Environmental Factors Affecting the Landscape-Scale Spatio-Temporal Distribution of Small Mammal Assemblages across the northern Great Plains of North America

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by
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Leanne Michelle Heisler, candidate for the degree of Master of Science in Biology, has presented a thesis titled, Environmental Factors Affecting the Landscape-Scale Spatio-Temporal Distribution of Small Mammal Assemblages Across the Northern Great Plains of North America, in an oral examination held on July 3, 2013. The following committee members have found the thesis acceptable in form and content, and that the candidate demonstrated satisfactory knowledge of the subject material.

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THESIS ABSTRACT

The logistic constraints of traditional sampling methods have limited our understanding of the effects of landscape-scale factors on the spatiotemporal distributions of rodents and shrews (small mammals), particularly in heterogeneous landscapes. I used owl pellets as an alternative sampling method, from which the remains of 60,972 individuals were identified and quantified in samples collected across 4.3 million hectares over 15 years. These remains were used to examine the influence of landscape-scale environmental factors on the spatial composition and annual abundances of small mammal species. I hypothesized that the spatial distribution of soil characteristics, agricultural land use, and weather patterns would largely determine the distributions of grassland small mammals within their geographic ranges, while annual weather variation would largely influence the temporal dynamics of grassland rodents across the landscape. I found soil texture was the primary landscape feature driving small mammal composition across my study area, whereas agricultural cropland significantly altered the composition of these assemblages. Cropland with clay soils was dominated by deer mice (*Peromyscus maniculatus*), whereas areas with higher proportions of native grassland and moderately sandy soils supported communities with more sagebrush voles (*Lemmiscus curatus*). Areas with clay soils and higher annual precipitation were associated with higher proportions of house mice (*Mus musculus*), meadow voles (*Microtus pennsylvanicus*), and shrews (*Blarina brevicauda* and *Sorex* species), whereas drier areas with sandier soils and lower annual precipitation were dominated by olive-backed pocket mice (*Perognathus fasciatus*) and northern grasshopper mice (*Onychomys leucogaster*). Furthermore, I found variation in weather had little influence on deer mouse or sagebrush
vole annual abundance, indicating that other factors (i.e., habitat availability) are more responsible for changes in the abundance of these species at the landscape scale. In contrast, meadow voles were positively associated with the duration of snow cover above the hiemal threshold (i.e., 20 cm), exhibiting up to five-fold increases (i.e., irruptions) in abundance following winters of persistent, deep snow cover. This is the largest study in spatial scale ever conducted on grassland small mammals, which provides a truly landscape-scale look at the environmental factors affecting their spatial composition and long-term, population-level responses to environmental change.
PREFACE

There are four chapters in this thesis. The first chapter is a general introduction, the second and third are research chapters, and the fourth consists of general conclusions. Chapters 2 and 4 were written as manuscripts for publication in peer-reviewed scientific journals. By the time this thesis was submitted to the Faculty of Graduate Studies & Research, Chapter 2 was tentatively accepted to be published and Chapter 3 was under peer-review for publishing. Both were submitted to the Journal of Mammalogy. The citation for Chapter 2 is listed below:

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DEDICATION

I’d like to dedicate this work to my father, Brian Heisler, and my significant other, Michael Bonnor. Without your love and support, I could not have achieved so much.
TABLE OF CONTENTS

THESIS ABSTRACT ............................................................................................................. i
PREFACE ............................................................................................................................. iii
ACKNOWLEDGEMENTS ......................................................................................................... iv
POST DEFENSE ACKNOWLEDGEMENTS ............................................................................. v
DEDICATION .......................................................................................................................... vi
TABLE OF CONTENTS ......................................................................................................... vii
LIST OF TABLES .................................................................................................................. ix
LIST OF FIGURES ................................................................................................................ xii

CHAPTER 1. GENERAL INTRODUCTION ........................................................................... 1
  1.1 Effects of scale on habitat selection .............................................................................. 1
  1.2 Small mammal habitat selection .................................................................................. 3
  1.3 Limits of conventional small mammal trapping ............................................................ 4
  1.4 Owl pellets as an alternative sampling technique for broad scale assessments ............ 6
  1.5 Research objectives and rationale .............................................................................. 7
  1.6 References .................................................................................................................... 8

CHAPTER 2. LANDSCAPE-SCALE FEATURES AFFECTING SMALL MAMMAL COMMUNITIES ON THE NORTHERN GREAT PLAINS OF NORTH AMERICA . . 15
  2.1 Introduction .................................................................................................................. 15
  2.2 Materials and methods ................................................................................................. 18
    2.2.1 Study area .............................................................................................................. 18
    2.2.2 Owl pellet data ...................................................................................................... 21
    2.2.3 Environmental data .............................................................................................. 27
2.2.4 Statistical analyses ............................................................... 30

2.3 Results .................................................................................... 31

2.3.1 Overall landscape patterns in small mammal species composition .......... 31

2.3.2 Agricultural influence on small mammal species composition .......... 39

2.4 Discussion ............................................................................. 44

2.5 References ........................................................................... 47

CHAPTER 3. LANDSCAPE-SCALE WEATHER PATTERNS EXPLAIN VOLE IRRUPTIONS ON THE NORTHERN GREAT PLAINS OF NORTH AMERICA ..... 54

3.1 Introduction ........................................................................ 54

3.2 Methods and Materials ........................................................ 56

3.2.1 Study area ........................................................................ 56

3.2.2 Small mammal sampling .................................................. 58

3.2.3 Weather data ..................................................................... 63

3.2.4 Statistical analyses ............................................................... 63

3.3 Results ................................................................................ 65

3.3.1 Deer Mice .......................................................................... 65

3.3.2 Sagebrush Voles ................................................................. 68

3.3.3 Meadow Voles ................................................................. 71

3.4 Discussion .......................................................................... 74

3.5 References .......................................................................... 78

CHAPTER 4. GENERAL DISCUSSION ........................................... 84

4.1 Conclusions ......................................................................... 84

4.2 References ......................................................................... 87
LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chapter 2</td>
<td></td>
</tr>
</tbody>
</table>

Table 2.1 Total abundances and relative abundances of small mammal species found within burrowing owl (BUOW) and great horned owl (GHOW) pellets, respectively. Bolded species were included in the multivariate regression tree analyses and comparison between a heavily cultivated region (Regina Plain) and a predominately native grassland region (Southeast Alberta). All *Sorex* and *Blarina* species were combined into a single group for the analyses (SHREW). .................................................... 23

Table 2.2 Means (±standard deviation) of average continuous environmental variables associated with burrowing owl (BUOW) and great horned owl (GHOW) pellet samples, as well as for the heavily cultivated (Regina Plain) and predominately native grassland (Southeast Alberta) regions.......................................................... 28

Table 2.3 Chi-Square analyses comparing the abundances of species within burrowing owl pellets from a heavily cultivated region (Regina Plain) and a predominately native grassland region (Southeast Alberta) to identify differences in small mammal composition. Observed species abundances were used to calculate expected abundances and adjusted residuals for comparison of small mammal composition and species abundances between regions, respectively. Marginal totals are in brackets. Acronyms represent species (DM = deer mouse, MV = meadow vole, SBV = sagebrush vole, SHREW = *Sorex* and *Blarina* as a collective group, OBPM = olive-backed pocket mouse, HM = house mouse, NGM = northern grasshopper mouse).... 40
CHAPTER THREE

Table 3.1 Total abundance and average annual abundance (± standard deviation) of small mammal species found within burrowing owl (BUOW). Bolded species were included in the generalized linear mixed models. .................................................................................................................. 60

Table 3.2 Top model, intercept only model, and all models within 10 delta AIC units of the top model (candidate set) explaining the annual dynamics of deer mice, followed by model averaged parameter estimates, standardized estimates, standard errors (Unconditional SE), and 95% confidence intervals (CI). Included in all models was the nest collection site as a random effect. Pseudo $R^2$ was calculated to determine the approximate amount of variation explained by the weather variables of the top model. Acronyms represent weather characteristics (GDD = accumulated growing degrees; PREC = precipitation; SNOW = number of days snow cover depth greater than 20 cm) and the year they were measured relative to small mammal sampling ($T_1$ = year prior to small mammal sampling, otherwise weather measured during same year of small mammal sampling). .................................................................................................................................................. 66

Table 3.3 Top model, intercept only model, and all models within 10 delta AIC units of the top model (candidate set) explaining the annual dynamics of sagebrush voles, followed by model averaged parameter estimates, standard error (Unconditional SE), and 95% confidence intervals (CI). Included in all models was the nest collection site as a random effect. Pseudo $R^2$ was calculated to determine the approximate amount of variation explained by the weather variables of the top model. Acronyms represent weather characteristics (GDD = accumulated growing degrees; PREC = precipitation; SNOW = number of days snow cover depth greater than 20 cm) and the year they
were measured relative to small mammal sampling ($T_1 =$ year prior to small mammal
sampling, otherwise weather measured during same year of small mammal sampling).

Table 3.4 Top model, intercept only model, parameter estimates, standard errors, and
confidence intervals explaining annual meadow vole dynamics. Included in both
models is the nest collection site as a random effect. Acronyms represent weather
characteristics (GDD = accumulated growing degrees; PREC = precipitation; SNOW
= number of days snow cover depth greater than 20 cm) and the year they were
measured relative to small mammal sampling ($T_1 =$ year prior to small mammal
sampling, otherwise weather measured during same year of small mammal sampling).
LIST OF FIGURES

CHAPTER 2

Figure 2.1 Pellet collection sites for burrowing owls (white circles) and great horned owls (black circles) on the mixed-grass prairie (dark gray) and aspen parkland (light gray) of the northern Great Plains of North America. The black circles outlined in white are reference points (right: Calgary, Alberta; left: Regina, Saskatchewan). Cross-hatching represents regions where owl pellet samples were used to determine similarity in small mammal composition between predominately native grassland (southeast Alberta) on the left and a heavily cultivated region (Regina Plain) on the right. ............................. 20

Figure 2.2 Small mammal assemblages predicted by multivariate regression tree analysis of small mammal relative abundances from burrowing owl pellet samples and landscape-scale environmental variables averaged within the owl foraging range. The hierarchy of nodes represents the environmental variables in decreasing order of influence on small mammal composition across the study region (Crop = proportion of cropland, Sand = proportion of sand, CH = chernozemic soil type, SZ = solonetec soil type, RG = regosolic soil type, VE = vertisolic soil type, Prec = average annual precipitation). Bar plots represent mean relative abundances of species occurring in each small mammal assemblage (from left to right: black = deer mouse, dark grey = meadow vole, light grey = sagebrush vole, black = Sorex and Blarina as a collective group, dark grey = olive-backed pocket mouse, light grey = house mouse, black = northern grasshopper mouse). Species that occur in high frequency and abundance
with specific environmental conditions were identified using the Dufrêne-Legendre Index (*; p < 0.05).

Figure 2.3 Mean relative abundance of deer mice (gray line) and sagebrush voles (black line) as the proportion of cropland increases and the percentage of sand in the soil (gray bars) decreases within owl foraging ranges.

Figure 2.4 Small mammal assemblages predicted by multivariate regression tree analysis of small mammal relative abundances from great horned owl pellet samples and landscape-scale environmental variables averaged within the owl foraging range. The hierarchy of nodes represents the environmental variables in decreasing order of influence on small mammal composition across the study region (Clay = proportion of clay, CH = chernozemic soil type, SZ = solonetzic soil type, RG = regosolic soil type, VE = vertisolic soil type). Bar plots represent mean relative abundances of species occurring in each small mammal assemblage (from left to right: black = deer mouse, dark grey = meadow vole, light grey = sagebrush vole, black = Sorex and Blarina as a collective group, dark grey = olive-backed pocket mouse, light grey = house mouse, black = northern grasshopper mouse). * (P < 0.05) represent indicator species that occur in high frequency and abundance with specific environmental conditions, identified using the Dufrêne-Legendre Index.

Figure 2.5 Small mammal assemblages predicted by multivariate regression tree analysis of small mammal relative abundances from burrowing owl pellet samples of the predominately native grassland region (southeast Alberta) and landscape-scale environmental variables averaged within the owl foraging range. The hierarchy of nodes represents the environmental variables in decreasing order of influence on small
mammal composition across the study region (CROP = proportion of cropland, SNOW = average annual snow cover). Bar plots represent mean relative abundances of species occurring in each small mammal assemblage (from left to right: black = deer mouse, dark grey = meadow vole, light grey = sagebrush vole, black = Sorex and Blarina as a collective group, dark grey = olive-backed pocket mouse, light grey = house mouse, black = northern grasshopper mouse). * (P < 0.05) represent indicator species that occur in high frequency and abundance with specific environmental conditions, identified using the Dufrêne-Legendre Index.

CHAPTER THREE

Figure 3.1 Burrowing owl pellet collection sites (black circles) and weather station locations (white circles) on the Mixedgrass prairie (dark gray) and Aspen Parkland (light gray) of the northern Great Plains of North America. Grey lines represent provincial boundaries, labelled at the top of the figure. The black circles outlined in white are reference points (right: Calgary, Alberta; left: Regina, Saskatchewan).

Figure 3.2 Average annual abundance of deer mice (light grey line), sagebrush voles (dark grey line), and meadow voles (black line) per owl nest between 1997 and 2011 across the northern Great Plains of central Canada.
1.1 Effects of scale on habitat selection

Composition of animal communities varies over space and time, depending on the availability of resources and biotic conditions. The variability of physical resources and biotic conditions are usually the basis for our definition of unique habitats (Mayor et al. 2009; Morris 2003). Individual animals associate with different habitats by selecting distinct areas disproportionate to their availability (habitat selection; Johnson 1980; Mayor et al. 2009; Morris 2003). Species with similar resource requirements exhibit similar habitat selection and associate with the same habitats, creating communities of distinct composition (Menge and Olson 1990). However, resources are unevenly distributed across space and fluctuate in abundance over time. The heterogeneity in resource distribution results in scale-dependent community composition, because species select habitat at different scales and populations respond to changing resource availability (Mayor et al. 2009; Menge and Olson 1990; Morris 2003). To investigate scale-dependent community composition, multi-scale approaches are used to assess which environmental factors drive community composition at different spatial and temporal scales.

Multi-scale studies suggest that environmental factors affecting animal community composition may not be detectable at any arbitrarily chosen spatial or temporal scale. Accurate assessment of the environmental factors affecting community composition depends on the scales at which these factors and corresponding species responses are measured (Mayor et al. 2009; Wiens 1989). However, approximately 70% of multi-scale studies since 1993 used arbitrarily chosen scales that were not associated
with any ecological rational for their use (Wheatley and Johnson 2009). Any species-habitat relationships observed in these studies may have been misappropriated to the wrong scale, while other existing relationships may have gone undetected (Mayor et al. 2009; Wheatley and Johnson 2009; Wiens 1989). Extrapolations from these single scale studies to explain species-habitat relationships at other scales may produce misleading conclusions because species can respond differently to the same environmental factor at different scales (Wheatley and Johnson 2009). To ensure ecological relevance, the scales chosen to examine species-habitat relationships governing community composition should be based on ecologically rational explanations for species-habitat associations occurring at each scale.

Habitat selection often exhibits a natural order in which specific selection processes occur at different spatial scales. The geographic range of a species depends on a consistent availability of all resources and biotic conditions required for the existence of that species. Within this range, selection of individual home ranges depends on the abundance of sites containing resources required throughout the life span of an individual. These selection processes represent the hierarchical nature of habitat selection, in which the availability of resources and biotic conditions required by individuals at finer scales is constrained by the diversity of habitats at broader scales (Johnson 1980). Community composition exhibits a similar hierarchical nature, where species partitioning resources within the same habitat are constrained by the diversity of habitats available to communities at broader scales (Menge and Olson 1990). This hierarchical basis for habitat selection provides a starting point for identifying the environmental factors determining community composition at different scales.
1.2 Small mammal habitat selection

Small mammals (i.e. mice, shrews, and voles) have important roles many terrestrial ecosystems. These species are characterized by high intrinsic rates of increase that allow populations to respond rapidly to changing environmental conditions (Korpimäki et al. 2004; Sieg 1987). This sensitivity often results in dramatic population fluctuations that affect other terrestrial species. For instance, fluctuating small mammal densities can affect prey availability for a variety of predators, plant community diversity and composition through small mammal foraging, and soil conditions or habitat availability through burrowing activities (Grant and French 1980; Sieg 1987). Thus, fluctuating small mammal densities at broad spatial and temporal scales can have significant impacts on other trophic levels, making small mammals vital components of many terrestrial ecosystems.

In ecosystems primarily limited by precipitation, small mammal community composition is driven by the distribution of rainfall across multiple spatiotemporal scales. Short term studies often observe increasing rodent densities when sporadic rainfall events produce flushes of primary productivity, increasing resource abundance within individual home ranges and improving individual survival and reproductive potential (Beatley 1969; Ernest et al. 2000; Meserve et al. 1995; Whitford 1976). However, this simple model does not hold up when examined over broader temporal scales. Although the distribution of precipitation primarily limits rodent densities at multiple scales, this relationship becomes nonlinear and confounded with the effects of other environmental factors (i.e. predation) when observed over longer time periods (Brown and Ernest 2002; Holmgren et al. 2006; Stapp 2010). These studies exemplify the differential responses of community
composition to the same environmental factor at different scales, justifying the importance of examining species-habitat relationships across different ecologically relevant spatial and temporal scales.

Similar to arid ecosystems, grassland small mammals are strongly influenced by the vegetative characteristics of their habitat as well. In particular, community composition in different grassland types may be facilitated by species partitioning resources along a gradient of vegetative cover (Batzli 1985; Grant and Birney 1979; Grant et al. 1977; Reed et al. 2006). Furthermore, dramatic shifts in community composition occur when vegetative cover is disturbed by anthropogenic (i.e. agriculture) or natural processes (i.e. fire and grazing), further emphasizing the importance of vegetative cover to small mammal community composition (Batzli 1985; Groves and Steenhof 1988; Jones et al. 2003; Swihart and Slade 1990). However, most of these studies employed trapping methods that sampled small areas (often less than one hectare) characterized by a specific vegetation type during short time periods (usually 1 to 4 years). Extrapolating the results of these studies to explain broader species-habitat associations and subsequent community composition may be misleading (Jorgensen 2004).

1.3 Limits of conventional small mammal trapping

The logistic constraints associated with the traditional method of sampling small mammal communities often limits studies to small spatial and/or temporal scales. The conventional method of sampling small mammal populations involves setting a series of traps along transects or within a grid, and collecting samples for several days consecutively at a chosen temporal resolution (i.e. sampling occurs monthly, seasonally,
annually, etc.). Trap stations must be set in all habitats occupied by the small mammal communities under question, and stations must be operated for a minimum of 4 or 5 days to capture a representative sample of the community. Unfortunately, this sampling method is expensive and time consuming (Glennon et al. 2002; Williams and Braun 1983), affecting the perspective of the research by limiting studies to a single, relatively small spatial and/or temporal scale. As a result, few studies using conventional trapping have sampled small mammal communities broadly across spatiotemporal scales (Hanser et al. 2011; Marti 1974). Consequently, little is known about which environmental factors consistently affect small mammal community composition across entire landscapes.

Limited sampling strategies have led to a number of studies extrapolating results from fine scale studies to explain broad scale variation in community composition. Fine scale studies often report associations between species and specific vegetative characteristics that provide essential resources for survival and reproduction (Brown and Ernest 2002; Batzli 1985). The results from these studies have been extrapolated to explain community composition at broader scales, suggesting that species partition resources along vegetative gradients in a way that allows coexistence of species in the same habitat without direct competition (Jorgensen 2004; Price 1978). However, many of these studies were conducted using arbitrary scales chosen due to the logistic constraints of conventional trapping, making them unsuitable for extrapolating across broader scales (Bowman et al. 2000; Coppeto et al. 2006; Jorgensen and Demarais 1999; Morris 1987; Oatway and Morris 2007). An alternative method of sampling small mammals is needed to fully examine the environmental factors affecting community composition within the geographic ranges of grassland small mammal species.
1.4 Owl pellets as an alternative sampling technique for broad scale assessments

Owl pellets provide an excellent opportunity to answer questions regarding the factors influencing the abundance and distribution of small mammals across broad spatial and temporal scales. Owls eat their prey whole and regurgitate the indigestible remains in compact pellets at nest and roost sites. They are selective regarding to breeding sites and are loyal to these sites during the breeding season, resulting in a concentration of pellets that can be collected systematically (Errington 1930; Glue 1970; Wooster 1936). The animals found within these pellets represent the prey captured within the foraging range of the individual owl (Porder et al. 2003; Schoener 1968; Terry 2010a). Compared to conventional trapping methods, owl pellets allow for the collection of a greater number of samples from a larger area at relatively low cost (Clark and Bunck 1990; Moreno and Barbosa 1992; Peña et al. 2003).

Like all trapping methods, using owl pellets to sample small mammal communities has potential biases. Ideally, any trap or owl should be able to sample the small mammal community in perfect correlation to the proportional abundance of species within the landscape. These perfect conditions are rarely possible but owls are likely to be at least as good as most conventional traps (Avenant 2005; Lyman 2012; Luiselli and Capizzi 1996; Terry 2010a; Terry 2010b; Torre et al. 2004). Many species of owls are generalist predators foraging relatively indiscriminately for small mammal prey in a variety of habitats (Schoener 1968; Terry 2010b). Many species also exhibit functional or numeric responses to changing prey densities, indicative of their sensitivity to fluctuating community composition among habitats within their foraging ranges (Jaksic and Simonetti 1987; Lyman 2012; Marti 1987). These generalist predators provide relatively
accurate representations of small mammal communities, facilitating the use of owl pellets to assess landscape-scale factors affecting small mammal community composition. Thus, the results from studies that have used owl pellets to sample small mammal communities must be analyzed within the context of these assumptions.

1.5 Research objectives and rationale

The northern Great Plains of western Canada is a heterogeneous landscape in vegetative composition and structure due to the effects of weather and soil characteristics (Coupland 1950). However, agriculture has dramatically transformed this region into a mosaic of land use types (Samson et al. 2004). Each of these three major environmental factors (weather, soil, and land use) has the potential to influence small mammal communities across the landscape. I hypothesize that the spatial distribution of these three environmental factors will largely determine the distributions of grassland small mammals within their geographic ranges, while climatic variation will largely influence the temporal dynamics of grassland small mammals across the landscape. I used pellets from burrowing (Athene cunicularia) and great horned (Bubo virginianus) owls to sample small mammal communities across the landscape instead of conventional trapping. Both species are generalist predators; however, great horned owls are capable of catching a larger diversity of nocturnal prey (due to their relatively large size) while burrowing owls are smaller and adapted to hunting arthropods and small vertebrates (Poulin and Todd 2006; Marti 1974). The generalist tendencies of these owls provide samples of the community according to the availability of most prey. The goal of my research was to examine the influence of environmental factors on landscape-scale small mammal community composition.
The specific objectives of my research were to:

1. Identify the magnitude of influence environmental factors have on the landscape-scale composition of small mammal communities on the northern Great Plains of western Canada. The results of this research have been accepted for publication in the *Journal of Mammalogy*.

The distributions of grassland small mammals at broad spatial scales have received little attention due to the logistic constraints associated with traditional trapping methods, particularly on the northern Great Plains of North America. My research will provide a unique perspective on which landscape-scale environmental factors largely determine the spatial distribution of these species within their geographic ranges.

2. Determine the effects of landscape-scale weather patterns on the annual abundances of rodent population on the northern Great Plains of western Canada.

Few studies have been conducted on the long-term, temporal dynamics of grassland species at a landscape scale, particularly on the northern Great Plains of North America. By examining these relationships, my research will provide insight into the implications of population-wide fluctuations in rodent densities on their trophic relationships with other grassland species.

1.6 References


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CHAPTER 2. LANDSCAPE-SCALE FEATURES AFFECTING SMALL MAMMAL COMMUNITIES ON THE NORTHERN GREAT PLAINS OF NORTH AMERICA


2.1 Introduction

Small mammals, such as mice, shrews, and voles, are vital components of most terrestrial ecosystems (Gibbons 1988); however, we know little about the factors affecting their distribution and abundance over landscape spatial scales. Small mammals influence ecosystems of the northern Great Plains by serving as a food source for a wide variety of predators, altering plant communities through caching or consuming vegetation and seeds, and altering soil conditions or providing habitat for other species through burrowing activities (Sieg 1987). Some of these influences can change species distributions by eliciting population-level responses across hundreds of kilometers (landscape-scale; Grant and French 1980; Jaksic and Simonetti 1987; Marti 1987). Despite their importance, most small mammal studies have focused on small-scale factors affecting habitat selection for specific resources, such as food, nest sites, or refuges, within individual home ranges (microhabitats). However, microhabitats are inherently constrained by the availability of the larger habitats encompassing the home ranges of entire populations (macrohabitats; Jorgensen and Demarais 1999; Mayor et al. 2009;
Morris 1987). These landscape-scale patterns may not be apparent in studies focusing on habitat selection within individual home ranges, warranting a closer look at how small mammals distribute themselves among macrohabitat types in heterogeneous landscapes.

The scope of most previous small mammal studies has been limited by conventional sampling techniques. Sampling small mammal assemblages generally involves conventional trapping methods that are relatively expensive and time consuming; limiting these studies to small spatial and/or temporal scales (Hanser et al. 2011). In addition, trapping is affected by sampling biases regardless of the type of trap or bait used. For example, the accuracy of the trapping session is dependent upon weather, season, moon phase, population density, food availability, the age, size, and sex of the small mammals (O’Farrell 1994; Wiener and Smith 1972), and is sensitive to sampling effort and location (Hanser et al. 2011). Also, trapping usually occurs in only a few distinguishable vegetation types, limiting the results to a small subset of the existing community (Hanser et al. 2011). These sampling constraints have led to a lack of landscape-scale studies, limiting the perspective of published research and effectively inhibiting investigation of the environmental factors affecting populations at broader spatial scales (Jorgensen 2004). To overcome this limitation, an alternative method is needed to sample small mammal communities across larger spatial scales.

I considered owls as another method for sampling small mammal communities. Owls tend to focus on small mammals while foraging and do so within a defined area (i.e., the foraging range of the individual owl; Feranec et al. 2007; Porder et al. 2003). Conveniently, owls regurgitate the indigestible parts of their prey (e.g. bones) and deposit these pellets in large quantities at their nest and roost sites (Errington 1930). The bones
found within the owl pellets are usually identifiable to species (depending on the species and the condition of the pellet contents) and allow researchers to quantify the animals eaten by the owls. However, similar to conventional trapping, owl pellet sampling is not without potential biases. In particular, owl pellets may be biased towards species that are more available as prey based on the hunting strategies and habitats owls use while foraging (Fulk 1976; Glue 1970; Torre et al. 2004; Wooster 1936). Despite this potential, some studies have found little difference in proportional abundance and taxonomic composition between conventional trapping results and prey assemblages inferred from owl pellet datasets (Terry 2010). In addition, several generalist owl species show clear functional relationships to fluctuating prey abundances, indicating that: (a) owls consume prey species that are the most available, and (b) owls are able to switch between prey species depending on their relative abundance (Jaksic and Marti 1984; Poulin et al. 2001; Rusch et al. 1972; Silva et al. 1995; Zimmerman et al. 1996). Together, these features of generalist owl diet suggest that pellet composition should be a good reflection of the small mammal assemblage in the foraging range of the owl. However, few studies have capitalized on widely distributed owls to examine small mammal communities over large spatial scales.

Here, I use great horned (\textit{Bubo virginianus}) and burrowing owl (\textit{Athene cunicularia}) pellets to examine factors that influence small mammal composition across the northern Great Plains of North America. This vast region of the Great Plains in western Canada is a heterogeneous landscape characterized by climatic, soil, and land use variation that has the potential to affect small mammal species composition (Coupland 1950). Burrowing and great horned owls are dietary generalist species that are
widespread across the Great Plains; they consume a variety of small mammal species, and their pellets provide an excellent opportunity to examine the landscape-scale composition of prairie small mammal assemblages and their macrohabitat associations. My objectives were to identify the environmental factors primarily responsible for small mammal composition across the landscape, as well as those potentially responsible for differences in composition between heavily cultivated regions and predominately native grassland regions.

2.2 Materials and methods

2.2.1 Study area

We collected owl pellets from across the mixed-grass prairie and aspen parkland of western Canada (Fig. 1). This region is covered in boulder clay soil deposits of varying texture, and experiences a continental climate of extreme variation in temperature and precipitation, with a short annual growing period of 3 to 5 months (Coupland 1950). Grain farming and livestock ranching have heavily affected the region since the late 1800s. Nearly 70% of the mixed-grass prairie has been converted to agriculture (Samson et al. 2004), severely altering the vegetative land cover and homogenizing the landscape in some regions. Variation in climate, soil characteristics, and land use across the whole region enables examination of small mammal communities in a diverse landscape, as well as a closer examination of regions dominated by single land use features. For instance, one part of the study area (Regina Plain of southern Saskatchewan) is a heavily cultivated landscape, whereas another part (southeast Alberta) remains predominantly native grassland. These regions also differ in soil and climate characteristics; the Regina Plain is
dominated by heavy clay soils and receives an average of 40% more precipitation than southeast Alberta.
Figure 2.1 Pellet collection sites for burrowing owls (white circles) and great horned owls (black circles) on the mixed-grass prairie (dark gray) and aspen parkland (light gray) of the northern Great Plains of North America. The black circles outlined in white are reference points (right: Calgary, Alberta; left: Regina, Saskatchewan). Cross-hatching represents regions where owl pellet samples were used to determine similarity in small mammal composition between predominately native grassland (southeast Alberta) on the left and a heavily cultivated region (Regina Plain) on the right.
2.2.2 Owl pellet data

We collected pellets from nest and roost locations of burrowing owls over a 15 year period (1997 to 2011) and great horned owls primarily in 2007 and 2008 (Fig. 1), which are now stored in the collections at the Royal Saskatchewan Museum. These pellets were collected as part of ongoing field studies on owls, during which researchers and bird banders made a focused effort to collect all pellets from each nest and associated roost. Burrowing owl pellets were collected an average 5 times during the breeding season of each year (April – July) from 1,181 nests, whereas great horned owl pellets were collected primarily during a single visit from 258 nests. We used a 10% sodium hydroxide solution to dissolve fur in the pellets and provide clean bones and teeth for identification. Prey species were identified via unique skeletal and dental traits using a reference collection when necessary. The abundance of each small mammal species was determined for each nest based on the number of individual craniomandibular elements present (i.e., minimum number of individuals).

The resulting dataset included 60,972 small mammal individuals, from which a total 19 species of rodents and shrews were identified (Table 1.). Seven species of *Sorex* were identified in the owl pellets; however, we could not reliably identify a large number (nearly 1500) of these individuals by specific dental or skeletal traits. The vast majority of *Sorex* shrews were most likely *S. haydeni* and *S. cinereus*, but to reduce error in the data set all *Sorex* and *Blarina brevicauda* specimens were consolidated into a single group referred to collectively as ‘shrews’. I included only remains of the six most abundant rodent species and shrews (*Sorex* species and *Blarina brevicauda*) in statistical analyses, which represented 99.7% of all small mammals identified (Table 1). The
remaining species were not included in these analyses because combined they made up less than 0.01\% of the diet of both owl species, the statistical results for which were overwhelmed by the more abundant species in the dataset. Collections were pooled by nest per year, and are referred to hereafter as a sample.
Table 2.1 Total abundances and relative abundances of small mammal species found within burrowing owl (BUOW) and great horned owl (GHOW) pellets, respectively. Bolded species were included in the multivariate regression tree analyses and comparison between a heavily cultivated region (Regina Plain) and a predominantly native grassland region (Southeast Alberta). All *Sorex* and *Blarina* species were combined into a single group for the analyses (SHREW).

<table>
<thead>
<tr>
<th>Species</th>
<th>Acronym</th>
<th>Species Abundance (BUOW)</th>
<th>Species Abundance (GHOW)</th>
<th>Species Relative Abundance (BUOW)</th>
<th>Species Relative Abundance (GHOW)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deer Mouse</td>
<td>DM</td>
<td>26199</td>
<td>10648</td>
<td>58%</td>
<td>68%</td>
</tr>
<tr>
<td><em>Peromyscus maniculatus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meadow Vole</td>
<td>MV</td>
<td>9189</td>
<td>2291</td>
<td>20%</td>
<td>15%</td>
</tr>
<tr>
<td><em>Microtus pennsylvanicus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sagebrush Vole</td>
<td>SBV</td>
<td>5738</td>
<td>705</td>
<td>13%</td>
<td>5%</td>
</tr>
<tr>
<td><em>Lemmiscus curtatus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>Code</td>
<td>Total</td>
<td>Alive</td>
<td>Actual</td>
<td>Relative</td>
</tr>
<tr>
<td>----------------------------------------------</td>
<td>------</td>
<td>-------</td>
<td>-------</td>
<td>--------</td>
<td>----------</td>
</tr>
<tr>
<td>Shrews (Sorex and Blarina)&lt;sup&gt;a&lt;/sup&gt;</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Olive-Backed Pocket Mouse</td>
<td>OBPM</td>
<td>915</td>
<td>799</td>
<td>2%</td>
<td>5%</td>
</tr>
<tr>
<td>House Mouse (Mus musculus)</td>
<td>HM</td>
<td>838</td>
<td>115</td>
<td>2%</td>
<td>1%</td>
</tr>
<tr>
<td>Northern Grasshopper Mouse</td>
<td>NGM</td>
<td>607</td>
<td>736</td>
<td>1%</td>
<td>5%</td>
</tr>
<tr>
<td>Western Jumping Mouse (Zapus princeps)</td>
<td></td>
<td>32</td>
<td>19</td>
<td>&lt;0.1%</td>
<td>&lt;0.1%</td>
</tr>
<tr>
<td>Ord’s Kangaroo Rat (Dipodomys ordii)</td>
<td></td>
<td>9</td>
<td>19</td>
<td>&lt;0.1%</td>
<td>&lt;0.1%</td>
</tr>
<tr>
<td>Southern Red-Backed Vole (Cleithrionomys gapperi)</td>
<td></td>
<td>5</td>
<td>45</td>
<td>&lt;0.1%</td>
<td>&lt;0.1%</td>
</tr>
<tr>
<td>Prairie Vole</td>
<td></td>
<td>2</td>
<td>30</td>
<td>&lt;0.1%</td>
<td>&lt;0.1%</td>
</tr>
</tbody>
</table>
(Microtus ochrogaster)

| Western Harvest Mouse | 2 | 0 | <0.1% | 0% |

(Reithrodontomys megalotis)

| Meadow Jumping Mouse | 2 | 0 | <0.1% | 0% |

(Zapus hudsonius)

This category includes *Blarina brevicauda, Sorex arcticus, Sorex cinerius, Sorex haydeni, Sorex hoyi, Sorex monticolus*, and *Sorex palustris*. 
The same six species and shrews comprised the majority of prey items in the pellets of both owl species, indicating that the diets of the two owls were generally similar. However, after the top 3 prey species, the order of importance was somewhat different; correlation analyses using Spearman’s Rho showed a moderately positive correlation between the rank abundances of the top 6 small mammal species (Table 1; rho = 0.61, p = 0.17). Thus, both owls are likely generalist predators exhibiting functional responses to changing prey densities (Terry 2010), but I did not pool pellet data across owl species for analyses.

Individual-based species accumulation curves were used to identify the minimum number of identified small mammal remains within which species richness (S) approached an asymptote; I used this value as the sample size needed to include a site for statistical analyses (Gotelli and Colwell 2004). This assessment was based on the sample size at which information content (species richness) reached an asymptote (Gotelli and Colwell 2004). Burrowing owl samples with less than 30 individual mammals and great horned owl samples containing less than 20 individual mammals were excluded from my analyses, which left 397 burrowing owl nests (557 samples; some nests were sampled in multiple years) with an average size of 59 (±31 SD) individuals, and 171 great horned owl nests (171 samples) with an average of 88 (±83 SD) individuals, to be included in statistical analyses. These samples were then standardized for sampling effort by dividing the abundance of each small mammal species by the total number of individuals of all species for statistical analyses.
2.2.3 Environmental data

Soil characteristics (i.e., percentage of sand and clay in the soil, soil texture, and soil order), spatial variation in climate (i.e., average annual precipitation, temperature, and snow depth), and land use type were included in all analyses of small mammal composition (Table 2). Land cover from vectorized, raster thematic data collected circa 2000 was provided by Geobase Canada® (Land Cover, Circa 2000-Vector). To avoid using outdated data for nests visited recently, I replaced land use within a four km radius of each nest visited between 2004 and 2011 with ground-truthed land use data collected the year these nests were visited. Soil variables were obtained from Agriculture & Agri-Food Canada (Soil Landscapes of Canada; v.3.2), which were compiled from existing soil survey maps. Annual averages of temperature, rainfall, and snow depth from 1997 to 2011 were taken from the national summaries of climate averages and extremes from Environment Canada. I used Geographic Information Systems to create circular buffers with 2500 and 5000 m radii from each pellet collection site for burrowing owl and great horned owl samples, respectively. These radii represent the typical foraging distances from roost/nest sites of each owl species (Baumgartner 1939; Rusch et al. 1972; Schoener 1968). Within foraging range buffers, average environmental conditions between 1997 and 2011 were determined for each pellet collection site. This approach provided a dataset containing annual small mammal composition and associated environmental conditions for each owl nest.
Table 2.2 Means (±standard deviation) of average continuous environmental variables associated with burrowing owl (BUOW) and great horned owl (GHOW) pellet samples, as well as for the heavily cultivated (Regina Plain) and predominately native grassland (Southeast Alberta) regions.

<table>
<thead>
<tr>
<th>Environmental Conditions</th>
<th>Condition</th>
<th>Acronym</th>
<th>Units</th>
<th>Canadian Prairies</th>
<th>Regina Plain</th>
<th>Southeast Alberta</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>BUOW</td>
<td>GHOW</td>
<td></td>
</tr>
<tr>
<td>Native Grass</td>
<td></td>
<td>NG</td>
<td>%</td>
<td>31 (±30)</td>
<td>17 (±18)</td>
<td>20 (±10)</td>
</tr>
<tr>
<td>Riparian^a</td>
<td></td>
<td>RIP</td>
<td>%</td>
<td>6 (±7)</td>
<td>3 (±4)</td>
<td>10 (±5)</td>
</tr>
<tr>
<td>Trees &amp; Shrubs</td>
<td></td>
<td>TV</td>
<td>%</td>
<td>0 (±1)</td>
<td>1 (±3)</td>
<td>0 (±0)</td>
</tr>
<tr>
<td>Tame Grass</td>
<td></td>
<td>TG</td>
<td>%</td>
<td>10 (±9)</td>
<td>10 (±10)</td>
<td>14 (±8)</td>
</tr>
<tr>
<td>Human Development^b</td>
<td></td>
<td>HUM</td>
<td>%</td>
<td>2 (±9)</td>
<td>1 (±2)</td>
<td>1 (±1)</td>
</tr>
<tr>
<td>Cropland</td>
<td></td>
<td>CROP</td>
<td>%</td>
<td>50 (±31)</td>
<td>67 (±24)</td>
<td>55 (±17)</td>
</tr>
<tr>
<td>Sand</td>
<td></td>
<td>SAND</td>
<td>%</td>
<td>26 (±19)</td>
<td>33 (±17)</td>
<td>6 (±8)</td>
</tr>
<tr>
<td>Clay</td>
<td></td>
<td>CLAY</td>
<td>%</td>
<td>43 (±20)</td>
<td>36 (±15)</td>
<td>70 (±12)</td>
</tr>
<tr>
<td>Soil Texture</td>
<td></td>
<td>TEXT</td>
<td>C/M</td>
<td>MF</td>
<td>M</td>
<td>VF</td>
</tr>
<tr>
<td>Soil Order</td>
<td></td>
<td>ORDER</td>
<td>C</td>
<td>VE</td>
<td>CH</td>
<td>VE</td>
</tr>
<tr>
<td>Description</td>
<td>Code</td>
<td>Unit</td>
<td>Values</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>------------------------------------</td>
<td>------</td>
<td>------</td>
<td>-----------------</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average Annual Precipitation</td>
<td>PREC</td>
<td>mm</td>
<td>260 (±160) 241 (±98) 340 (±91) 205 (±96)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average Annual Snow Depth</td>
<td>SNOW</td>
<td>Cm</td>
<td>58 (±47) 64 (±42) 83 (±25) 41 (±40)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>TEMP</td>
<td>°C</td>
<td>3.16 (±1.26) 2.15 (±1.46) 4.16 (±1.24) 3.38 (±2.05)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) Refers to surface area of permanent water bodies only (i.e. lakes, reservoirs, rivers, and streams)

\(^b\) Human development refers to roads, railways, buildings, paved surfaces, urban areas, industrial sites, farmsteads, excavation pits, and dumping sites.

\(^c\) Categorical Variable
2.2.4 Statistical analyses

Multivariate regression tree (MVRT) analyses were used to identify the broad scale environmental factors influencing small mammal composition (De’Ath 2002; Larsen and Speckman 2004). This method is suitable for complex datasets like owl pellets because it relies on few statistical assumptions, tolerates collinearity and higher-order interactions among predictor variables, and can analyze large datasets with multiple response variables efficiently (De’Ath 2002; Larsen and Speckman 2004). The hierarchy of branches represents the environmental variables in decreasing order of influence on the composition of small mammal assemblages across the study region. Each branch is characterized by a threshold value chosen to maximize homogeneity within the resulting nodes (De’Ath 2002). The terminal nodes represent small mammal assemblages characterized by the environmental factors used to separate the small mammal species data into homogeneous groups. Cross-validation relative error (CVRE) identifies the optimal tree size by determining the predictive accuracy of the tree, and the amount of variation in small mammal species composition unexplained by the tree is quantified by the relative error (RE). Trees with the smallest CVRE tend to be overly optimistic in their predictive capacity because they include redundant or irrelevant branching. Thus, final models were chosen from models above or below the minimum CVRE plus one standard error (SE) threshold (De’Ath 2002). Principal component analysis was used to determine the homogeneity of samples representing each small mammal assemblage identified with MVRT (De’Ath 2002). The Dufreîne-Legendre index was used to identify individual species that were associated with specific environmental conditions based on the relative
abundance and relative frequency of occurrence within small mammal assemblages (Dufrêne and Legendre 1997).

I used MVRT to identify overall landscape patterns in small mammal composition across the entire study area. I analyzed pellet samples from burrowing owls and great horned owls separately to account for differential sampling effort between the two pellet datasets. I used the Chi Square test to determine similarities in composition of small mammal assemblages between a heavily cultivated region (Regina Plain) and a predominately native grassland region (southeast Alberta; Everitt 1977). MVRT analyses of the burrowing owl samples from these two regions identified which environmental variables affected small mammal species composition. There were too few great horned owl samples in either region to conduct this analysis, so only burrowing owl samples were used.

I used ArcMap 10.0 for all data preparation (ESRI 2011); all statistical computations were conducted in R Project for Statistical Computing 2.14.1 (R Development Core Team 2011), using vegan 2.0-5 (Oksanen et al. 2012), mpart 1.6-0 (Therneau et al. 2012) and MVPARTwrap 0.1-9 packages (Ouellette and Legendre 2012).

2.3 Results

2.3.1 Overall landscape patterns in small mammal species composition

The proportion of cropland and the percentage of sand in the soil had the greatest influence on small mammal species composition in the MVRT of all burrowing owl pellet samples, in which foraging ranges were comprised of 1,962 hectares (Fig. 2). The model explained 47% of the variation in small mammal species composition and predicted the relative abundance of all six individual species plus shrews based on four of
the twelve environmental variables considered. The relative abundance of deer mice in assemblages increased with the proportion of cropland, whereas the relative abundance of sagebrush voles showed the opposite trend, particularly in regions with moderately sandy soils (Fig. 3). Meadow voles, house mice, olive-backed pocket mice, northern grasshopper mice, and shrews were associated with soil orders characteristic of grassland environments (chernozemic or solonetizic soils). These species were split further into two small mammal assemblages along a gradient of precipitation. In regions receiving an average annual precipitation higher than 439 mm, the average relative abundance of meadow voles, house mice, and shrews were 29%, 4%, and 4% higher, respectively. In the same regions characterized by soils made up of more than 40% sand, the average relative abundance of northern grasshopper mice and olive-backed pocket mice were 5% and 2% higher, respectively.
Figure 2.2 Small mammal assemblages predicted by multivariate regression tree analysis of small mammal relative abundances from burrowing owl pellet samples and landscape-scale environmental variables averaged within the owl foraging range. The hierarchy of nodes represents the environmental variables in decreasing order of influence on small mammal composition across the study region (Crop = proportion of cropland, Sand = proportion of sand, CH = chernozemic soil type, SZ = solonetzic soil type, RG = regosolic soil type, VE = vertisolic soil type, Prec = average annual precipitation). Bar plots represent mean relative abundances of species occurring in each small mammal
assemblage (from left to right: black = deer mouse, dark grey = meadow vole, light grey = sagebrush vole, black = *Sorex* and *Blarina* as a collective group, dark grey = olive-backed pocket mouse, light grey = house mouse, black = northern grasshopper mouse).

Species that occur in high frequency and abundance with specific environmental conditions were identified using the Dufrène-Legendre Index (*; p < 0.05).
Figure 2.3 Mean relative abundance of deer mice (gray line) and sagebrush voles (black line) as the proportion of cropland increases and the percentage of sand in the soil (gray bars) decreases within owl foraging ranges.
Soil characteristics had the greatest influence on small mammal species composition across the landscape in the MVRT of all great horned owl pellet samples from foraging ranges comprised of 7,850 hectares (Fig. 4). This is similar to the results of the burrowing owl pellet samples, where soil characteristics occur at four of the six branches of the resulting MVRT. Soil texture and soil order explained 35% of the variation in small mammal species composition and predicted the relative abundances of five individual species (all except house mice) and shrews. Deer mice and meadow voles were split into separate small mammal species assemblages based on soil texture and soil order. In particular, average deer mouse relative abundance was 43% higher in regions where soils contained more than 28% clay, whereas meadow vole relative abundance was an average 9% higher in the same regions characterized by solonetzic soils. The remaining species were an average 12% more abundant in regions where soils contained less than 18% clay (average species relative abundance: sagebrush voles = 3%, shrews = 2%, olive-backed pocket mouse = 26%, northern grasshopper mouse = 17%). However, northern grasshopper mice and olive-backed pocket mice were almost nine times more abundant than sagebrush voles and shrews in these regions. These results corroborate the relationship between soil texture and small mammal species composition exhibited in the previous MVRT of burrowing owl samples.
Figure 2.4 Small mammal assemblages predicted by multivariate regression tree analysis of small mammal relative abundances from great horned owl pellet samples and landscape-scale environmental variables averaged within the owl foraging range. The hierarchy of nodes represents the environmental variables in decreasing order of influence on small mammal composition across the study region (Clay = proportion of clay, CH = chernozemic soil type, SZ = solonetzic soil type, RG = regosolic soil type, VE = vertisolic soil type). Bar plots represent mean relative abundances of species occurring in each small mammal assemblage (from left to right: black = deer mouse, dark grey = meadow vole, light grey = sagebrush vole, black = Sorex and Blarina as a collective group, dark grey = olive-backed pocket mouse, light grey = house mouse, black = northern grasshopper mouse). * (P < 0.05) represent indicator species that occur in high
frequency and abundance with specific environmental conditions, identified using the Dufrène-Legendre Index.
2.3.2 Agricultural influence on small mammal species composition

Small mammal assemblages in the heavily cultivated Regina Plain differed significantly from those in the predominately native grassland region of southeast Alberta ($\chi^2 = 3864.3$, df = 6, p<0.05; Table 3). Deer mice made up 41% of the assemblage in the heavily cultivated region (Regina Plain), but only 16% of the assemblage in the predominately native grassland region (southeast Alberta). In contrast, sagebrush voles made up only 1% of the assemblage in the heavily cultivated region but up to 21% of the assemblage in the predominately native grassland. To confirm that differences in soil and climate between the two regions didn’t confound these results, another Chi Square test comparing the composition of small mammal assemblages from samples with owl foraging ranges comprised of ≥90% cropland or native grassland across the entire sampled region showed almost identical results (data not shown; $\chi^2 = 2717.8$, df = 6, p<0.05). These results are also similar to the relationship identified in the first split of the MVRT of all burrowing owl samples where deer mice and sagebrush voles were inversely associated with cropland. Thus, it appears that land use may be largely responsible for shifts in assemblage composition between these two regions, despite the differences in soil and weather characteristics.
Table 2.3 Chi-Square analyses comparing the abundances of species within burrowing owl pellets from a heavily cultivated region (Regina Plain) and a predominately native grassland region (Southeast Alberta) to identify differences in small mammal composition. Observed species abundances were used to calculate expected abundances and adjusted residuals for comparison of small mammal composition and species abundances between regions, respectively. Marginal totals are in brackets. Acronyms represent species (DM = deer mouse, MV = meadow vole, SBV = sagebrush vole, SHREW = Sorex and Blarina as a collective group, OBPM = olive-backed pocket mouse, HM = house mouse, NGM = northern grasshopper mouse).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Regina Plain</th>
<th>Southeast Alberta</th>
<th></th>
<th>Marginal</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
<td>Residuals</td>
<td>P Value</td>
</tr>
<tr>
<td>DM</td>
<td>5492</td>
<td>4223</td>
<td>42.39</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>MV</td>
<td>1992</td>
<td>1929</td>
<td>2.50</td>
<td>0.05</td>
</tr>
<tr>
<td>SBV</td>
<td>153</td>
<td>1491</td>
<td>-57.96</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>SHREW</td>
<td>218</td>
<td>275</td>
<td>-5.29</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>OBPM</td>
<td>71</td>
<td>70</td>
<td>0.104</td>
<td>&gt;0.05</td>
</tr>
</tbody>
</table>

<sup>a</sup> Indicates statistical significance.
<table>
<thead>
<tr>
<th></th>
<th>HM</th>
<th>264</th>
<th>161</th>
<th>12.39</th>
<th>&lt;0.001</th>
<th>22</th>
<th>125</th>
<th>-12.39</th>
<th>286</th>
<th>&lt;0.001</th>
</tr>
</thead>
<tbody>
<tr>
<td>NGM</td>
<td>23</td>
<td>64</td>
<td>-7.74</td>
<td>&lt;0.001</td>
<td>90</td>
<td>49</td>
<td>7.74</td>
<td>113</td>
<td></td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Marginal</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Column</td>
<td>8213</td>
<td></td>
<td>6364</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\[a_\alpha = 0.05\]
The proportion of cropland in the MVRT of pellet samples from the predominantly native grassland region had the greatest influence on small mammal species composition, further identifying this land use type as a dominant factor affecting assemblages. Thirty seven percent of the variation in small mammal species composition and the predicted distributions of four species were explained by the proportion of cropland and average annual snow cover (Fig. 5). Deer mouse and northern grasshopper mouse average relative abundances were 25% and 2% higher in regions with greater than 6% cropland, respectively. In contrast, sagebrush vole and meadow vole average relative abundances exhibited a corresponding decrease by 17% and 9%, respectively. Interestingly, the MVRT of pellet samples from the heavily cultivated region explained less than 1% of the variation in small mammal species composition and had no predictive value.
Figure 2.5 Small mammal assemblages predicted by multivariate regression tree analysis of small mammal relative abundances from burrowing owl pellet samples of the predominately native grassland region (southeast Alberta) and landscape-scale environmental variables averaged within the owl foraging range. The hierarchy of nodes represents the environmental variables in decreasing order of influence on small mammal composition across the study region (CROP = proportion of cropland, SNOW = average annual snow cover). Bar plots represent mean relative abundances of species occurring in each small mammal assemblage (from left to right: black = deer mouse, dark grey = meadow vole, light grey = sagebrush vole, black = Sorex and Blarina as a collective group, dark grey = olive-backed pocket mouse, light grey = house mouse, black = northern grasshopper mouse). * (P < 0.05) represent indicator species that occur in high frequency and abundance with specific environmental conditions, identified using the Dufrêne-Legendre Index.
2.4 Discussion

Using owls to sample small mammal assemblages enabled us to conduct a landscape-scale study of a size that would have been inconceivable with traditional sampling methods. All sampling methods have inherent biases, and do not provide a perfect spatial representation of small mammal communities (Torre et al. 2004). For example, traps can be species- and size-selective (O’Farrell et al. 1994), whereas owls may be selective through non-random habitat and prey choices (Yom-Tov and Wool 1997). However, despite the differences in habitat use, body size, and foraging strategies of the two owl species I used, the overall small mammal species composition of great horned and burrowing owl diets were similar. Also, land use and soil characteristics were important predictors in the MVRTs using pellets from both owl species. The similarity in diet composition across such a large landscape area suggests that both owls are generalist predators, and the similarity in results of the MVRTs suggests the relative abundance of small mammals within pellet samples is reflective of their relative abundance in the environment. Thus, owl pellets should be considered a useful method of small mammal sampling (Terry 2010). Also, the efficiency of collecting pellet samples and the potential for acquiring datasets encompassing large geographic areas and long time periods compared to traditional trapping methods (Hanser et al. 2011) suggest that owl pellets should be considered an alternative method for future large-scale small mammal studies.

Species-habitat associations at spatial scales that encompass the distributions of entire populations (macrohabitat) provide important insight into the factors affecting small mammal composition. Most microhabitat studies sample areas less than 2 hectares and focus on a few vegetation types at most (Bowman et al. 2000; Jorgensen 2004).
Although some of these studies found explicit relationships between resource distribution and local species abundance, they were less successful in determining how species distribute themselves across landscapes (Jorgensen 2004). My study sampled small mammals from more than four million hectares irrespective of vegetation type, making this a truly landscape-scale study of small mammal species composition. My results were similar to several multi-scale studies that suggest small mammals have greater affiliations with macrohabitats than other spatial scales, potentially due to species distributing themselves according to microhabitat abundance within macrohabitats (Jorgensen and Demarais 1999; Morris 1987; Stevens and Tello 2009). Thus, including macrohabitat associations in studies of small mammal composition markedly enhances our perspective on the importance of both scale and important habitat features beyond that gained from studies focused solely on microhabitat selection.

Agriculture has changed the native grassland ecosystem from one with a diverse assemblage of small mammals to a system completely dominated by deer mice. Approximately 60% of the mixed-grass prairie in North America was cultivated for agricultural purposes (Henwood 2010), in many areas this proportion reaches over 90% of the land area (Poulin et al. 2005). Conversion of native grassland to cropland homogenizes vegetative structure and alters resource availability across the landscape, redistributing resources in a way that appears to benefit some species while imposing a cost on others. In particular, the high relative abundances of deer mice in agricultural areas are likely due to high seed productivity and the use of ephemeral burrows for nesting and reproduction in cropland (White et al. 2012; Witmer et al. 2012). Conversely, the inverse relationship sagebrush voles have with the prevalence of cropland is likely
due to cultivation eliminating many resources this species depends on, such as vegetative structure for food and shelter, as well as a lack of a stable underground environment for extensive burrowing activities (Witmer et al. 2007). The overall result is that the conversion of native grassland to cropland has significantly altered small mammal assemblages and populations across the northern Great Plains of North America. The ecological consequences of altering the dynamics of such a key species group to predator-prey dynamics and disease or parasite transmission among animals and humans should be the focus for future large-scale studies.

Previous studies of grassland small mammal assemblages have concluded that precipitation is a dominant contributing factor to small mammal species composition (Grant and Birney 1979; Reed et al. 2006); however, my findings suggest that soil characteristics may have been overlooked as a potential driving force at the landscape scale. Microhabitat studies have extrapolated that precipitation is responsible for the variation in resource distribution that species use to partition microhabitats, thereby allowing coexistence across the landscape (Price 1978; Reed et al. 2006). In my study only a weak relationship existed between precipitation and small mammal species composition, whereas soil texture and soil order were dominant environmental factors determining small mammal species composition. Soil characteristics have been considered in some microhabitat studies, but few found associations between small mammal density and the edaphic features measured (Feldhamer 1979; Stevens and Tello 2009). The lack of evidence for soil characteristics, such as texture and order, as a determining factor for small mammal abundance at microhabitat scales may stem from
the fact that these species are associating with habitats characterized by differing edaphic characteristics at the macrohabitat level.

The importance of soil texture as a predictor of small mammal species composition is likely due to its indirect influence on primary productivity and vegetative structure. Several small mammal microhabitat studies suggest litter-dwelling herbivorous and insectivorous species associate with consistent vegetative structure for food, shelter, and predator avoidance, whereas granivorous species associate with heterogeneous structure for easier access to seeds (Reed et al. 2006; Wrigley et al. 1979). Fine-textured clay maintains soil moisture and nutrient availability closer to the soil surface for more consistent, natural vegetative cover. In contrast, sandy soils drain moisture and nutrients away from the soil surface, leaving them unavailable for most plant growth except forbs and shrubs. Thus, large areas with sandy soils often exhibit heterogeneous vegetative structure and cover (Epstein et al. 1997; Hook and Burke 2000; Lane et al. 1998). These concepts are consistent with the patterns observed in my study; olive-backed pocket mice (i.e., granivore) were associated with coarse textured soils more so than voles or shrews (i.e., litter-dwelling species). Regardless of the specific mechanism, my data suggest that soil texture plays a role as a natural macrohabitat feature responsible for variance in small mammal species composition across the prairie landscape.

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CHAPTER 3. LANDSCAPE-SCALE WEATHER PATTERNS EXPLAIN VOLE IRRUPTIONS ON THE NORTHERN GREAT PLAINS OF NORTH AMERICA

3.1 Introduction

Rodents are characterized by high intrinsic rates of increase that prompt rapid population responses to acute factors. Substantial evidence suggests that changing predator densities can cause oscillations in prey populations. In particular, specialist predators may induce regular, high amplitude oscillations, while generalist predators may stabilize rodent communities by preventing irregular outbreaks (Gilg et al. 2003; Hansson and Henttonen 1988; Korpimäki et al. 2004). Diseases and parasites may cause large declines in high-density populations (Hansson and Henttonen 1988; Korpimäki et al. 2004). However, mounting evidence suggests that these top-down compensatory processes are regulated by bottom-up processes caused by factors such as weather (Mutshinda et al. 2009; Power 1992; White 2004).

Different aspects of the weather are largely responsible for the temporal fluctuations in food and shelter, factors known to affect rodent abundance. Most rodents exhibit diets and foraging strategies that allow them to take advantage of temporal fluctuations in primary productivity (Hansson and Henttonen 1988). Effects of food limitation on rodent dynamics have been documented extensively in arid and semi-arid regions, where densities respond to the changes in primary productivity associated with the distribution of precipitation and temperature (Brown and Ernest 2002; Hansson 1979; Holmgren et al. 2006). Some species are also positively associated with winters characterized by deep, prolonged snow cover (Bilodeau et al., in press; Kausrud et al. 2008). These effects have been documented in northern North America and northern...
Eurasia, where snow cover depth is often above the hiemal threshold (i.e., 20-30 centimeters) – a depth of snow that usually results in small mammals remaining under the snow pack as opposed to regularly venturing to the surface. These rodents use the subnivian space under the snow to avoid predation while foraging and continuing to reproduce during the winter season. Despite the potential for these weather characteristics to influence rodent abundance, the effects of these extrinsic factors on rodent populations across broad spatial scales are not well understood.

Despite their importance to terrestrial communities on the northern Great Plains, few studies have examined landscape-scale fluctuations in abundance of grassland rodents. Rodents are prey to a wide diversity of predators, alter plant communities through consumption of vegetation and seeds, and provide habitat for other species through burrowing activities (Gibbons 1988; Sieg 1987). The highly variable, seasonal weather associated with the continental climate of the northern Great Plains has the potential to influence grassland rodent abundance across the landscape in several ways. Precipitation and temperature during the growing season may indirectly influence rodent abundance through their direct effect on primary productivity (Garsd and Howard 1981; Reed et al. 2007), whereas extreme winter conditions may influence the survival of these species. However, few studies have examined the effects of landscape-scale weather variation on the annual abundance of rodents in grassland ecosystems over long periods of time, particularly on the northern Great Plains of North America.

The objective of this study was to identify species-specific, rodent population responses to seasonal weather variation on the northern Great Plains of North America.
Annual variation in factors such as snow cover, rainfall, and temperature was hypothesized to influence annual rodent abundance across the landscape.

3.2 Methods and Materials

3.2.1 Study area

My study area encompassed 1.3 million hectares of the northern Great Plains in Alberta, Manitoba, and Saskatchewan, Canada (Fig. 1). This region has been heavily influenced by anthropogenic activities since the late 1800s; nearly 70% of the mixed-grass prairie has been converted for agricultural purposes, such as the production of cereal crops and livestock ranching (Samson et al. 2004). The northern Great Plains experiences a continental climate with a short growing season of 3 to 5 months (May – September), followed by long, cold winters (October – April). Annual mean precipitation is 454 mm and annual mean maximum and minimum temperatures are 8.1 and -4.1 °C, respectively. Extreme seasonal variation results in summer mean temperatures that are 22 – 28 °C higher than temperatures during the winter months. The majority of the annual average precipitation (70-80%) falls during the summer, most of which falls in June and July (Coupland 1950; McGinn 2010). The spatial distribution of precipitation also varies; Saskatchewan and Alberta receive the least amount of precipitation with annual averages of 300 - 350 mm falling as rainfall during the summer, and approximately 40 millimetres as snowfall during the winter. Manitoba receives the most precipitation with annual averages of 500 – 550 millimetres as rainfall and 60 millimetres or more as snowfall (McGinn 2010).
Figure 3.1 Burrowing owl pellet collection sites (black circles) and weather station locations (white circles) on the Mixedgrass prairie (dark gray) and Aspen Parkland (light gray) of the northern Great Plains of North America. Grey lines represent provincial boundaries, labelled at the top of the figure. The black circles outlined in white are reference points (right: Calgary, Alberta; left: Regina, Saskatchewan).
3.2.2 Small mammal sampling

I characterized the annual changes in abundance of several small mammal species by identifying their remains within burrowing owl (*Athene cunicularia*) pellets collected across the study area. Burrowing owls forage primarily for small mammals and do so within a foraging radius often no greater than 2 km from their nest (Haug and Oliphant 1990; Marsh 2012; Sissons et al. 2001). They exhibit functional relationships to fluctuating prey abundances, indicating that they prey on the most available species within flying distance of their nest (Marsh 2012; Poulin et al. 2001; Silva et al. 1995). Burrowing owls also cache prey items in the burrow entrances to their nests, suggesting that these owls kill more than the nest occupants can eat, capturing the variation in annual rodent abundances above the limits of predator satiation (Poulin and Todd 2006). The indigestible parts (i.e., bones and teeth) of the prey eaten by owls are regurgitated as pellets and deposited in large quantities at their nest or roost sites (Marti 1974). The bones within these pellets allow identification and quantification of the animals eaten by the owls.

Owl researchers made a focused effort to collect burrowing owl pellets from 1997 to 2011 at nesting sites across the Canadian prairies (Fig. 1). A total 1,181 burrowing owl nests were visited an average of 5 times during the breeding season (April – July). All nests visited between 1997 and 2002 were located on the Regina Plain south of Regina, Saskatchewan (Fig. 1). Nests visited between 2003 and 2011 were located in all three provinces; however, the nests located in Manitoba were visited in either 2010 or 2011 only (Fig. 1). To standardize the data for uneven sampling effort between nests and years, I included data only from nests where two or more visits occurred between May and June.
of each year, with the first and last visit occurring at least 14 days apart. Standardization was important because rodents identified from a single nest approximate all individuals depredated in May and June of each year; this level of approximation is applied to all nests included in statistical analyses. Of the 1,181 nests visited, 682 met criteria to be used in the statistical analyses. From these nests, a mean of 66 ± 43 $SD$ nests were visited annually with a mean of 36 ± 5 $SD$ days between the first and last pellet collection.

Pellets were processed in a 10% sodium hydroxide solution to dissolve the fur and provide clean bones and teeth for identification and quantification of species. Cranial and dental traits were used to identify species, and the minimum count of craniomandibular elements from either the left or right side was used to determine the minimum number of individuals of each species present in the pellets. Species abundances were then summed for each nest per year (using collections from May and June only). This produced a data set representing the annual abundances of rodent species at each nest; raw abundances were used in all subsequent statistical analyses. A total of 33,697 individuals were identified, representing eleven different rodent species (Table 1). Deer mice made up 64% of these individuals, followed by meadow voles at 19%, and sagebrush voles at 13% of the total individuals sampled (Fig. 2). The remaining species were not included in analyses because combined they made up less than 4% ($n = 1,128$) of the total individuals sampled, and all had a mean abundance of less than one individual per sample (Table 1).
Table 3.1 Total abundance and average annual abundance (± standard deviation) of small mammal species found within burrowing owl (BUOW). Bolded species were included in the generalized linear mixed models.

<table>
<thead>
<tr>
<th>Species</th>
<th>Total Abundance</th>
<th>Annual Average (± SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deer Mouse (Peromyscus maniculatus)</td>
<td>21,701</td>
<td>14 ± 18</td>
</tr>
<tr>
<td>Meadow Vole (Microtus pennsylvanicus)</td>
<td>6,473</td>
<td>4 ± 9</td>
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<tr>
<td>Sagebrush Vole (Lemmiscus curtatus)</td>
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<tr>
<td>Olive-Backed Pocket Mouse (Perognathus fasciatus)</td>
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<td>Northern Grasshopper Mouse (Onychomys leucogaster)</td>
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<td>Western Harvest Mouse (Reithrodontomys megalotis)</td>
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<td>0 ± 0</td>
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<tr>
<td>Western Jumping Mouse (Zapus princeps)</td>
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<td>0 ± 0</td>
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</tr>
<tr>
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<td>0 ± 0</td>
</tr>
<tr>
<td>Red-Backed Vole</td>
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<td>0 ± 0</td>
</tr>
<tr>
<td>Species</td>
<td>Abundance</td>
<td>Rarity</td>
</tr>
<tr>
<td>-------------------------</td>
<td>-----------</td>
<td>--------</td>
</tr>
<tr>
<td><em>Myodes gapperi</em></td>
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<td>0 ± 0</td>
</tr>
<tr>
<td><em>Dipodomys ordii</em></td>
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</table>
Figure 3.2 Average annual abundance of deer mice (light grey line), sagebrush voles (dark grey line), and meadow voles (black line) per owl nest between 1997 and 2011 across the northern Great Plains of central Canada.
3.2.3 Weather data

Weather stations were an average 31 ± 14 kilometres from burrowing owl nests. I used a weather data set generated from interpolating weather measurements from known locations to estimate the weather measurements for surrounding locations where it was not measured, assuming that weather exhibits autocorrelation across geographic space. Daily precipitation, snow depth, minimum temperature, and maximum temperature between 1995 and 2011 were taken from 35 to 64 weather stations maintained by Environment Canada (Fig 1.). Daily snow depth was used to determine the number of days snow cover depth was at least 20 centimeters deep (snow cover duration) for the winter of (current year) and the winter before (previous year) small mammal sampling. Daily rainfall was used to determine total rainfall during May and June of the current spring and from May to September of the previous summer. Growing degrees were calculated as the sum of average temperatures above the base temperature required for plant growth, in this case 5°C (Miller et al. 2002). Growing degrees of the current spring included only May and June, while accumulated growing degrees of the previous summer included May to September. Growing degrees, rainfall, and snow cover duration of the current and previous year for each nest location was then interpolated using the Inverse Distance Weighted tool in ArcGIS 10 (ESRI 2011). This provided a data set characterizing weather variation of the current and previous year for each nest.

3.2.4 Statistical analyses

The influence of weather on the annual abundance of each species was examined using generalized linear mixed models and Akaike Information Criterion (AIC) model selection. Generalized linear mixed models with a Poisson distribution and log link were
used to account for the uneven influence of spatial variation between nests, and the potential non-linear relationships between species count data and weather variation (Gillies et al. 2006). Fixed effects included growing degrees, rainfall, and snow cover duration of the current and previous year. Nest site locations were used as a random effect to minimize the influence of spatial variation between nests (Gillies et al. 2006). The model parameter estimates and standard errors were standardized to a mean of 0 ± 0.5 SD prior to model selection, allowing comparison of the strength of parameter estimates relative to each other (Grueber et al. 2011).

Maximum likelihoods from all possible subsets of the global model containing all variables were used to obtain AIC scores and build the candidate set of explanatory models for each species. The most parsimonious model (top model) was that with the lowest AIC score (i.e., greatest support) out of the candidate set. Competing models were those within two delta AIC units of the top model (Burnham and Anderson 2002). Model averaging and 85% confidence intervals of all models within 10 delta AIC units of the top model were used when competing models were present to provide more robust parameter estimates (Grueber et al. 2011). Inference was made from parameters whose confidence intervals did not pass through zero. Pseudo $R^2$ was calculated for each top model to determine the approximate amount of temporal variation in the annual abundance of each species that was explained by the weather.

ArcMap 10 was used for all species and weather data preparation (ESRI 2011), and all statistical analyses were conducted in R Project for Statistical Computing 2.15.2 (R Development Core Team 2012), using packages lme4 (Bates et al. 2012), arm (Gelman and Su 2013), and MuMIn (Barton 2013).
3.3 Results

3.3.1 Deer Mice

The top model characterizing deer mouse abundance included all fixed effects of the current year and summer precipitation of the previous year, accounting for 6% of the variation in annual deer mouse abundance (Table 2). Snow cover duration of the previous winter and growing degrees of the previous summer were included in three competing models. However, model averaged 85% confidence intervals passed through zero for both of these parameters (85% CI\textsubscript{GDDT1} = -0.08, 0.02; 85% CI\textsubscript{SNOWT1} = -0.01, 0.06; Table 2), indicating little potential influence on deer mouse populations. Snow cover duration of the current winter had the greatest relative effect; deer mouse abundance decreased 23% following a winter with above average deep snow cover duration. Deer mouse abundance also exhibited negative associations with precipitation of the current spring and previous summer, corresponding to 9% and 29% decreases in abundance with above average precipitation, respectively. In contrast, deer mouse abundance was positively associated with growing temperatures of the current spring, corresponding to a 5% increase in abundance during years of above average growing temperatures. Thus, weather variation had little effect on deer mouse abundance, but populations generally responded positively to warm, dry summers and winters with little snow.
Table 3.2 Top model, intercept only model, and all models within 10 delta AIC units of the top model (candidate set) explaining the annual dynamics of deer mice, followed by model averaged parameter estimates, standardized estimates, standard errors (Unconditional SE), and 95% confidence intervals (CI). Included in all models was the nest collection site as a random effect. Pseudo $R^2$ was calculated to determine the approximate amount of variation explained by the weather variables of the top model. Acronyms represent weather characteristics ($\text{GDD} =$ accumulated growing degrees; $\text{PREC} =$ precipitation; $\text{SNOW} =$ number of days snow cover depth greater than 20 cm) and the year they were measured relative to small mammal sampling ($T_1 =$ year prior to small mammal sampling, otherwise weather measured during same year of small mammal sampling).

<table>
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<th>$w_i$</th>
<th>Pseudo $R^2$</th>
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<td>0.03</td>
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3.3.2 Sagebrush Voles

Sagebrush vole annual abundance was affected by all fixed effects of the previous year, as well as summer precipitation and winter snow cover duration of the current year (Table 3). The top model accounted for 19% of the variation in sagebrush vole annual abundance, indicating a three-fold higher effect compared to deer mouse populations. Three competing models also included growing degrees of the current spring as a fixed effect. However, model averaged 85% confidence intervals suggested all parameters except growing degrees of the current spring had an effect on the spring abundance of sagebrush voles (85% CI$_{\text{GDD}}$ = -0.25, 0.08; Table 3). Sagebrush vole abundance decreased 50% when summer growing temperatures and deep snow cover duration were above average during the previous year. There was a 17% decrease in abundance when precipitation was above average in the previous summer. Fixed effects of the previous year had the greatest relative influence, indicating that this species responds to weather variation a year after the change in weather occurs. These results suggest sagebrush vole populations increase following cool, dry summers and winters with little snow.
Table 3.3 Top model, intercept only model, and all models within 10 delta AIC units of the top model (candidate set) explaining the annual dynamics of sagebrush voles, followed by model averaged parameter estimates, standard error (Unconditional SE), and 95% confidence intervals (CI). Included in all models was the nest collection site as a random effect. Pseudo $R^2$ was calculated to determine the approximate amount of variation explained by the weather variables of the top model. Acronyms represent weather characteristics (GDD = accumulated growing degrees; PREC = precipitation; SNOW = number of days snow cover depth greater than 20 cm) and the year they were measured relative to small mammal sampling ($T_1$ = year prior to small mammal sampling, otherwise weather measured during same year of small mammal sampling).

<table>
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<th>Model</th>
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<th>Model Averaging</th>
<th>Parameter</th>
<th>Estimate</th>
<th>Unconditional SE</th>
<th>85% CI (lower)</th>
<th>85% CI (upper)</th>
</tr>
</thead>
</table>

69
<table>
<thead>
<tr>
<th></th>
<th>Intercept</th>
<th>1.47</th>
<th>0.06</th>
<th>1.39</th>
<th>1.56</th>
</tr>
</thead>
<tbody>
<tr>
<td>SNOW$_{T1}$</td>
<td>-0.94</td>
<td>0.10</td>
<td>-1.09</td>
<td>-0.79</td>
<td></td>
</tr>
<tr>
<td>PREC$_{T1}$</td>
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<td>-0.84</td>
<td>-0.56</td>
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</tr>
<tr>
<td>GDD$_{T1}$</td>
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<td>-0.70</td>
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</tr>
<tr>
<td>PREC</td>
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</tr>
<tr>
<td>SNOW</td>
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<td>0.11</td>
<td>0.38</td>
<td></td>
</tr>
<tr>
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<td>0.11</td>
<td>-0.25</td>
<td>0.08</td>
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3.3.3 Meadow Voles

Weather had the greatest influence on meadow vole annual abundance; the top model included all fixed effects and explained 32\% of the variation in their annual abundance. Thus, weather explained five times more variation in meadow vole abundance compared to deer mice, and two times more variation compared to sagebrush voles (Table 3). Model averaging was not necessary because there were no competing models and none were within 10 delta AIC units of the top model. Evaluation of the 85\% confidence intervals found all parameters affected the annual abundance of meadow voles. Snow cover duration of the current year was at least three times as influential as all other fixed effects, and associated with meadow vole populations exhibiting up to five-fold increases in abundances (population irruption) following winters with above average deep snow cover duration. Meadow vole abundances decreased 50\% and 11\% in years of above average precipitation during the current spring and previous summer, respectively. Thus, meadow voles appear to be considerably influenced by weather variation; population abundances increased following summers with little rainfall and irrupted following winters characterized by prolonged deep snow cover.
Table 3.4 Top model, intercept only model, parameter estimates, standard errors, and confidence intervals explaining annual meadow vole dynamics. Included in both models is the nest collection site as a random effect. Acronyms represent weather characteristics (GDD = accumulated growing degrees; PREC = precipitation; SNOW = number of days snow cover depth greater than 20 cm) and the year they were measured relative to small mammal sampling ($T_1 =$ year prior to small mammal sampling, otherwise weather measured during same year of small mammal sampling).

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>AIC</th>
<th>ΔAIC</th>
<th>$w_i$</th>
<th>Pseudo R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>GDD+PREC+SNOW+GDD$<em>{T_1}$+PREC$</em>{T_1}$+SNOW$_{T_1}$</td>
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<tr>
<td>INTERCEPT-ONLY</td>
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<td>1518</td>
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</table>

<table>
<thead>
<tr>
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<th>Standard Error</th>
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<th>85% CI (upper)</th>
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</tr>
<tr>
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<td>1.13</td>
</tr>
<tr>
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<td>0.46</td>
<td>0.30</td>
</tr>
<tr>
<td>PREC$_{T_1}$</td>
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<td>-0.41</td>
</tr>
<tr>
<td>SNOW$_{T_1}$</td>
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<td>0.06</td>
<td>0.36</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>GDD_{T1}</td>
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<td></td>
</tr>
<tr>
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<td>-------</td>
</tr>
<tr>
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<td>-0.22</td>
<td>0.06</td>
<td>-0.13</td>
<td>-0.30</td>
</tr>
<tr>
<td>PREC</td>
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<td>0.05</td>
<td>-0.10</td>
<td>-0.24</td>
</tr>
</tbody>
</table>
3.4 Discussion

This is the first long-term study of rodent population fluctuations on the northern Great Plains of North America. Most studies of this nature represent rodent dynamics in desert ecosystems limited primarily by precipitation. In these arid regions, positive associations between the amount and distribution of precipitation and rodent densities are indicative of the crucial role weather plays in the dynamics of desert rodent communities (Brown and Ernest 2002; Ernest et al. 2000; Meserve et al. 2011; Shenbrot et al. 2010; Thibault et al. 2010). Precipitation is less limiting to primary productivity on the northern Great Plains of North America, although still a contributing factor to vegetation structure and composition. This region is also characterized by a cool, continental climate of extreme seasonal variation (Barker and Whitman 1988; Coupland 1950; McGinn 2010) that has the potential for considerable effects on landscape-scale rodent population fluctuations. However, only one of the three most abundant rodent species was largely influenced by fluctuating weather conditions, suggesting that weather variation may not play as dominant a role in driving rodent population fluctuations in grassland ecosystems compared to more arid regions.

Habitat type may influence rodent population responses to environmental change. Deer mice and sagebrush voles exhibited the weakest associations with weather variation of the three species considered, indicating that weather had little effect on the annual abundance of these two species. However, using the same data set, I found both species make up notably greater proportions of small mammal composition in cropland and native grassland compared to other habitat types at the landscape scale, respectively (data not shown). Sagebrush vole average annual abundances across the landscape were higher
(8 ± 3 individuals/sample) compared to regions dominated by cropland (2 ± 1 individuals/sample), whereas deer mice exhibited the inverse relationship (landscape = 18 ± 6 individuals/sample; cropland dominated = 24 ± 9 individuals/sample). These habitat affinities suggest that weather variation causing population-level fluctuations in rodent abundances may be detectable only within habitats where their densities are notably higher. My study occurred at a scale encompassing many different habitat types and did not differentiate population fluctuations between habitats, which may have limited my ability to identify the true relationship between rodents, their affiliated habitats, and weather variation. Future studies of fluctuations in deer mice and sagebrush vole populations should examine not only other environmental factors occurring across the landscape, but also whether temporal patterns in population fluctuations differ between habitat types.

Meadow voles were the only species whose annual abundances were largely influenced by weather variation across the landscape. Population densities were positively associated with years characterized by deep snow cover that persisted throughout the winter. Snow cover reaching a depth of 20 cm or more (hiemal threshold) insulates the ground surface against cold and variable ambient temperatures, maintaining a stable ground temperature close to freezing (Courtin et al. 1991; Pruitt 1957). These temperatures increase individual survival of species adapted to inhabiting snow cover close to the ground surface (subnivian space) by reducing physiological stress associated with maintaining body temperatures in extreme environments (Bilodeau et al., in press; Courtin et al. 1991; Duchesne et al. 2011; Reid et al. 2012). Snow cover also reduces mortality due to predation by providing protective cover, under which individuals carry
out most daily activities during the winter (Duchesne et al. 2011; Korpimäki et al. 2004; Reid et al. 2012). Furthermore, these conditions facilitate rapid population growth by extending the reproductive season past the limits of the plant growing season (Bilodeau et al., in press; Reid and Krebs 1996; Reid et al. 2012), resulting in irruptions of meadow vole populations across the landscape.

Weather plays an important role in determining the cyclicity, or lack thereof, in the dynamics of rodent populations. Rodent populations characterized by recurring high densities at regular intervals (population cycles) are often found in highly seasonal environments, where weather indirectly affects population growth by increasing resource availability and subsequent secondary productivity and/or individual survival (Andreassen et al., in press; Bilodeau et al., in press; Duchesne et al. 2011; Hansson and Henttonen 1985; Kausrud et al. 2008; Korpimäki et al. 2004; Reid and Krebs 1996; Reid et al. 2012). Consistent patterns in the frequency and magnitude of specific weather events (i.e., snow cover or drought) are proposed to drive cyclicity in the dynamics of rodent species inhabiting highly seasonal environments (Korpimäki et al. 2004). For example, several studies have found that snow conditions (i.e., depth, duration, density) can affect the amplitude and periodicity of lemming population cycles on different continents (Bilodeau et al., in press; Duchesne et al. 2011; Kausrud et al. 2008; Reid and Krebs 1996; Reid et al. 2012). However, regions where snow cover reaches the hiemal threshold infrequently or irregularly are characterized by rodent dynamics with corresponding infrequent or irregular irruptions (Hansson and Henttonen 1985; Kausrud et al. 2008). The irregular irruptions of meadow vole populations on the northern Great
Plains further emphasize the important role weather plays in the population fluctuations of rodents in highly seasonal environments.

Irruptions in meadow vole populations may have significant effects on rodent community dynamics and predator-prey relationships on the northern Great Plains. Over the last 15 years, meadow vole abundances increased two to five fold above average annual abundance for this time period following winters of above average snow cover duration (i.e., irruptive years). Furthermore, average annual abundance of meadow voles changed from 26% of the total individuals from all three species combined to 53% in irruptive years, supplanting deer mice as the most abundant rodent during these irruptions. These high densities may alter rodent composition further through the propensity of meadow voles to exclude deer mice and red-backed voles (*Myodes gapperi*) from local habitats on the northern Great Plains (Findley 1954; Morris 1969; Reich 1981). Previous studies have also observed the effects of these irruptions cascade through higher trophic levels as regional predator densities respond by increasing reproduction and/or immigration in regions experiencing local meadow vole irruptions (Poulin et al. 2001). These cascading effects have significant implications for population fluctuations and geographic distributions of many species across the landscape, illustrating the importance of the mechanisms behind meadow vole irruptions (i.e., persistent deep snow cover) for trophic dynamics on the northern Great Plains.

Meadow vole irruptions on the northern Great Plains have been observed in previous studies; however, until now, we knew little about the mechanisms driving these population changes. Previous studies focused on identifying predator responses to changing prey densities, noting in particular the meadow vole irruption in 1997 (Poulin
My study is the first to examine the effects of weather on these irruptions at the landscape scale, the scope of which was logistically only possible through the use of owl pellets. My results identify the influence of the duration of deep snow cover (i.e., above 20 cm) on meadow vole densities and provide further insight into the role weather plays in driving fluctuations in the abundances of grassland rodent species.

3.5 References


CHAPTER 4. GENERAL DISCUSSION

4.1 Conclusions

The objectives of my thesis were to examine the influence of landscape-scale environmental factors on the spatial composition and annual abundance of rodents and shrews (small mammals) on the northern Great Plains of North America. I hypothesized that weather conditions, soil characteristics, and agricultural land use would determine the distributions of small mammals within their geographic ranges, while weather conditions would largely affect population fluctuations in abundance of grassland small mammals across the landscape. In chapter 2, I show that soil texture is the primary landscape feature driving small mammal composition across the landscape, whereas agricultural land use significantly altered the spatial composition of these assemblages. In chapter 3, I show that weather had little influence on some rodent species annual abundances (deer mice and sagebrush voles), but was responsible for landscape-scale population irruptions in meadow voles. These results emphasize the importance of examining species-habitat associations at multiple spatial and temporal scales to identify the hierarchical nature in which species are affected by the heterogeneous distributions of available resources.

My study provides an unprecedented perspective on species-habitat associations across broad spatial and temporal scales in grassland environments. Most small mammal research is conducted at scales that limit perspective to individual habitat selection and specific vegetation or habitat types (Bowman et al. 2000; Hanser et al. 2011; Jorgensen 2004; Morris 1987). Results of these studies are often extrapolated to explain species distributions and dynamics across broader scales (Jorgensen 2004). My study
encompassed 4.3 million hectares of the northern Great Plains using 1,823 burrowing and
great horned owl samples collected over 15 years. The area sampled by an individual owl
is equivalent to a single trapping grid, indicating that my study included the equivalent of
1,823 trapping grids, much greater than the typical small mammal study (> 50% studies
used ≤ 3 trapping grids; Jorgensen 2004). Furthermore, individual burrowing and great
horned owls were capable of sampling 1,963 hectares and 7,850 hectares of landscape
heterogeneous in habitat types, respectively, whereas most small mammal studies are
limited to a few vegetation types (>77% studies used ≤ 2 vegetation types; Jorgensen
2004). To my knowledge, this is the largest study in spatial scale ever conducted on
grassland small mammals, which provides a truly landscape-scale look at the
environmental factors affecting their spatial composition and long-term, population-level
responses to environmental change.

The scale of this study could not have been achieved without the use of owl
pellets to sample small mammal assemblages. Compared to conventional trapping
methods, owl pellets allow for the collection of a greater number of samples from a larger
area at relatively low cost. Both owl species forage relatively indiscriminately among
habitat types, indicating that the small mammal composition of their pellets is an accurate
representation of their proportional abundance within foraging radii of nest and roost sites
(Jaksic and Marti 1984; Poulin et al. 2001; Rusch et al. 1972; Silva et al. 1995;
Zimmerman et al. 1996). In contrast, trapping occurs in only a few distinguishable habitat
types, which may introduce biases by focusing on human perceived habitat differences
rather than habitats perceived by the small mammals themselves (Jorgensen 2004; Morris
1987). Owl pellet collection also allowed me to sample all small mammal species
available as prey to burrowing and great horned owls. Some of these species are difficult to sample using traditional sampling methods because traps can be biased towards certain species depending on a variety of factors (i.e., trap size and type, location, bait type, etc.; Hanser et al. 2011; O’Farrell 1994; Wiener and Smith 1972). Thus, owl pellets proved to be a useful method for sampling small mammal assemblages across broad spatial and temporal scales, which should be considered for future broad scale studies on small mammal assemblages.

Like all trapping methods, using owl pellets also has its potential biases, the results from which should be analysed within the context of some assumptions. Any trap or owl should be able to sample small mammal communities in perfect correlation to the proportional abundance of species within the landscape. However, some small mammal species exhibit habitat associations and/or behavioral attributes that limit their availability as prey to owls. For example, jumping mice often occur in dense vegetation and use saltatorial locomotion to avoid predators, which may make them more difficult to catch (Hart et al. 2004; Whitaker 1972). Both owl species also exhibit differential habitat associations and hunting strategies that most likely affect where and when they forage for prey. For instance, burrowing owls select nesting sites at least partially based on soil characteristics, suggesting they are constrained to foraging within areas of specific soil characteristics (Poulin et al. 2005). Burrowing owls may also avoid foraging in dense vegetation (i.e. crops), indicating that they may select foraging habitat where predator vigilance can be maintained (Haug and Oliphant 1990; Marsh 2012; Sissons et al. 2001). Great horned owls are strictly nocturnal predators, indicating that they depredate only species active at night (Marti 1974; Zimmerman et al. 1996). Despite these differences, a
comparison of the composition of my two owl pellet datasets found both owl species
depredated the most available species within foraging range of their nest and roost sites,
indicating that the prey remains within their pellets is reflective of the proportional
abundance of these species within habitats surrounding their nest or roost sites.
Therefore, I believe that using both owl species to sample small mammals on the northern
Great Plains provided a relatively accurate representation of their assemblages across the
landscape at a scale that would have been impossible to examine using conventional
trapping grids.

4.2 References

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