FORAGING ECOLOGY OF RANGELAND BATS

A Thesis
Submitted to the Graduate Faculty
of the
North Dakota State University
of Agriculture and Applied Science

By

Rebecca Therese Trubitt

In Partial Fulfillment of the Requirements
for the Degree of
MASTER OF SCIENCE

Major Program:
Range Science

November 2017

Fargo, North Dakota

North Dakota State University
Graduate School

Title

Foraging Ecology of Rangeland Bats

By

Rebecca Therese Trubitt

The Supervisory Committee certifies that this ***disquisition*** complies with North Dakota

State University's regulations and meets the accepted standards for the degree of

MASTER OF SCIENCE

SUPERVISORY COMMITTEE:

Torre Hovick

Chair

Erin Gillam

Devan McGranahan

Approved:

November 13th, 2017	Francis Casey
Date	Department Chair

ABSTRACT

Land-use and land cover changes impact the distribution of landscape features in rangelands and wildlife use of the landscape. To balance the requirements of wildlife groups that respond differently to landscape features, managers need more information on how these species use rangelands. Here, we investigate bat use of rangelands. We investigated the associations between bat activity and landscape features using acoustic monitoring and generalized linear mixed effect models. Trees and open water were positively associated with bat activity. We also investigated bat use of rangeland tree patches using a hierarchical modelling framework to build generalized linear models that included landscape, patch, and local level variables. Bats selected contiguous patches with low basal area. These studies show the importance of riparian forests for rangeland bats, and guide management of these areas. This data will aid managers in conserving rangeland bats and balancing their habitat requirements with those of other rangeland wildlife.

ACKNOWLEDGEMENTS

DEDICATION

This thesis is dedicated to:

My mom, Mary Beth Trubitt, who is a source of inspiration for me in both academia and life,

My dad, Brian Trubitt, who taught me to always WIWAP- Walk In With A Plan,

My sister, Kate the Great, who always keeps me smiling, and

My partner, Paul Rogers, my rock, without whom this thesis would not exist.

Also to Wash, the world's best cat.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

HABITAT ASSOCIATIONS OF BATS IN A WORKING RANGELAND LANDSCAPE

Abstract

Land-use change has resulted in rangeland loss and degradation globally. These losses include conversion of native grasslands for row-crop agriculture as well as degradation of remaining rangeland due to fragmentation and changing disturbance patterns. Understanding the factors that impact wildlife use of rangelands is important for conservation in these landscapes. We investigated bat habitat associations in a working rangeland in southeastern North Dakota throughout the summer of 2016. We used Petterson d500x acoustic detectors to systematically sample bat activity across the study area on a 1 km point grid. We identified calls using Sonobat autoclassification software. We detected five species using this working rangeland, which included *Lasionycteris noctivagans* (2,722 detections), *Lasiurus cinereus* (2,055 detections), *Eptesicus fuscus* (749 detections), *Lasiurus borealis* (62 detections) and *Myotis lucifugus* (1 detection). We developed generalized linear mixed effect models for the four most commonly detected species based on their known ecology. The modeling results for all focal species highlighted the importance of trees and water at both proximate and landscape scales. The scale of selection varied between the four focal species, with all three investigated scales being explanatory for at least one bat species. The importance of other factors, particularly those associated with direct human development, also differed between species. The broad importance of trees to rangeland bats may put their conservation needs at odds with those of obligate grassland species. Focusing rangeland bat conservation on areas that were treed prior to European settlement, such as riparian forests, can provide important areas for bat conservation while minimizing negative impacts on other grassland species.

1

Introduction

　　Rangelands cover approximately 27% of the world's surface (MA, 2005), but land-use and land cover change have affected the distributions of landscape features throughout these systems (Foley et al., 2005). Human-driven shifts in land cover caused by changing patterns of disturbance, construction of buildings and water sources, and tree planting have also altered the distributions of landscape features on remaining rangelands (Polasky et al., 2005; Fuhlendorf et al., 2012; Lawler et al., 2014; Briggs et al., 2005). Global patterns of rangeland land-use and cover change are reflected in the Great Plains of North America, where 49.5% of land has been converted to agricultural or urban uses (Swaty et al., 2011). In addition to continued conversion to row crops, mismanagement and increasing development of energy infrastructure have led to an overall decline in the quality and quantity of grasslands that persist in the region (Allred et al., 2015; Kreuter et al., 2016; Fuhlendorf et al., 2012). Fragmentation and changing disturbance patterns have also prompted changes in land cover, affecting the distribution of landscape features (Briggs et al., 2005; Engle et al., 2008). In these rangeland landscapes, informed and effective conservation and management requires understanding the features that impact wildlife distributions and habitat associations (Nielsen et al., 2006).

　　Afforestation is a primary example of changing land cover due to alteration of historic disturbance regimes. Afforestation occurs globally and is particularly rampant in the Great Plains of North America (Engle et al., 2008; Price & Morgan, 2008). Prior to European settlement, tree distribution within North American prairies was limited to areas that were moist and fire inhibited, such as riparian areas and steep draws (Briggs et al., 2005; Engle et al., 2008). However, human development has changed the distribution of trees in rangelands both directly and indirectly. Following the Dust Bowl, shelterbelt plantings became widespread, particularly

around homesteads and in agricultural areas (Hess & Bay, 2000). Indirect afforestation is driven largely by landscape fragmentation and changes to the fire regimes (Briggs et al., 2005). In an undisturbed landscape, woody cover can increase rapidly, sometimes leading to major regime shifts (Twidwell et al., 2013). Increased woody cover in rangelands promotes generalist and woodland-adapted species while threatening grassland obligate species (Coppedge et al., 2001; Brennan & Kuvlesky, 2005; Ratajczak et al., 2012). In addition to negative impacts on wildlife, woody encroachment can influence other ecosystem functions such as hydrology and nutrient cycling (Huxman et al., 2005; Wine et al., 2012).

Changing hydrology due to land cover changes can have broad ecological impacts (Gordon et al., 2008; Poff et al., 2006). Agricultural expansion and intensification, dam building, afforestation and urbanization all cause changes in hydrology, including changes in stream or river flooding and flow patterns, soil water content, and runoff patterns (Gordon et al., 2008; Poff et al., 2006; Nilsson & Berggren, 2000). One important example of ecological change induced by changes to hydrology is the development and destruction of *Populus* riparian forests (Rood & Mahoney, 1990; Johnson, 1994). Riparian forests are important for some wildlife species, including bats, birds, and small mammals (Holloway & Barclay, 2000; Doyle, 1990; Tubbs, 1980). Changing land uses can also alter water distributions at finer scales. For example, agricultural development has led to the draining of many wetlands (Zedler, 2003), and the simultaneous development of dugouts or well-fed water troughs for cattle water access in working rangeland landscapes, which are managed for both conservation and production goals (Polasky et al., 2005). Although some wildlife utilize these water sources (Tuttle et al., 2006; Rosenstock et al., 2004), the utility of creating water developments for wildlife conservation is debated (Broyles, 1995).

Animals that rely heavily on landscape features undergoing change, such as trees and water, present an interesting case for investigating habitat associations in rangelands. Rangeland bats are one such group. Trees are vital to the life histories of many North American bat species, as they are used during both roosting (Barclay & Kurta, 2007; Carter & Menzel, 2007) and foraging (Prevedello et al., 2017). Access to open water for both drinking and foraging is also important to bats, which experience high evaporative water loss during day roosting (Adams & Hayes, 2008). Previous work in rangelands has noted higher bat activity in treed riparian areas (Holloway & Barclay, 2000). The importance of trees to rangeland bats may put their habitat requirements at odds with many grassland obligate species, which generally respond negatively to woody cover (Coppedge et al., 2001; Brennan & Kuvlesky, 2005; Ratajczak et al., 2012).

Studies of rangeland bat habitat associations are also necessary because these populations provide ecosystem services, face growing threats, and are highly under-studied. Bats provide several important ecosystem services, including insect control (Kunz et al., 2011). Insectivorous bats consume several species of crop pests, an ecosystem service with high value in regions with extensive row-crop agriculture (Kunz et al., 2011; Boyles et al., 2011). North American bats also face growing threats, including white-nose syndrome, wind energy development, and habitat loss (Frick et al., 2015; Arnett & Baerwald, 2013; Mickleburgh et al., 2002). Combating these challenges requires ecosystem-specific information on bat habitat requirements. Although the bat species inhabiting the Great Plains have distributions covering multiple ecosystems (International Union for the Conservation of Nature, 2015), most of the ecological studies of these species have been conducted in forested areas of their ranges (Amelon et al., 2014; Ethier & Fahrig, 2011; Jung et al., 1999; Menzel et al., 2005) while relatively little work has been done on rangeland populations. The relative importance of different landscape features to the habitat

selection process may vary between populations inhabiting different ecosystems, as the underlying distributions of these features change (Bolnick et al., 2011). Addressing conservation concerns in rangeland bats will require rangeland-specific information.

Managing Great Plains rangelands for wildlife requires an understanding of how landscape features, such as tree patches and open water sources, influence animal behavior (Nielsen et al., 2006). Understanding these influences is especially important when managing landscapes to conserve species with differing responses to landscape features, such as rangeland bats and grassland birds. In this study, we evaluated the habitat associations of bats in a rangeland landscape in eastern North Dakota. We investigated landscape features that may provide roosting resources (trees, human built structures) and foraging or drinking resources (trees, open water, herbaceous wetlands), and landscape features that may disrupt access to these resources (roads, row crops) (Barclay & Kurta, 2007; Carter & Menzel, 2007; Harvey et al., 2011; Prevedello et al., 2017; Adams & Hayes, 2008; Zurcher et al., 2010; Frey-Ehrenbold et al., 2013). We evaluated the relationships between bat activity and these landscape features at both proximate and landscape levels at multiple spatial scales. This study will help inform the management and conservation of rangeland bats, and will also aid in balancing the conservation needs of bats with those of grassland obligate species to preserve biodiversity and important ecosystem services.

Methods

Study Area

This study took place on the United States Forest Service's Sheyenne National Grassland, The Nature Conservancy's Brown Ranch and Pigeon Point Preserve, and North Dakota State University's Albert Ekre Grassland Preserve, which are all located in southeast North Dakota.

5
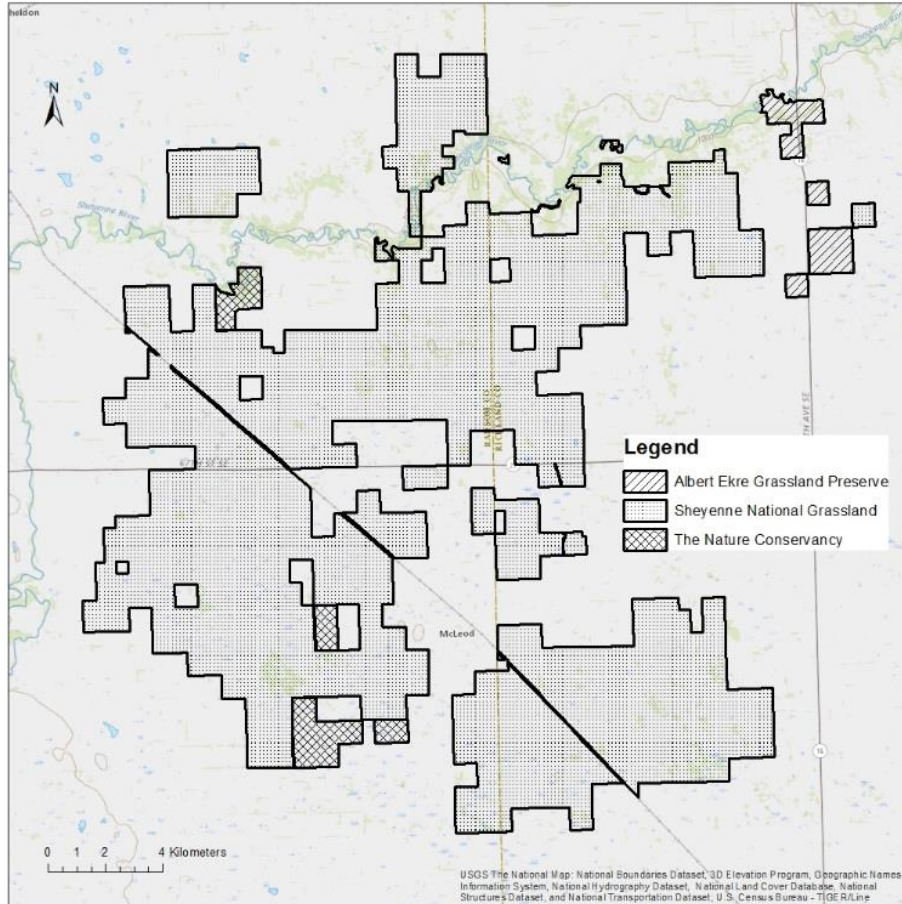
Figure 1.1. Map of study area land ownership. The Sheyenne National Grassland, which is managed by the U.S. Forest Service, is marked with stippling. The Nature Conservancy's Brown Ranch and Pigeon Point Preserve are marked with crosshatches, and North Dakota State University's Albert Ekre Grassland Preserve is marked with lines.

(Fig. 1.1). The total study area is 28,822.12 ha. The climate of this area is temperate, with cold winters and warm summers. During the study period (May to August), monthly average temperatures range from 14.4^0C (May) to 22.2^0 C (July). Most of the yearly precipitation falls during this period, with an average of 31cm from May to August (NDAWNCenter, 2015). The area is characterized by sandy soils and dunes deposited in the delta of the glacial Lake Agassiz, forming a rolling landscape with a mosaic of wetland and upland grasslands (Knudson et al., 2015). The Sheyenne River flows through the northern part of the study area, and the area is surrounded by mostly agricultural plains (Knudson et al., 2015). The Sheyenne National

6

Grasslands encompass the only remaining tallgrass prairie in the Red River region (Samson et al., 2003), and mixed prairie, prairie wetlands, oak-aspen savanna, and mixed deciduous forest are also present in the area (Knudson et al., 2015). All the lands within the study area are grazed and managed as working ranches.

Bat Survey

We collected acoustic data from May 15 to August 14, 2016 to evaluate bat activity across the Sheyenne National Grasslands and surrounding area. This period encompasses pregnancy, lactation, and early flight of juveniles. We used Pettersson d500x bat detectors that were elevated approximately 1.5 m above ground to record echolocation calls (U.S. Fish and Wildlife Service, 2015). We recorded for three consecutive nights at each survey point, recording from sunset to sunrise each night (Skalak et al., 2012). The sampling period was extended up to 5 nights if rainfall was experienced during the recording period, as bat activity can be depressed during rainstorms (Erickson & West, 2002). We drew 237 survey points randomly from a 1 km point grid across the study area, which contained 304 total points. This systematic approach allowed thorough coverage of the full study area, regardless of landcover type. We retrieved bat detectors after the third night and downloaded recordings which were then analyzed using Sonobat autoclassification software (Sonobat 3.1, MT_Plains package, Arcata, CA). Only calls classified with 95% confidence or higher were accepted as detections, and these calls were manually vetted to ensure accuracy (Barnhart & Gillam, 2014).

Landscape Variables

We collected data on both proximate and landscape level variables using ArcGIS 10 (ESRI, Redlands, CA) and the R statistical environment (version 3.3.1; R Core Team, 2017). We delineated tree, open water, and crop cover manually in ArcGIS 10 using orthoimagery collected

by the National Agriculture Imagery Program (NAIP 2014). Because herbaceous wetlands were difficult to identify using aerial imagery, we used the National Wetlands Inventory (U.S. Fish and Wildlife Service, 2016) to delineate these areas. Open cover was determined by subtracting the four measured cover class areas from the total buffer area. Land cover was ground truthed during later fieldwork focused on tree cover extent. We then used R to calculate the cover area (m^2) of these classes and tree patch perimeter length (edge length, m) within 250 m, 500 m, 1000 m and 3000 m buffers of each sampling point. The ratio of tree patch edge length to tree area was used in modelling to separate the effects of edge from those of cover. We also used R to measure the road density within these buffers, using State and Federal and City and County road datasets from the North Dakota Department of Transportation (NDDOT, 2016). Distances from each sampling point to the nearest live tree, open water source, and human-built structure were also measured using ArcGIS 10.

Data Analysis

We developed generalized linear mixed effect models (GLMMs) to assess the relative contributions of each variable to observed bat activity. Nine models were developed based on the known biology of our study species (Table 1.1). For all models, we used minutes with a detection as the response variable. Using this measure avoids inflated counts caused by individual behavior, such as bats circling the detector (Miller, 2001). We included detector ID as a random variable to account for differences in detector sensitivity. We assessed the influence of tree, water, wetland, and crop cover, road density, tree edge length, and the proximity of trees, open water and human-built structures on bat activity (Table 1.2).

Table 1.1

Chapter 1 analysis model set

Model Name	Model Variables
Global	TreeDist + WaterDist + StructDist + TreeCover + WaterCover + WetlandCover + CropCover + EdgeRatio + RoadDensity
Landscape	TreeCover + WaterCover + WetlandCover + CropCover + EdgeRatio + RoadDensity
Proximate	TreeDist + WaterDist + StructDist
Landcover	TreeCover + WaterCover + WetlandCover + CropCover
Roost	TreeDist + StructDist* + TreeCover
Tree	TreeDist + TreeCover + EdgeRatio
Water	WaterDist + WaterCover + WetlandCover
Development	StructDist + CropCover + RoadDensity
Null	1

Generalized linear mixed models tested for 2016 bat activity data on and near the Sheyenne National Grasslands. Due to the less robust dataset, the global model could not be tested for *L. borealis*. *Structure Distance was only included in Roost models for *L. noctivagans* and *E. fuscus*, which have been reported to roost in buildings.

Table 1.2

Summary of variables for Chapter 1 analysis

Variable Name	Mean	St. Dev.	Range	Description
TreeDist	186	227	0 - 1071	Distance to nearest live tree (m)
WaterDist	398	227	2 - 1227	Distance to nearest open water (m)
StructDist	1795	1027	10 - 5817	Distance to nearest human-built structure (m)
TreeCover250	7.7%	13.3%	0 - 75.8%	Percent tree cover within 250m of sampling point
TreeCover500	8.1%	11.9%	0 - 64.6%	Percent tree cover within 500m of sampling point
TreeCover1000	8.3%	10.7%	0 - 57.9%	Percent tree cover within 1km of sampling point
WaterCover250	0.2%	0.6%	0 - 7.1%	Percent open water cover within 250m of sampling point
WaterCover500	0.1%	0.5%	0 - 6.1%	Percent open water cover within 500m of sampling point
WaterCover1000	0.2%	0.4%	0 - 3.2%	Percent open water cover within 1km of sampling point
WetlandCover250	10.6%	14.1%	0 - 70.7%	Percent herbaceous wetland cover within 250m of sampling point
WetlandCover500	10.9%	12.0%	0 - 55.2%	Percent herbaceous wetland cover within 500m of sampling point
WetlandCover1000	10.1%	10.4%	0 - 43.7%	Percent herbaceous wetland cover within 1km of sampling point
CropCover250	1.6%	7.4%	0 - 44.6%	Percent crop cover within 250m of sampling point
CropCover500	2.3%	7.9%	0 - 49.2%	Percent crop cover within 500m of sampling point
CropCover1000	4.3%	9.5%	0 - 50.2%	Percent crop cover within 1km of sampling point
EdgeRatio250	0.22	0.28	0 - 2.0	Tree edge/tree cover ratio within 250m of sampling point
EdgeRatio500	0.19	0.17	0 - 1.21	Tree edge/tree cover ratio within 500m of sampling point
EdgeRatio1000	0.15	0.09	0 - 0.68	Tree edge/tree cover ratio within 1km of sampling point
RoadDensity250	103	204	0 - 974	Meters of road within 250m of sampling point
RoadDensity500	290	494	0 - 1987	Meters of road within 500m of sampling point
RoadDensity1000	1143	1185	0 - 4405	Meters of road within 1km of sampling point

Summary of measured variables used for modelling 2016 bat activity in and near the Sheyenne National Grasslands.

For all of these variables, we used z-scores to allow the comparison of variables with different scales. The z-score is found by subtracting the mean from each observation then dividing by the standard deviation (Hovick et al., 2015a). We evaluated pairwise correlations using the function "ggpairs" in package "GGally" in R. Variable pairs with correlation coefficients of >0.6 were not tested together (Hovick et al., 2015b; Emerson et al., 2013). This eliminated the open cover class, as it was correlated with other variables at multiple scales, and the 3000 m scale, which had a high number of variable correlations. There was also a high level of correlation in landcover variables between scales, so models at each scale were considered individually rather than averaged when models at multiple scales were explanatory.

Four species had sufficient detections to use in modelling, although one species (*Lasiurus borealis*) did not have a robust enough dataset to support the large global model. An abbreviated model set, using the eight non-global models, was tested for this species (Table 1.2). To evaluate models, we used Akaike's Information Criterion (AIC) adjusted for small sample sizes (AIC_c) to rank models at each of three landscape scales (250 m, 500 m, 1000 m) for each species (Burnham & Anderson, 2002). Then, the top models for each scale were ranked using AIC_c to determine the scale of selection for each species (Burnham & Anderson, 2002). The significance of variables included in explanatory models for each species were determined using 95% confidence intervals as calculated by function "confint" in R.

Results

We collected 5,589 detections from five species of North American bats. We detected *Lasionycteris noctivagans* 2,722 times (78% of points), *Lasiurus cinereus* 2,055 times (60% of points), *Eptesicus fuscus* 749 times (51% of points), *Lasiurus borealis* 62 times (11% of points), and *Myotis lucifugus* 1 time (0.4% of points).

All species responded to tree and water distributions at either proximate or landscape scales or both. Three species, *L. noctivagans, L. cinereus* and *L. borealis*, responded positively to landscape level tree cover (Fig. 1.2). *E. fuscus* responded negatively to landscape level tree cover, but positively to trees at a proximate level (Fig. 1.2). *L. noctivagans* and *L. cinereus* were also positively associated with tree proximity (Fig. 1.2). Landscape level water cover was positively associated with activity of all four focal species, and all species but *L. borealis* were negatively associated with distance to the nearest open water source (Fig. 1.2). Water proximity was not included in the *L. borealis* model. The importance of these variables highlights the importance of riparian forests, where both trees and water are available.

Bat responses to other variables showed more interspecific variation. Wetland cover was negatively associated with the activity of all species but *L. borealis*, for which it was not significant (Fig. 1.2). Responses to human infrastructure (crop cover, road density, and distance from human built structures) were largely not significant or not included in the most explanatory models. Areas with high crop cover were avoided only by *E. fuscus* (Fig. 1.2). Road density was negatively associated with both *E. fuscus* and *L. cinereus* activity (Fig. 1.2). Both *L. noctivagans* and *L. cinereus* activity was reduced as the distance to the nearest human-built structure increased (Fig. 1.2).

Although all four species responded to landscape-level variables, the scale at which they responded varied. The 1000 m global model best explained *E. fuscus* activity. Both *L. noctivagans* and *L. cinereus* activities were best explained by the 500 m global models. The 250 m and 500 m landcover models were equally explanatory for *L. borealis,* and responses to cover variables were the same at both scales.

12

Discussion

Bats are important ecosystem service providers, but relatively little is known about their habitat requirements in rangeland landscapes (Kunz et al., 2011; Barclay, 1993; Chung-MacCoubrey, 1996; Holloway & Barclay, 2000). We analyzed the use of landscape features by bats across multiple scales in the Great Plains of North America. We found that trees and water were positively associated with bat activity for all four species investigated, which is consistent with previous findings (Holloway & Barclay, 2000; Brigham, 2007; Adams & Hayes, 2008). Although some species were affected by variables reflecting direct human development (road density, crop cover, distance to human built structure), these effects were not as consistent as the responses to tree and water distributions at both proximate and landscape levels. The importance of trees and open water highlights the value of riparian forests to bats in rangeland ecosystems (Holloway & Barclay, 2000). These results will be important in guiding conservation efforts for bats in landscapes where trees are commonly viewed as a negative feature, but may serve an important ecological function in the appropriate context (Prevedello et al., 2017).

The availability of trees at both proximate and landscape scales was positively associated with bat activity. Three of four species (*L. noctivagans, L. cinereus* and *L. borealis*) responded positively to landscape-level tree cover, and three of four (*L. noctivagans, L. cinereus,* and *E. fuscus*) were negatively associated with the distance to the nearest live tree. Many North American bats, including the four focal species, utilize trees for roosting. *L. cinereus* and *L. borealis* are migratory and roost in foliage year-round, and *L. noctivagans* and *E. fuscus* often roost in cavities and beneath sloughing bark (Harvey et al., 2011). Trees also provide foraging opportunities (Prevedello et al., 2017), and shelter from weather and predators (Verboom & Spoelstra, 1999). At the landscape level, the positive responses to tree cover we found in this
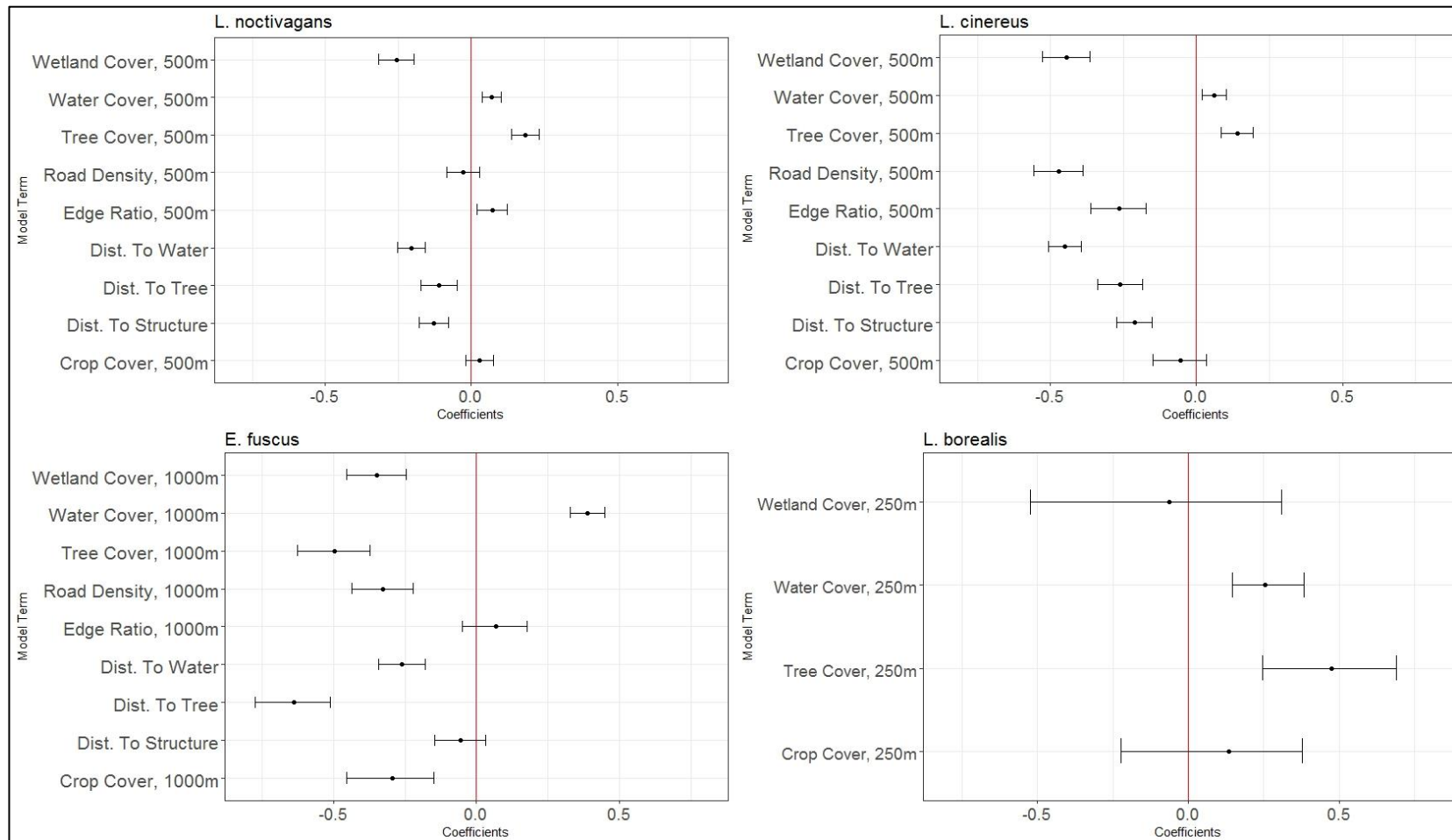
Figure 1.2. Model output for Chapter 1 analysis. Variable coefficients for the most explanatory models for the activity levels of *L. noctivagans, L. cinereus, E. fuscus* and *L. borealis* on and near the Sheyenne National Grasslands during the summer of 2016. Coefficient values are indicated by the black dots, and error bars represent 95% confidence intervals. Positive coefficients indicate that bat activity is positively associated with that variable, and negative coefficients indicate a negative association. Effect size is represented by the magnitude of the variable.

study reflect those found in forested systems (Amelon, 2007; Ethier & Fahrig 2011; Starbuck et al., 2015). Three of our focal species, *L. cinereus*, *E. fuscus* and *L. borealis*, have been reported to have a positive or neutral response to landscape level tree cover (Amelon, 2007; Ethier & Fahrig 2011; Starbuck et al., 2015). However, our results for *L. noctivagans* and *E. fuscus* tree cover responses differ from those reported in forested regions (Ethier & Fahrig, 2011; Starbuck et al., 2015). In our study, *L. noctivagans* was positively associated with higher tree cover and *E. fuscus* was negatively associated with tree cover. In previous studies, *L. noctivagans* has responded negatively to forest cover (Ethier & Fahrig 2011), and favors clearcuts and open spaces (Patriquin & Barclay, 2003). It has been suggested that some species have thresholds of necessary cover, and that may influence the patterns we find here (Amelon, 2007). At the local scale, the use of treed areas is mediated by bat morphology, particularly wing morphology (Norberg & Rayner, 1987). Smaller, more maneuverable bats are able to utilize areas with higher vegetative clutter (i.e. forest interiors), while larger, faster, less maneuverable bats utilize open areas and edges (Norberg & Rayner, 1987). All four of our focal species are considered open-area or edge foraging species (Loeb & O'Keefe, 2011), and at proximate scales, positive responses to areas of non-forest have been reported (Amelon, 2007). However, the lower levels of tree cover available on rangeland landscapes promotes the selection of tree patches rather than open areas.

All four of our focal species responded positively to water cover, and three of four responded to the proximity of water. Our study species have been reported to respond positively to water cover and proximity in previous studies (Amelon et al., 2014; Dixon, 2012; Brooks & Ford, 2005). Water availability is important to bats, as open water provides both drinking and foraging opportunities (Korine et al., 2016). Roosting bats experience high evaporative water

15

loss and replenish 20-22% of these losses by drinking (Adams & Hayes, 2008). The availability

of drinking water is particularly important to lactating individuals, which have been reported to

visit drinking holes 13 times more than non-reproductive females (Adams & Hayes, 2008). Open

water also provides emergent aquatic insect prey and can concentrate insects (Hagen & Sabo,

2011). Riverine sources may also provide corridors for commuting and migration

(Furmankiewicz & Kucharska, 2009). In working rangelands, cattle production is also

accompanied by water development. In our study area, six percent of the water cover was

provided by dirt and metal stock tanks, and these sources provided much of the water cover away

from the Sheyenne River (which accounted for 54% of water cover in the study area). Bats have

been documented to use artificial water sources, including dirt and metal stock tanks (Vindigni et

al., 2009; Geluso & Geluso, 2016; Tuttle et al., 2006), and were observed using stock tanks

during this study.

　　　　Use of acoustic detectors in our study allowed us to cover a broad area efficiently.

Although this approach was needed for our study, the technique does have some drawbacks. Due

to the function of echolocation calls, which are used to locate surrounding objects rather than to

advertise identity, some calls are not able to be identified to species (Barclay, 1999). This

difficulty is compounded when call quality is low. We have addressed this concern by accepting

only calls with high-certainty identifications made by Sonobat (≥95% discrete probability) and

hand vetting these calls to ensure accuracy. Several authors recommend a combination of

acoustic and mist netting techniques for bat surveys to compensate for the shortcomings of each

technique (Barclay, 1999; O'Farrell & Gannon, 1999). Although logistical constraints did not

allow for a systematic netting effort comparable to our acoustic sampling, opportunistic netting

throughout the summer of 2016 confirmed the presence of all four focal bat species in the area,

lending credence to our inventory. The use of acoustic survey techniques also left information on age and sex structure and intraspecific variation in landscape use undiscovered. These questions may be productive avenues for future research.

This study shows a strong positive association between tree and open water availability and bat activity in rangeland landscapes. From a range management perspective, the importance of tree cover to rangeland bats appears to put bat management goals at odds with the needs of obligate grassland wildlife (Coppedge et al., 2001; Brennan & Kuvlesky, 2005; Ratajczak et al., 2012). However, some tree cover existed on rangelands prior to European settlement in areas where sufficient water is available and fire is infrequent- riparian areas and steep draws (Knopf et al., 1988; Briggs et al., 2005). Riparian forests are small but important parts of the broader rangeland landscape (Knopf et al., 1988). Their importance to bats has been demonstrated both in rangeland and forested systems, and our systematic, landscape-level approach has reaffirmed the importance of these natively high tree cover areas (Holloway & Barclay, 2000; Grindal et al., 1999). Riparian forests are also important to other wildlife, including some species of birds and small mammals (Doyle, 1990; Tubbs, 1980). The optimal management of these areas for bats and other wildlife is an important question for future research. Riparian forest dynamics are affected by both stream-associated and upland-associated sources of disturbance, including flooding patterns, fire and grazing (Scott et al., 2003; Rood & Mahoney, 1990; Kozlowski, 2002; Abrams, 1985; Ohmart, 1996). Understanding the roles of these disturbances, particularly fire and grazing, which are more accessible methods for managers, is important for retaining native structure and disturbance regimes in these important areas.

Our landscape-level modelling of bat foraging activity in rangelands illustrates the complexity of the factors associated with habitat use in these animals. Relationships between bat

activity and landscape features varied between bat species, and several variables, including the distributions of trees and water, were significant predictors of bat activity at both proximate and landscape scales. These results corresponded to findings from rangelands and forested ecosystems (Holloway & Barclay, 2000; Amelon, 2007; Ethier & Fahrig, 2011, Adams & Hayes 2008). The models also left significant amounts of variation unexplained, showing that there are variables influencing bat activity that we have not accounted for. Questions remain about the importance of tree patches away from riparian areas, and the importance of patch size and tree species composition. Despite the complexity demonstrated, this study shows the importance of water and trees at both proximate and landscape. This in turn highlights the importance of natively treed areas, particularly riparian forests, to rangeland bats (Holloway & Barclay, 2000). Focusing management efforts on these areas can provide important core areas for bat populations that fit into the historical context of the rangeland landscape.

Literature Cited

Abrams, M. D. (1985). Fire history of oak gallery forests in a northeast Kansas tallgrass prairie. *American Midland Naturalist*, 188-191.

Adams, R. A., & Hayes, M. A. (2008). Water availability and successful lactation by bats as related to climate change in arid regions of western North America. *Journal of Animal Ecology*, *77*(6), 1115-1121.

Allred, B. W., Smith, W. K., Twidwell, D., Haggerty, J. H., Running, S. W., Naugle, D. E., & Fuhlendorf, S. D. (2015). Ecosystem services lost to oil and gas in North America. *Science*, *348*(6233), 401-402.

Amelon, S. K. (2007). Multi-scale factors influencing detection, site occupancy and resource use by foraging bats in the Ozark Highlands of Missouri (Doctoral dissertation, University of Missouri--Columbia).

Amelon, S. K., Thompson, F. R., & Millspaugh, J. J. (2014). Resource utilization by foraging eastern red bats (Lasiurus borealis) in the Ozark region of Missouri. *The Journal of Wildlife Management*, *78*(3), 483-493.

Anonymous (2015). The IUCN Red List of Threatened Species. http://www.iucnredlist.org/.

Arnett, E. B., & Baerwald, E. F. (2013). Impacts of wind energy development on bats: implications for conservation. In R. A. Adams & S. C. Pederson (Eds.), *Bat Evolution, Ecology, and Conservation* (pp. 435-456). Springer New York.

Barclay, R. M. R. (1993). The biology of prairie bats. *Proceedings of the 3rd Prairie Conservation and Endangered Species Workshop* (Vol. 19, pp. 353-357).

Barclay, R. M. R. (1999). Bats are not birds—a cautionary note on using echolocation calls to identify bats: a comment. *Journal of Mammalogy*, *80*(1), 290-296.

Barclay, R. M., & Kurta, A. (2007). Ecology and behavior of bats roosting in tree cavities and under bark. In M. J. Lacki, J. P. Hayes & A. Kurta (Eds.), *Bats in Forests: Conservation and Management* (pp. 17-59). Johns Hopkins University Press, Baltimore, Maryland.

Barnhart, P. R., & Gillam, E. H. (2014). The impact of sampling method on maximum entropy species distribution modeling for bats. *Acta Chiropterologica*, *16*(1), 241-248.

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., ... Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, *26*(4), 183-192.

Boyles, J. G., Cryan, P. M., McCracken, G. F., & Kunz, T. H. (2011). Economic importance of
bats in agriculture. *Science*, *332*(6025), 41-42.

Brennan, L. A., & Kuvlesky Jr, W. P. (2005). North American grassland birds: an unfolding
conservation crisis?. *Journal of Wildlife Management*, *69*(1), 1-13.

Briggs, J. M., Knapp, A. K., Blair, J. M., Heisler, J. L., Hoch, G. A., Lett, M. S., & McCarron, J.
K. (2005). An ecosystem in transition: causes and consequences of the conversion of
mesic grassland to shrubland. *BioScience*, *55*(3), 243-254.

Brigham, R. M. (2007). Bats in forests: what we know and what we need to learn. In M. J. Lacki,
J. P. Hayes & A. Kurta (Eds.), *Bats in Forests: Conservation and Management* (pp. 1-
15). Johns Hopkins University Press, Baltimore, Maryland.

Brooks, R. T., & Ford, W. M. (2005). Bat activity in a forest landscape of central
Massachusetts. *Northeastern Naturalist*, *12*(4), 447-462.

Broyles, B. (1995). Desert wildlife water developments: questioning use in the
Southwest. *Wildlife Society Bulletin (1973-2006)*, *23*(4), 663-675.

Burnham, K. P. & Anderson, D. R. (2002). Model selection and multimodal inference: A
practical information-theoretic approach (2nd ed.). New York, NY: Springer New York.

Carter, T. C., & Menzel, J. M. (2007). Behavior and day-roosting ecology of North American
foliage-roosting bats. In M. J. Lacki, J. P. Hayes & A. Kurta (Eds.), *Bats in Forests:
Conservation and Management* (pp. 61-81). Johns Hopkins University Press, Baltimore,
Maryland.

Chung-MacCoubrey, A. L. (1996). Grassland bats and land management in the Southwest.
*Ecosystem Disturbance and Wildlife Conservation in Western Grasslands: A Symposium
Proceedings*. 54-63.

Coppedge, B. R., Engle, D. M., Masters, R. E., & Gregory, M. S. (2001). Avian response to landscape change in fragmented southern Great Plains grasslands. *Ecological Applications*, *11*(1), 47-59.

Dixon, M. D. (2012). Relationship between land cover and insectivorous bat activity in an urban landscape. *Urban Ecosystems*, *15*(3), 683-695.

Doyle, A. T. (1990). Use of riparian and upland habitats by small mammals. *Journal of Mammalogy*, *71*(1), 14-23.

Emerson, J. W., Green, W. A., Schloerke, B., Crowley, J., Cook, D., Hofmann, H., & Wickham, H. (2013). The generalized pairs plot. *Journal of Computational and Graphical Statistics*, *22*(1), 79-91.

Engle D. M., Coppedge B. R., & Fuhlendorf S. D. (2008). From the Dust Bowl to the Green Glacier: Human activity and environmental change in Great Plains grasslands. In O. Van Auken (Ed.), *Western North American Juniperus Communities: A Dynamic Vegetation Type* (pp. 253-271). New York, NY: Springer New York.

Erickson, J. L., & West, S. D. (2002). The influence of regional climate and nightly weather conditions on activity patterns of insectivorous bats. *Acta Chiropterologica*, *4*(1), 17-24.

Ethier, K., & Fahrig, L. (2011). Positive effects of forest fragmentation, independent of forest amount, on bat abundance in eastern Ontario, Canada. *Landscape Ecology*, *26*(6), 865-876.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., ... & Helkowski, J. H. (2005). Global consequences of land use. *Science*, *309*(5734), 570-574.

Frey-Ehrenbold, A., Bontadina, F., Arlettaz, R., & Obrist, M. K. (2013). Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. *Journal of Applied Ecology*, *50*(1), 252-261.

Frick, W. F., Puechmaille, S. J., Hoyt, J. R., Nickel, B. A., Langwig, K. E., Foster, J. T., ... & Herzog, C. (2015). Disease alters macroecological patterns of North American bats. *Global Ecology and Biogeography*, *24*(7), 741-749.

Fuhlendorf, S. D., & Engle, D. M. (2001). Restoring Heterogeneity on Rangelands: Ecosystem Management Based on Evolutionary Grazing Patterns. *BioScience*, *51*(8), 625-632.

Fuhlendorf, S. D., Engle, D. M., Elmore, R. D., Limb, R. F., & Bidwell, T. G. (2012). Conservation of pattern and process: developing an alternative paradigm of rangeland management. *Rangeland Ecology & Management*, *65*(6), 579-589.

Furmankiewicz, J., & Kucharska, M. (2009). Migration of bats along a large river valley in southwestern Poland. *Journal of Mammalogy*, *90*(6), 1310-1317.

Geluso, K. N., & Geluso, K. (2016). Bats of Kimball and Cheyenne counties in the panhandle of Nebraska. *Special Publications*, 183.

Gordon, L. J., Peterson, G. D., & Bennett, E. M. (2008). Agricultural modifications of hydrological flows create ecological surprises. *Trends in Ecology & Evolution*, *23*(4), 211-219.

Grindal, S. D., Morissette, J. L., & Brigham, R. M. (1999). Concentration of bat activity in riparian habitats over an elevational gradient. *Canadian Journal of Zoology*, *77*(6), 972-977.

Hagen, E. M., & Sabo, J. L. (2011). A landscape perspective on bat foraging ecology along

rivers: does channel confinement and insect availability influence the response of bats to

aquatic resources in riverine landscapes?. *Oecologia*, *166*(3), 751-760.

Harvey, M. J., Altenbach, J. S., & Best T. L. (2011). Bats of the United States and

Canada. The Johns Hopkins University Press. Baltimore, Maryland, USA.

Hess, G. R., & Bay, J. M. (2000). A regional assessment of windbreak habitat

suitability. *Environmental Monitoring and Assessment*, *61*(2), 239-256.

Holloway, G. L., & Barclay, R. M. (2000). Importance of prairie riparian zones to bats in

southeastern Alberta. *Ecoscience*, *7*(2), 115-122.

Hovick, T. J., Allred, B. W., Elmore, R. D., Fuhlendorf, S. D., Hamilton, R. G., & Breland, A.

(2015a). Dynamic disturbance processes create dynamic lek site selection in a prairie

grouse. *PloS one*, *10*(9), e0137882.

Hovick, T. J., Elmore, R. D., Fuhlendorf, S. D., Engle, D. M., & Hamilton, R. G. (2015b).

Spatial heterogeneity increases diversity and stability in grassland bird

communities. *Ecological Applications*, *25*(3), 662-672.

Huxman, T. E., Wilcox, B. P., Breshears, D. D., Scott, R. L., Snyder, K. A., Small, E. E., ... &

Jackson, R. B. (2005). Ecohydrological implications of woody plant

encroachment. *Ecology*, *86*(2), 308-319.

Johnson, W. C. (1998). Adjustment of riparian vegetation to river regulation in the Great Plains,

USA. *Wetlands*, *18*(4), 608-618.

Jung, T. S., Thompson, I. D., Titman, R. D., & Applejohn, A. P. (1999). Habitat selection by

forest bats in relation to mixed-wood stand types and structure in central Ontario. *The

Journal of Wildlife Management*, 1306-1319.

Knopf, F. L., Johnson, R. R., Rich, T., Samson, F. B., & Szaro, R. C. (1988). Conservation of riparian ecosystems in the United States. *The Wilson Bulletin*, *100*(2), 272-284.

Knudson, M. D., VanLooy, J. A., & Hill, M. J. (2015). A Habitat Suitability Index (HSI) for the Western Prairie Fringed Orchid (Platanthera praeclara) on the Sheyenne National Grassland, North Dakota, USA. *Ecological Indicators*, *57*, 536-545.

Korine, C., Adams, R., Russo, D., Fisher-Phelps, M., & Jacobs, D. (2016). Bats and water: anthropogenic alterations threaten global bat populations. In C. C. Voigt & T. Kingston (Eds.). *Bats in the Anthropocene: Conservation of Bats in a Changing World* (pp. 215-241). Springer International Publishing.

Kozlowski, T. T. (2002). Physiological-ecological impacts of flooding on riparian forest ecosystems. *Wetlands*, *22*(3), 550-561.

Kreuter, U. P., Iwaasa, A. D., Theodori, G. L., Ansley, R. J., Jackson, R. B., Fraser, L. H., ... & Moya, E. G. (2016). State of knowledge about energy development impacts on North American rangelands: An integrative approach. *Journal of Environmental Management*, *180*, 1-9.

Kunz, T. H., Braun de Torrez, E., Bauer, D., Lobova, T., & Fleming, T. H. (2011). Ecosystem services provided by bats. *Annals of the New York Academy of Sciences*, *1223*(1), 1-38.

Lawler, J. J., Lewis, D. J., Nelson, E., Plantinga, A. J., Polasky, S., Withey, J. C. ... & Radeloff, V. C. (2014). Projected land-use change impacts on ecosystem services in the United States. *Proceedings of the National Academy of Sciences*, *111*(20), 7492-7497.

Loeb, S. C., & O'Keefe, J. M. (2011). Bats and gaps: the role of early successional patches in the roosting and foraging ecology of bats. In C. Greenberg, B. Collins, F. Thompson III. (Eds.) *Sustaining Young Forest Communities* (pp. 167-189). Springer Netherlands.

Menzel, J. M., Menzel, M. A., Kilgo, J. C., Ford, W. M., Edwards, J. W., & McCracken, G. F. (2005). Effect of habitat and foraging height on bat activity in the coastal plain of South Carolina. *Journal of Wildlife Management*, *69*(1), 235-245.

Mickleburgh, S. P., Hutson, A. M., & Racey, P. A. (2002). A review of the global conservation status of bats. *Oryx*, *36*(1), 18-34.

Millennium Ecosystem Assessment [MA] (2005). *Current State and Trends*, 626. Washington, DC: Island Press.

Miller, B. W. (2001). A method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. *Acta Chiropterologica*, *3*(1), 93-105.

National Agriculture Imagery Program. (2014). Accessed from https://www.fsa.usda.gov/programs-and-services/aerial-photography/imagery-programs/naip-imagery/index, 4/29/2016.

Nielsen, S. E., Stenhouse, G. B., & Boyce, M. S. (2006). A habitat-based framework for grizzly bear conservation in Alberta. *Biological Conservation*, *130*(2), 217-229.

Nilsson, C., & Berggren, K. (2000). Alterations of riparian ecosystems caused by river regulation: Dam operations have caused global-scale ecological changes in riparian ecosystems. How to protect river environments and human needs of rivers remains one of the most important questions of our time. *AIBS Bulletin*, *50*(9), 783-792.

Norberg, U. M., & Rayner, J. M. (1987). Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *316*(1179), 335-427.

North Dakota Agricultural Weather Network. (2015). NWS Monthly Normal Weather Data.

Accessed from https://ndawn.ndsu.nodak.edu/station-info.html?station=75, 9/21/2015.

North Dakota Department of Transportation. (2016). City and County Roads, shapefile.

Accessed from https://gishubdata.nd.gov/dataset/city-and-county-roads.

North Dakota Department of Transportation. (2016). State and Federal Roads, shapefile.

Accessed from https://gishubdata.nd.gov/dataset/state-and-federal-roads.

O'Farrell, M. J., & Gannon, W. L. (1999). A comparison of acoustic versus capture techniques

for the inventory of bats. *Journal of Mammalogy*, *80*(1), 24-30.

Ohmart, R. D. (1996). Historical and present impacts of livestock grazing on fish and wildlife

resources in western riparian habitats. *Rangeland Wildlife. Society for Range

Management, Denver, CO*, 245-279.

Patriquin, K. J., & Barclay, R. M. (2003). Foraging by bats in cleared, thinned and unharvested

boreal forest. *Journal of Applied Ecology*, *40*(4), 646-657.

Poff, N. L., Bledsoe, B. P., & Cuhaciyan, C. O. (2006). Hydrologic variation with land use

across the contiguous United States: geomorphic and ecological consequences for stream

ecosystems. *Geomorphology*, *79*(3), 264-285.

Polasky, S., Nelson, E., Lonsdorf, E., Fackler, P., & Starfield, A. (2005). Conserving species in a

working landscape: land use with biological and economic objectives. *Ecological

Applications*, *15*(4), 1387-1401.

Prevedello, J. A., Almeida-Gomes, M., & Lindenmayer, D. B. The importance of scattered trees

for biodiversity conservation: a global meta-analysis. *Journal of Applied Ecology*.

Price, J. N., & Morgan, J. W. (2008). Woody plant encroachment reduces species richness of

herb-rich woodlands in southern Australia. *Austral Ecology*, *33*(3), 278-289.

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/.

Ratajczak, Z., Nippert, J. B., & Collins, S. L. (2012). Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology*, *93*(4), 697-703.

Rood, S. B., & Mahoney, J. M. (1990). Collapse of riparian poplar forests downstream from dams in western prairies: probable causes and prospects for mitigation. *Environmental Management*, *14*(4), 451-464.

Rosenstock, S. S., Rabe, M. J., O'Brien, C. S., & Waddell, R. B. (2004). Studies of wildlife water developments in southwestern Arizona: wildlife use, water quality, wildlife diseases, wildlife mortalities, and influences on native pollinators. *Arizona Game and Fish Department, Research Branch Technical Guidance Bulletin*, *8*, 1-15.

Samson, F. B., Knopf, F. L., McCarthy, C. W., Noon, B. R., Ostlie, W. R., Rinehart, S. M., ... & Byer, T. W. (2003). Planning for population viability on northern Great Plains national grasslands. *Wildlife Society Bulletin*, 986-999.

Scott, M. L., Skagen, S. K., & Merigliano, M. F. (2003). Relating geomorphic change and grazing to avian communities in riparian forests. *Conservation Biology*, *17*(1), 284-296.

Skalak, S. L., Sherwin, R. E., & Brigham, R. M. (2012). Sampling period, size and duration influence measures of bat species richness from acoustic surveys. *Methods in Ecology and Evolution*, *3*(3), 490-502.

Starbuck, C. A., Amelon, S. K., & Thompson, F. R. (2015). Relationships between bat occupancy and habitat and landscape structure along a savanna, woodland, forest gradient in the Missouri Ozarks. *Wildlife Society Bulletin*, *39*(1), 20-30.

Swaty, R., Blankenship, K., Hagen, S., Fargione, J., Smith, J., & Patton, J. (2011). Accounting
for ecosystem alteration doubles estimates of conservation risk in the conterminous
United States. *PloS one*, *6*(8), e23002.

Tubbs, A. A. (1980). Riparian bird communities of the Great Plains. *US Forest Service,
Intermountain Forest and Range Experiment Station, General Technical Report*, (INT-
86), 419-433.

Tuttle, S. R., Chambers, C. L., & Theimer, T. C. (2006). Potential effects of livestock water-
trough modifications on bats in northern Arizona. *Wildlife Society Bulletin*, *34*(3), 602-
608.

Twidwell, D., Fuhlendorf, S. D., Taylor, C. A., & Rogers, W. E. (2013). Refining thresholds in
coupled fire–vegetation models to improve management of encroaching woody plants in
grasslands. *Journal of Applied Ecology*, *50*(3), 603-613.

U.S. Fish and Wildlife Service. (2015). 2015 Range-wide Indiana bat summer survey guidelines.
Accessed at
http://www.fws.gov/midwest/endangered/mammals/inba/inbasummersurveyguidance.ht
ml, 11/11/2015.

U.S. Fish and Wildlife Service. (2016). National Wetlands Inventory. Accessed at
https://www.fws.gov/wetlands/, 11/14/2016.

Verboom, B., & Spoelstra, K. (1999). Effects of food abundance and wind on the use of tree
lines by an insectivorous bat, Pipistrellus pipistrellus. *Canadian Journal of
Zoology*, *77*(9), 1393-1401.

Vindigni, M. A., Morris, A. D., Miller, D. A., & Kalcounis-Rueppell, M. C. (2009). Use of modified water sources by bats in a managed pine landscape. *Forest Ecology and Management*, *258*(9), 2056-2061.

Wine, M. L., Ochsner, T. E., Sutradhar, A., & Pepin, R. (2012). Effects of eastern redcedar encroachment on soil hydraulic properties along Oklahoma's grassland-forest ecotone. *Hydrological Processes*, *26*(11), 1720-1728.

Zedler, J. B. (2003). Wetlands at your service: reducing impacts of agriculture at the watershed scale. *Frontiers in Ecology and the Environment*, *1*(2), 65-72.

Abstract

Increased tree cover presents a challenging paradox for rangeland managers, as trees are detrimental to some wildlife species but beneficial for others. Human development has led to increased tree cover in the Great Plains of North America, which negatively affects grassland obligate wildlife such as grassland passerines, small mammals, and prairie chickens. However, some species, such as rangeland bats, benefit from increased tree cover. To inform the process of balancing the conservation needs of grassland obligate wildlife and rangeland bats, we investigated the associations between bat use of individual rangeland tree patches and tree patch attributes at landscape, patch, and local scales. We used acoustic detection to evaluate bat activity at the edges of 82 tree patches ranging from isolated, single trees to large stretches of riparian forest. We detected five species using these sites, which included *Lasionycteris noctivagans*, *Lasiurus cinereus, Eptesicus fuscus, Lasiurus borealis,* and *Myotis lucifugus,* and developed generalized linear models for the four most commonly detected species using a hierarchical modelling framework. We found that patch shape and basal area were consistent predictors of bat activity across species, as all four focal species were negatively associated with the ratio of tree edge to patch area and tree basal area. The activity of *L. noctivagans* and *E. fuscus* was positively associated with patch size, but *L. cinereus* was negatively associated with this variable. Bat activity was associated with larger average tree size in *L. cinereus* and with smaller average tree size in *L. borealis*. *L. cinereus* activity was also positively associated with higher canopy cover. Our findings will help inform management of rangeland tree patches, including tree removal or retention and the management of existing patches. Furthermore, our

results will aid managers in balancing the habitat requirements of grassland obligate and tree dependent rangeland wildlife such as bats.

Introduction

Tree distributions and stand structure in rangelands are determined by a combination of water availability and disturbances, including fire, grazing, and river flow changes (Briggs et al., 2005; Engle et al., 2008; Friedman et al., 1998). Before European settlement, trees were limited to riparian areas and steep draws within grasslands by water availability and frequent disturbance (Briggs et al., 2005). Human activity has led to an expansion of trees present in grasslands through fragmentation and changing disturbance regimes (Briggs et al., 2005). Moreover, tree planting following the Dust Bowl has also driven increases in tree cover and impacts via increased tree dispersal from plantings and resulting fragmentation (Engle et al., 2008). The expansion of trees is a major conservation concern for remaining grasslands in North America (Engle et al., 2008) because woody plant cover negatively affects many grassland organisms, including grassland passerines (Brennan & Kuvlesky, 2005; Grant et al., 2004; Coppedge et al., 2008), small mammals (Horncastle et al., 2005) and prairie chickens (Fuhlendorf et al., 2002). However, some species in rangelands, such as bats, rely on tree cover (Holloway & Barclay, 2000). This paradox makes understanding the use of trees by facultative grassland species necessary for managers to make informed decisions regarding the removal, retention, and management of tree patches.

Trees are vital to the life histories of many North American bat species (Harvey et al., 2011; Brigham, 2007). Several bat species use foliage, tree cavities, or sloughing bark as roosts (Barclay & Kurta, 2007; Carter & Menzel, 2007). Trees also provide foraging opportunities by concentrating insect prey, and provide shelter from weather and predators (Prevedello et al.,

31

2017; Verboom & Spoelstra, 1999). Despite the importance of trees for bats, very little is known about the influence of tree patch attributes, such as size and structure. Investigating the role of these attributes in tree patch selection by bats can help land managers balance the conservation needs of tree-dependent rangeland bats and obligate grassland wildlife.

The influence of tree patch structure on bat activity is mediated by bat morphology (Norberg & Rayner, 1987). Wing morphology and body size influence the ability of a bat to maneuver in areas with high vegetative clutter (Norberg & Rayner, 1987). Clutter adapted species, such as *Myotis septentrionalis*, typically have low wing loading, fly at slower speeds, and utilize echolocation calls with a broad range of frequencies that allow for the detection of high levels of detail (Norberg & Rayner, 1987; Aldridge & Rautenbach, 1987). Open or edge adapted species, such as *Lasiurus cinereus*, have high wing loading, fly quickly, and typically utilize constant-frequency echolocation calls (Norberg & Rayner, 1987; Aldridge & Rautenbach, 1987). Stand density and vegetative clutter affect the utility of stands for foraging bats (Crampton & Barclay, 1998; Jung et al., 1999; Patriquin & Barclay, 2003; Loeb & Waldrop, 2008; Perry, 2012; Yates & Muzika, 2006). Stand structure, particularly the density of large trees and snags, can also affect roost availability. Roost selection varies considerably between species, and the density and diversity of available roosting structures (i.e. snags, large trees) can influence bat activity and species richness (Crampton & Barclay, 1998; Boyles & Aubrey, 2006; Perry, 2012; Yates & Muzika, 2006).

The effects of tree patch size on bat use are less understood than the effects of tree stand structure. Generally, patch size has a strong influence on specialist wildlife species that utilize interior or edge habitats, and are negligible for generalist species (Bender et al., 1998). Bat species range from generalists to open area or forest interior specialist species (Harvey et al.,

2011). Bat use of forest edges or interiors is mediated by their morphology (Norberg & Rayner, 1987), with less maneuverable bat species restricted to using edge or open areas for foraging (Norberg & Rayner, 1987). Because flight offers high mobility, bats can travel to isolated tree patches, such as isolated remnant or savanna trees (Fischer et al., 2010). However, larger tracts of forest may provide more roosting opportunities (Hutchinson & Lacki, 2000). Several studies have shown no significant difference in bat activity between remnant forest patches and contiguous, intact forest (Law et al., 1999; Zielinski & Gellman, 1999). Little is known about the influence of patch size on bat activity in rangeland landscapes.

In the Great Plains of North America, the size and structure of tree patches are influenced by natural disturbances including fire, grazing, and river flow (Briggs et al., 2005; Engle et al., 2008; Friedman et al., 1998). Both fire and browsing activity can influence the extent and age structure of patches by reducing sapling recruitment (Ripple & Beachta, 2007; Bond & Keeley, 2005). Additionally, fires affect snag abundance by both creating and destroying snags, which are important roosting resources for several bat species (Bagne et al., 2008; Barclay & Kurta, 2007). The ability of fire to create snags is mediated by fuel loads, which are in turn affected by grazing activity (Van Langevelde et al., 2003). Riparian forest extent and structure are affected by these upland disturbances, and are additionally affected by flooding and flow reduction, which affects recruitment and mortality, particularly in *Populus* riparian forests (Pettit & Naiman, 2007; Ohmart, 1996; Rood & Mahoney, 1990; Friedman et al., 1998). Interacting natural disturbances affect the size and structure of tree patches within the rangeland, which in turn affects the value of these areas for wildlife.

Increasing tree cover is a conservation challenge in the Great Plains (Engle et al., 2008). Grassland species may avoid trees due to increased predation near tree patches, general edge

avoidance, or as part of an avoidance response to vertical structure (Renfrew et al., 2005; Thompson et al., 2014, Hovick et al., 2015). Tree removal using cutting, bulldozing, or chemical means can be an important part of management for grassland-obligate species in areas where the development of tree cover is too advanced for methods like prescribed fire to be effective (Engle et al., 2006; Thompson et al., 2014; Thompson et al., 2016; Twidwell et al., 2013). However, tree patches provide vital resources for other wildlife, including rangeland bats (Holloway & Barclay, 2000). Our objective in this study is to profile the influences of landscape, patch and local level attributes of tree extent and structure on rangeland bat use of tree patches. We expect that multiple scales will be influential, and that patch size and local structural attributes will be correlated with bat activity. This study will inform management decisions, particularly those concerning tree patch removal, retention, and management.

Methods

Study Area

We investigated bat use of tree patches on the United States Forest Service's Sheyenne National Grassland, The Nature Conservancy's Brown Ranch and Pigeon Point Preserve and North Dakota State University's Albert Ekre Grassland Preserve. The total study area was 28,822.12 ha. The area has a temperate climate, and during the study period (May to August), monthly average temperatures ranged from 14.4^0C (May) to 22.2^0 C (July). The majority of the area's yearly precipitation falls during this period, with an average of 31cm from May to August (NDAWNCenter, 2015). The area is characterized by sandy soils and dunes, which form a rolling landscape with a mosaic of wetland and upland grassland habitat (Knudson et al., 2015). The Sheyenne River flows through the northern part of the study area, and the area is surrounded by mostly agricultural plains (Knudson et al., 2015). The area includes tallgrass and mixed grass

prairie, prairie wetlands, oak-aspen savanna, and mixed deciduous forest (Samson et al., 2003;

Knudson et al., 2015). All the lands within the study area are grazed and managed as working

ranches.

Survey Site Selection

We manually delineated tree patches using orthoimagery collected by the National

Agriculture Imagery Program (NAIP) in 2014 (NAIP, 2014). In order to encompass the wide

variability of patch size in the study area, we randomly selected twenty-four patches from four

size classes, which ranged from 5-500 m^2, 500-5000 m^2, 5000-50,000 m^2, and 50,000-500,000

m^2. For site standardization, we selected monitoring sites from the edge of these patches rather

than the patch interior. We did not expect this to eliminate detections of common species, as the

four most common bat species detected previously at this study area (*L. noctivagans, L. cinereus,*

L. borealis and *E. fuscus*) are typically open or edge foraging species (Loeb & O'Keefe, 2011).

We required monitoring sites to be at least 75 m from other tree patches or open water sources

(Adams, 2013). This was to avoid the detection of bats foraging over other tree patches or water

sources. We also required sites to be less than 500 m from an open water source, as proximity to

open water has been shown to be positively correlated with bat activity in previous seasons at

this study site (Trubitt, unpublished data). Patches that did not have an appropriate site along

their perimeter were replaced until a total of 24 sites in each class were selected.

Data Collection

We used acoustic monitoring to evaluate bat activity at focal tree patches. We used

Pettersson d500x bat detectors to collect acoustic data from May 15 to August 15, 2017. We

elevated detectors 1.5 m to provide clear recordings (U.S. Fish and Wildlife Service, 2015) and

recorded for three nights at each site, extending the recording period up to five nights if rain

events occurred during the overnight period. We analyzed the collected recordings using Sonobat

autoclassification software (Sonobat 3.1- MT Plains, Arcata, CA). We accepted calls classified

with 95% confidence or higher as detections, and hand vetted these detections to ensure

accuracy.

We collected landscape, patch, and local level data at each survey site. At the landscape

level, we recorded tree cover at 500 m and 1000 m buffers surrounding each sampling point

using R (version 3.3.1; R Core Team, 2017). We delineated tree cover manually using

orthoimagery collected by the National Agriculture Imagery Program in 2014 (NAIP, 2014). At

Table 2.1

Summary of variables for Chapter 2 analysis

Variable Name	Mean	St. Dev.	Range	Description
TreeCover500m	15.37	15.14	0.004 – 61.85	Tree cover within 500m radius of survey point (%)
TreeCover1000m	13.86	12.97	0.09 – 55.00	Tree cover within 1km radius of survey point (%)
PatchArea	111,387.80	524,955.60	14.07 – 4,507,551.32	Size of focal patch, (m^2)
PatchEdge/PatchArea	0.21	0.27	0.0001 – 1.24	Ratio of focal patch perimeter to focal patch area
BA Total	3.79	2.97	1 – 14	Count of all trees in 10 factor prism variable radius sample
Average DBH Total	44.23	25.18	5.57 - 92.36	Average diameter of breast height of all trees in 10 factor prism sample (cm)
Canopy Cover	29.58	25.63	0 - 86.45	Percent tree canopy cover, measured from top of detector

Summary of measured variables used for modelling 2017 bat activity in and near the
Sheyenne National Grasslands.

the patch level, we measured the area and perimeter length of each focal tree patch using ArcGIS 10 (Esri, Redlands CA). The ratio of patch perimeter to patch area was used to evaluate the effect of patch shape on bat activity. We estimated basal area (BA) using a 10-factor prism at each sampling point (Yates & Muzika, 2006), and recorded the species, diameter at breast height (DBH) and whether the tree was alive or dead for all trees in this sample (Yates & Muzika, 2006). We evaluated canopy cover at each sampling point by taking a photograph of the canopy from the top of the detector and analyzing canopy cover using the digital image analysis program CanopyDigi (Goodenough & Goodenough, 2012).

Data Analysis

We evaluated pairwise correlation between the collected variables using the function "ggpairs" in package "GGally" in R. Variable pairs with correlation coefficients of >0.6 were not used in the same models (Hovick et al., 2015a; Emerson et al., 2013). This left us with one landscape level variable, two patch level variables, and three local level variables (Table 2.1). All six variables were standardized using z-scores to allow the comparison of regression coefficients between variables with different scales (Gelman & Hill, 2007). To avoid inflated counts of bats based on individual behavior, such as an individual circling the detector, we used minutes with a detection as the response variable in all models (Miller, 2001). We also eliminated sites that included outliers in bat activity (>7 standard deviations from the mean) leaving us with 82 sites (Jantzen & Fenton, 2013). All tested models were generalized linear models with a Poisson family and "log" link function and were run using the "lme4" package in R (Bates et al., 2015).

Because of the multiple levels of variables (landscape, patch, and local), we used a hierarchical modeling scheme for model development. This approach allows for the development of more potential models than a strictly *a priori* approach while still narrowing the field of and

37

avoiding a completely exploratory modeling scheme (Winter et al., 2006; Fondell et al., 2008; Hovick et al., 2012). We added parameters in a landscape to local order, as it is generally accepted that wildlife make selections based on large scale filters before selecting at smaller scale features (Mayor et al., 2009). In each step, the selected model from the previous step is used as the base model, and if none of the additional parameters in a step produce a more parsimonious model, we moved ahead with that base model. Parsimony was assessed by comparing AIC_c values (Burnham & Anderson, 2002), and the guidelines suggested by Arnold (2010) were used to avoid the inclusion of uninformative variables when selecting the best supported models. Arnold (2010) suggests ignoring models that include an additional variable without overcoming the +2 AIC unit penalty for that variable when considering a set of explanatory models. We used the approach of Burnham and Anderson (2002) to make inferences based on the resulting model set.

We used the landscape level tree cover variable in the first modelling step. The scale at which tree cover was measured was determined by the most explanatory scale for each species in a previous study at this site (Trubitt, unpublished data). Tree cover was evaluated at a 500 m radius of each sampling site for *Lasiurus cinereus, Lasionycteris noctivagans,* and *Lasiurus borealis* and was measured within 1000 m for *Eptesicus fuscus*. The intercept only model was used as the base model for this step. In the second modelling step, we investigated the patch level variables of patch size and patch shape as measured by the patch edge/patch area ratio. The most explanatory model from the first step was used as the base model in this second step, and the patch level variables were added individually and in combination to create three models in addition to the base model. In the third and final modelling step, we investigated the three local level variables that included BA, average DBH, and canopy cover at the sampling point. These

variables were assessed individually and in all possible combinations, yielding seven additional models. If adding variables at one step did not improve model parsimony, the best model from the previous step was retained.

Results

We collected 2977 detections of five bat species. After removal of two outlier sites, 1914 detections were retained for analysis. We detected *Lasiurus noctivagans* 927 times (72% of sites), *Lasiurus cinereus* 643 times (63% of sites), *Eptesicus fuscus* 317 times (57% sites), *Lasiurus borealis* 26 times (16% of sites) and *Myotis lucifugus* 1 time (1% of sites). We developed models for the four most commonly detected species (Table 2.2).

At the broadest, landscape scale, tree cover within 500 m improved model parsimony in *L. noctivagans* and *L. cinereus,* but was not significant in the final models (Table 2.3, Table 2.4, Fig. 2.1). At the patch scale, the ratio of patch edge length to patch area (patch shape) was negatively associated with the activity of all four focal species (Fig. 2.1). This indicates a

Table 2.2

Overview of focal bat species

Scientific Name	Common Name	Weight	Wingspan	Summer Roosts
Eptesicus fuscus	Big brown bat	14-21g	32-39cm	Trees, human-built structures
Lasionycteris noctivagans	Silver-haired bat	8-11g	27-31cm	Tree cavities, beneath bark, occasionally in human-built structures
Lasiurus borealis	Eastern red bat	9-15g	28-33cm	Foliage
Lasiurus cinereus	Hoary bat	25-30g	34-41cm	Foliage

Scientific names, common names, and selected natural history traits of the four focal bat species found on the Sheyenne National Grassland and adjacent properties in the summers of 2016 and 2017 (Harvey et al., 2011).

preference for rounder, more contiguous patches that provide less edge. Responses to patch area were more variable, as *L. noctivagans* and *E. fuscus* were positively associated with patch area and *L. cinereus* was negatively associated with patch (Fig. 2.1). At the local scale, basal area was negatively associated with the activity of three bat species (*L. noctivagans, E. fuscus,* and *L. borealis*) (Fig. 2.1). Average diameter at breast height was significant in predicting patch use by *L. cinereus* and *L. borealis* (Table 2.4, Table 2.6). *L. cinereus* activity was positively associated with average DBH and *L. borealis* activity was negatively associated with this variable. (Fig. 2.1). Canopy cover positively associated with *L. cinereus* activity (Fig. 2.1).

Tables 2.3.-2.6. Hierarchical model summaries. Models explaining the effects of tree cover within 500 m (Tables 2.3, 2.4, 2.6) or 1000 m (Table 2.5) of each sampling site (Cover), patch area (Area), the ratio of patch edge length to patch area (Shape), basal area (BA), average diameter at breast height of sampled trees (DBH) and tree canopy cover (Canopy) on the activity of *L. noctivagans* (Table 2.3), *L. cinereus* (Table 2.4), *E. fuscus* (Table 2.5), and *L. borealis* (Table 2.6) at the Sheyenne National Grasslands and adjacent properties in the summer of 2017. New factors are added at each step, and the most explanatory model from the previous step is used as the base model. The two most explanatory models (Lowest AIC_c) from each step are shown.

Table 2.3

Lasionycteris noctivagans hierarchical model summary

Model	Number of Parameters	AIC$_c$	ΔAIC$_c$	Model Weight
Step 1: Landscape Level				
Cover	1	1560.6	0	1
Null	0	1611.04	50.397	0
Step 2: Patch Level				
Cover + Area + Shape	3	1524.5	0	0.78
Cover + Area	2	1527.02	2.475	0.22
Step 3: Local Level				
Cover + Area + Shape + BA	4	1502.4	0	0.58
Cover + Area + Shape + BA + DBH	5	1504.62	2.264	0.19

Table 2.4

Lasiurus cinereus hierarchical model summary

Model	Number of Parameters	AIC$_c$	ΔAIC$_c$	Model Weight
Step 1: Landscape Level				
Cover	1	1334.7	0	0.67
Null	0	1336.05	1.388	0.33
Step 2: Patch Level				
Cover + Area + Shape	3	1273.5	0	1
Cover + Shape	2	1286.1	12.572	0
Step 3: Local Level				
Cover + Area + Shape + DBH + Canopy	5	1260.2	0	0.60
Cover + Area + Shape + BA + DBH + Canopy	6	1262.59	2.382	0.18

Table 2.5

Eptesicus fuscus hierarchical model summary

Model	Number of Parameters	AIC$_c$	ΔAIC$_c$	Model Weight
Step 1: Landscape Level				
Null	0	743.396	0	0.74
Cover	1	745.476	2.0798	0.26
Step 2: Patch Level				
Area + Shape	2	653.351	0	0.59
Shape	1	654.116	0.7646	0.41
Step 3: Local Level				
Area + Shape + BA	3	625.48	0	0.40
Area + Shape + BA + Canopy	4	626.29	0.813	0.27

Table 2.6

Lasiurus borealis hierarchical model summary

Model	Number of Parameters	AIC$_c$	ΔAIC$_c$	Model Weight
Step 1: Landscape Level				
Null	0	145.74	0	0.66
Cover	1	147.101	1.3626	0.34
Step 2: Patch Level				
Shape	1	143.57	0	0.52
Area + Shape	2	145.41	1.8387	0.21
Step 3: Local Level				
Shape + BA + DBH	3	128.007	0	0.58
Shape + BA + DBH + Canopy	4	130.051	2.044	0.21
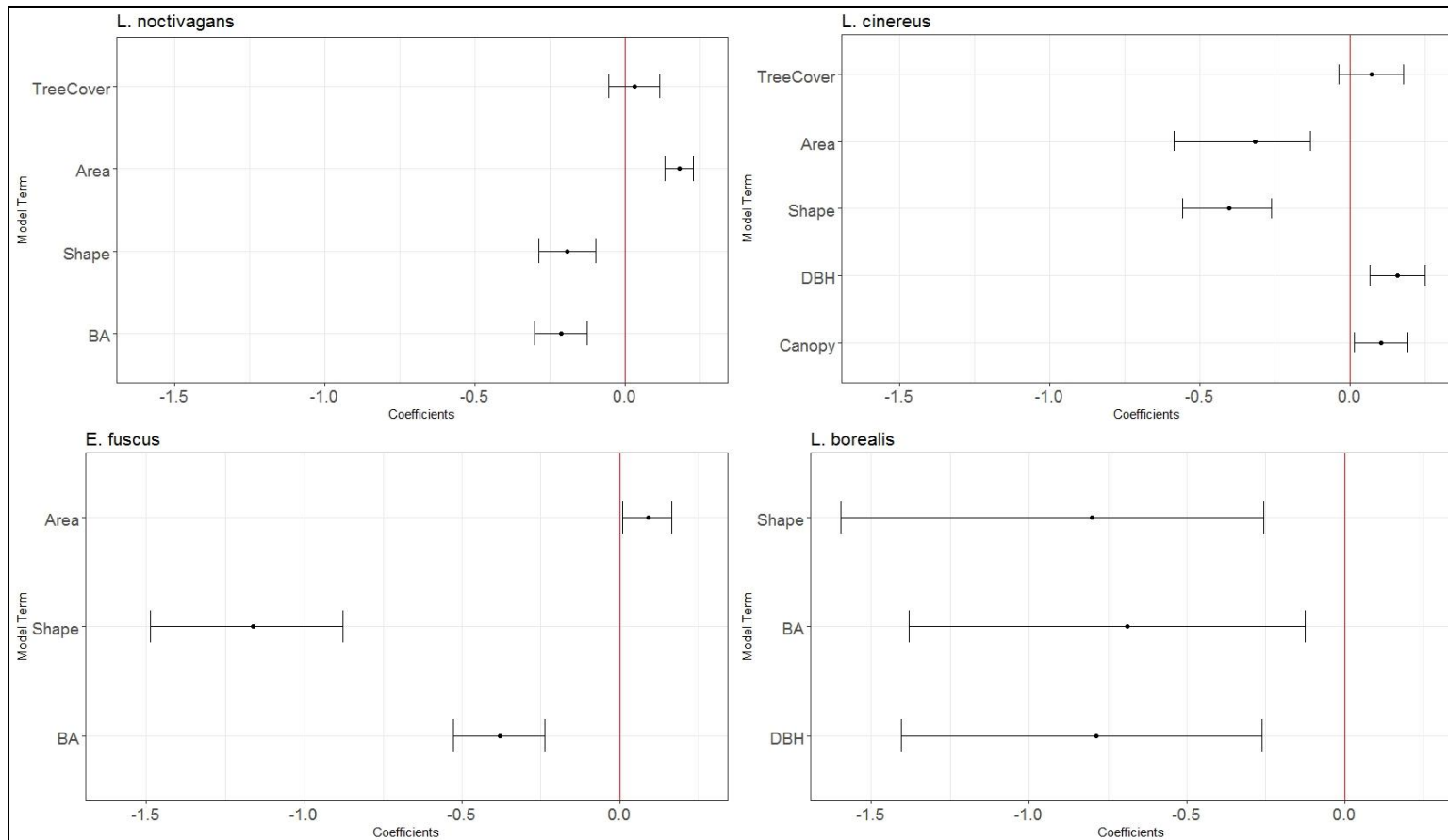
Figure 2.1. Model output for Chapter 2 analysis. Standardized regression coefficients (dots) and 95% confidence intervals (error bars) for the most competitive model for each focal species after modelling step 3. Variables with positive coefficients positively associated with bat activity, variables with negative coefficients are negatively associated with activity, and effect size is indicated by coefficient magnitude. Variables are significant if their confidence interval does not cross zero.

Discussion

Increasing tree cover in rangelands is an important conservation concern for grassland obligate wildlife (Brennan & Kuvlesky, 2005; Grant et al., 2004; Coppedge et al., 2008; Horncastle et al., 2005; Fuhlendorf et al., 2002). However, trees are vital to the life histories of other rangeland wildlife, such as rangeland bats (Harvey et al., 2011; Holloway & Barclay, 2000). This paradox makes understanding the use of tree patches by bats necessary for developing rangeland management approaches that balance the needs of both grassland obligate species and tree-dependent bats. In our assessment of tree patch use by bats, we found that bats responded to tree distributions and structure across multiple scales. Bat activity was consistently correlated with patch shape and tree density, with all four focal species negatively associated with higher patch edge to patch area ratio and higher basal area. This is the first study to investigate relationships between bat use of tree patches and tree patch attributes in rangelands at multiple scales. Similar studies in forested systems have shown a similar, negative response to tree density (Humes et al., 1999; Loeb & Waldrop, 2008; Yates & Muzika, 2006; Perry, 2012). However, the negative response to tree patches with longer edges found in this study was surprising, as the four focal species have shown positive responses to edge density and fragmentation in previous studies (Ethier & Fahrig, 2011; Grindal & Brigham, 1999). The high amounts of open habitat available in this landscape may shift selection towards contiguous forest as bats move towards their optimal balance of open cover and tree cover (Boughey et al., 2011).

Tree cover at a landscape scale (i.e., 500 and 1000 m) had little influence on the activity of the four focal species in this study. Despite the importance of trees to the life histories of these bat species, mixed responses have been observed in previous research (Ethier & Fahrig, 2011; Amelon, 2007; Starbuck et al., 2015). Negative responses to landscape level tree cover or

44

positive responses to non-forest cover have been reported for *L. noctivagans* (Ethier & Fahrig, 2011), *L. cinereus* (Amelon, 2007), *E. fuscus* (Trubitt, unpublished data) and *L. borealis* (Amelon, 2007). Additionally, neutral responses have been reported for *L. cinereus* and *E. fuscus* (Ethier & Fahrig, 2011), while positive responses have been reported for *L. noctivagans* (Trubitt, unpublished data), *L. cinereus* (Trubitt, unpublished data), *E. fuscus* (Starbuck et al, 2015; Amelon, 2007) and *L. borealis* (Trubitt, unpublished data; Ethier & Fahrig, 2011; Starbuck et al., 2015). The variety of reported responses within species may be due to requirements for a particular range of forest and non-forest, with species selecting for non-forest when tree cover is high and for forest when tree cover is low (Amelon, 2007; Boughey et al., 2011). In this study, we may be seeing neutral responses to landscape-level tree cover because monitoring sites were located directly at tree patches that provided. The local effects of these patches may ameliorate effects of landscape-level tree cover seen in previous studies at this site (Trubitt, unpublished data).

Patch level attributes were consistently important in describing variation in tree use by rangeland bats. Patch area was significant in three of four top models, but had diverging effects between species. Patch area was positively associated with both *L. noctivagans* and *E. fuscus* activity*,* and negatively associated with *L. cinereus* activity. However, even the species that preferred larger patch sizes showed some activity at small tree patches. Bat use of isolated or remnant trees has been well documented, particularly in heavily altered systems (Le Roux et al., 2017; Lumsden & Bennett, 2004; Fischer et al., 2010; Manning et al., 2006). Nonetheless, large, continuous patches of forest may promote species richness (De Jong, 1995) or increased foraging activity (Law et al., 1999). In rangelands, riparian forests have historically provided the largest

areas of tree cover (Briggs et al., 2005), and are important areas for rangeland bats (Holloway & Barclay, 2000). Large riparian patches appear to be beneficial for our focal species.

The activity of all four bat species was negatively associated with the ratio of patch edge length to patch area. This indicates a preference for rounder, more contiguous patches. This finding is unexpected, as all four of the focal bat species are typically considered edge or open foraging species due to their wing morphology (Loeb & O'Keefe, 2011). Linear features, which have relatively high edge to area ratios, are generally considered positive features for bats in landscapes with low tree cover, particularly for those species which are better adapted to flight in open areas (Fuentes-Montemayor et al., 2013; Frey-Ehrenbold et al., 2013; Verboom & Huitema, 1997). Edge density and landscape fragmentation have also been positive for edge and open foraging bats (Ethier & Fahrig, 2011; Grindal & Brigham, 1999). It is possible that the high amount of non-treed and tree-edge areas in this landscape shift selection towards areas of contiguous tree cover, as bats search for their optimal level of contiguous forest cover (Boughey et al., 2011).

At fine scales, structural attributes were important for all four focal species. Basal area was negatively associated with the activity of three of four species, and was not included in the top model for *L. cinereus*, indicating a preference for more open stands. This pattern is also reported in forested systems (Humes et al., 1999; Loeb & Waldrop, 2008; Yates & Muzika, 2006; Perry, 2012). Our focal species are all reported to be edge or open adapted foragers, and their morphology may preclude their ability to maneuver effectively inside dense stands (Loeb & O'Keefe, 2011; Norberg & Rayner, 1987). Tree size was important to the two lasiurine bats, *L. cinereus* and *L. borealis*. However, these two bats had divergent responses to this variable, as *L. cinereus* was positively associated and *L. borealis* was negatively associated with tree size. This

46

is in contrast to reports of roost tree preferences for these species, which both roost in foliage. *L. borealis* has been reported to prefer large roost trees, while reported roost trees of *L. cinereus* are not larger than random surrounding trees (Menzel et al., 1998; Mager & Nelson, 2000; Willis & Brigham, 2005; Klug et al., 2012). Differences in patch selection during foraging and roosting may explain this discrepancy. During foraging, the density of large trees has been reported to be positively related to activity in *L. noctivagans* and *L. cinereus,* and neutral responses to the size of isolated trees have been reported in other systems (Jung et al., 1999; Le Roux et al., 2017).

The importance of patch configuration and structure can direct rangeland management activities as managers work to balance the needs of grassland obligate and tree-dependent species in rangeland landscapes. This data informs choices concerning both tree removal or retention and management of existing tree patches. The selection of more contiguous patches indicates that bat management activities should be focused on larger, more intact tree patches such as riparian forest areas. These areas provide tree cover for bats while fitting into the historical context of the rangeland (Briggs et al., 2005). Managers can use both natural disturbances, such as fire, and mechanical or chemical means to regain or maintain an open structure within these forest patches, promoting use by the large-bodied bats profiled in this study (Engle et al., 2006; Norberg & Rayner, 1987). While this study suggests that these larger tree patches provide an important focus for bat conservation in rangelands, isolated or small tree patches may also provide benefits to rangeland ecosystems. Small patches were used by bats in this study despite preferences for more contiguous, intact tree patches, and have been documented previously as important keystone structures in rangelands, where they were used by bats, tree-dependent birds, and other wildlife (Prevedello et al., 2017; Fischer et al., 2010). However, the removal of isolated trees and small tree patches may benefit grassland obligate

wildlife that demonstrate tree avoidance (Thompson et al., 2014). Further investigations on use these trees by rangeland bats, particularly their utility as roosting structures, will continue to refine tree removal choices. Well informed tree removal, retention, and management can help balance the needs of tree-dependent and grassland-obligate rangeland wildlife, preserving biodiversity and important ecosystem services.

Literature Cited

Adams, A. M. (2013). Assessing and analyzing bat activity with acoustic monitoring: challenges and interpretations (Doctoral dissertation, University of Western Ontario).

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

Amelon, S. K. (2007). Multi-scale factors influencing detection, site occupancy and resource use by foraging bats in the Ozark Highlands of Missouri (Doctoral dissertation, University of Missouri--Columbia).

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management*, *74*(6), 1175-1178.

Bagne, K. E., Purcell, K. L., & Rotenberry, J. T. (2008). Prescribed fire, snag population dynamics, and avian nest site selection. *Forest Ecology and Management*, *255*(1), 99-105.

Barclay, R. M., & Kurta, A. (2007). Ecology and behavior of bats roosting in tree cavities and under bark. In M. J. Lacki, J. P. Hayes & A. Kurta (Eds.), *Bats in Forests: Conservation and Management* (pp. 17-59). Johns Hopkins University Press, Baltimore, Maryland.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*. 67(1):1-48.

Bender, D. J., Contreras, T. A., & Fahrig, L. (1998). Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology*, *79*(2), 517-533.

Bond, W. J., & Keeley, J. E. (2005). Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, *20*(7), 387-394.

Boughey, K. L., Lake, I. R., Haysom, K. A., & Dolman, P. M. (2011). Effects of landscape-scale broadleaved woodland configuration and extent on roost location for six bat species across the UK. *Biological Conservation*, *144*(9), 2300-2310.

Boyles, J. G., & Aubrey, D. P. (2006). Managing forests with prescribed fire: implications for a cavity-dwelling bat species. *Forest Ecology and Management*, *222*(1), 108-115.

Brennan, L. A., & Kuvlesky Jr, W. P. (2005). North American grassland birds: an unfolding conservation crisis?. *Journal of Wildlife Management*, *69*(1), 1-13.

Briggs, J. M., Knapp, A. K., Blair, J. M., Heisler, J. L., Hoch, G. A., Lett, M. S., & McCarron, J. K. (2005). An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. *BioScience*, *55*(3), 243-254.

Brigham, R. M. (2007). Bats in forests: what we know and what we need to learn. In M. J. Lacki, J. P. Hayes & A. Kurta (Eds.), *Bats in Forests: Conservation and Management* (pp. 1-15). Johns Hopkins University Press, Baltimore, Maryland.

Burnham, K. P. & Anderson, D. R. (2002). Model selection and multimodal inference: A practical information-theoretic approach (2nd ed.). New York, NY: Springer New York.

Carter, T. C., & Menzel, J. M. (2007). Behavior and day-roosting ecology of North American foliage-roosting bats. In M. J. Lacki, J. P. Hayes & A. Kurta (Eds.), *Bats in Forests: Conservation and Management* (pp. 61-81). Johns Hopkins University Press, Baltimore, Maryland.

Crampton, L. H., & Barclay, R. M. (1998). Selection of roosting and foraging habitat by bats in

    different-aged aspen mixedwood stands. *Conservation Biology*, *12*(6), 1347-1358.

De Jong, J. (1995). Habitat use and species richness of bats in a patchy landscape. *Acta*

    Theriologica, *40*(3), 237-248.

Emerson, J. W., Green, W. A., Schloerke, B., Crowley, J., Cook, D., Hofmann, H., & Wickham,

    H. (2013). The generalized pairs plot. *Journal of Computational and Graphical*

    Statistics, *22*(1), 79-91.

Engle, D. M., Bodine, T. N., & Stritzke, J. F. (2006). Woody plant community in the cross

    timbers over two decades of brush treatments. *Rangeland Ecology & Management*, *59*(2),

    153-162.

Engle D. M., Coppedge B. R., & Fuhlendorf S. D. (2008). From the Dust Bowl to the Green

    Glacier: Human activity and environmental change in Great Plains grasslands. In O. Van

    Auken (Ed.), *Western North American Juniperus Communities: A Dynamic Vegetation*

    Type (pp. 253-271). New York, NY: Springer New York.

Ethier, K., & Fahrig, L. (2011). Positive effects of forest fragmentation, independent of forest

    amount, on bat abundance in eastern Ontario, Canada. *Landscape Ecology*, *26*(6), 865-

    876.

Fischer, J., Stott, J., & Law, B. S. (2010). The disproportionate value of scattered

    trees. *Biological Conservation*, *143*(6), 1564-1567.

Fondell, T. F., Miller, D. A., Grand, J. B., & Anthony, R. M. (2008). Survival of dusky Canada

    goose goslings in relation to weather and annual nest success. *Journal of Wildlife*

    Management, *72*(7), 1614-1621.

Frey-Ehrenbold, A., Bontadina, F., Arlettaz, R., & Obrist, M. K. (2013). Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. *Journal of Applied Ecology*, *50*(1), 252-261.

Friedman, J.M., Osterkamp, W.R., Scott, M.L., Auble, G.T. (1998). Downstream effects of dams on channel geometry and bottomland vegetation: Regional patterns in the Great Plains. *Wetlands*, *18*(4), 619-633.

Fuentes-Montemayor, E., Goulson, D., Cavin, L., Wallace, J. M., & Park, K. J. (2013). Fragmented woodlands in agricultural landscapes: the influence of woodland character and landscape context on bats and their insect prey. *Agriculture, Ecosystems & Environment*, *172*, 6-15.

Fuhlendorf, S. D., Woodward, A. J., Leslie, D. M., & Shackford, J. S. (2002). Multi-scale effects of habitat loss and fragmentation on lesser prairie-chicken populations of the US Southern Great Plains. *Landscape Ecology*, *17*(7), 617-628.

Gelman, A., & Hill, J. (2007). *Data analysis using regression and multilevel hierarchical models* (Vol. 1). New York, NY, USA: Cambridge University Press.

Goodenough, A. E., & Goodenough, A. S. (2012). Development of a rapid and precise method of digital image analysis to quantify canopy density and structural complexity. *ISRN Ecology*, *2012*.

Grant, T. A., Madden, E., & Berkey, G. B. (2004). Tree and shrub invasion in northern mixed-grass prairie: implications for breeding grassland birds. *Wildlife Society Bulletin*, *32*(3), 807-818.

Grindal, S. D., & Brigham, R. M. (1999). Impacts of forest harvesting on habitat use by foraging insectivorous bats at different spatial scales. *Ecoscience*, 25-34.

Harvey, M. J., Altenbach, J. S., & Best T. L. (2011). Bats of the United States and

      Canada. The Johns Hopkins University Press. Baltimore, Maryland, USA.

Holloway, G. L., & Barclay, R. M. (2000). Importance of prairie riparian zones to bats in

      southeastern Alberta. *Ecoscience*, *7*(2), 115-122.

Horncastle, V. J., Hellgren, E. C., Mayer, P. M., Ganguli, A. C., Engle, D. M., & Leslie, D. M.

      (2005). Implications of invasion by Juniperus virginiana on small mammals in the

      southern Great Plains. *Journal of Mammalogy*, *86*(6), 1144-1155.

Hovick, T. J., Allred, B. W., Elmore, R. D., Fuhlendorf, S. D., Hamilton, R. G., & Breland, A.

      (2015b). Dynamic disturbance processes create dynamic lek site selection in a prairie

      grouse. *PloS one*, *10*(9), e0137882.

Hovick, T. J., Elmore, R. D., Fuhlendorf, S. D., Engle, D. M., & Hamilton, R. G. (2015a).

      Spatial heterogeneity increases diversity and stability in grassland bird

      communities. *Ecological Applications*, *25*(3), 662-672.

Hovick, T. J., Miller, J. R., Dinsmore, S. J., Engle, D. M., Debinski, D. M., & Fuhlendorf, S. D.

      (2012). Effects of fire and grazing on grasshopper sparrow nest survival. *The Journal of*

      Wildlife Management, *76*(1), 19-27.

Humes, M. L., Hayes, J. P., & Collopy, M. W. (1999). Bat activity in thinned, unthinned, and

      old-growth forests in western Oregon. *The Journal of Wildlife Management*, 553-561.

Hutchinson, J. T., & Lacki, M. J. (2000). Selection of day roosts by red bats in mixed

      mesophytic forests. *The Journal of Wildlife Management*, 87-94.

Jantzen, M. K., & Fenton, M. B. (2013). The depth of edge influence among insectivorous bats at

      forest–field interfaces. *Canadian Journal of Zoology*, *91*(5), 287-292.

Jung, T. S., Thompson, I. D., Titman, R. D., & Applejohn, A. P. (1999). Habitat selection by

    forest bats in relation to mixed-wood stand types and structure in central Ontario. *The*

    Journal of Wildlife Management, 1306-1319.

Klug, B. J., Goldsmith, D. A., & Barclay, R. M. (2012). Roost selection by the solitary, foliage-

    roosting hoary bat (Lasiurus cinereus) during lactation. *Canadian Journal of*

    Zoology, *90*(3), 329-336.

Knudson, M. D., VanLooy, J. A., & Hill, M. J. (2015). A Habitat Suitability Index (HSI) for the

    Western Prairie Fringed Orchid (Platanthera praeclara) on the Sheyenne National

    Grassland, North Dakota, USA. *Ecological Indicators*, *57*, 536-545.

Law, B. S., Anderson, J., & Chidel, M. (1999). Bat communities in a fragmented forest

    landscape on the south-west slopes of New South Wales, Australia. *Biological*

    Conservation, *88*(3), 333-345.

Le Roux, D. S., Ikin, K., Lindenmayer, D. B., Manning, A. D., & Gibbons, P. (2017). The value

    of scattered trees for wildlife: Contrasting effects of landscape context and tree

    size. *Diversity and Distributions*.

Loeb, S. C., & O'Keefe, J. M. (2011). Bats and gaps: the role of early successional patches in the

    roosting and foraging ecology of bats. In C. Greenberg, B. Collins, F. Thompson III.

    (Eds.) *Sustaining Young Forest Communities* (pp. 167-189). Springer Netherlands.

Loeb, S. C., & Waldrop, T. A. (2008). Bat activity in relation to fire and fire surrogate treatments

    in southern pine stands. *Forest Ecology and Management*, *255*(8), 3185-3192.

Lumsden, L. F., & Bennett, A. F. (2005). Scattered trees in rural landscapes: foraging habitat for

    insectivorous bats in south-eastern Australia. *Biological Conservation*, *122*(2), 205-222.

Mager, K. J., & Nelson, T. A. (2001). Roost-site selection by eastern red bats (Lasiurus borealis). *The American Midland Naturalist*, *145*(1), 120-126.

Manning, A. D., Fischer, J., & Lindenmayer, D. B. (2006). Scattered trees are keystone structures–implications for conservation. *Biological Conservation*, *132*(3), 311-321.

Mayor, S. J., Schneider, D. C., Schaefer, J. A., & Mahoney, S. P. (2009). Habitat selection at multiple scales. *Ecoscience*, *16*(2):238-247.

Menzel, M. A., Carter, T. C., Chapman, B. R., & Laerm, J. (1998). Quantitative comparison of tree roosts used by red bats (Lasiurus borealis) and Seminole bats (L. seminolus). *Canadian Journal of Zoology*, *76*(4), 630-634.

Miller, B. W. (2001). A method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. *Acta Chiropterologica*, *3*(1), 93-105.

National Agriculture Imagery Program. (2014). Accessed from https://www.fsa.usda.gov/programs-and-services/aerial-photography/imagery-programs/naip-imagery/index, 4/29/2016.

Norberg, U. M., & Rayner, J. M. (1987). Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *316*(1179), 335-427.

North Dakota Agricultural Weather Network. (2015). NWS Monthly Normal Weather Data. Accessed from https://ndawn.ndsu.nodak.edu/station-info.html?station=75, 9/21/2015.

Ohmart, R. D. (1996). Historical and present impacts of livestock grazing on fish and wildlife resources in western riparian habitats. *Rangeland Wildlife. Society for Range Management, Denver, CO*, 245-279.

Patriquin, K. J., & Barclay, R. M. (2003). Foraging by bats in cleared, thinned and unharvested

    boreal forest. *Journal of Applied Ecology*, *40*(4), 646-657.

Perry, R., (2012). A review of fire effects on bats and bat habitat in the eastern oak region.

    Proceedings of the 4ᵗʰ Fire in Eastern Oak Forests Conference. 170-191.

Pettit, N. E., & Naiman, R. J. (2007). Fire in the riparian zone: characteristics and ecological

    consequences. *Ecosystems*, *10*(5), 673-687.

Prevedello, J. A., Almeida-Gomes, M., & Lindenmayer, D. B., (2017). The importance of

    scattered trees for biodiversity conservation: a global meta-analysis. *Journal of Applied*

    Ecology.

R Core Team (2017). R: A language and environment for statistical computing. R Foundation for

    Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/.

Renfrew, R. B., Ribic, C. A., & Nack, J. L. (2005). Edge avoidance by nesting grassland birds: a

    futile strategy in a fragmented landscape. *The Auk*, *122*(2), 618-636.

Ripple, W. J., & Beschta, R. L. (2007). Hardwood tree decline following large carnivore loss on

    the Great Plains, USA. *Frontiers in Ecology and the Environment*, *5*(5), 241-246.

Rood, S. B., & Mahoney, J. M. (1990). Collapse of riparian poplar forests downstream from

    dams in western prairies: probable causes and prospects for mitigation. *Environmental*

    Management, *14*(4), 451-464.

Samson, F. B., Knopf, F. L., McCarthy, C. W., Noon, B. R., Ostlie, W. R., Rinehart, S. M., ... &

    Byer, T. W. (2003). Planning for population viability on northern Great Plains national

    grasslands. *Wildlife Society Bulletin*, 986-999.

Starbuck, C. A., Amelon, S. K., & Thompson, F. R. (2015). Relationships between bat
occupancy and habitat and landscape structure along a savanna, woodland, forest gradient
in the Missouri Ozarks. *Wildlife Society Bulletin*, *39*(1), 20-30.

Thompson, S. J., Arnold, T. W., & Amundson, C. L. (2014). A multiscale assessment of tree
avoidance by prairie birds. *The Condor*, *116*(3), 303-315.

Thompson, S. J., Arnold, T. W., Fieberg, J., Granfors, D. A., Vacek, S., & Palaia, N. (2016).
Grassland birds demonstrate delayed response to large-scale tree removal in central North
America. *Journal of Applied Ecology*, *53*(1), 284-294.

Twidwell, D., Fuhlendorf, S. D., Taylor, C. A., & Rogers, W. E. (2013). Refining thresholds in
coupled fire–vegetation models to improve management of encroaching woody plants in
grasslands. *Journal of Applied Ecology*, *50*(3), 603-613.

U.S. Fish and Wildlife Service. (2015). 2015 Range-wide Indiana bat summer survey guidelines.
Accessed at
http://www.fws.gov/midwest/endangered/mammals/inba/inbasummersurveyguidance.ht
ml, 11/11/2015.

Van Langevelde, F., Van De Vijver, C. A., Kumar, L., Van De Koppel, J., De Ridder, N., Van
Andel, J., ... & Prins, H. H. (2003). Effects of fire and herbivory on the stability of
savanna ecosystems. *Ecology*, *84*(2), 337-350.

Verboom, B., & Huitema, H. (1997). The importance of linear landscape elements for the
pipistrelle Pipistrellus pipistrellus and the serotine bat Eptesicus serotinus. *Landscape
ecology*, *12*(2), 117-125.

Verboom, B., & Spoelstra, K. (1999). Effects of food abundance and wind on the use of tree lines by an insectivorous bat, Pipistrellus pipistrellus. *Canadian Journal of Zoology*, *77*(9), 1393-1401.

Willis, C. K., & Brigham, R. M. (2005). Physiological and ecological aspects of roost selection by reproductive female hoary bats (Lasiurus cinereus). *Journal of Mammalogy*, *86*(1), 85-94.

Winter, M., Johnson, D. H., Shaffer, J. A., Donovan, T. M., & Svedarsky, W. D. (2006). Patch size and landscape effects on density and nesting success of grassland birds. *Journal of Wildlife Management*, *70*(1), 158-172.

Yates, M. D., & Muzika, R. M. (2006). Effect of forest structure and fragmentation on site occupancy of bat species in Missouri Ozark forests. *Journal of Wildlife Management*, *70*(5), 1238-1248.

Zielinski, W. J., & Gellman, S. T. (1999). Bat Use of Remnant Old-Growth Redwood Stands. *Conservation Biology*, *13*(1), 160-167.

Zurcher, A. A., Sparks, D. W., & Bennett, V. J. (2010). Why the bat did not cross the road?. *Acta Chiropterologica*, *12*(2), 337-340.

Table A.1

Full model summary for L. noctivagans, Chapter 1

L. noctivagans			
Model	DF	AIC$_c$	ΔAIC$_c$
250 m Models			
LN.global.250	11	3452.47	0
LN.landscape.250	8	3583.53	131.064
LN.landcover.250	6	3583.65	131.185
LN.water.250	5	3599.88	147.412
LN.roost.250	5	3658.72	206.252
LN.proximate.250	5	3671.73	219.259
LN.tree.250	5	3698.65	246.185
LN.devo.250	5	3887.4	434.932
LN.null.250	2	3975.9	523.429
500 m Models			
LN.global.500	11	3418.31	0
LN.landscape.500	8	3527.3	108.994
LN.landcover.500	6	3530.81	112.504
LN.water.500	5	3542.1	123.795
LN.roost.500	5	3598.78	180.469
LN.tree.500	5	3625.74	207.427
LN.proximate.500	5	3671.73	253.42
LN.devo.500	5	3896.7	478.39
LN.null.500	2	3975.9	557.59
1000 m Models			
LN.global.1000	11	3468.73	0
LN.water.1000	5	3560.2	91.476
LN.landscape.1000	8	3587.73	119.005
LN.landcover.1000	6	3605.4	136.677
LN.roost.1000	5	3661.82	193.09
LN.proximate.1000	5	3671.73	203.002
LN.tree.1000	5	3692.69	223.962
LN.devo.1000	5	3890.63	421.905
LN.null.1000	2	3975.9	507.172
Scale Comparison			
LN.global.500	11	3418.31	0
LN.global.250	11	3452.47	34.161
LN.global.1000	11	3468.73	50.418

Degrees of freedom (DF), AIC$_c$ and ΔAIC$_c$ values for all generalized linear mixed effect models used to model *L. noctivagans* activity on the Sheyenne National Grasslands and adjacent properties from May to August of 2016. See Table 1.1 for variables present in each model.

Table A.2

Full model summary for L. cinereus, Chapter 1

L. cinereus			
Model	DF	AIC$_c$	ΔAIC$_c$
250 Models			
LC.global.250	11	3250.76	0
LC.landscape.250	8	3589.94	339.172
LC.water.250	5	3596.68	345.919
LC.landcover.250	6	3662.72	411.952
LC.proximate.250	5	3705.76	455.001
LC.roost.250	4	3765.92	515.153
LC.tree.250	5	3871.89	621.128
LC.devo.250	5	4122.46	871.698
LC.null.250	2	4289.12	1038.353
500 Models			
LC.global.500	11	3141.15	0
LC.landscape.500	8	3485.64	344.494
LC.water.500	5	3536.31	395.163
LC.landcover.500	6	3617.47	476.324
LC.proximate.500	5	3705.76	564.616
LC.tree.500	5	3754.47	613.323
LC.roost.500	4	3800.77	659.623
LC.devo.500	5	4132.45	991.302
LC.null.500	2	4289.12	1147.968
1000 Models			
LC.global.1000	11	3162.33	0
LC.landscape.1000	8	3512.22	349.893
LC.water.1000	5	3551.09	388.763
LC.proximate.1000	5	3705.76	543.437
LC.landcover.1000	6	3721.61	559.285
LC.tree.1000	5	3898.56	736.234
LC.roost.1000	4	3918.4	756.072
LC.devo.1000	5	4007.29	844.961
LC.null.1000	2	4289.12	1126.789
Scale Comparison			
LC.global.500	11	3141.15	0
LC.global.1000	11	3162.33	21.179
LC.global.250	11	3250.76	109.615

Degrees of freedom (DF), AIC$_c$ and ΔAIC$_c$ values for all generalized linear mixed effect models used to model *L. cinereus* activity on the Sheyenne National Grasslands and adjacent properties from May to August of 2016. See Table 1.1 for variables present in each model.

Table A.3

Full model summary for E. fuscus, Chapter 1.

E. fuscus			
Model	DF	AIC$_c$	ΔAIC$_c$
250 Models			
EF.global.250	11	1603.94	0
EF.landscape.250	8	1714.74	110.798
EF.water.250	5	1723.98	120.034
EF.landcover.250	6	1745.52	141.579
EF.proximate.250	5	1750.56	146.622
EF.tree.250	5	1822.78	218.842
EF.roost.250	5	1823.48	219.538
EF.devo.250	5	1917.45	313.505
EF.null.250	2	1941.38	337.433
500 Models			
EF.global.500	11	1638.15	0
EF.water.500	5	1740.84	102.688
EF.proximate.500	5	1750.56	112.415
EF.landscape.500	8	1751.88	113.731
EF.landcover.500	6	1768.91	130.76
EF.tree.500	5	1821.9	183.751
EF.roost.500	5	1822.78	184.626
EF.devo.500	5	1926.61	288.459
EF.null.500	2	1941.38	303.226
1000 Models			
EF.global.1000	11	1534.04	0
EF.landscape.1000	8	1686.23	152.191
EF.landcover.1000	6	1715.32	181.277
EF.water.1000	5	1740.51	206.462
EF.proximate.1000	5	1750.56	216.521
EF.tree.1000	5	1820.84	286.793
EF.roost.1000	5	1822.36	288.315
EF.devo.1000	5	1901.93	367.883
EF.null.1000	2	1941.38	407.332
Scale Comparison			
EF.global.1000	11	1534.04	0
EF.global.250	11	1603.94	69.899
EF.global.500	11	1638.15	104.106

Degrees of freedom (DF), AIC$_c$ and ΔAIC$_c$ values for all generalized linear mixed effect models used to model *E. fuscus* activity on the Sheyenne National Grasslands and adjacent properties from May to August of 2016. See Table 1.1 for variables present in each model.

Table A.4

Full model summary for L. borealis, Chapter 1

L. borealis			
Model	DF	AIC_c	ΔAIC_c
250 Models			
LB.landcover.250	6	246.868	0
LB.landscape.250	8	249.681	2.8131
LB.water.250	5	258.736	11.8679
LB.roost.250	4	265.051	18.1833
LB.tree.250	5	266.846	19.9776
LB.proximate.250	5	322.255	75.3871
LB.devo.250	5	329.535	82.6664
LB.null.250	2	337.825	90.9568
500 Models			
LB.landcover.500	6	248.427	0
LB.landscape.500	8	251.592	3.1647
LB.roost.500	4	254.102	5.6746
LB.tree.500	5	254.995	6.5681
LB.water.500	5	260.49	12.0627
LB.proximate.500	5	322.255	73.8281
LB.devo.500	5	332.05	83.6225
LB.null.500	2	337.825	89.3978
1000 Models			
LB.landcover.1000	6	267.474	0
LB.landscape.1000	8	270.246	2.7717
LB.water.1000	5	275.671	8.1967
LB.roost.1000	4	280.349	12.8745
LB.tree.1000	5	281.733	14.2586
LB.proximate.1000	5	322.255	54.7811
LB.devo.1000	5	331.917	64.4428
LB.null.1000	2	337.825	70.3508
Scale Comparison			
LB.landcover.250	6	246.868	0
LB.landcover.500	6	248.427	1.559
LB.landcover.1000	6	267.474	20.606

Degrees of freedom (DF), AIC_c and ΔAIC_c values for all generalized linear mixed effect models used to model *L. borealis* activity on the Sheyenne National Grasslands and adjacent properties from May to August of 2016. See Table 1.1 for variables present in each model.

Table A.5

Full model summary for L. noctivagans, Chapter 2

L. noctivagans				
Model	DF	AIC_c	ΔAIC_c	Weight
Step 1: Landscape Level				
Cover	2	1560.6	0	1
Null	1	1611.04	50.397	0
Step 2: Patch Level				
Cover + Area + Shape	4	1524.5	0	0.78
Cover + Area	3	1527.02	2.475	0.22
Cover + Shape	3	1560.25	35.706	0.00
Cover	2	1560.64	36.096	0.00
Step 3: Local Level				
Cover + Area + Shape + BA	5	1502.4	0	0.58
Cover + Area + Shape + BA + DBH	6	1504.62	2.264	0.19
Cover + Area + Shape + Canopy + BA	6	1504.69	2.329	0.18
Cover + Area + Shape + BA + DBH + Canopy	7	1507.01	4.653	0.06
Cover + Area + Shape + Canopy	5	1523.91	21.555	0.00
Cover + Area + Shape	4	1524.55	22.19	0.00
Cover + Area + Shape + Canopy + DBH	6	1526.23	23.876	0.00
Cover + Area + Shape + DBH	5	1526.73	24.37	0.00

Degrees of freedom (DF), AIC_c and ΔAIC_c values, and model weights for all generalized linear models evaluated at each level of hierarchical model development used to model *L. noctivagans* activity on the Sheyenne National Grasslands and adjacent properties from May to August of 2017.

Table A.6

Full model summary for L. cinereus, Chapter 2

L. cinereus				
Model	DF	AIC$_c$	ΔAIC$_c$	Weight
Step 1: Landscape Level				
Cover	2	1334.7	0	0.67
Null	1	1336.05	1.388	0.33
Step 2: Patch Level				
Cover + Area + Shape	4	1273.5	0	1
Cover + Shape	3	1286.1	12.572	0
Cover + Area	3	1320.24	46.707	0
Cover	2	1334.66	61.128	0
Step 3: Local Level				
Cover + Area + Shape + DBH + Canopy	6	1260.2	0	0.60
Cover + Area + Shape + BA + DBH + Canopy	7	1262.59	2.382	0.18
Cover + Area + Shape + DBH	5	1263.01	2.8	0.15
Cover + Area + Shape + BA + DBH	6	1264.58	4.371	0.07
Cover + Area + Shape + Canopy	5	1269.2	8.991	0.01
Cover + Area + Shape + Canopy + BA	6	1271.45	11.238	0.00
Cover + Area + Shape	4	1273.53	13.318	0.00
Cover + Area + Shape + BA	5	1274.29	14.077	0.00

Degrees of freedom (DF), AIC$_c$ and ΔAIC$_c$ values, and model weights for all generalized linear models evaluated at each level of hierarchical model development used to model *L. cinereus* activity on the Sheyenne National Grasslands and adjacent properties from May to August of 2017.

Table A.7

Full model summary for E. fuscus, Chapter 2

E. fuscus				
Model	DF	AIC$_c$	ΔAIC$_c$	Weight
Step 1: Landscape Level				
Null	1	743.396	0	0.74
Cover	2	745.476	2.0798	0.26
Step 2: Patch Level				
Area + Shape	3	653.351	0	0.59
Shape	2	654.116	0.7646	0.41
Area	2	734.742	81.3915	0.00
Null	1	743.396	90.0455	0.00
Step 3: Local Level				
Area + Shape + BA	4	625.48	0	0.40
Area + Shape + BA + Canopy	5	626.29	0.813	0.27
Area + Shape + BA + DBH	5	626.8	1.3175	0.21
Area + Shape + BA + DBH + Canopy	6	627.947	2.467	0.12
Area + Shape + Canopy + DBH	5	645.257	19.7769	0.00
Area + Shape + Canopy	4	646.029	20.5484	0.00
Area + Shape + DBH	4	650.8	25.3198	0.00
Area + Shape	3	653.351	27.8705	0.00

Degrees of freedom (DF), AIC$_c$ and ΔAIC$_c$ values, and model weights for all generalized linear models evaluated at each level of hierarchical model development used to model *E. fuscus* activity on the Sheyenne National Grasslands and adjacent properties from May to August of 2017.

Table A.8

Full model summary for L. borealis, Chapter 2

L. borealis				
Model	DF	AIC$_c$	ΔAIC$_c$	Weight
Step 1: Landscape Level				
Null	1	145.74	0	0.66
Cover	2	147.101	1.3626	0.34
Step 2: Patch Level				
Shape	2	143.57	0	0.52
Area + Shape	3	145.41	1.8387	0.21
Null	1	145.738	2.1672	0.18
Area	2	147.074	3.5027	0.09
Step 3: Local Level				
Shape + BA + DBH	4	128.007	0	0.58
Shape + BA + DBH + Canopy	5	130.051	2.044	0.21
Shape + Canopy + DBH	4	131.684	3.6768	0.09
Shape + DBH	3	131.807	3.7991	0.09
Shape + BA	3	135.152	7.1441	0.02
Shape + Canopy + BA	4	135.901	7.8935	0.01
Shape + Canopy	3	140.445	12.438	0.00
Shape	2	143.571	15.5635	0.00

Degrees of freedom (DF), AIC$_c$ and ΔAIC$_c$ values, and model weights for all generalized linear models evaluated at each level of hierarchical model development used to model *L. borealis* activity on the Sheyenne National Grasslands and adjacent properties from May to August of 2017.