	1	0	100.00	0.00
MYVO	1	1	50.00	50.00
Total	64	269	19.22	80.78

Numbers of bats captured by sex with associated gender ratios in North Dakota, 2009-2012. COTO= *C. townsendii*, EPFU= *E. fuscus*, LANO= *L. noctivagans*, LABO= *L. borealis*, LACI= *L. cinereus*, MYCI=*M. ciliolabrum*, MYEV= *M. evotis*, MYLU= *M. lucifugus*, MYSE= *M. septentrionalis*, MYTH= *M. thysanodes*, MYVO= *M. volans*.

APPENDIX C. ADDITIONAL OCCURRENCE MAPS

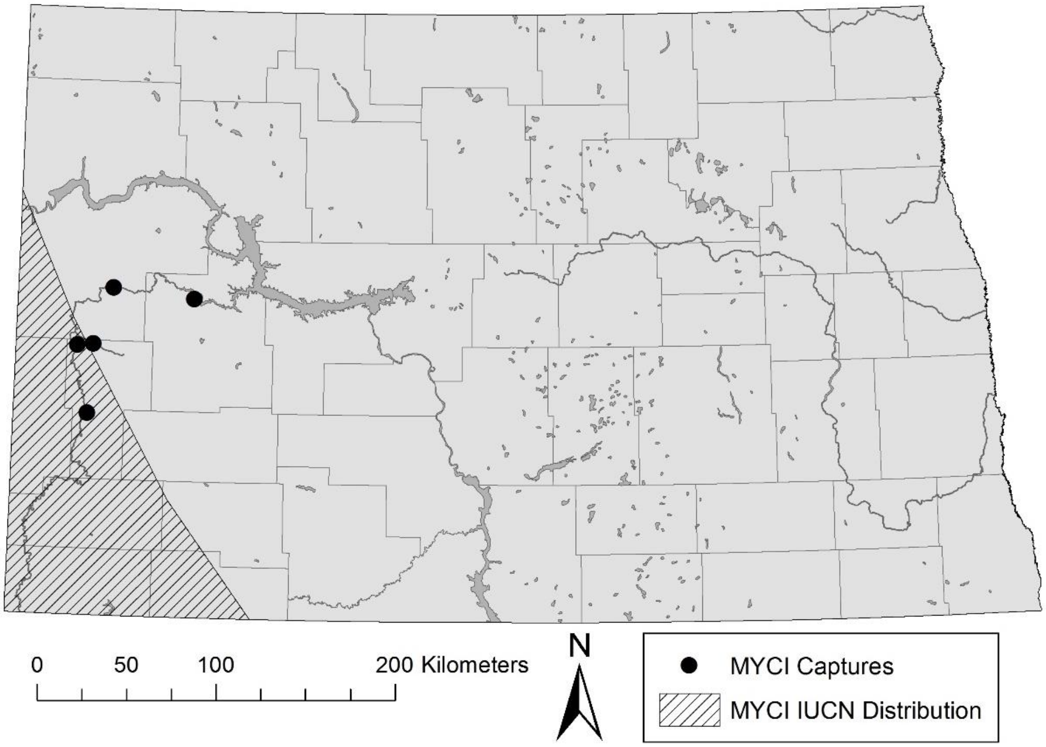

Figure C1. Occurrence Map with IUCN Distribution for *M. ciliolabrum*
Map of *M. ciliolabrum* captures and the current IUCN species distribution.

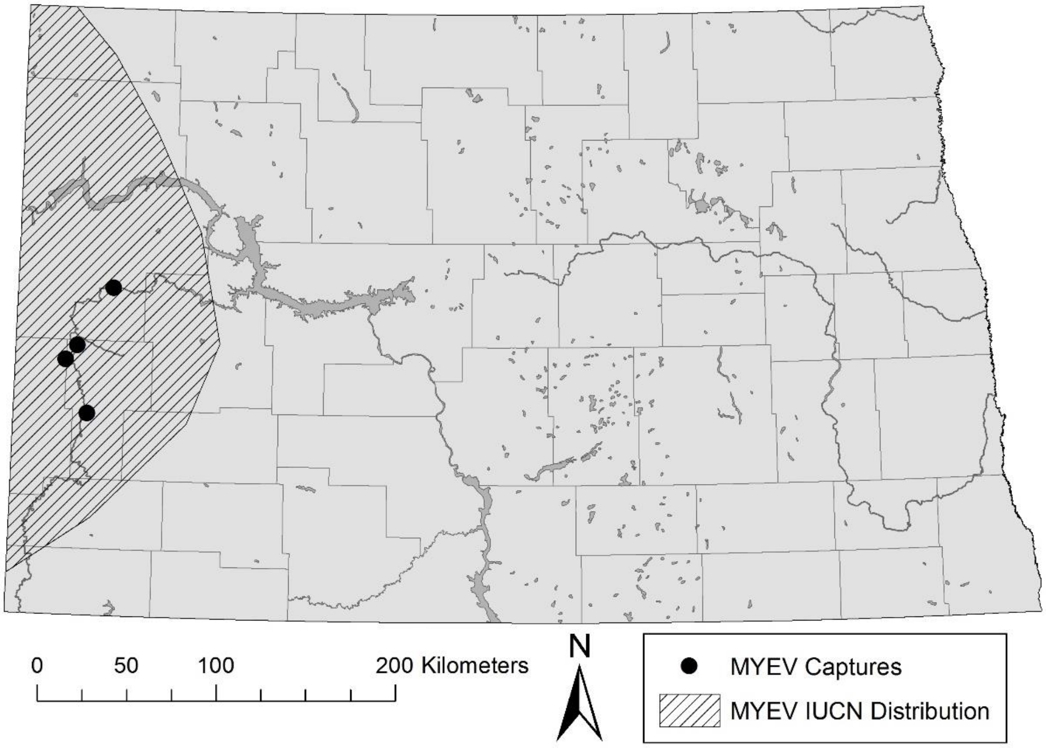

Figure C2. Occurrence Map with IUCN Distribution for *M. evotis*
Map of *M. evotis* captures and the current IUCN species distribution.

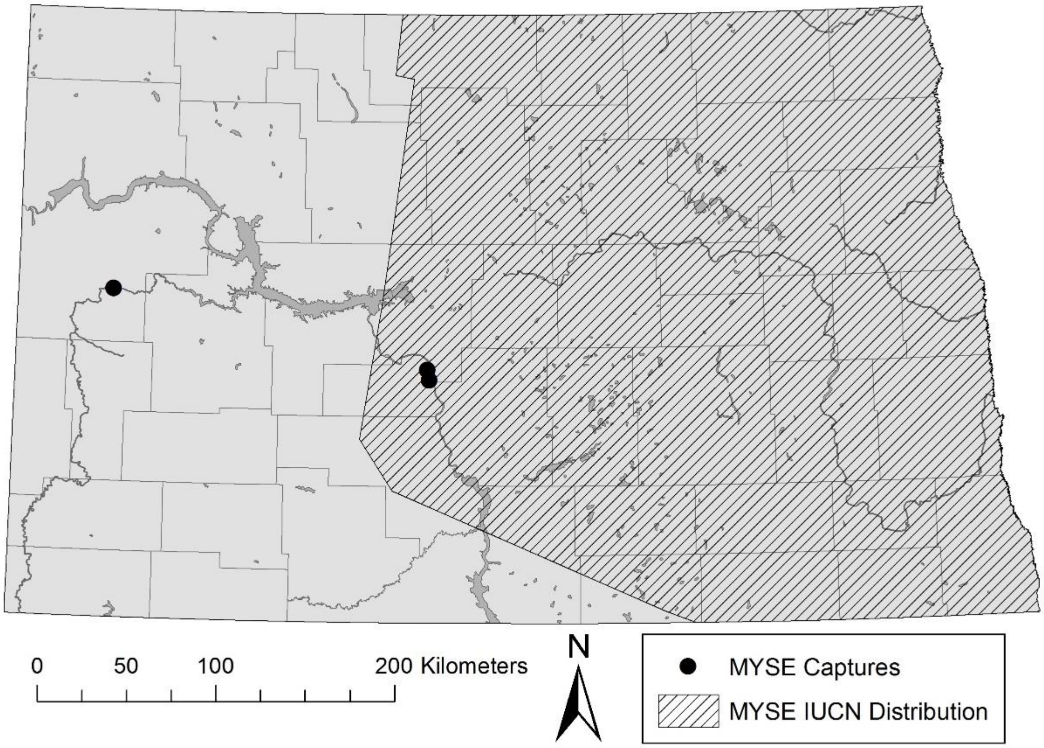

Figure C3. Occurrence Map with IUCN Distribution for *M. septentrionalis*
Map of *M. septentrionalis* captures and the current IUCN species distribution.

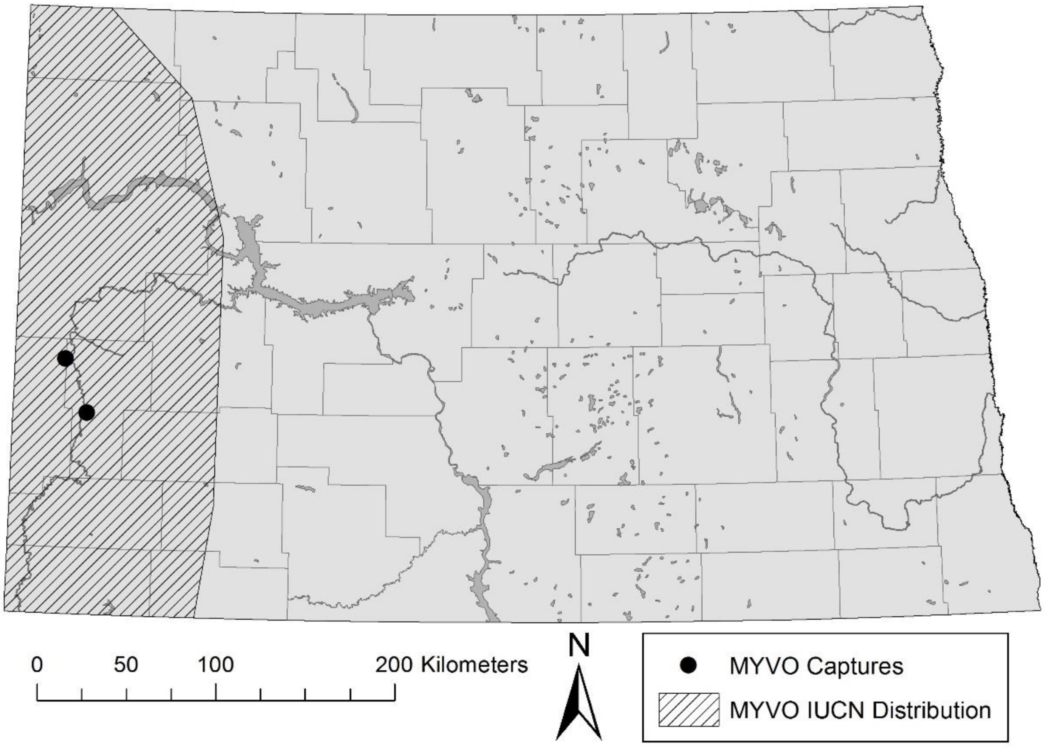

Figure C4. Occurrence Map with IUCN Distribution for *M. volans*
Map of *M. volans* captures and the current IUCN species distribution.

APPENDIX D. HABITAT SELECTION MATRICES

Table D1. Habitat Selection Matrix of *Myotis lucifugus* for Theodore Roosevelt National Park

	Mixed Forest	Cottonwood Forest	Grass/Herb	Mowed	Barren	Shrubs	Marsh	Grass/Herb Edge	Water Edge	Dev/Mowed Edge	Corridor	River	Stream	Buildings	Roadway
Mixed Forest	0	++	+	++	+	+	-	++	+	+	++	+	+	++	+
Cottonwood Forest	--	0	--	-	--	--	--	+	-	--	--	-	--	--	--
Grass/Herb	-	++	0	+	--	--	--	++	-	-	-	-	--	+	-
Mowed	--	+	-	0	--	-	--	+	-	--	--	-	-	+	-
Barren	-	++	++	++	0	+	-	++	+	+	+	+	+	++	++
Shrubs	-	++	++	+	-	0	-	++	-	+	+	-	++	++	++
Marsh	+	++	++	++	+	+	0	++	+	++	+	+	++	++	++
Grass/Herb Edge	--	-	--	-	--	--	--	0	-	--	-	-	--	-	--
Water Edge	-	+	+	+	-	+	-	+	0	+	+	+	+	+	+
Dev/Mowed Edge	-	++	+	++	-	-	--	++	-	0	-	-	+	++	++
Corridor	--	++	+	++	-	-	-	+	-	+	0	-	+	+	+
River	-	+	+	+	-	+	-	+	-	+	+	0	+	+	+
Stream	-	++	++	+	-	--	--	++	-	-	-	-	0	++	+
Buildings	--	++	-	-	--	--	--	+	-	--	-	-	--	0	--
Roadway	-	++	+	+	--	--	--	++	-	--	-	-	-	++	0

Habitat selection for habitat types in TRNP. A double sign (++, --) indicates significant ($p < 0.05$) selection of habitat in row in reference to habitat in column.

Table D2. Habitat Selection Matrix of *Myotis lucifugus* for Cross Ranch State Park

	Mixed Forest	Cottonwood Forest	Grass/Herb	Crops	Mowed	Barren	Shrubs	Marsh	Grass/Herb Edge	Water Edge	Crops Edge	Dev/Mowed Edge	Corridor	Marsh Edge	River	Pond	Buildings	Roadway	Developed Other
Mixed Forest	0	--	--	+	-	-	-	+	--	-	++	+	-	+	-	-	-	--	-
Cottonwood Forest	++	0	+	++	++	-	++	++	-	-	++	++	++	++	-	++	++	++	++
Grass/Herb	++	-	0	++	++	-	++	++	--	-	++	++	+	++	-	++	++	++	++
Crops	-	--	--	0	-	--	-	-	--	--	-	-	-	-	--	-	--	--	-
Mowed	+	--	--	+	0	-	+	+	--	-	+	+	-	+	-	-	-	--	-
Barren	+	+	+	++	+	0	+	+	+	-	++	+	+	+	-	+	+	+	+
Shrubs	+	--	--	+	-	-	0	+	--	-	+	+	-	+	-	-	-	--	-
Marsh	-	--	--	+	-	-	-	0	--	-	+	+	-	+	-	-	-	--	-
Grass/Herb Edge	++	+	++	++	++	-	++	++	0	-	++	++	++	++	-	++	++	++	++
Water Edge	+	+	+	++	+	+	+	+	+	0	++	+	+	++	-	+	+	+	+
Crops Edge	--	--	--	+	-	--	-	-	--	--	0	-	-	-	--	-	--	--	-
Dev/Mowed Edge	-	--	--	+	-	-	-	-	--	-	+	0	-	+	-	-	-	--	-
Corridor	+	--	-	+	+	-	+	+	--	-	+	+	0	+	-	++	+	-	++
Marsh Edge	-	--	--	+	-	-	-	-	--	--	+	-	-	0	-	-	--	--	-
River	+	+	+	++	+	+	+	+	+	+	++	+	+	+	0	+	+	+	+
Pond	+	--	--	+	+	-	+	+	--	-	+	+	--	+	-	0	+	-	+
Buildings	+	--	--	++	+	-	+	+	--	-	++	+	-	++	-	-	0	--	+
Roadway	++	--	--	++	++	-	++	++	--	-	++	++	+	++	-	+	++	0	+
Developed/ Other	+	--	--	+	+	-	+	+	--	-	+	+	--	+	-	-	-	-	0

Habitat selection for habitat types in Cross Ranch State Park. A double sign (++, --) indicates significant ($p < 0.05$) selection of habitat in row in reference to habitat in column.

Table D3. Individual Selection Ratios of *Myotis lucifugus* in Theodore Roosevelt National Park

Bat ID	Mixed Forest	Cottonwood Forest	Grass/Herb	Mowed	Barren	Shrubs	Marsh	Grass/Herb Edge	Water Edge	Dev/Mowed Edge	Corridor	River	Stream	Buildings	Roadway
ML173	0.94	1.04	0.98	1.20	0.67	1.00	0.85	1.01	1.12	1.08	1.01	1.12	1.17	1.27	1.00
ML174	1.44	0.93	0.93	1.04	1.14	1.07	1.30	0.89	1.41	1.10	1.23	1.41	1.00	0.94	1.03
ML176	1.31	0.89	0.98	0.99	1.24	1.15	1.32	0.87	1.29	1.09	1.16	1.29	1.06	0.91	1.03
ML178	1.02	0.87	1.05	0.91	1.23	1.22	1.24	0.90	0.89	1.06	0.97	0.89	1.13	0.92	1.01
ML180	1.04	0.77	1.11	0.75	1.17	1.45	1.57	0.86	0.36	1.09	0.85	0.36	1.24	0.84	0.98
ML181	1.35	0.89	0.98	0.97	1.05	1.18	1.39	0.89	1.03	1.11	1.11	1.03	1.09	0.94	1.01
ML184	1.48	0.85	0.96	1.04	1.48	1.12	1.27	0.81	1.62	1.13	1.30	1.62	1.06	0.90	1.08

Matrix of individual selection ratios of bats at Theodore Roosevelt National Park. Individual bats in rows with habitat types in columns.

Table D4. Individual Selection Ratios of *Myotis lucifugus* in Cross Ranch State Park

Bat ID	Mixed Forest	Cottonwood Forest	Grass/Herb	Crops	Mowed	Barren	Shrubs	Marsh	Grass/Herb Edge	Water Edge	Crop Edge	Dev/Mowed Edge	Corridor	Marsh Edge	River	Pond	Buildings	Roadway	Developed Other
ML10	0.48	1.16	1.09	0.02	0.73	1.17	0.67	0.64	1.15	1.35	0.16	0.60	0.81	0.63	1.46	0.73	0.64	0.83	0.72
ML11	0.49	1.35	1.21	0.02	0.33	0.56	0.32	0.26	1.39	0.95	0.08	0.25	0.79	0.13	1.09	0.41	0.18	0.69	0.39
ML12	0.20	1.09	1.11	0.01	0.30	1.71	0.28	0.25	1.20	2.13	0.07	0.24	0.35	0.20	2.46	0.33	0.35	0.66	0.32
ML13	0.63	1.11	1.00	0.08	1.06	0.95	0.97	1.04	1.06	1.12	0.28	0.96	0.95	1.34	1.18	0.87	0.97	0.97	0.89
ML14	0.28	1.14	1.12	0.00	0.38	1.47	0.35	0.32	1.21	1.85	0.08	0.30	0.49	0.25	2.12	0.42	0.38	0.69	0.40
ML15	0.25	1.12	1.11	0.01	0.35	1.48	0.33	0.30	1.21	1.93	0.08	0.28	0.43	0.27	2.23	0.37	0.35	0.68	0.36
ML16	0.70	1.36	1.16	0.02	0.74	0.24	0.68	0.64	1.30	0.43	0.16	0.60	1.14	0.58	0.41	0.76	0.49	0.85	0.75
ML17	0.45	1.24	1.19	0.02	0.48	1.30	0.45	0.38	1.25	1.25	0.11	0.36	0.77	0.22	1.34	0.57	0.48	0.75	0.55
ML18	0.39	1.15	1.15	0.05	0.52	1.67	0.49	0.43	1.18	1.57	0.15	0.41	0.66	0.30	1.70	0.59	0.59	0.76	0.57
ML19	0.48	1.16	1.10	0.11	0.65	1.25	0.61	0.57	1.16	1.39	0.21	0.53	0.77	0.49	1.51	0.68	0.59	0.81	0.67
ML20	0.40	1.23	1.19	0.03	0.40	1.43	0.38	0.31	1.26	1.39	0.10	0.30	0.68	0.15	1.51	0.49	0.44	0.72	0.47
ML22	0.07	1.08	1.20	0.00	0.05	2.52	0.04	0.04	1.24	2.42	0.01	0.03	0.11	0.02	2.76	0.06	0.43	0.58	0.05
ML23	0.46	1.23	1.19	0.00	0.56	1.53	0.53	0.44	1.21	1.22	0.11	0.41	0.84	0.21	1.25	0.69	0.60	0.78	0.66
ML24	0.31	1.18	1.18	0.03	0.32	1.65	0.31	0.26	1.25	1.70	0.09	0.25	0.52	0.14	1.90	0.39	0.42	0.68	0.37
ML161	0.79	1.17	0.96	0.02	1.34	0.36	1.22	1.28	1.04	0.62	0.28	1.18	1.25	1.59	0.59	1.14	1.05	1.07	1.16
ML162	0.75	1.41	1.19	0.01	0.78	0.11	0.73	0.61	1.31	0.21	0.16	0.57	1.32	0.30	0.11	0.96	0.42	0.86	0.91
ML163	0.51	1.24	1.18	0.02	0.62	1.30	0.59	0.49	1.21	1.09	0.14	0.46	0.92	0.24	1.11	0.77	0.58	0.80	0.73

Matrix of individual selection ratios of bats at Cross Ranch State Park. Individual bats in rows with habitat types in columns.