THE DISTRIBUTION AND HABITAT USE OF NORTH DAKOTA BATS

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Distribution and Habitat Use of North Dakota Bats

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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

Prior to 2009, a comprehensive statewide survey of occurrence and distribution of bats in North Dakota had not been conducted. From 2009 to 2012, mist netting, radio telemetry, and acoustic monitoring were conducted to document species presence and habitat associations across North Dakota. We surveyed multiple sites at 17 locations, captured a total of 309 bats, documented habitat associations, and identified roosting sites. Data was then used to: 1) build habitat suitability maps (also called species distribution maps or SDMs) for each species in the state, 2) examine the environmental and climatic variables that influence bat habitat use along the periphery of their distribution, 3) assess the effect of sampling technique on habitat suitability models, and 4) determine if North Dakota's badlands region contains overwintering bat populations that may be susceptible to white nose syndrome, an emerging fungal disease of hibernating bats. We confirmed the presence of 11 species in the state and found that five species were present in areas outside their ND IUCN distribution. Maximum-entropy modeling showed that temperature was the most important variable for SDM production. We found that sampling technique (physical capture vs. acoustic detection) led to pronounced differences in habitat suitability maps for some species (33.9% overlap; *Myotis septentrionalis*) while models from other species were highly similar (80.4% overlap; *Myotis lucifugus*). Our findings show that acoustic detection results in better SDMs for *Myotis* spp. while physical capture was best for *Eptesicus fuscus* and *Lasionycteris noctivagans*. During the winter, we positively identified four species based on both acoustic detection and physical capture: *E. fuscus*, *Myotis evotis*, *Myotis ciliolabrum,* and *Corynorhinus townsendii*. Based on known and potential hibernacula locations, we produced a habitat suitability map that was successfully used to locate additional potential hibernacula. We also recorded temperature in confirmed and potential hibernacula, finding that temperatures were within the optimum range of fungal growth. The information gathered from these studies will be used to develop the first statewide conservation action plan for North Dakota bats. Also, the habitat suitability maps produced will be used by managers to target areas of high priority for conservation of bat communities.

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CHAPTER 1. INTRODUCTION

1.1. Bats of North Dakota

Insectivorous bats form a diverse group of mammals with complex ecological niches and habitat requirements. As would be expected, many bat species have become threatened or endangered due to destruction of roosting and foraging habitat (Carmel and Safriel 1998). Although bats play key ecological roles in many ecosystems, conservation efforts can be challenging due to a lack of information on habitat requirements for some species. Characterizing the natural history of a species is critical for asking more advanced questions about ecology and behavior, as well as developing effective conservation plans (Stebbings 1988).

A basic component of an organism's natural history is an understanding of the resources used for obtaining food and gaining protection from predators and weather (Brigham 1991). For bats, such information can be obtained through direct capture, acoustic monitoring and radio telemetry surveys. Although technological advances have produced superior bat detectors and telemetry equipment, the majority of habitat use studies focus on a single species (Dodd et al. 2008; Russo et al. 2002; Mackie and Racey 2007; Farrow and Broders 2011; Elmore et al. 2004), with few researchers (e.g., Rydell et al. 1996) collecting data on several bat species. Research oriented at the ecological requirements of a bat community can provide quicker and more appropriate conservation actions as they relate to habitat use.

Bats are an integral component of a variety of ecosystems found in North Dakota. As nocturnal insectivores, bats can have significant impacts on the size of insect prey populations, including some pest species that cause major damage to agricultural and forest habitats (Cleveland et al. 2006). Despite their importance, little work has focused on assessing the distribution and habitat use of bats in North Dakota. Before 2009, little was known about the ecology and behavior of bat species in North Dakota. Bailey (1926) noted anecdotal sightings and scattered museum specimens of *Lasiurus cinereus*, *Lasiurus borealis*, *Eptesicus fuscus*, *Myotis ciliolabrum*, *M. evotis* and *M. lucifugus*. Museum of Natural History field collections in the southwestern ND documented the presence of *M. ciliolabrum*, *M. evotis*, *M. lucifugus*, *M. volans* and *E. fuscus* (Genoways 1967; Jones and Genoways 1966; Jones and Stanley 1962). More recently, separate studies along the Little Missouri River 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* (Lenard and Lausen, 2010; Tigner 2006). Eleven species of bats have been reported in the state, three of which are listed as *Species of Conservation Priority* by the ND Game and Fish Department. To our knowledge, the most recent peer-reviewed research study on any bat in the state was published in 1978 (Jones and Choate 1978). Further, most previous studies only reported the occurrence of a species in one area of the state, contained few capture records, and provided little or no information about habitat use (Genoways 1966; Genoways and Jones 1972; Jones and Choate 1978; Jones and Genoways 1966; Jones and Stanley 1962; Seabloom et al. 1978).

Bat populations are currently facing serious threats, including White Nose Syndrome (WNS), a fungal disease significantly impacting cave-dwelling species (Blehert et al. 2009), as well as anthropogenic changes, such as suburban sprawl and extensive energy development. Bats have low reproductive rates, making rapid recovery from population disturbances difficult (Barclay and Harder 2003). Given these impending threats to bat populations, it is critical to not only determine where bats are found in North Dakota, but also to understand what types of habitats are essential for the foraging and roosting needs of each species. Gathering such information is crucial for developing an effective bat conservation and management plan for the state.

1.2. White Nose Syndrome (WNS)

White Nose Syndrome (WNS) is an epizootic caused by the fungus *Pseudogymnoascus destructans* (formerly *Geomyces destructans*). Since it was discovered in a cave system in upstate New York in 2006, the disease has spread through 25 states and 5 Canadian provinces, killing millions of bats of multiple species, including three species native to North Dakota: *E. fuscus*, *M. lucifugus* and *M. septentrionalis*. In some circumstances the death rate in affected caves has reached 100% and many endangered species are now on the edge of extinction. With no cure in sight, North Dakota must prepare for mitigation efforts needed to combat WNS. Since WNS is found only in colonial hibernating bats, a habitat usage study in North Dakota could help show areas that would be more susceptible to harboring the fungus (USFWS 2014).

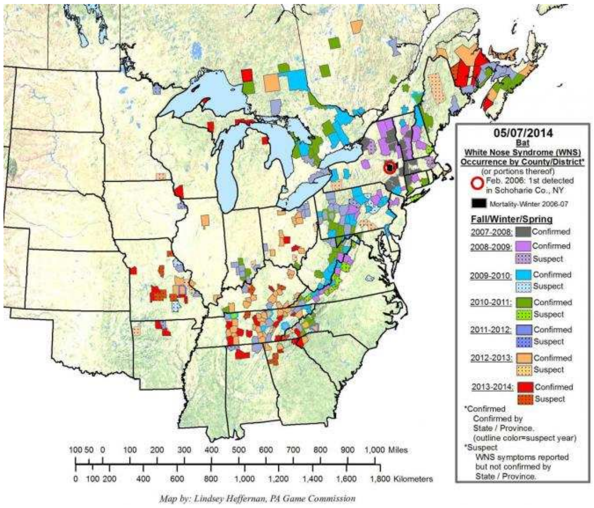

Figure 1.1. Map depicting the spread of WNS across the United States and Canada (USFWS 2014).

1.3. Energy Development In North Dakota

North Dakota is among the nation's leaders in the production of wind energy, and many studies show that wind turbines are affecting bat populations in a substantial way (Arnett et al. 2007). A habitat usage study that identifies areas where construction of wind turbines would negatively affect bats would be valuable for minimizing the impacts of wind energy on bat populations in North Dakota. In addition, accelerated oil production from the Bakken and Three Forks Formations in the western part of the state has impacted the badlands ecosystem in a variety of ways. Infrastructure development encroaches on wildlife and habitat, and the demand for workers has led to increased land conversion, water usage, generation of wastes and pollution, as well as greater recreational use of public lands and waters (Dyke et al. 2012). Multiple spills have been reported in the area and heavy metals and other toxic substances are released into the air from flare-offs that regulate gas pressure (Dyke et al. 2012).

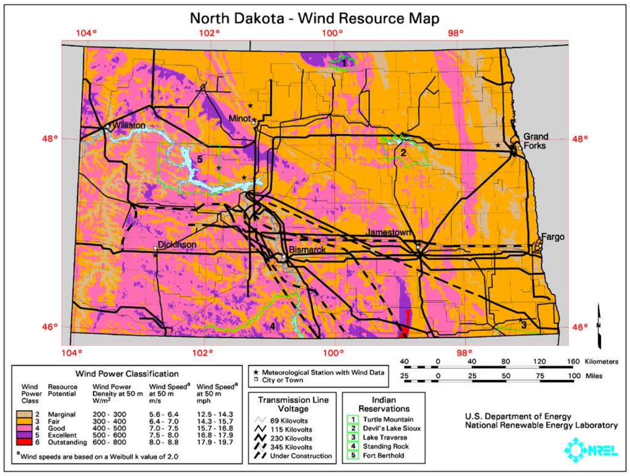

Figure 1.2. Map depicting wind energy potential in North Dakota (USDOE 2014).

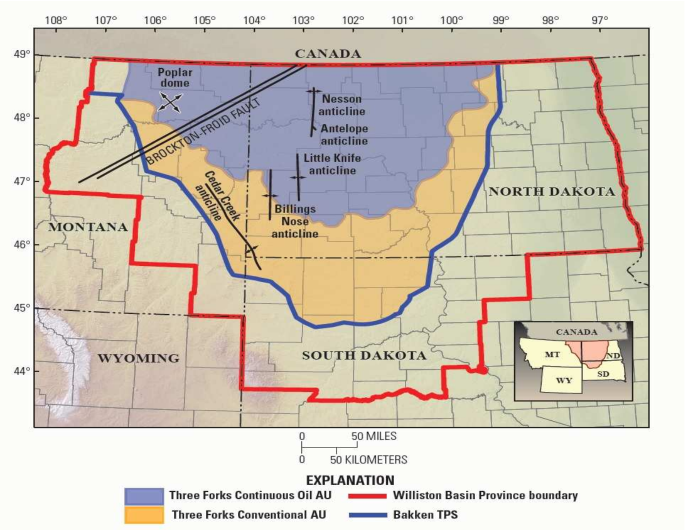

Figure 1.3. Map depicting the Bakken oil formation within the larger Williston Basin (USGS 2014).

1.4. Primary Objectives

The primary objective of this research project was to obtain key ecological information about bat populations resident in the state of North Dakota. Specific objectives include: 1) confirming the presence/absence of bat species that have previously been recorded in North Dakota, 2) documenting the current distribution of each bat species in the state, 3) determining the locations and types of key foraging habitats used by bats in North Dakota, 4) determining the importance of sampling technique on species distribution modeling in maximum-entropy modeling, 5) examining the ecological differences between bat populations in the peripheral margins of North Dakota, and 6) confirming the presence/absence of bat species during the winter hibernation period in the North Dakota badlands.

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CHAPTER 2. THE IMPACT OF SAMPLING METHOD ON MAXIMUM ENTROPY SPECIES DISTRIBUTION MODELING FOR BATS

2.1. Introduction

Understanding the ecological and climatic factors that drive limitations of a species distribution is of fundamental importance for many conservation issues. Documentation of a species' distribution provides the baseline information needed for future studies assessing range modifications, habitat use, genetic robustness, and conservation mitigation efforts (Austin 2002; Carvalho et al. 2011). Unfortunately, range maps are often too simplistic and lead to misinformed interpretation of a species' true distribution. These maps typically do not accurately depict the exact locations of populations, as most are simple polygons (Brown et al. 1996) that do not include information about “islands” of species presence outside of the main distribution and/or include areas within the polygon that do not represent suitable habitat. The lack of biologically relevant information (i.e. climatic and habitat data) and associations of the focal species with these variables means that polygon range maps provide limited information, especially when attempting to ask more advanced questions about the ecology and behavior of a species, or when developing effective conservation plans (Stebbings 1988).

Maximum-entropy modeling is a relatively new method for producing species distribution models (SDMs) that relies on presence data alone (i.e. information about areas of species absence is not needed). Such presence-only modeling has been shown to be very reliable and competitive with other high performing modeling techniques (Elith et al. 2010). This method allows for habitat suitability maps, where species presence is scored across small geographic areas as likely (score near 1) or unlikely (score near 0) (Phillips and Dudik 2008). To develop these suitability estimations, the researcher selects key climatic and ecological variables for a given region and correlates each record of a species' presence with these parameters. Ultimately, the maps produced from maximum-entropy modeling represent areas of highest to lowest suitability for the given species across the geographic range. Researchers can then use these maps to focus management decisions, conservation actions, or to implement further research endeavors.

As presence-only modeling becomes more widely used and implemented by researchers, the techniques and methods used to obtain presence data should be carefully considered. For example, in many cases, information about species presence can be gathered in multiple ways via different metrics. In such cases, researchers need to consider the pros and cons of each technique and assess which will best represent a species' distribution given the foreseen biases with each sampling technique (Phillips et al. 2009; Yesson et al. 2012). Such issues may be particularly relevant for certain species where the most effective method of detection/sampling differ from other species within the same ecological community.

Although bats play key ecological roles, many species have become endangered due to habitat destruction (Carmel and Safriel 1998), and conservation efforts can be hampered due to lack of information regarding distributions. For bats, presence data are most commonly obtained through direct capture and/or acoustic monitoring. Despite common use of both sampling methods, it is not clear if these distinct "presence" datasets lead to different SDMs, which could potentially result in disparate management decisions.

We conducted a survey of bat activity, diversity, and habitat use throughout the state of North Dakota in Summers 2009-2012. The major goal of this study was to compare SDMs generated from: 1) acoustic monitoring, and 2) physical capture for each species found in the state. Since our study collected both types of presence data during the same times and in the same geographic locations, we predicted that if both physical capture and acoustic monitoring are sampling bat populations in a similar manner that the SDMs generated separately for each method would exhibit extensive overlap with each other.

2.2. Materials and Methods

2.2.1. Location and Capture

For sampling purposes, we divided North Dakota into 5 sampling regions: The Red River Valley, Pembina Gorge, Turtle Mountains, Missouri River Valley, and the Badlands of southwestern North Dakota. The only regions of the state not sampled were the Drift Plains and Missouri Coteau, as previous sampling found that activity is particularly low in these regions and that there is a severe lack of natural roosting structures available (Erin H Gillam and Paul R Barnhart, personal observations 2009). A total of 17 sites were sampled across the 5 regions between 2009 and 2012. At each site, we sampled for species presence for 4 to 7 nights at one or more sub-sites within each location. At each sub-site, we sampled using two methods: direct capture of bats via mist-netting and ultrasonic recording of echolocation calls from free-flying bats using bat detectors. All capture and sampling techniques were approved by the North Dakota State University Institutional Animal Care and Use Committee.

Direct capture involved deploying a total of two to five mistnets (Avinet, Dryden, NY) at each sub-site each night. No harp-traps were used in this study due to the lack of known colony roosting sites and the open landscape of North Dakota. Mistnets were configured to maximize capture success given the local topography and environmental conditions; hence configurations differed between sub-sites. Mistnets were opened each night just before sunset and closed either shortly before sunrise or 2 hrs after the last capture of a bat. Physical and acoustic captures sites were areas that had an abundance of potential roosting and foraging habitat, such as ponds, flyways and riparian zones. Upon capture, we assessed the following for each individual: species, sex, age, mass, forearm length, and reproductive condition.

Ultrasonic detectors were deployed as either active or passive systems. The active detection system involved acoustic monitoring for bat activity at or near mistnets where the researcher would manually record the echolocation calls of free-flying bats. Each night, two broadband Pettersson D240x bat detectors (Pettersson Elektronik, Uppsala, Sweden) were manually deployed at the selected sub-site. This time-expansion bat detection system was set to record for 1.7 sec and then broadcast the recorded calls at one-tenth the original speed. Time-expanded calls were stored on either an iRiver (iRiver iFP-890 digital audio recorder, iRiver Inc., Irvine, CA) player or an H2 Zoom (Samson Technologies, Hauppauge, NY) recorder attached to the detector. For the passive system, a different ultrasonic detector (Pettersson D500X) was housed in a protective casing and placed within 2 miles of the netting site at a location classified by the researchers as high-quality foraging habitat. The protected bat detector was manually activated before sunset and set to automatically record sounds when an amplitude threshold was crossed. The detector ran until the following morning, when the researchers returned to the site to manually deactivate the unit, or until batteries died (generally occurred 4 hours after sunrise).

2.2.2. Sound Analysis

Echolocation calls were analyzed and classified to species using Sonobat 3-Great Plains (Sonobat, Arcata, CA). This system uses a decision engine based on the quantitative analysis of known recordings from species across the Great Plains of North America to identify each recording to the species level. Since variation in call structure between geographic locations is a possibility, we also included our recordings from light tagging in the known recordings database. Sonobat 3 generates a spectrogram and measures 72 parameters that characterize call structure, such as highest frequency, lowest frequency, and duration of each individual call in the recorded sequence. We used only echolocation call sequences for species identification that had a 95% classification quality value or higher based on the algorithms employed in Sonobat 3 for analysis.

2.2.3. Ecological Niche Modeling

To assess impacts of capture technique (i.e. physical or acoustic) in producing species distribution models we used ecological niche modeling, also known as species distribution modeling (SDM), with the program MaxEnt for six bat species in the state of North Dakota: *Eptesicus fuscus*, *Lasionycteris noctivagans*, *Myotis ciliolabrum*, *M. septentrionalis*, *M. lucifugus*, and *M. evotis*. Such presence-only modeling has been shown to be very reliable and competitive with other high performing modeling techniques (Elith et al. 2010). MaxEnt has also been shown to perform well with small samples sizes (Hernandez et al. 2006; Wisz et al. 2008), which could prove useful for cryptic, volant species such as bats. Although the study positively identified eleven species, only these six species had large enough sample sizes for both physical capture and acoustic detection to produce useful results within the MaxEnt environment (Hernandez et al. 2006; Elith et al. 2011). Species distribution modeling requires input of: 1) eco-geographical data, generally in the form of raster datasets, and 2) locations where a species is known to occur. For each species, we used presence data collected from our field data based on acoustic monitoring and physical capture. Eco-geographical data was selected from 19 "Bioclim" variables and other bioclimatic variables that describe monthly precipitation and temperature (Hijmans et al. 2005; http://www.worldclim.org). Selected variables were deemed ecologically relevant based on knowledge about the biology and annual activity patterns of North American bats (Razgour et al. 2011). The following variables were initially isolated for modeling: altitude;

roads; rivers; annual precipitation; summer precipitation; winter temperatures; and a landcover dataset (Zhang et al. 2008; Fry et al. 2011; http://www.nd.gov/gis/data-portal.html; reclassified into 16 classes) that describes the "vegetational and artificial constructions covering the land surface" (Burley 1961). A fundamental assumption of MaxEnt is that the entire geographic area of interest has been sampled (Kramer-Schadt et al. 2013), yet this is typically not the case as presence locations are gathered in better-surveyed areas. Because of this, background samples used when developing distribution models can have significant consequences on the model results (Elith et al. 2011). For our study, MaxEnt was only allowed to select background pseudo-absence locations within the same counties as the study took place. This provides MaxEnt with a pseudo-absence file that has the same bias as the presence locations (Young et al. 2011).

Due to landscape heterogeneity seen across the study sites, we used high-resolution (30" or 1km²) raster datasets for all modeling analysis. We developed SDMs using the program MaxEnt (ver. 3.3.3, Phillips et al. 2006). For each species, we partitioned each set of presence data into test and training data (80% and 20%, respectively) and ran the jackknife validation function to minimize biases associated with small sample sizes. Because MaxEnt chooses which presence data to use in model training and testing, we ran 50 model replications and then averaged them into a single distribution model for each species based on sampling technique. All MaxEnt outputs were in RAW format as this is the only format that can be used with ENMTools (see below). We also combined acoustic detection locations and physical capture locations to produce a "master" SDM for each of the six species. Models generated for each species sampling technique would then be compared to this master SDM to determine which technique is better for surveying each species. Using the “autofeatures” function in Maxent, we produced response curves and did a jackknife analysis to measure variable importance in each model.

2.2.4. Model Evaluation

All MaxEnt models were evaluated for fit based on the Area Under the Curve (AUC) of the Receiver Operator Characteristics, which measures the models' likelihood of correctly distinguishing between presence and random locations; an AUC value of 0.5 indicates the model was no better than random at depicting the species distribution while values closer to 1.0 indicate good model performance (see Phillips et al. 2006 for further explanation). We considered a model to be good if both the training and test AUC were higher than 0.75 (Elith et al. 2006).

Models were run using the default MaxEnt settings, with the exception of the number of iterations (5000 instead of the default 500). To evaluate model complexity and reduce over-parameterization/over-fitting, we ran each model using different regularization betamultiplier values (1-12). These values affect the fitting of the output distribution, with large values being more generalized, geographically spread out and can be thought of as a smoothing parameter. This resulted in running 36 models for each species, (12 for each sampling technique alone + 12 for the master combined model). To find the most parsimonious models, we used AIC scores produced in ENMTools v. 1.3. To evaluate the correlation between these variables (i.e. test for multicollinearity), we used the variable correlation analysis in ENMTools v. 1.3 (Warren et al. 2010). For variables that were highly correlated ($R^2 > 0.75$), the less ecologically relevant variable was removed. Only variables that contributed more than 1% to the model were included in the final models. This resulted in eight final variables to be used for modeling (Table 2.1).

Table 2.1. Environmental variables* used in the final models generated for each species**. Variables that did not contribute >1% were removed before final models were calculated.

Species	Alt	Roads	A.P	Rivers	M.O.T.	M.P.	J.P.	Land
Epfu	A,M	M	P,M	A,M	A,P,M		P,M	A,P,M
Lano	A,M		A,M	A,M	A,P,M	M	P,M	A,P,M
Myci	A	P	P	A,M	A,P,M	P		A,P,M
Myev	A	P	A,P,M	A,P,M	A,P,M	A		A,P,M
Mylu	A			P,M	A,P,M		P	A,P,M
Myse	P	M	P	A,P	A,P,M	A,P,M	A,P,M	A,P,M

*Alt = Altitude; A.P. = Annual Precipitation; M.O.T. = Mean October Temperature; M.P. = May Precipitation; J.P. = June Precipitation; Land = Landcover. A = used for acoustic detection models; P = used for physical capture models; M = used for master model

**Epfu = *Eptesicus fuscus*; Lano = *Lasionycteris noctivagans*; Myci = *Myotis ciliolabrum*; Myev = *Myotis evotis*; Mylu = *Myotis lucifugus*; Myse = *Myotis septentrionalis*

2.2.5 Niche Overlap Analysis

We evaluated the amount of overlap between the physical capture and acoustic monitoring SDMs generated for each species using the niche overlap function in ENMTools v.1.3 (Thompson et al. 2011; Levsen et al. 2012). Schoener's *D* quantifies niche overlap from 0, indicating no overlap between SDMs, to 1, where all grid cells are of equal suitability for both species (Warren et al. 2010). This methods was also used to evaluate the amount of overlap between each sampling technique alone and the master SDM for each species.

2.3. Results

2.3.1. Acoustic vs. Physical Overlap

Both physical and acoustic capture SDMs resulted in high AUC statistics (Table 2.2), which demonstrates that each capture method has high habitat suitability predictive capabilities within MaxEnt. However, ENMTools niche overlap analysis (D statistic) showed differences between the amount of overlap generated for the SDMs of each species based on capture technique (Table 2.3). Interestingly, within the *Myotis* genus there were notable differences in the amount of overlap among species; *Myotis septentrionalis* had the lowest amount of overlap (33.9%) between the acoustic and physical capture models, while *Myotis lucifugus* had the highest amount of overlap (80.4%). The remaining *Myotis* spp. had very similar amounts of overlap (*Myotis evotis* = 48.2% and *Myotis ciliolabrum* = 48.6%). Comparable degrees of overlap were also seen *E. fuscus* (64.4%,) and *L. noctivagans* (66.4%).

Table 2.2. MaxEnt AUC values for the SDMs generated for each species* using either acoustic monitoring or physical capture data.

Species	Physical Capture AUC	Acoustic Detection AUC
Epfu	0.916	0.892
Lano	0.931	0.877
Myci	0.757	0.894
Myev	0.855	0.946
Mylu	0.848	0.855
Myse	0.887	0.849

*Epfu = *Eptesicus fuscus*; Lano = *Lasionycteris noctivagans*; Myci = *Myotis ciliolabrum*; Myev = *Myotis evotis*; Mylu = *Myotis lucifugus*; Myse = *Myotis septentrionalis*.

Table 2.3. ENMTools niche overlap analysis (Schoener's *D* statistic) for each species*. Results are shown for overlap analyses of the: 1) acoustic monitoring and physical capture methods, 2) acoustic monitoring and master models, and 3) physical capture and master models.

Species	Acoustic vs Physical	Acoustic vs Master	Physical vs Master
Epfu	0.644	0.576	0.646
Lano	0.664	0.505	0.574
Myci	0.486	0.735	0.648
Myev	0.482	0.732	0.546
Mylu	0.804	0.842	0.712
Myse	0.339	0.812	0.403

*Epfu = *Eptesicus fuscus*; Lano = *Lasionycteris noctivagans*; Myci = *Myotis ciliolabrum*; Myev = *Myotis evotis*; Mylu = *Myotis lucifugus*; Myse = *Myotis septentrionalis*.

2.3.2. Overlap Between Detection Method and All Occurrence Locations

To determine if certain detection techniques were better at representing a species SDM, we compared the best models for the two detection techniques against a master SDM generated using all occurrence locations. For all *Myotis* species,. acoustic detection SDMs had the highest amount of overlap with the master SDM (Table 2.3). For *E. fuscus* and *L. noctivagans,* the physical capture model had greater overlap with the master SDM than the acoustic monitoring model (Table 2.3).

2.4. Discussion

Presence-only modeling is becoming more widely used as an effective means to produce SDMs (Kumar and Stohlgren 2009) and inform managers about the conservation needs of species. Our results highlight that when presence data can be gathered in multiple ways, SDMs produced from the different collection methods can sometimes generate disparate habitat suitability predictions. Since our study collected acoustic and physical capture data at the same time and in the same study area, we anticipated high levels of overlap between physical capture and acoustic monitoring models if these methods are sampling bat populations in a similar manner. Instead, we found that the amount of overlap between acoustic and physical capture SDMs varied substantially between species, ranging from 33.9% for *M. septentrionalis* to 80.4% for *M. lucifugus*. Given the similarity in the foraging ecology, echolocation and behavior of these two species (Ratcliffe and Dawson 2003), which can be viewed as proxy for the likelihood of detection by either method, one would expect similar levels of detection regardless of the sampling technique employed.

2.4.1. Overlap Within Species

Some of the intraspecific differences in SDMs could be related to the foraging behavior, habitat use and/or echolocation structure of a given species. For example, the hoary bat, *L. cinereus*, forages in relatively open areas, such as above tree canopies (Caire et al. 1984; Kalcounis et al. 1999), making it difficult to capture in mistnets. If one used physical captures alone to build an SDM of *L. cinereus*, this bias would lead to the species not being scored as present at sites where it is actually found. Yet, hoary bats produce loud, low frequency echolocation calls that travel long distances (Barclay et al. 1999), resulting in high detectability by bat detectors and potentially making acoustic monitoring systems a more appropriate method for accurately assessing the distribution of this species. Alternatively, bats that produce highly directional calls (i.e. “whispering bats”; Brinkløv et al. 2009), rely on prey-generated sounds for navigation (Marimuthu and Neuweiler 1987; Faure and Barclay 1994; Eklöf and Jones 2003), or produce high frequency echolocation (Fenton and Bell 1981; Faure and Barclay 1994), may be particularly difficult to document with acoustic detection methods alone. For such species, physical capture data may be more reliable for building SDMs. These life history characteristics are presumably responsible for the difference we found when comparing each species to the master SDM.

2.4.2. Differences In Overlap Between Species

The differences in SDM overlap observed among the four *Myotis* species is likely not an artifact of species-specific ecological differences. Within the myotids, we can look at the similarity of echolocation call structure as one proxy for similarity in general foraging ecology (Aldridge and Rautenbach 1987; Crome and Richards 1988) and potentially niche partitioning (Kingston et al. 1999; Kingston et al. 2000). The four *Myotis* species found in North Dakota produce similar echolocation calls (high frequency, FM), which are ideal for detecting prey within cluttered habitats (Schnitzler and Kalko 2001). Because of these similarities, we would expect that the probability of detection, either acoustic or physical, would be roughly the same for each *Myotis* species in North Dakota. However, we found differences within this group. The differences between sampling methods in the production of SDMs is particularly noticeable when comparing two congeners, *M. lucifugus* and *M. septentrionalis* (Figure 2.1). In *M. lucifugus*, highly correlated suitability models were produced (80.4% overlap between SDMs), while for *M. septentrionalis*, each technique produced substantially different suitability models (33.9% overlap between SDMs). The discrepancies between the *M. septentionalis* models cannot be attributed to poor sampling coverage, as this was the one of the most common species captured in mistnets and was also common in acoustic recordings. The reasons behind these technique-specific differences are not always clear; further research focusing on the potential factors driving such discrepancies would be valuable. It is plausible that fine-scale differences in the foraging ecology of these species (Broders et al. 2004), beyond what is detectable from basic differences in call structure, are responsible for differences in detectability via acoustic and physical capture. For example, the generalist foraging strategy of *M. lucifugus* (Belwood and Fenton 1976; Wund 2006) means that bats readily move among considerably different habitats, which may increase the probability of the species being detected when an area is sampled with mistnets or bat detectors. Alternatively, gleaning bats (Audet 1990; Barclay 1991), like *M. septentrionalis,* are considered specialists, presumably leading to a more clumped distribution across the landscape, which could reduce the probability of detection. When selecting which method of detection to use for presence-only modeling, researchers should first consider the foraging strategy of their study species, particularly in reference to the geographic scale of the proposed study.

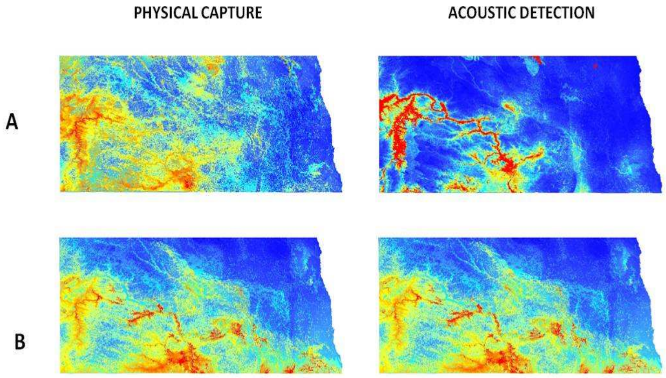

Figure 2.1. SDM physical and acoustic presence data for: a) *M. lucifugus* and b) *M. septentrionalis*. Areas of high suitability are shown in red/yellow while areas of low suitability are shown in blue.

<u>*2.4.3. General Considerations*</u>

When deciding how to collect presence data, researchers should consider which sampling method/s will result in more accurate SDM production for their specific research goals. Acoustic sampling suffers from issues with identifying species based solely on call structure (while modern classification programs have made this less of a problem, issues still exist). The primary problem is that many bat species show overwhelming similarity and/or flexibility in call structure, making positive identification based solely on echolocation difficult, if not impossible in some cases. For example, *E. fuscus* and *L. noctivagans* produce echolocation calls that are sometimes indistinguishable from each other (Fenton et al. 1983; Thomas et al. 1987; Crampton and Barclay 1995) and therefore SDMs produced for these species could actually be representing a compilation of both species. Geographic variation in echolocation structure, as a result of variation in body size or habitat differences (Barclay et al. 1999) can further compound the difficulty of species-specific classifications (Thomas et al. 1987). Despite these drawbacks, the major benefit of acoustic sampling is that it allows researchers to sample a large area, potentially detecting more species and collecting a greater number of samples. Current studies (Jennings et al. 2008; Adams et al. 2010) show that automated classification systems perform well, however a future study examining the effects of acoustic identification technique on SDM production could prove quite useful. Alternatively, physical capture via mistnets allows for definitive identification of species, thus greatly reducing or eliminating issues of misclassification, but only allows for sampling a small space, which limits sample size and increases the probability of missing a species.

Because maximum entropy modeling allows for predicting species distributions in both contemporary environments, as well as making future projections, the consequences of developing unrealistic or misleading habitat suitability maps can be large in terms of conservation and management efforts. Although these models were produced for only part of each species’ distribution (i.e. North Dakota), the SDMs generated can still be useful in guiding management, research, and conservation decisions, as none of the environmental variables selected for modeling represented annual averages/variations during times when the study was not conducted. SDMs generated from these annual averages/variations can greatly bias the resulting model if the study species is not a year round resident (such as our study species' in North Dakota). Our study should represent a cautionary note for researchers who rely solely on one method for obtaining presence data. As presence-only modeling continues to expand and grow in use within the research community, particularly when applied to bats, we encourage researchers to use a combination of research methods rather than focusing on one alone, as this leads to greater success at capturing the full range of presence data (Kuenzi and Mornson 1998). For species-specific studies, we encourage researchers to consider which sampling method is most appropriate to produce adequate sample sizes needed for SDM development. Although each capture method resulted in high AUC values, the need for accurate and detailed habitat suitability maps is becoming increasingly important in the face of increased urban sprawl, agricultural production and, for bats in particular, the spread of white-nose syndrome.

Although the consideration of sampling bias is not novel (Kunz and Brock 1975; Kuenzi and Mornson 1998) many current studies using presence-only modeling continue to employ only one sampling method (Lamb et al. 2008; Hughes et al. 2010; Stoffberg et al. 2012; Hughes et al. 2012) or use georeferenced distribution records, which typically do not contain information as to what sampling method was used (Rebelo et al. 2010; Lee et al. 2012; Pinto et al. 2013). Due to species-specific differences in behavior, energetics, ecology and physiology, using only one sampling method or georeferenced data could produce biased SDMs. Although georeferenced presence locations can provide insight into changes in distribution and habitat use from previously recorded location information, changes such as urban sprawl and climate change can impact the usefulness of these comparisons. We recommend that researchers select the most appropriate sampling method based on the ecology of their study species, and provide justification for why that sampling technique was chosen.

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CHAPTER 3. UNDERSTANDING PERIPHERAL BAT POPULATIONS USING MAXIMUM ENTROPY SUITABILITY MODELING

3.1. Introduction

Understanding the ecological and climatic factors that drive limitations of a species distribution is of fundamental importance for many conservation issues. Documentation of a species' distribution provides the baseline information needed for assessing range modifications, habitat use, genetic robustness, and conservation mitigation efforts (Jones et al. 2001; Zhang et al. 2008; Carvalho et al. 2011). A species distribution is also the fundamental characteristic used by local managers to employ species-specific environmental research, habitat management and biological reserve design (Franklin 2009).

It has long been known that populations become increasingly fragmented or isolated at the periphery of a species' distribution (Kluth and Bruelheide 2005) and that individuals residing in these peripheral margins experience more challenging environmental conditions than their conspecifics in the center of the distribution (Brussard 1984). Peripheral populations, especially those at or near the leading-edge of a distribution are often more vulnerable to decline (Peterman et al. 2013) and are of significant importance for conservation and management. Debate still exists as to the importance of peripheral populations in the evolution and persistence of a species (Garner et al. 2004). Due to small population sizes, isolation, and the resulting threat of local extinction, some studies have concluded that these populations are unimportant for a species' persistence (Lesica and Allendorf 1995), while others argue that they contain important genetic information that natural selection can act upon (Kirkpatrick and Barton 1997).

Unfortunately, range maps are often too simplistic and lead to misinformed interpretation of a species' true distribution limits. These maps typically do not accurately depict the exact locations of peripheral populations, as most are simply polygons with no information about "islands" of species presence outside the continuous distribution (Brown et al. 1996). Recently, a new method for producing habitat suitability maps has become increasingly incorporated into the ecological literature, maximum entropy modeling. This method allows for the production of habitat suitability maps based on the known presence locations of the target species and ecogeographical variables describing the constructs of the environment of the study area. Unlike other methods, no information about locations of species absence is required. This method is especially important for cryptic or volant species, where precise documentation of the true distribution is difficult. Habitat suitability modeling can be valuable, informing research and guiding future studies examining the peripheral margins of a species distribution. Research aimed at documenting exact locales and potential areas (i.e. suitable habitat) of range expansion of a species distribution in the peripheral margins is critical for asking more advanced questions about ecology and behavior, as well as developing effective conservation plans (Stebbings 1988) as they relate to peripheral population dynamics.

Although many studies have looked at the distribution and ecological requirements of individual bat species (Russo et al. 2002; Elmore et al. 2004; Mackie and Racey 2007; Dodd et al. 2008; Farrow and Broders 2011) only recently has statistical environmental modeling been incorporated into habitat studies. Such modeling has the ability to accurately depict environmental data as they relate to more suitable habitat within or outside a species distribution in a more streamlined and standardized way through GIS.

In North Dakota, eleven species of bats have been reported, of which three are listed as conservation priority by the state. From a biogeographical viewpoint, North Dakota is an interesting location, as seven species reach the border of their IUCN distribution within the state

(The IUCN Red List of Threatened Species, http://www.iucnredlist.org). Previous research on bats in North Dakota has been limited to studies reporting species occurrence in one area of the state and generally contain few capture records (Jones Jr. and Stanley 1962; Genoways 1966; Jones Jr. and Genoways 1966; Genoways and Jones Jr. 1972; Jones Jr. and Choate 1978; Seabloom et al. 1978; Tigner 2006; Lenard and Lausen 2010). Due to North Dakota's geographic position and large agricultural expansions that are characteristic of the Great Plains, studies assessing characteristics of peripheral populations in the state can provide insight as to how and under what circumstances range expansions occur in the northern latitudes of North America.

The major goals of this study were to: 1) document patterns of species presence throughout the state of North Dakota to determine if any species are found outside their known distributions; 2) use habitat suitability modeling to identify areas along the peripheral margins of species distribution that contain highly suitable habitat; and 3) identify key environmental variables driving species distributions in the state.

3.2. Methods

3.2.1. Ethics Statement

All procedures followed a protocol approved by the North Dakota State University Animal Care and Use Committee (Permit Number: A12040). No animals were euthanized during this study and no federally protected species were sampled.

3.2.2. Data Collection

For sampling purposes, we divided North Dakota into 5 sampling regions (Figure 3.1): The Red River Valley, Pembina Gorge, Turtle Mountains, Missouri River Valley, and the Badlands of southwestern North Dakota. These regions spanned the entire state so that the proposed boundary of each species distribution was sampled. The only regions of the state not sampled were the Drift Plains and Missouri Coteau, as previous sampling found that activity is particularly low in these regions and that there is a severe lack of natural roosting structures available (EHG and PRB, personal observations 2009). A total of 17 locations were sampled across the 5 regions, with 4 to 7 nights of sampling within each location. At each location, we collected data at 3-7 sites, to ensure that we captured the diversity of habitats in the area. Selected sites spanned a variety of land types, including wildlife management areas, private land, state parks, federal parks, and wildlife refuges. At each site, we sampled using two methods: direct capture of bats via mist-netting and ultrasonic recording of echolocation calls from free-flying bats. Previous studies have found that using both mist-nets and ultrasonic detectors provides a more accurate estimate of species diversity than either one alone (Kuenzi and Mornson 1998).

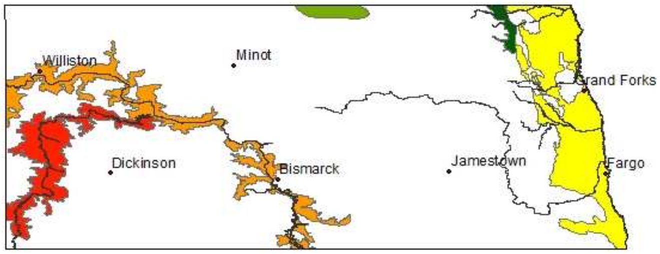

Figure 3.1. Map of North Dakota depicting the 5 sampling region in the state. Red = Badlands; Orange = Missouri River Valley; Light Green = Turtle Mountains; Dark Green = Pembina Gorge; Yellow = Red River Valley. Major cities are labeled for reference.

A total of two to five mist-nets were deployed at each sampling site each night. At each site, the primary vegetation dominating the landscape (e.g. mixed ponderosa pine/juniper woodlands) was characterized. Mist nets were opened each night just before sunset and closed shortly before sunrise, or 2 hours after the last capture of a bat. Upon capture, we assessed the following for each individual using spring scales (Avinet, Dryden, NY), digital calipers (Avinet, Dryden, NY), and palpation: species, sex, mass, forearm length, and reproductive condition.

Recordings of the echolocation calls of captured bats, which had been identified in the hand to species, were used to build a call library for analysis of unknown calls. To obtain these calls, captured bats were housed in clean cloth bags and transported to an open release site within 2 miles of the capture site. A 1.5" chemoluminescent tag (Rod-N-Bobb's Inc., Eau Claire, Wisconsin) was attached between the scapulae of the bat using non-toxic Elmer's glue. The release site was continually monitored for bat activity; when no bats had been detected for >60 seconds, one light-tagged individual was released and tracked with an ultrasonic bat detector (see Ultrasonic Detection below). All bats were released within two hours of capture.

Active ultrasonic detection was conducted on every sampling night 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 to 3.4 seconds) and then broadcasts the recorded calls at one-tenth the original speed. Time-expanded calls were stored as an MP3 file on an iRiver player attached to the detector. Detectors were deployed as either passive or active systems. For the passive system, a D500x Pettersson bat detector was housed in a protective casing and placed within 2 miles of the netting site at a location containing high-quality bat habitat, such as a forest edge or riparian area. The protected bat detector was manually activated before sunset and automatically recorded sounds when an amplitude threshold was crossed. The active detection system involved monitoring and recording bat activity at mist-net sites using a second bat detector. All physical captures of specimens were done on private and protected land under the following permits: (1) The National Park Service (Permit Number: THRO-2009-SCI-0003); (2) North Dakota Game and Fish Department (Permit Number: GNF02778109); (3) North Dakota Parks and Recreation Department.

3.2.3. Sound Analysis

Recorded echolocation calls were analyzed using Sonobat 3 (Sonobat, Arcata, CA). This system 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. Since variation in call structure between geographic locations is a possibility, we also included our recordings from light tagging in the known recordings database. Sonobat 3 generates a spectrogram and measures 72 parameters that characterize call structure, such as highest frequency, lowest frequency, and duration of each individual call in the recorded sequence. We used only echolocation call sequences for species identification that had a 95% classification quality value or higher based on the algorithms employed in Sonobat 3 for analysis.

3.2.4. Ecological Niche Modeling

We used ecological niche modeling, also known as habitat suitability modeling, to assess the climatic and environmental constraints for six bat species (*Lasiurus borealis*, *Myotis ciliolabrum*, *M. volans*, *M. septentrionalis*, *M. evotis*, and *Corynorhinus townsendii*) in the state. Although we documented 11 species in the state, low sample size for *M. thysanodes* (6 individuals) caused us to eliminate this species from further habitat suitability modeling. We used our presence data, gathered from both acoustic monitoring and physical capture, to delineate locations where each species is known to occur. These presence points were then added to a habitat suitability modeling tool. Due to landscape heterogeneity seen across the study sites, we used high-resolution (30" or $1km^2$) raster datasets for all climatic modeling analysis.

We developed species distribution models using the program MaxEnt v.3.3.3 (Phillips et al. 2006). Such presence-only modeling has been shown to be very reliable and competitive with other high performing modeling techniques (Elith et al. 2010). MaxEnt has also been shown to perform well with small samples sizes (Hernandez et al. 2006; Wisz et al. 2008), which could prove useful for cryptic, volant species such as bats. This method produces probability density maps, where species presence is scored across small geographic areas as likely (score near 1) or unlikely (score near 0) (Phillips and Dudik 2008).

For each species, we separated the presence data into test and training datasets (80% and 20%, respectively) and ran the jackknife validation function to minimize biases associated with small sample sizes. Because MaxEnt chooses which presence data to use in modeling training and testing, we ran 50 model replications and then averaged them into a single distribution model for each species. Using the autofeatures function, we produced response curves and did a jackknife analysis to measure variable importance in each model. Eco-geographical data were selected from 19 "Bioclim" variables and other bioclimatic variables that describe monthly precipitation and temperature (Hijmans et al. 2005;http://www.worldclim.org). Selected variables were deemed ecologically relevant based on knowledge about the biology and annual activity patterns of North American bats (Razgour et al. 2011). The following variables were initially isolated for modeling: altitude; roads; rivers; annual precipitation (i.e. precipitation for each month); summer precipitation (i.e. precipitation for each month during summer); winter temperatures (i.e. temperatures for each month during winter); and a landcover dataset (Zhang et al. 2008; Fry et al. 2011; http://www.nd.gov/gis/data-portal.html; reclassified into 15 classes) that describes the "vegetational and artificial constructions covering the land surface" (Burley, 1961) .

A fundamental assumption of MaxEnt is that the entire geographic area of interest has been sampled (Kramer-Schadt et al. 2013), yet this is typically not the case as presence locations are gathered in better-surveyed areas. Because of this, background samples used when developing distribution models can have significant consequences on the model results (Elith et al. 2011). For our study, MaxEnt was only allowed to select background pseudo-absence locations within the same counties as the study took place. This provides MaxEnt with a pseudo-absence file that has the same bias as the presence locations (Young et al. 2011).

3.2.5. Model Evaluation

All MaxEnt models were evaluated for fit based on the Area Under the Curve (AUC) of the Receiver Operator Characteristics, which measures the models' likelihood of correctly distinguishing between presence and random locations; an AUC value of 0.5 indicates the model was no better than random at depicting the species distribution while values closer to 1.0 indicate good model performance (see Phillips et al. 2006 for further explanation). We considered a model to be good if both the training and test AUC were higher than 0.75 (Elith et al. 2006).

Models were run using the default MaxEnt settings, with the exception of the number of iterations (5000 instead of the default 500). To evaluate model complexity and reduce over-parameterization/over-fitting, we ran each model using different regularization betamultiplier values (1-12). These values affect the fitting of the output distribution, with large values being more generalized, geographically spread out and can be thought of as a smoothing parameter. This resulted in running 12 models for each species, (12 for each sampling technique). To find the most parsimonious models, we used AIC scores produced in ENMTools v. 1.3. To evaluate the correlation between these variables (i.e. test for multicollinearity), we used the variable correlation analysis in ENMTools v. 1.3 (Warren et al. 2010). For variables that were highly correlated ($R^2 > 0.75$), the less ecologically relevant variable was removed. Only variables that contributed more than 1% to the model were included in the final models. This resulted in eight final variables to be used for modeling: Altitude, roads, annual precipitation, rivers, mean

October temperature, Map precipitation, June precipitation, and landcover. The landcover dataset was reclassified into 15 classes (Table 3.1).

Table 3.1. Landcover reclassifications. Reclassifications were done based on current knowledge of the study sites and North Dakota ecoregion characteristics.

Landcover Reclassifications
Mosaic cropland
Mosaic vegetation
Closed broadleaved evergreen forest
Closed broadleaved deciduous forest
Open broadleaved deciduous forest
Closed needleleaved evergreen forest
Open needleleaved deciduous or evergreen forest
Closed mixed broadleaved and needleleaved forest
Mosaic grassland
Closed shrubland
Closed herbaceous vegetation
Sparse vegetation
Broadleaved forest regularly flooded
Broadleaved forest or shrubland permanently flooded
Woody vegetation on regularly flooded or waterlogged soil

Using the statistical outputs of the most parsimonious MaxEnt models, we extracted the three variables for each species that had the most explanatory power in building the SDMs (Table 3.2). Using the final habitat suitability models for each species, we evaluated the amount of overlap between all 10 species using the niche overlap function in ENMTools v.1.3 (Warren et al. 2010). We used the measure Schoener's *D* to evaluate the amount of overlap between species habitat suitability maps (Table 3.3). Schoener's *D* quantifies niche overlap from 0, meaning there is no overlap between habitat suitability maps (0% overlap), to 1, where all grid cells are of equal suitability for both species (100% overlap). We then qualitatively compared the

SDMs to look for areas throughout the state where modeling predicted areas of high suitability for multiple species.

Table 3.2. Three most relevant predictive environmental variables used for MaxEnt habitat suitability modeling for each species. Species abbreviations are as follow: *Corynohinus townsendii* = Coto; *Lasiurus borealis* = Labo; *Myotis ciliolabrum* = Myci; *Myotis evotis* = Myev; *Myotis septentrionalis* = Myse; *Myotis volans* = Myvo.

Species	Predictive EGVs In MaxEnt Model	
Coto		
	1	Max Temperature of Warmest Month
	2	Mosaic grassland/forest or shrubland ; Closed to open shrubland; Sparse vegetation
	3	Min Temperature of Coldest Month
Labo		
	1	Max Temperature of Warmest Month
	2	Mosaic grassland /forest or shrubland ; Closed to open shrubland; Sparse vegetation
	3	Annual Mean Temperature
Myci		
	1	Mosaic forest or shrubland /grassland; Sparse vegetation
	2	Max Temperature of Warmest Month
	3	Annual Mean Temperature
Myev		
	1	Mean Temperature of Coldest Quarter
	2	Max Temperature of Warmest Month
	3	Mosaic forest or shrubland /grassland; Sparse vegetation
Myse		
	1	Mosaic forest or shrubland /grassland
	2	Max Temperature of Warmest Month
	3	Mean Temperature of Warmest Quarter
Myvo		
	1	Mosaic forest or shrubland /grassland
	2	Annual Mean Temperature
	3	Mean Temperature of Warmest Quarter

Table 3.3. Schoener's D niche overlap statistic for six bat species in North Dakota (excludes *M. thysanodes*).

SPECIES	Coto	Labo	Myci	Myev	Myse	Myvo
Coto†	1					
Labo†/††	0.804	1				
Myci†	0.748	0.72	1			
Myev†	0.738	0.661	0.784	1		
Myse†	0.676	0.668	0.825	0.624	1	
Myvo††	0.714	0.720	0.869	0.685	0.869	1

†Species Documented outside known IUCN distribution.
†† Species whose MaxEnt SDM depicts suitable habitat outside known IUCN distribution.

3.3. Results

3.3.1. Species Distributions

We documented eleven bat species in North Dakota, with seven having an IUCN distribution range limit intersecting the state (*C. townsendii*, *M. thysanodes*, *M. ciliolabrum*, *M. septentrionalis*, *M. evotis*, *L. borealis*, and *M. volans)*. Of these seven species, five were captured or recorded outside their known IUCN distribution (*C. townsendii*, *M. thysanodes*, *M. septentrionalis*, *M. ciliolabrum*, and *L. borealis*) and habitat suitability maps show areas of high suitability outside IUCN range limits of North Dakota for all six species analyzed (Figure 3.2).

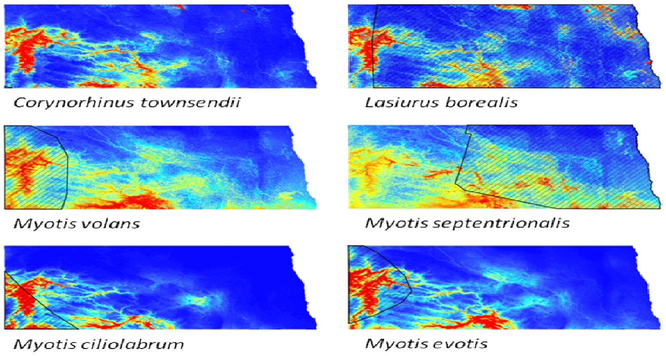

Figure 3.2. MaxEnt habitat suitability maps for six species either found outside the known IUCN distribution or showed areas of high suitability outside the known IUCN distribution in North Dakota. IUCN distribution depicted by black 10% hatch overlaid on habitat suitability map. Areas depicted as red are of high suitability and areas depicted as blue are of low suitability.

Our capture/monitoring results confirm that *C. townsendii and M. thysanodes* are summer residents of North Dakota (Tigner 2006; Lenard and Lausen 2010). We positively identified *M. thysanodes* by 3 physical captures and 3 echolocation sequences, indicating this species is rare in the state. We also positively identified 3 *C. townsendii* by physical capture and >200 echolocation sequences from acoustic monitoring. *C. townsendii* was also acoustically detected in the Turtle Mountains region of North Central North Dakota, suggesting that this species may be expanding its distribution to higher latitudes.

Statistical analysis within MaxEnt showed several important environmental variables for each species (Table 3.1). Maximum temperature of warmest month was one of the top three environmental variables used for MaxEnt SDM production for all but one species, *M. volans*. For all species, mosaic landscapes containing forests and shrubland were also important. However, *C. townsendii* and *L. borealis* were primarily associated with deciduous and needleleaf forests, while the myotids were more strongly associated with grasslands and shrubland open areas. Surprisingly, precipitation was not important for shaping the habitat suitability model in any species.

With the exception of *M. lucifugus*, Schroener's D statistic (Table 3.2) showed that *Myotis* species had the greatest habitat overlap with other *Myotis* species, with these four species being categorized in the Grassland/Shrubland group. Interestingly, *M. lucifugus* had the greatest habitat overlap with *L. cinereus*. Of the remaining species that were either documented or predicted to be outside their known distribution in North Dakota, MaxEnt analysis showed that *C. townsendii* and *L. borealis* both were associated with deciduous and coniferous forest stands. Habitat suitability maps clearly showed four distinct areas in the state that contain highly suitable habitat for all species: 1) the badlands region of western North Dakota, 2) the Missouri River Valley, 3) the Little Missouri Grasslands, and 4) the Heart River.

3.4. Discussion

We positively identified, either by physical capture or acoustic identification, five bat species outside their known IUCN distribution. This finding highlights the importance of continued monitoring efforts and the lack of precision that contemporary distribution maps are able to depict. With imminent threats, such as white-nose syndrome and wind energy development, such oversight could have significant impacts on bat populations, especially those populations along the periphery of the species distribution. With the recent advent and use of habitat suitability modeling, managers and researchers can better identify areas that contain a higher likelihood of species presence and therefore avoid such oversights. For our study, MaxEnt modeling revealed four key areas of the state that have significant roosting and foraging potential for all bat species. These include the badlands region, the Missouri River (which bisects the state into eastern and western halves), the Heart River, and the Little Missouri Grasslands. The river systems that connect these areas could act as a migratory route between the species-rich Badlands region and the comparably species-poor Missouri River Valley and Turtle Mountains regions. For instance, The Heart River extends as a tributary of the Missouri River, arising in the South Unit of Theodore Roosevelt National Park, which is part of the species-rich badlands region of North Dakota. It is presumable that species are using this river as both a fall and spring migratory route, and future work should be conducted to determine the river's influence on dispersal patterns throughout West Central North Dakota. The majority of riparian areas in the state are dominated by aspen and *Populus* stands (Potter and Moir 1961; PB personal observation) and could allow for seasonal movement of bats into and out of these more peripheral areas. Large broadleaf trees and dense understory are also characteristics of these habitat types, making them more structurally complex and potentially increasing trophic complexity. Since the majority of North Dakota has limited tree cover, species might be using riparian corridors throughout the state to locate and exploit more diverse roosting and foraging resources. Future research should be aimed at monitoring these potential corridors to determine if bats are indeed using them as routes for movement between local foraging grounds and/or as migratory corridors for longer, seasonal movements.

The vegetative and landscape characteristics of North Dakota have the potential to be important for other species distributions in northern regions. *C. townsendii* has previously been reported to occur in riparian corridors, coniferous and deciduous forests, and avoid open grasslands (Kunz and Martin 1982; Adam et al. 1994; Baker and Laci 2006). Our study showed that this species was associated, through MaxEnt modeling, with grassland systems that are characteristic of the badlands region of North Dakota. This finding suggests that *C. townsendii* has different foraging and roosting habitat preferences in the periphery of their distribution. However, other species, such as *M. ciliolabrum,* have previously been shown to occur in badlands terrain, juniper-pinyon stands, and coniferous and deciduous forests (Halloway and Barclay 2001). Our analysis seemed to confirm these finding in the peripheral margins of the species distribution. We found *M. ciliolabrum* and *M. septentrionalis* to be associated with grassland/shrublands and tall hardwood forests, respectively. These findings are similar to habitat preferences of this species in more central populations, suggesting that *M. ciliolabrum* and *M. septentrionalis* are not altering their habitat preferences along the peripheral margins (Foster and Kurta 1999; Caceres and Barclay 2000; Kruic et al.1996; Owen et al. 2003; Loeb and O'Keefe 2006). However, the full array of environmental and climatic characteristics that actively influence a species habitat use are not measurable within a MaxEnt environment. Further fine-scale habitat analysis, especially information gathered on roosting preferences for bats, could show a greater contrast between central and peripheral populations. Since the datasets available for species distribution modeling are mostly limited in scope, many models do not fully depict key ecological characteristics of a species. Future research attempts to document differences between central and peripheral populations should focus on fine-scale habitat assessments conducted in the field. For example, *C. townsendii* is known to preferentially roost in caves (Kunz and Martin 1982), although tree roosting has been documented (Fellers and Pierson 2002). Our physical and acoustic captures documented this species in locations where caves are not known to occur, such as the Turtle Mountains and Missouri River Valley, suggesting that individuals are potentially exploiting different aspects of the habitat in the northern Great Plains. Further work needs to be done to confirm such differences and the potential for exploitation of man-made structure as roosting resources.

Of the eleven species of bats found in North Dakota, we positively identified five outside of their known IUCN distribution. This result highlights the importance of continuous monitoring of population trends and distributions, especially when relying on range maps constructed from simple polygons, which do not reflect changing characteristics of populations from the interior towards the periphery. Two species (*M. thysanodes* and *C. townsendii*) were documented far outside their IUCN distributions, which did not include North Dakota as part of their range. This documentation of species outside of their known IUCN distributions could represent two scenarios. First, these species have expanded their distribution range limits since the time of the last monitoring study. Second, these species may have always occupied these areas and simply went undetected during the limited monitoring studies that have been conducted in the past. Our results cannot distinguish between these two scenarios, but instead highlight that much information about species distributions is still unknown for many bats, and habitat suitability modeling coupled with monitoring surveys can greatly influence the contemporary knowledge of species distribution and range limits.

Using maximum-entropy modeling and high-resolution climatic and vegetative datasets, we documented the top three environmental variables driving distributions for each species in North Dakota. Though there were discrepancies between which variables were important for modeling SDMs for each species, the presence of mixed heterogeneous habitat was common for all species. Temperature was an especially important climactic factor driving SDMs, although, interestingly, precipitation was not. For the bats of the northern Great Plains, the impacts of climate change on temperature could be the most important factor in determining how the contemporary distributions of bat species will shift over time. Our analysis provides insight into the climactic and vegetation characteristics that are important for supporting peripheral populations of bats in the northern Great Plains, which can potentially inform future research and management decisions in this region.

An additional problem for contemporary modeling studies is that in most cases it is difficult, if not impossible, to quantitatively compare results of past studies that have primarily made qualitative assessments with those studies using data from GIS raster datasets and habitat suitability analyses. The majority of literature we included in our analysis defined habitat associations loosely, typically only describing the immediate vegetation with little or no insight into the surrounding forest stand. Due to these discrepancies, it is difficult to make highly reliable comparisons between modern and historical environmental analysis. Habitat suitability modeling is becoming widely used in many taxa, including bats (Tingley et al. 2009; Carpenter

2010; Razgour et al. 2011). As MaxEnt modeling continues to become established as an important ecological tool, it is imperative that researchers obtain information that can be used collaboratively by others to provide a baseline for habitat use comparisons. Such information may be critical in the face of global climate change and increasing concerns about effective conservation of bat species, as well as other taxa.

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CHAPTER 4. DOCUMENTATION OF OVERWINTER BAT SPECIES PRESENCE AND HIBERNACULA USE IN THE BADLANDS OF NORTH DAKOTA

4.1 Introduction

The 2006 introduction of *Pseudogymnoascus destructans*, the fungus that causes white-nose syndrome (WNS), has led to an alarming decrease in many bat species across eastern North America. To date, 5.7 million hibernating bats, including11 species, have died from this infectious disease (USFWS 2014). The 2012-2013 discovery of the disease in eastern Minnesota (Minnesota Department of Natural Resources; Naumann et al. 2013) indicates that *P. destructans* has not yet reached its limit and is continuing its progression westward and northward in North America. While hibernacula are well documented in the eastern United States, information about such sites in the northwestern US and western Canada is not as well established.

North Dakota is one of the states with the least amount of documented information about the occurrence and characteristics of summer or winter bat populations. Previous studies have focused only on isolated areas of the state (i.e. one sampling location), generally contained few capture records, and examined only summer resident bats (Jones Jr. and Stanley 1962, Genoways 1966, Jones Jr. and Genoways 1966, Genoways and Jones Jr. 1972, Jones Jr. and Choate 1978, Seabloom et al. 1978, Tigner 2006, Lenard and Lausen 2010). More recent work has studied the summer bat community across the entire state of ND, documenting key foraging and roosting habitats using maximum entropy modeling (Barnhart and Gillam, under review). Eleven bat species are known to be resident in North Dakota during the summer months; *Eptesicus fuscus, Corynorhinus townsendii, Lasiurus borealis, Lasiurus cinereus, Lasionycteris noctivagans, Myotis ciliolabrum, Myotis evotis, Myotis lucifugus, Myotis septentrionalis, Myotis thysanodes, and Myotis volans*.

To date, it has been assumed that all bats leave North Dakota during the winter months, migrating to cave systems in western Minnesota or western South Dakota (Seabloom et al. 2011). Yet, documentation of hibernacula in similar habitat types at more northern latitudes suggests that bats could potentially overwinter in North Dakota (Lausen and Barclay 2006). Accurate assessment of winter bat distributions is especially important given the continued spread of WNS and the high likelihood that it will very soon impact bat populations in the Great Plains of the United States and Canada.

The purpose of this study was to: 1) determine if any of the eleven bat species known to inhabit North Dakota in the summer are also resident in the state during the winter hibernation period (October to April), 2) assess the characteristics of any identified hibernacula to potentially determine habitat preferences, and 3) determine if confirmed or potential hibernacula are within the range of temperatures suitable for *P. destructans* growth.

4.2. Methods

In Winters 2010-2013, we sampled for bats in the south unit of Theodore Roosevelt National Park (TRNP-SU), a badlands region of western North Dakota where all eleven species have been documented, and which includes the only naturally occurring cave systems in the state. The geology of the badlands region is dominated by clays, with erosion producing varying cavities, ranging from small crevices to large cave systems (Bell 1968). TRNP-SU follows the Little Missouri River and its tributaries, which have shaped the unique landscape. TRNP-SU is an arid environment, typically averaging <385mm of rainfall per year, and extreme temperatures during the winter months can routinely reaching -20˚C (National Park Service).

4.2.1 Passive Acoustic Monitoring

In Winter 2010-2011, we deployed four Anabat SD-1 (Titley Scientific, Columbia, Missouri) zero-crossing bat detectors at a variety of locations in the TRNP-SU. In subsequent winters, we deployed six AnaBat SD-1 and two Anabat SD-2 units in the national park (Figure 4.1). These AnaBat units are meant to detect the calls of bats that have temporarily aroused from hibernation and have left their hibernacula in search of water or other resources. All AnaBats were housed in weather-proof boxes and mounted on wood support beams 1.5 meters above the ground. Previous research has shown that acoustic detectors provide much higher quality echolocation calls when they are placed off the ground (Weller and Zabel 2002). Each system was powered by a 12 V battery charged by a solar panel. Data from each AnaBat unit was downloaded every 2 to 4 weeks. Anabats were continuously in record mode (day and night), in which sounds exceeding a pre-set amplitude threshold would trigger recording. We selected AnaBat recording locations based on general habitat preferences of the 11 summer resident species, such as sites with tree cover or near water sources. Sites were also chosen based on their accessibility, as many areas of the park are not accessible during the winter months due to deep snow and limited road access. Units were initially deployed on 12 September 2010, 1 September 2011, and 4 September 2012. Units were removed from the field on 3 May 2011, 24 April 2012 and 14 May 2013. AnaBat units were placed in the field shortly before fall migration was expected to begin and were removed from the field when there was a dramatic increase in detected echolocation calls noting arrival of spring migrants. Echolocation call files were visually inspected for quality using AnaLook W (ver. 3.3; Corben 2006) and classified to species using Kaliedoscope (ver.1.1.22, Wildlife Acoustics, MA, USA; Agranat 2013).

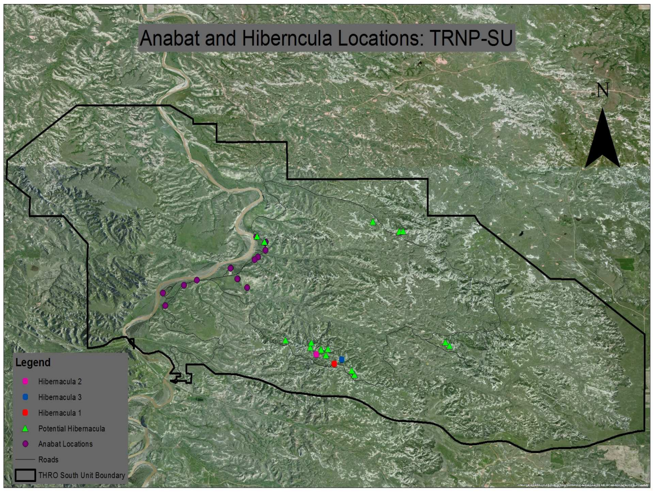

Figure 4.1. Winter 2012-2013 Anabat recording sites (purple circles), potential hibernacula (green triangles), hibernacula 1 (red circle), hibernacula 2 (pink circle), and hibernacula 3 (blue circle) in the South Unit of Theodore Roosevelt National Park, Medora ND.

4.2.2. Physical Capture of Bats Via Mistnetting

Mistnetting for bats during the winter months is especially difficult due to the very low levels of active, flying bats at any given time. In Winters 2011-2013, we mistnetted at a variety of sites within TRNP-SU, including: 1) habitats that would potentially be attractive to bats that have aroused from hibernation, such as sites with tree cover or near water sources, and 2) at known or potential hibernacula. Mistnets were opened shortly before sunset and monitored for bat captures until sunrise or 90 minutes after the last successful capture. Mistnetting was conducted during warm weather bouts, which were characterized by temperatures above -18C. To reduce the risk to bats captured in mistnets at such low temperatures (between 0 C to -15C), nets were continuously monitored so that bats could be quickly removed (within 5 minutes) and taken to a heated vehicle. All procedures followed a protocol approved by the North Dakota State University Animal Care and Use Committee (Permit Number: A12040). No animals were euthanized during this study and no federally protected species were sampled during the study period.

4.2.3. Documenting Known Hibernacula and Temperature Recordings In Known Hibernacula

Once a bat was captured, a 0.35 g radio transmitter (Model LB-2N, Holohil Systems, Canada) was attached between the scapulae using Osto-Bond latex adhesive (Osto-Bond, Canada). Radiotransmitters were only attached to bats in which the transmitter weighed less than five percent of the bats total body weight (Aldridge and Brigham 1988). Tagged bats were released and not tracked until the following day to allow the establishment of normal roosting behavior. Bats were tracked using a 3-pronged directional Yagi antenna and receiver (R1000, Communication Specialists, CA, USA).

In Winter 2012-2013, we used Ibuttons (Model DS1921G, Embedded Data Systems, KY, USA) to collect temperature data from the three hibernacula identified in Winter 2011-2012. Temperature data in hibernacula 1 (HIB 1) were collected from 12-14 March 2013 at 60 sec intervals at a location ~12 m within the cave near the area that two bats had been observed hibernating (Table 4.1). Two additional Ibuttons were deployed from 14-15 March 2013 at different locations within the cave; one was placed ~1 m from the terminal end of the cave and the other was placed ~10 m from the entrance to the cave. We also collected temperature data in hibernacula 2 (HIB 2, 10 October 2012) and hibernacula 3 (HIB 3, 11-19 October 2012; Table 4.1). All entry into hibernacula followed the WNS protocol set by the United State Fish and Wildlife Service (USFWS 2012).

Table 4.1. Temperatures collected from Hibernacula 1-3. Temperatures are shown in C˚.

Hibernacula	ONE		TWO		THREE	
Ibutton	1	2	3	4	5	6
AVG	5.37	5.36	4.91	5.21	8.62	7.84
SD	1.09	1.18	0.89	1.08	3.19	4.05
MIN	4	4	4	4	1	-2
MAX	7	7.5	8	8.5	13	16.5

4.2.4. Identification of Potential Hibernacula

Due to a paucity of information about the location of caves in the badlands of Western North Dakota, we took several scouting trips on foot into the backcountry of TRNP-SU between 18-28 February 2013 and 3-10 October 2013 in search of potential hibernacula. Our second scouting trip was guided by our MaxEnt mapping efforts (see below). We considered a cave to be a potential hibernacula if it appeared deep enough to not be influenced by fluctuating external temperatures. Figure 1 depicts the location of the seven potential hibernacula we initially identified via scouting. Although scouting via vehicle is more efficient, the limited number of roads in the park and complete lack of documentation of cave sites left surveying on foot as our only option for further exploration.

Based on the location of the three known and seven potential hibernacula (Figure 4.1) we developed a habitat suitability map using MaxEnt (ver. 3.3.3, Phillips et al. 2006). This habitat suitability map was produced to guide future hibernacula scouting efforts made within TRNP-SU. Such presence-only modeling has been shown to be very reliable and competitive with other high performing modeling techniques (Elith et al. 2010). The analysis included a digital elevation map (DEM) obtained through the USGS (National Elevation Dataset; Gesch et al. 2002; Gesch 2007). The DEM was then converted into two separate raster datasets, slope and aspect, using ArcGIS. These variables were deemed ecologically relevant because of their importance in cave formation and based on knowledge about the biology and ecology of cave roosting North American bats (Razgour et al. 2011). We partitioned our location points into test and training datasets (80% and 20%, respectively) and ran the jackknife validation function to minimize biases associated with small sample sizes. Using the "autofeatures" function in Maxent, we produced response curves and conducted a jackknife analysis to measure variable importance in each model. We then added the aspect and slope datasets and the locations of known and potential hibernacula into MaxEnt to develop a habitat suitability map for TRNP-SU. Because Maxent chooses which presence data to use in model training and testing, we ran 50 model replications and then averaged them into a single habitat suitability model. The resulting map depicts areas of high (red) and low (blue) suitability in which new potential hibernacula can be found.

4.2.5. Model Evaluation

All MaxEnt models were evaluated for fit based on the Area Under the Curve (AUC) of the Receiver Operator Characteristics, which measures the models' likelihood of correctly distinguishing between presence and random locations; an AUC value of 0.5 indicates the model was no better than random at depicting the species distribution while values closer to 1.0 indicate good model performance (see Phillips et al. 2006 for further explanation). We considered a model to be good if both the training and test AUC were higher than 0.75 (Elith et al. 2006). A fundamental assumption of MaxEnt is that the entire geographic area of interest has been sampled (Kramer-Schadt et al. 2013), yet this is typically not the case as presence locations are gathered in more heavily surveyed areas. Because of this, background samples used when developing distribution models can have significant consequences on the model results (Elith et al. 2011). For our study, MaxEnt was only allowed to select background pseudo-absence locations within the same county as the study took place. This provides MaxEnt with a pseudo-absence file that has the same bias as the presence locations (Young et al. 2011).

Models were run using the default MaxEnt settings, with the exception of the number of iterations (5000 instead of the default 500). To evaluate model complexity and reduce over-parameterization/over-fitting, we ran each model using different regularization betamultiplier values (1-12). These values affect the fitting of the output distribution, with large values indicating more geographical dispersion. The large values can be thought of as smoothing parameters. This resulted in running 12 total models, (1 for each betamultiplier). To find the most parsimonious models, we used the model selection function in ENMTools v. 1.3. (Warren et al. 2010), which evaluates the models using AIC scores.

4.3. Results

4.3.1. Passive Acoustic Monitoring

During the sampling period, we collected 1,297 recordings of bat calls across the eight AnaBat Units (328 in Winter 2010-2011; 646 in Winter 2011-2012; 323 in Winter 2012-2013). An example of a high-quality call is shown in Figure 4.2. Of the 1,297 total call files, 962 were positively classified to the species level. We positively identified 3 species: *E. fuscus* (486), *L. noctivagans* (349), and *M. lucifugus* (127). The majority of calls (88%) were recorded during September. Due to the overwhelming majority of calls during September, we believe this month represents the fall migration of bats from North Dakota. However, we positively identified bat calls in all other months from October to April (Table 4.2). No recordings were captured during the daylight hours, suggesting bats primarily aroused from hibernation and flew outside at night (Boyles et al. 2006). During the sampling period, nightly temperatures ranged from 5.9˚C to 20.3˚C. An example of an Anabat recording is shown in Figure 4.2.

Table 4.2. Number of echolocation calls identified during the winter hibernation period in TRNP-SU 2010-2013.

Month	Number of Echolocation Calls
September	1156
October	59
November	25
December	25

Table 4.2. Number of echolocation calls identified during the winter hibernation period in TRNP-SU 2010-2013 (continued).

Month	Number of Echolocation Calls
January	8
February	4
March	8
April	24

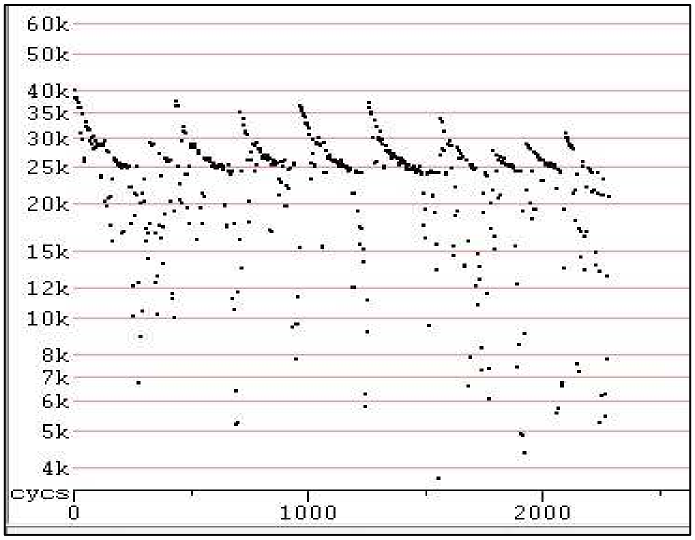

Figure 4.2. An example spectrogram (Frequency x time representation) of a sequence of bat calls recorded from an Anabat detector during the Winter 2012-2013 field season.

<u>4.3.2. Physical Capture of Bats Via Mistnetting</u>

We deployed mistnets on 16 nights throughout the sampling period. HIB 1 was identified as a summer roost during a separate study in 2010. On 10 March 2011, we visually inspected the cave and found two hibernating big brown bats, *E. fuscus*, ~12m from the entrance. This visual sighting was the first confirmation of bats overwintering in a natural habitat in North Dakota. On 11 March 2011, we deployed a mistnet across the entrance to the cave and captured an *E. fuscus* entering the cave when the ambient temperatures was ~ 0˚C. After being tagged, the bat was tracked back to HIB 1 and remained in the cave for the next 10 days, after which the transmitter battery died. On 9 October 2012 we captured and radiotagged one western small-footed myotis, *M. ciliolabrum* emerging from a small cave entrance. We tracked the individual to two hibernacula, the first of which it remained in for one night (HIB 2) and the second of which it remained in for eight nights (HIB 3), after which the transmitter failed. Both of these hibernacula were considerably smaller in size than HIB 1, appearing to be thin rock crevices, although we were unable to assess how deep the crevices ran or if they opened up into larger spaces.

On 12-14 September 2012, we set up a 2.6m mistnet to block the entrance to HIB 1. This was done to determine if HIB 1 was again being used during a different winter, as this site was the largest and deepest known hibernacula in the study area. During this time, we captured one long-eared myotis (*M. evotis*, emerging), one big brown bat (*E. fuscus*, emerging), and one Townsend's big-eared bat (*C. townsendii*, entering). Emergence or entrance was noted by the side of the mistnet in which the bat was captured.

4.3.3. Hibernacula Temperature and P. destructans Susceptibility

The average temperatures for hibernacula are shown in Table 4.3. Temperatures were more stable in the larger HIB 1 compared to the two smaller HIB 2 and 3. In addition, average temperatures were lower in HIB 1 (5.21 +/- 1.06 °C; 4 Ibuttons) compared to HIB 2 (8.62 +/- 3.19 °C; 1 Ibutton) and HIB 3 (7.84 +/- 5.05 °C; 1 Ibutton). Temperatures reported in all three hibernacula are within the growing range of *P. destructans* (Verant et al. 2012). However, Verant et al. (2012) noted that the optimum growing range for *P. destructans* is 12.5˚C to 15.8˚C, in which case all hibernacula but HIB 3 are outside of the thermal optima.

4.3.4. Potential Hibernacula Identification

Our first scouting trip in February 2013 positively identified seven potential hibernacula. These locations (and those for the confirmed hibernacula) were placed into the MaxEnt modeling program to produce a map of habitat suitability. MaxEnt modeling revealed multiple areas within

TRNP-SU that contain suitable habitat for hibernacula (Figure 4.3). Model performance was high (AUC = 0.974) and betamultiplier 2 was the most parsimonious model indicating the default betamultiplier value of 1 was over-fitting the output distribution. Areas of high suitability were identified as those on steep, south-facing slopes. On our second scouting trip in October 2013, we used this map to select our search areas, which led to the documentation of eleven new potential hibernacula. This model will be used in the future to guide scouting trips to locate potential hibernacula that could be susceptible to *P. destructans* growth.

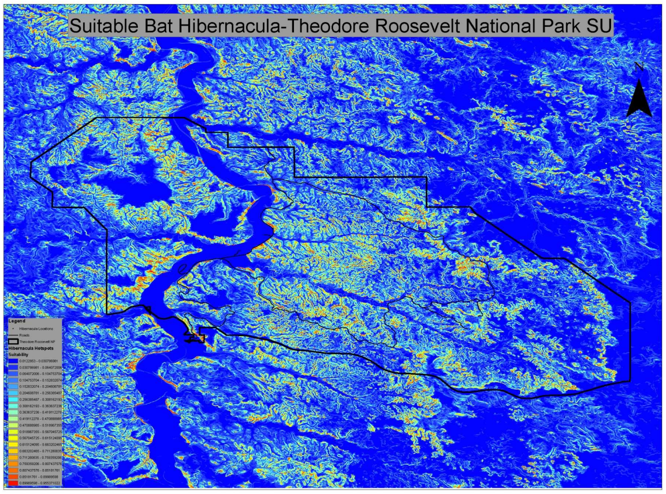

Figure 4.3. Habitat suitability map build from known and potential hibernacula sites. Red areas indicated areas of high suitability, while blue indicates an area of low suitability. The border of the South Unit of Theodore Roosevelt National Park is outlined in black.

4.4. Discussion

This is the first study to document bats overwintering in natural habitats in North Dakota. Through both acoustic monitoring and physical capture, we positively identified *M. ciliolabrum* and *E. fuscus*. These results mirror the findings of Lausen and Barclay (2006), who identified the same two species overwintering in Dinosaur Provincial Park in northern Alberta, Canada. Lausen and Barclay (2006) also documented overwintering *M. lucifugus* and *M. evotis*; given that these species are very common summer residents of our study area, it seems likely that *M. lucifugus* and *M. evotis* also overwinter in ND, but simply went undetected in our study. The similarities between our findings and those of Lausen and Barclay (2006) likely reflect the similar habitats available to overwintering bats. Like TRNP-SU, Dinosaur Provincial Park is characterized by badlands terrain with many rock and mud crevices available for roosting bats. Both sites are also arid, typically experiencing similar amounts of annual rainfall and extreme temperatures during the winter. Overall, the similar findings of these two studies, which were conducted >500 miles apart, likely indicate which species we would expect to be winter residents in other badland habitats of the northern Great Plains.

Our temperature data show that all three known hibernacula were regularly within the thermal optimum for *P. destructans* growth. Due to the overwhelming number of potential overwintering sites for bats within the badlands environment, we believe there to be many more sites at which this fungus could grow at an optimal temperature. Despite these ideal thermal properties, previous studies have documented that hibernacula in the northern badlands regions have low relative humidity (28+/-1%, Lausen 2001). Because *P. destructans* growth is restricted to hibernacula with >90% relative humidity (Foley et al. 2011), it is possible that if hibernation sites in western ND also have low relative humidity, the growth rate of *P. destructuans* could be slowed. Further, our limited temperature data demonstrated regular fluctuation of hibernacula temperatures outside of the optimal growth range for *P. destructans,* which could further hinder the fungus from rapidly establishing at sites in western North Dakota. Also, *P. destructans* has not demonstrated a growth rate at or below 0˚C, suggesting that all confirmed hibernacula in North Dakota, except HIB 3, were continuously within the growth range but not the thermal optimum range. Ongoing research in the study area is focused on collecting relative humidity data to see if this may be the case.

Habitat suitability modeling can be a valuable research and conservation tool for potentially identifying habitat “hotspots” that have not been previously identified. In our study, a habitat suitability model helped to direct our searches when attempting to document locations of potential hibernacula. This can not only help to quickly identify areas that could potentially be impacted by WNS spread, but also allow researchers and managers to expend fewer in-the-field expenses, such as gas and manpower. Using our habitat suitability map produced from three confirmed hibernacula and seven potential hibernacula (Figure 4.3), directed ground scouting helped us identify eleven additional potential hibernacula within TRNP-SU (Figure 4.1). Areas of high suitability on the map appear to receive high levels of direct sunlight during the winter months, and contain steep slopes that regularly experience erosion via running water during the spring, summer and fall months. Our results highlight that habitat suitability maps can be especially valuable for regions lacking information about the location of hibernacula.

Information as to what environmental features drive roost selection in the overwintering bat populations of western North Dakota is lacking. Specifically, variables related to potential warming by the sun (in high latitudes, south facing slopes receive the most ambient sunlight), slope (Thomas et al. 1987, Russo et al. 2004, Greaves et al. 2006, Nixon et al. 2009), and proximity to water can provide more accurate habitat suitability maps. In addition, more information, such as depth, entrance size, and geological features could further assist on-foot scouting trips since these data are not available in a GIS environment.

Mistnetting at HIB 1 on 12-14 September 2012, which resulted in the capture of *M. evotis*, *E. fuscus*, and *C. townsendii*,, is an interesting case. Early September is likely a time of transition, with some species migrating out of the region and others establishing hibernation sites. Hence, the bats captured in mid September could possibly be winter residents, which would increase the number of species known to hibernate in the state to four. Due to the lack of information about this species in ND, future work should be oriented at determining if *C. townsendii* is indeed a winter resident.

Our findings highlight the need for additional work in the northern Great Plains in preparation for the potential invasion of *P. destructans*. Future research should focus on conducting an in-depth survey of the potential hibernacula in the region, as well as using radiotracking and acoustic monitoring within caves to confirm the presence of hibernating bats. More extensive temperature data, including information about relative humidity, should also be collected throughout the winter at potential and known hibernacula. Finally, regular sampling of soil at known hibernacula for the presence of *P. destructans* should be conducted to determine if the fungus reaches the study area.

The northern Great Plains have recently been put on alert after the documentation of WNS in eastern Minnesota. Though much of the regions does not provide optimal habitat for hibernating bat populations, due to a lack of large, permanent caves, our study shows that the relatively ephemeral caves and crevices produced in the clay soils of the ND badlands are capable of sustaining populations of hibernating bats. As *P. destructans* continues to spread across North America, it is imperative to gather information about overwintering bat populations, as well as determine the potential suitability of hibernacula sites for colonization by the fungus. Our study is a stark reminder that many areas in the predicted path of white-nose syndrome still have little to no information about the vulnerability of resident bats. Future work should focus on filling in these information gaps so that proper mitigation efforts can be made.

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CHAPTER 5. CONCLUSIONS

5.1. Overview of Need

Understanding the distributions and habitat usage of resident bats is a critical component to establishing a statewide conservation plan. Several factors are currently affecting bat populations throughout the United States. Two of the most critical are White Nose Syndrome (WNS) and the rapid expansion of wind energy. The increasing number of wind turbine facilities in North Dakota could have significant impacts on bat populations through mortality due to direct strikes and barotrauma (Arnett et al. 2008; Baerwald et al. 2008). Our habitat suitability maps can be used to minimize this impact if used by managers and wind energy developers to note areas that are of high suitability for bat species in North Dakota. Avoiding or minimizing the number of wind turbines placed in these high suitability locations could have great consequences for the conservation of bats in the state. Also, the rapid spread of WNS across the United States and Canada, with the latest documentation in Minnesota, is currently threatening winter bat populations in North Dakota. With no cure in sight, North Dakota must prepare for mitigation efforts needed to combat WNS. Since WNS is found only in colony roosting bats during hibernation, a habitat usage study in North Dakota could help highlight areas that are more susceptible to harboring the fungus that causes WNS. The results of this research can be used by the North Dakota Game and Fish Department to limit human entrance into areas that prove likely for harboring WNS-infected bats and inform wind energy companies about the location of critical roosting and foraging habitats of bats.

Since the discovery of oil in the Bakken formation, oil production and the resulting habitat damage has exploded in the western part of the state. Although Theodore Roosevelt National Park is immune to such an invasion, the National Grasslands and other lands within the Bakken, which are preferred habitat for all ND bat species, are in critical danger of exploitation and degradation. Land acquisition in this part of the state for forming new Wildlife Management Areas should be a top priority for state managers.

5.2. Overview of Results

Our study includes the first statewide survey of bat distributions and habitat use in North Dakota, and is the first work to address the potential for WNS spread into the state. Our data are currently providing managers the most contemporary image of bat habitat use during the summer and winter months, which will be used to produce mitigation and conservation efforts. We positively identified eleven species of bats in North Dakota and also reported the first occurrence of winter bat residency in the state. This data was then used to examine the impacts of sampling technique on maximum entropy modeling, how peripheral populations of bats in North Dakota differ in habitat use from conspecifics near the center of each species distribution, and winter habitat use of bats in the badlands region of North Dakota.

5.2.1. Sampling Technique and Maximum-Entropy Modeling

Maximum-entropy modeling is a relatively new method for assessing species habitat requirements that is becoming more widely used for ecological applications. Maximum-entropy modeling requires only the input of presence locations and environmental variables (i.e. no absence information is required). Therefore, this method of habitat assessment is especially useful for cryptic and volant species and has been proven as a high performance modeling technique (Elith et al. 2010). However, for bats in particular, presence locations can be gathered in two ways: 1) physical capture via mistnets for identification in the hand or 2) acoustic detection via ultrasonic detectors for identification by echolocation structure. Our study examined the influence of each sampling technique on the production of habitat suitability models produced in the program MaxEnt. We then determined the amount of overlap between the two sampling techniques. We hypothesized that if both techniques sample populations in the same manner, then the amount of overlap between detection technique models should be high. Results showed that both sampling techniques produced high suitability predictive capabilities for ten bat species. For the Myotids, we found differences between species in the amount of overlap. For example, *M. septentrionalis* had only 33.9% overlap while *M. lucifugus* had 80.4% overlap. The two other Myotids in our study, *M. evotis* and *M. ciliolabrum*, had strikingly similar amounts of overlap (48.2% and 48.6%, respectively). This same trend was seen between *E. fuscus* (64.4%) and *L. noctivagans* (66.4%). We then compared the best detection technique model to a master model that included all presence locations from both detection techniques. It was found that acoustic detection most accurately depicted habitat suitability for all *Myotis* species and physical capture most accurately depicted habitat suitability for *E. fuscus* and *L. noctivagans*. We conclude that researchers should consider the pros and cons of each sampling technique when conducting maximum-entropy modeling and assess which will best represent a species true habitat use patterns (Phillips et al. 2009; Yesson et al. 2012).

5.2.2. Understanding Peripheral Populations

Assessing range modifications, habitat use, and genetic robustness is essential for proper management of peripheral populations. For managers and researchers, it is imperative to document the true distribution of a species so that more advanced questions can be addressed (Jones et al. 2001; Zhang et al. 2008; Carvalho et al. 2011). Current distribution maps are often too simplistic and do not accurately depict or predict fragmented and island populations, which prohibits the proper management of peripheral populations (Brown et al. 1996). Documenting exact locales of species presence and predicting areas of potential range expansion is critical for developing effective conservation plans, especially in the face of global climate change, urban expansion, and for bats in particular, WNS (Stebbings 1988).

We documented five bat species outside their known IUCN distribution in North Dakota. This finding highlights the importance of continued monitoring along the periphery of species' distributions. Also, maximum entropy modeling was able to reveal multiple areas of high suitability outside the IUCN distribution for six additional species. For maximum-entropy modeling, maximum temperature of warmest month was one of the top three environmental variables used to produce the models for all but one species, *M. volans*. Mosaic landscapes that contained forests and shrubland was also a defining variable of habitat suitability for North Dakota bats. Two species, *C. townsendii* and *L. borealis*, were associated with deciduous and needleleaf forests, while the myotids were more strongly associated with grasslands and shrubland open areas. Precipitation was not important for shaping the habitat suitability model in any species, which is surprising given the aridity of the badlands region that contains the highest bat diversity in North Dakota.

Schroener's D statistic showed that Myotis species had the greatest habitat overlap with other Myotis species (expect for *M. lucifugus*). Interestingly, *M. lucifugus*, which was grouped with riparian areas and forests, had the greatest habitat overlap with *L. cinereus,* which was associated with grasslands/shrublands. Although *M. lucifugus* was documented across North Dakota, the majority of physical and acoustic captures came from the badlands region, the same is true for *L. cinereus*. However, with the evident lack of roost availability for *L. cinereus*, which is considered an obligate tree rooster (Shump and Shump 1982), in grasslands/shrublands this finding is deserving of further research. Of the remaining species, *C. townsendii* and *L. borealis* were associated with mixed land types containing both deciduous and coniferous stands. The areas with highest suitability for all species included the Turtle Mountains in north-central North Dakota, the Missouri River, and the Heart River. We recommend that managers focus on these regions for the protection of bat communities.

5.2.3. Winter Residency and Habitat Use

This study was the first attempt to document bats overwintering in North Dakota. Although it was expected that some bats remained in the state in anthropogenic structures, our study examined bats overwintering in natural roosts. The badlands region of North Dakota constitutes the only known natural cave systems in the state (Bell 1968). These caves are ephemeral in nature due to erosion from wind and water. This region also goes through extreme temperature and weather patterns during the winter months, making it a harsh environment for winter resident bat populations. However, we were able to positively identify two species during the winter months in the South Unit of Theodore Roosevelt National Park in southwestern North Dakota, *E. fuscus* and *M. ciliolabrum.* Confirmed captures of *M. evotis* and *C. townsendii* during September suggest the number of overwintering species could be as high as four.

Between 2010 and 2013 we recorded the echolocation calls of *E. fuscus*, *L. noctivagans*, and *M. lucifugus* during the winter months. Although the majority of calls (88%) were recorded in September, which could be during the migratory period, we also documented echolocation call activity from October to April. These calls are from winter resident bats, and constitute the first documentation of bat echolocation in the winter months of North Dakota. No echolocation calls were recorded during daylight hours, suggesting bats primarily arouse from hibernation and flew outside at night (Boyles et al. 2006). Temperatures during these night flights ranged from 5.9˚C to -20.3˚C.

We were also able to physically capture *E. fuscus*, *M. ciliolabrum, M. evotis,* and *C. townsendii*. Of the three hibernacula we documented, HIB 1 was the most commonly used by the most species. This cave is relatively large, having an entrance ~3m in diameter and a depth of ~15m. Areas deeper in the cave, which is where bats were found roosting, maintained more stable temperatures than area near the entrance. Since acoustic detection is hampered by the lack of 100% confidence in species identification, we can only confirm the presence of *E. fuscus, M. ciliolabrum,* and *M. evotis.* Since *C. townsendii* was captured in September, which could be considered the migration period in North Dakota, we cannot confirm this species as a winter resident. This finding mirrors that of Lausen and Barclay (2006), in which the same species were documented in the badlands region of Alberta, Canada. These findings suggest that these three species are likely found overwintering throughout the badlands region of the northern Great Plains.

To improve future exploration efforts for overwintering bat populations in North Dakota, we developed a habitat suitability map based on three known hibernacula and seven potential hibernacula. The map identified several areas in TRNP-SU suitable for hibernacula formation and ground-truthing of select “hotspots” resulted in the identification of eleven new potential hibernacula. Current research is ongoing and echolocation detectors have been placed in a set of potential hibernacula to assess bat presence.

5.3. Future Work

This work has laid the baseline needed to ask more advanced questions about the bats of North Dakota. With the impending threat of WNS, wind energy production, oil production, and increased urban sprawl, especially in the badlands region of North Dakota, future work should be oriented at monitoring how the issues addressed here change due to these environmental threats.

Currently, a microhabitat use study is underway to determine how species are partitioning ecological niches in relatively small geographic areas. The knowledge from this study will then be used to better narrow conservation actions within a habitat based on foraging needs. Also, future work should be oriented at determining how bat populations in North Dakota will respond to climate change. Very little work has examined the impacts of climate change on the habitat suitability of bat species, and contemporary modeling techniques are currently being developed to better understand these responses to climate change.

Almost no research has been conducted in North Dakota assessing bat species composition or habitat use in urban, agricultural, or prairie environments. Since these land types occupy the majority of the North Dakota eco-regions, this work is imperative to fully understand how bat species are using the North Dakota landscape and how threats will likely impact these populations. Bats are known to be predators of many agricultural pest species (Boyles et al. 2011) and within the agro-ecosystem of North Dakota, this benefit could be quite attractive to local farmers. Collaborative work with entomologists could give great insight into how bats are providing an agro-economic benefit to North Dakota.

With the potential spread of WNS into North Dakota, one of the most imperative research endeavors needed is the continued monitoring of bat populations and hibernacula in the badlands region. Our work, which started in Winter 2010, has confirmed the presence of bats spending the winter months in North Dakota. We also provided a first glimpse into the hibernacula conditions that exist in the ephemeral cave systems of western North Dakota. Future work should be aimed at continuous monitoring, both acoustically and by physical capture, during the winter months in western ND and continued assessment of confirmed and potential hibernacula. Also, future work should be focused on monitoring of substrate samples within hibernacula to confirm the presence of *P. destructans*. Since no large bat colony has been found in the winter months in North Dakota, documentation of WNS will most likely not come from physical inspection of captured bats, but rather from soil samples taken within confirmed and potential hibernacula. A large research effort should be dedicated to such monitoring due to the potential consequences of *P. destructans* invasion to North Dakota.

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