SMALL MAMMAL COMMUNITIES IN TWO GRASSLAND ECOSYSTEMS IN BRITISH COLUMBIA, CANADA

by

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DEDICATION

To all the mice, voles and shrews who begrudgingly allowed themselves to captured, handled, tagged and weighed during the course of this study.

To the ones who led us on a merry chase:

Big Hungry Joe
Brandine
Buckshot
Cilantro
Cousin Merl
Daisy Duke
Dirty Rotten Scoundrel
Dozer
Muffy
Penelope
Ruprecht the Monkey Boy
Sir Sniffs-A-Lot
Veruca Salt

To Barbie Lightning II, who carried my gear and never once let me down.

And finally to deer mouse # 2101,
whose contribution shall not be forgotten.

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ABSTRACT

This study compared small mammal communities between upper and lower elevation grassland systems using mark-recapture, and examined third and fourth order resource selection of daytime refuge sites by deer mice (*Peromyscus maniculatus*) in lower elevation grasslands using radio telemetry, near Kamloops, British Columbia, Canada. Small mammal densities showed high levels of variability. Deer mice were found in both habitat types, and survival rates between the two grassland types were not significantly different. Voles (*Microtus* spp.) were confined to the upper grasslands. Radio-collared deer mice selected daytime refuge sites in areas with increased slope and decreased litter (third order), at sites with large-diameter shrubs, decreased levels of bare ground and increased levels of coarse woody debris (fourth order). Land managers can use this information to begin filling knowledge gaps in species-specific recovery plans, and to help inform anthropogenic-related activities in grasslands so as to maintain rodent populations on the landscape.

Key words: British Columbia, grassland, mark-recapture, *Microtus*, *Peromyscus maniculatus*, radio telemetry, resource selection, small mammal

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CHAPTER 1 – INTRODUCTION: OF MICE AND MEN AND GRASSLANDS

Why are some species abundant in certain habitats, and yet absent from others? This seemingly simple question has formed the basis of a large body of scientific work, and is a matter ecologists continue to investigate. In general, the distribution and abundance of a particular species can be influenced by dispersal habits, biotic (e.g. competition) and abiotic (e.g. weather) factors, and by the selection and exploitation of resources (e.g. food, shelter) available on the landscape (Krebs 1994). As adequate quantities of resources are needed to support populations, understanding which resources are important to animals provides valuable insights into how they meet their requirements for survival (Manly et al. 2002).

The manner in which certain organisms choose to occupy a particular habitat or exploit a resource can be viewed as a hierarchical process in which individuals make selection choices at varying spatial scales. Johnson (1980) described this hierarchy of choices as ordered selections. For example, members of a species may occupy a number of distinct areas (e.g. forest vs. grassland) within the extent of its range: a first order selection. Within each area, individuals may occupy a home range (second order selection), and within each home range select areas for specific activities such as feeding or nesting (third order selection). The location where a specific activity occurs (e.g. nest site location) may be considered a fourth order selection. The selection criteria may vary at each level (Johnson 1980, Orians and Wittenberger 1991), and so to gain better insight into why a species occupies a certain area or displays changes in abundance, it is essential to understand which resources may be important to it at various spatial scales.

Research on species within the Order *Rodentia* can offer excellent insights into resource and habitat selection processes, and these animals have been extensively studied with respect to this field (Krebs 1994). Their ubiquitous nature (i.e. found on all continents except Antarctica and in a vast range of habitats), relatively short breeding cycle and varied social structures have allowed scientists to use rodents to study a host of ecological processes, including population cycles (e.g. Krebs et al. 1973, Korpimäki and Krebs 1996, Krebs 1996, Boonstra et al. 1998, Korpimäki et al. 2004, Getz et al. 2006) and competition and community assembly rules (e.g. Valone and Brown 1995, Brown et al. 2000, 2002, Eccard and Ylönen 2003). Rodents have been extensively studied in forest systems (e.g. Carey and Johnson 1995, Carey and Harrington 2001, Moses and Boutin 2001, Sullivan and Sullivan 2001, 2004, Sullivan et al. 2001, Klenner and Sullivan 2003, 2009, Larsen et al. 2007, Oaten and Larsen 2008), in desert and desert/grassland systems (e.g. Brown and Heske 1990, Valone and Brown 1995, Brown et al. 2000, Brown and Ernest 2002, Hernandez et al. 2005) and in the temperate grasslands of North America (e.g. French et al. 1976, Grant and Birney 1979, Grant et al. 1982, Brady and Slade 2001, 2004, Howe and Brown 2001, Howe et al. 2002, 2006, Howe and Lane 2004, Reed et al. 2007).

Grasslands, not surprisingly, are those areas where grasses (*Poaceae*) and grass-like plants and/or forbs dominate the vegetative cover. As with rodents, grasslands are found on every continent except Antarctica, and generally fall into two broad categories: temperate and savannah. The former is characterized by the complete lack of trees, and the latter containing scattered individual trees (Daubenmire 1978, Wikeem and Wikeem 2004). Temperate grasslands are known by many names, from the "puszta" of Hungary and the "pampas" of Argentina and Uruguay, to the "veldts" of South Africa and the "steppes" of Russia (Campbell et al. 1999). In North America, grasslands occupy approximately 28% of the continent's land area (Wikeem and Wikeem 2004), with the most prominent grassland being the central great plains of the United States of America.

Small mammals are important in the structuring and functioning of grasslands. In these systems, rodents play vital roles as consumers of invertebrate species (Churchfield et al. 1991), as seed dispersers (La Tourrette et al. 1971, McAdoo et al. 1983) and consumers (Hulme 1994, Edwards and Crawley 1999), and as consumers of herbaceous and woody material (Lindroth and Batzli 1984, Howe et al. 2002, 2006). They provide ecological functions as prey for a variety of grassland predators (Reich 1981, Sera and Early 2003), and as dispersers of spores of mycorrhizal fungi (Maser et al. 1988). Further to their important trophic position in grassland systems, some rodents act as ecological engineers who increase landscape heterogeneity by establishing unique patches different from the surrounding landscape, and create habitat for other plant and wildlife species (Davidson and Lightfoot 2008, Davidson et al. 2008). Their exceptional abilities to drastically alter grassland vegetation and processes (Keesing 2000, Howe and Lane 2004, Howe et al. 2006) highlight the need to understand how rodent populations change temporally and spatially across different grassland ecosystems.

In British Columbia, Canada, grasslands cover only about 1% of the land base (0.74 million hectares) scattered over 11° of latitude and 25° of longitude, and can be divided into two broad groups: the cooler grasslands found north of 52° N latitude, and the hotter semi-arid grasslands which occur south of 52° N latitude where almost 90% of the province's grasslands occur (Wikeem and Wikeem 2004). Previous studies into the organization of these semi-arid grasslands revealed they have a definite sequence of vegetative zones that occur on an elevation/precipitation gradient and divide the grasslands into three fairly distinct zones: the lower, middle and upper grassland zones (Tisdale 1947, van Ryswyk et al. 1966). The lower grasslands are confined to valley bottoms, and are the hottest and driest of the grassland systems (Figure 1.1). Vegetation in this zone consists of widely spaced bunchgrasses such as bluebunch wheatgrass (*Pseudoroegneria spicata*) associated with big sagebrush (*Artemisia tridentata*). The inter-shrub areas often are bare or partially lichen-covered (Tisdale 1947, van Ryswyk et al. 1966). The cooler, more mesic upper grassland zone is characterized by nearly continuous grass coverage, the lack of shrubs, greater plant richness, higher amounts of yield and substantive levels of vegetative litter (Figure 1.1). In this zone, rough fescue (*Festuca campestris*) can be the dominant plant species on northern and eastern slopes, and often co-dominates with *P. spicata* on more xeric sites (Tisdale 1947, van Ryswyk et al. 1966). The middle grasslands are transitional areas between the lower and upper grassland zones, with moderate levels of grass coverage, plant richness, and vegetative litter. Shrub species prevalent in the lower grasslands mostly are absent from this zone, as are most specimens of *F. campestris*. Instead, species such as needle-and-thread grass (*Hesperostipa comata*), Sandberg bluegrass (*Poa secunda*) and *P. spicata* can dominate

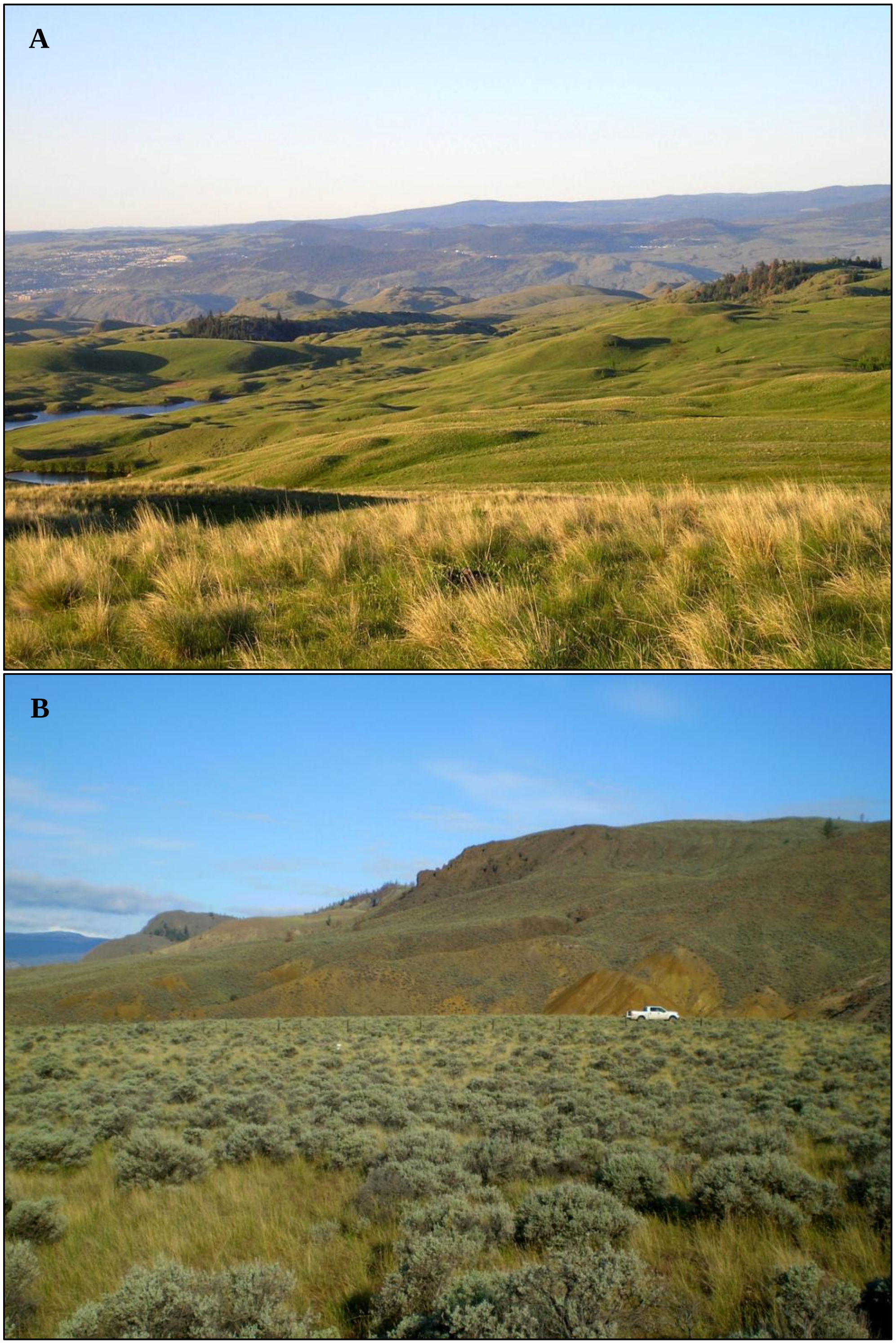

Figure 1.1. Photographs of typical upper grassland (A) and lower grassland (B) landscapes.

the landscape of middle grassland climax communities (Tisdale 1947, van Ryswyk et al. 1966).

Although British Columbia's grasslands constitute only 1% of the province's land base, they are utilized to some degree by 30% of the at-risk species in the province (Wikeem and Wikeem 2004). A number of these species, including the burrowing owl (*Athene cunicularia*), badger (*Taxidea taxus*), Great Basin gopher snake (*Pituophis catenifer deserticola*), and the western rattlesnake (*Crotalus oreganus*) depend on small mammals as sources of prey, further highlighting the need to understand small mammal community dynamics in grassland settings.

The ultimate goal of my research was to increase the knowledge of small mammal communities in temperate grasslands of British Columbia, Canada. To gain a more complete understanding of these communities, my investigation had two fundamental objectives:

1. To collect and compare small mammal population and demographic information, as well as habitat data, across two grassland communities; and
2. To examine the third and fourth order resource selection of a specific habitat feature by a dominant semi-arid grassland rodent.

To accomplish the first objective, an intensive small mammal live-trapping and mark-recapture program took place from 2006 through 2008 using study sites in the upper and lower grasslands. Small mammal densities, demographics and rates of apparent survival were compared between the two grassland types, as were a number of habitat characteristics, in order to confirm differences between the two grassland types. This work is presented in Chapter 2 of this thesis. My second objective was accomplished by examining the use of daytime refuge sites by deer mice (*Peromyscus maniculatus*) in the lower grasslands using radio telemetry techniques. Chapter 3 details this work. In Chapter 4, I discuss the potential management implications of my study.

My research was conducted in grassland systems near Kamloops, British Columbia, Canada (50°43’ N; 120°25’ W). In total 10 sites were used for the study, with 5 occurring in each grassland type. Eight sites were utilized for the majority of the small mammal trapping activities, while an additional two were established in the fall of 2007 to investigate the over-winter survival of small mammals (Figure 1.2). Following provincial terminology, all of the lower grassland sites occurred within the Thompson Very Dry Hot Bunchgrass Variant biogeoclimatic zone, and the upper grassland sites were situated within the grassland phase of the Thompson Very Dry Hot Interior Douglas-Fir Variant (termed ‘BGxh2’ and ‘IDFxh2a’ respectively, by Meidinger and Pojar 1991). The eight main sites were established in 2006 by researchers at Thompson Rivers University (M. Rankin working under the supervision of K. Larsen and L. Fraser), and some trapping data also were collected that year. I incorporated these data into parts of this thesis, using it to provide a more thorough picture of the small mammal communities through time.

Climate in the area of my study generally is driven by weather systems moving east from the Pacific Ocean, as well as by local topography (Tisdale 1947). As the study area is situated within the rain shadow of the Coast and Cascade mountains, the local climate is typical of the dry interior portion of the province. Precipitation levels follow the previously-described elevation gradient, varying from about 240 mm in lower grasslands at the valley bottom to 380 mm in grasslands above 850 m elevation (Wikeem and Wikeem 2004), with the 30-year average (1976-2005) annual precipitation, as recorded at the Kamloops International Airport within the lower grasslands, being 287 mm (data compiled from Environment Canada’s National Climate Data and Information Archive available at: http://climate.weatheroffice.gc.ca/). Much of the precipitation falls during the summer months in the form of thunder showers (Tisdale 1947), and relatively less during winter months. An examination of the mean monthly total precipitation for the 30 years previous to the study and the mean monthly total precipitation that occurred during the study indicates that the study period may have been drier than the years preceding it (Figure 1.3).

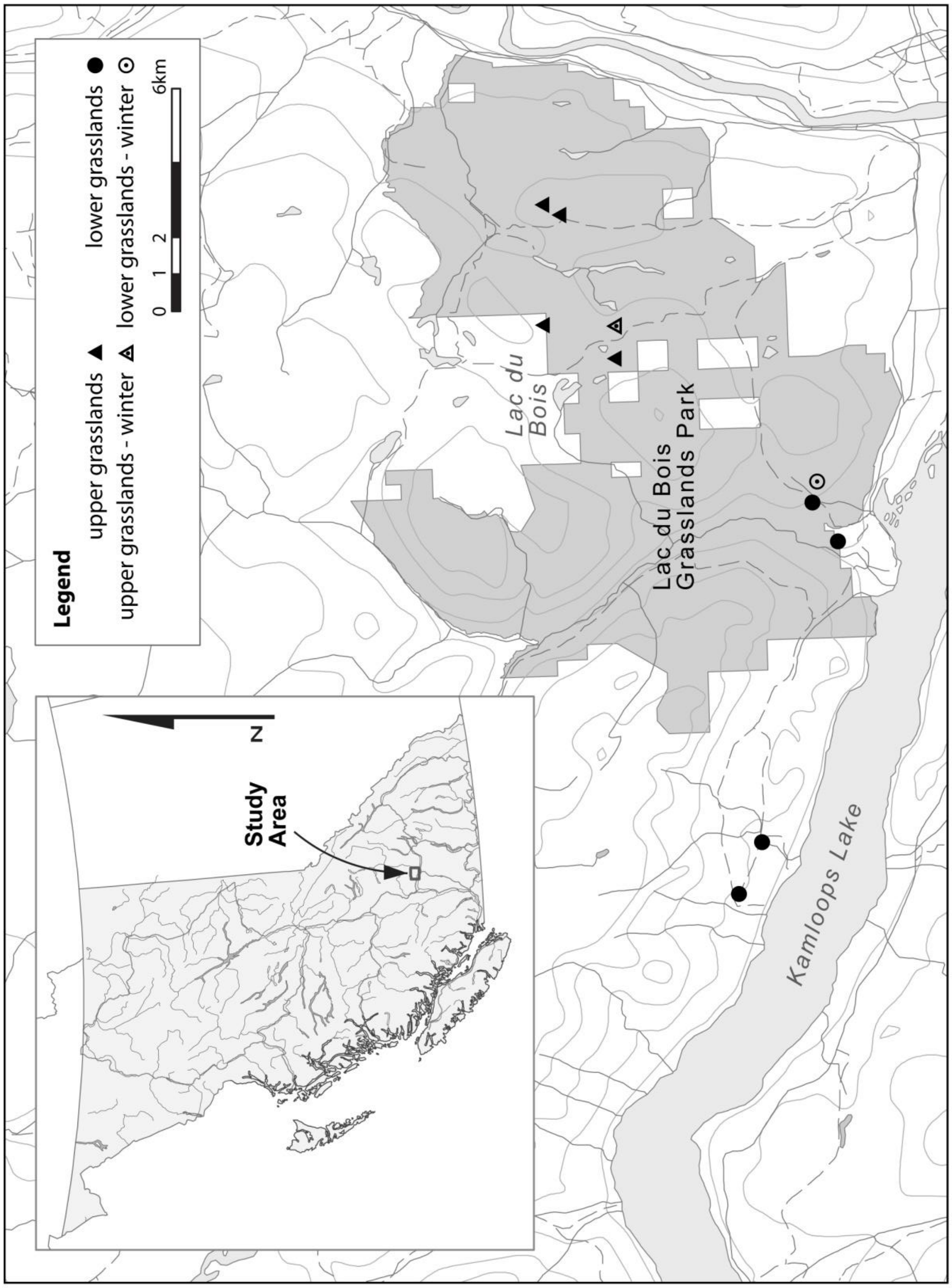

Figure 1.2. Study site locations in and around Lac du Bois Grasslands Provincial Park, near Kamloops, British Columbia, Canada. Map developed by M. Wolowicz.

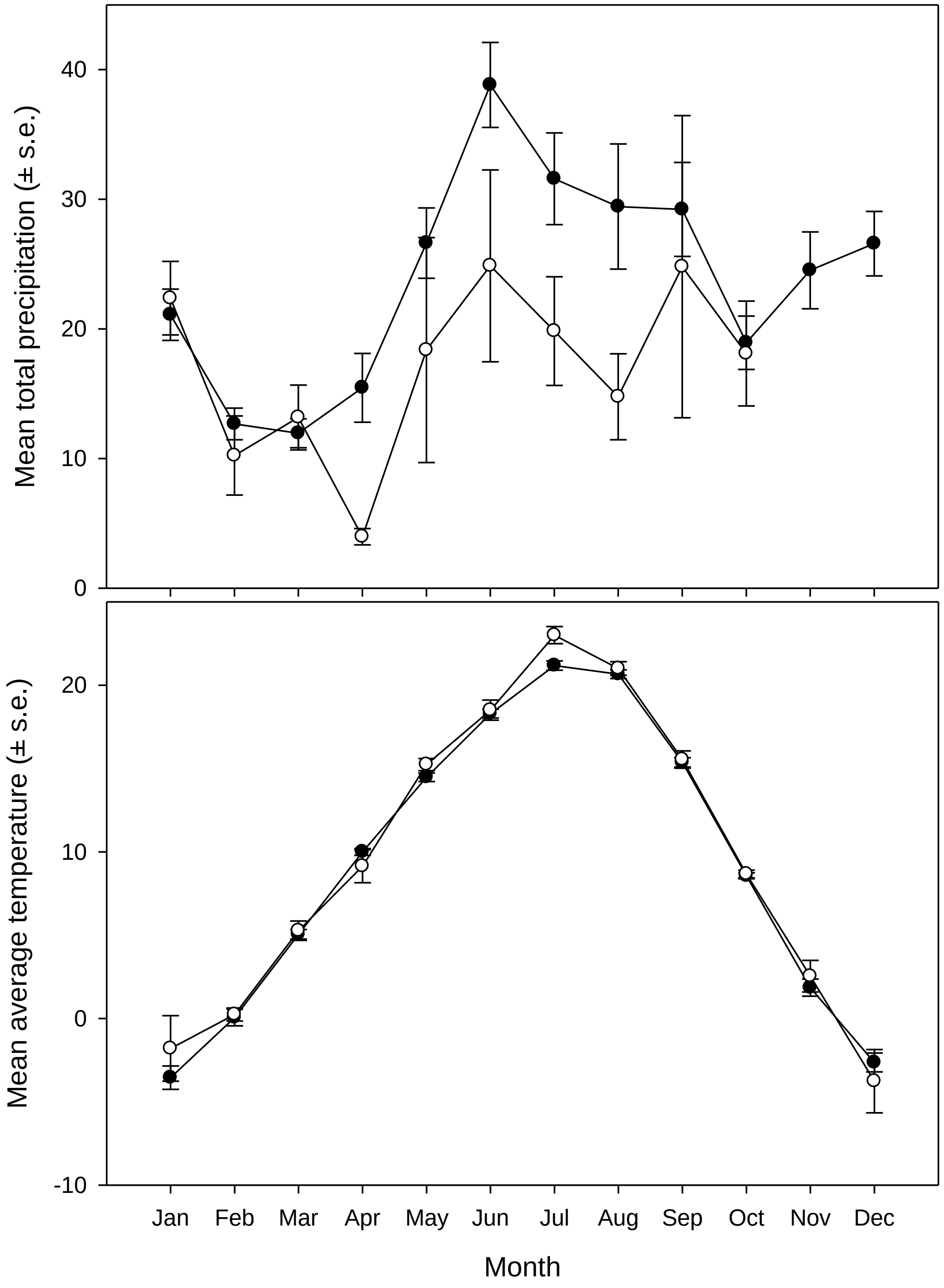

Figure 1.3. Mean monthly total precipitation (mm) and mean monthly average temperature (°C) for the 1976-2005 (●) and the 2006-2008 (○) time periods. Data compiled from Environment Canada's National Climate Data and Information Archive available at: http://climate.weatheroffice.gc.ca/. November and December 2008 data for mean total precipitation was not available.

Average annual snowfall in the lower grasslands is 75 cm, and 126 cm in the upper grasslands (Wikeem and Wikeem 2004). Rarely is a prolonged continuous snow cover established in the lower grassland, as ground snow is intermittently removed by warmer Chinook winds (Tisdale 1947). Snow in the upper grasslands can, however, form a continuous and often deep snow layer that may last through April (Tisdale 1947). Snow depth in the upper grasslands is highly variable, with winter winds creating snowdrifts across the local topography.

Low elevation grasslands are considered to have some of the most extreme temperature conditions in the province. Wikeem and Wikeem (2004) reported average July temperatures in the lower grasslands to be 22.7°C, but daily highs can exceed 40°C. Average January temperatures are relatively mild at -10°C, but extreme cold events can decrease the temperature to below -20°C. Upper grasslands have milder summer conditions, with average July temperatures being 18.9°C, but colder average January temperatures (-13.4°C; Wikeem and Wikeem 2004). Mean monthly average temperatures during the study period appear to closely mirror the mean monthly average temperatures of the preceding 30 years (Figure 1.3).

The majority of the sites used in this study occurred either within, or very near to, Lac du Bois Grasslands Provincial Park (Figure 1.2). Established in 1996, the park is one of only three in the province that provides a significant amount of protection for grassland ecosystems (Ministry of Environment, Lands and Parks 2000). Its proximity to the city of Kamloops means it receives extensive amounts of anthropogenic use, including all-terrain vehicle and motorcycling, horseback riding, cycling and hiking, and the grazing of livestock. In general, these uses were not felt to exert a direct effect on the results of this study, but their presence on the landscape must be acknowledged as part of the general ecological stressors operating in the area of study.

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CHAPTER 2 – SMALL MAMMAL COMMUNITIES IN TWO TEMPERATE GRASSLAND ECOSYSTEMS OF BRITISH COLUMBIA, CANADA

INTRODUCTION

The processes that drive small mammal community structures are complex and have a lengthy history of debate. One long-standing theory involves the idea of resource availability, wherein increased primary productivity is positively associated with rodent densities (Hernandez et al. 2005, Krebs et al. 2010). Simply put, increased precipitation (or sunlight, heat, nutrients, etc.) leads to increased plant growth and reproduction, which can support higher populations of consumers such as rodents (Brown and Ernest 2002). This form of bottom-up trophic cascade has been shown to be particularly prevalent in arid, pulse-driven systems (Beatley 1969, Ernest et al. 2000, Baez et al. 2006), and in other terrestrial systems (Ostfeld and Keesing 2000, Falls et al. 2007). Moisture gradients also have been found to be dominant drivers of rodent community structure in a number of North American grassland systems (Grant and Birney 1979, Reed et al. 2007). These changes often are observed at the functional group level, with increased plant productivity and the accumulation of litter (dead plant matter) resulting in increased abundances of herbivore species such as voles, and a decrease in granivorous small mammals through processes such as a reduction in seed foraging efficiency (Kaufman and Kaufman 1990, Reed et al. 2006a, 2006b). Yet primary productivity alone does not dictate the structure of small mammal communities. Top-down forces (i.e. predation) also have been shown to affect small mammal community structures (Hairston et al. 1960, Meserve et al. 1999), as have other biotic and abiotic factors such as competition (Redfield et al. 1977, Valone and Brown 1995, Brady and Slade 2001) and microhabitat availability (Morris 1984, 1987).

Understanding the mechanisms that affect small mammal communities is important, as rodent populations often play vital roles in their ecosystems. In grassland systems, rodents act as consumers of invertebrate species (Churchfield et al. 1991), as seed dispersers (La Tourrette et al. 1971, McAdoo et al. 1983) and consumers (Hulme 1994, Edwards and Crawley 1999), and as consumers of herbaceous and woody material

(Lindroth and Batzli 1984, Howe et al. 2002, 2006). They provide ecological functions as prey for a variety of grassland predators (Reich 1981, Sera and Early 2003), and as dispersers of spores of mycorrhizal fungi (Maser et al. 1988). Further to their important trophic position in grassland systems, some rodents act as ecological engineers and habitat modifiers who increase landscape heterogeneity by establishing unique patches different from the surrounding landscape, and create habitat for other plant and wildlife species (Davidson and Lightfoot 2008, Davidson et al. 2008).

The abilities of small mammals to drastically alter grassland vegetation and processes (Keesing 2000, Howe and Lane 2004, Howe et al. 2006) highlight the need to understand how their populations change temporally and spatially across different grassland ecosystems. This need is particularly acute with respect to the grasslands of British Columbia, Canada, which make up approximately 1% of the provincial land base (0.74 million hectares) yet are home to nearly 30% of the threatened and endangered species in the province (Wikeem and Wikeem 2004). And while small mammal communities have been studied extensively in other semi-arid and grassland systems throughout the world (see previous references), they have received little attention in temperate British Columbia grassland systems where they often are subject to extreme summer and winter conditions.

Plant productivity and precipitation have been positively correlated in North American grasslands (Sala et al. 1988). In some British Columbia grasslands, an elevation gradient exists with precipitation increasing with increased elevation. This results in the establishment of three distinct zones of vegetation: the lower, middle and upper elevation grassland zones (Tisdale 1947, van Ryswyk et al. 1966). Low elevation sites (valley bottoms to about 700 m elevation) are the hottest and driest of the grassland systems, and are characterized by low plant diversity and the dominance of big sagebrush (*Artemisia tridentata*), and large, bare inter-shrub areas with widely spaced bunchgrasses. Upper elevation sites (850 m to 1130 m) are relatively more mesic, and are characterized by increased plant species diversity, the lack of big sagebrush, nearly complete grass coverage and a layer of dead vegetation, and by species such as rough fescue (*Festuca* *campestris*) and bluebunch wheatgrass (*Pseudoroegneria spicata*) which often co-dominate in the mid- to late-seral stages of these communities (van Ryswyk et al. 1966, Wikeem and Wikeem 2004). Given this elevation increase in plant productivity, one might expect upper grasslands to support higher densities of small mammal species, particularly litter-dwelling species that require higher amounts of vegetative litter and cover to persist.

The primary objective of this study was to examine and compare the abundance, composition and apparent survival of small mammal communities in two distinct grassland ecosystems (lower and upper elevation grasslands). It is predicted that 1) total small mammal densities and densities of herbivorous small mammal species (e.g. *Microtus* spp.) will be higher in upper elevation grassland sites; 2) densities of more omnivorous small mammal species will generally be higher in the lower grasslands; and 3) small mammal apparent survival rates will be higher in upper grassland sites.

METHODS

Study Area and Site Selection

This study took place in grassland ecosystems near Kamloops, British Columbia, Canada (50°43' N; 120°25' W). Eight sites were utilized for the majority of the study, and two supplementary sites were established in 2007 for winter surveys of small mammal communities (see Figure 1.2). Five of the sites occurred within the lower grasslands, and the other five sites within the upper grasslands. The four main sites in the lower grasslands ranged in elevation from 434 m to 584 m, and the four main upper grassland sites from 846 m to 981 m.

Small Mammal Trapping – Spring, Summer and Fall

Small mammals were live-trapped for three sessions between June and September 2006, and for six sessions between May and October in both 2007 and 2008. Most trap sessions were separated by approximately 28 days (Getz et al. 2006). At each site, small mammals were sampled with a 10 × 5 trapping grid (50 traps total) with 14.3 metres between trap stations. A single Longworth-style live trap (Little Critter Traps, Rogers Manufacturing, Kelowna, BC) was placed within a 2 m radius of each trap station, and covered with a 15 × 30 cm board to provide protection from exposure to sun and rain. Synthetic cotton bedding was added to the nesting chamber of each trap, and traps were locked open and placed at each study site a week before the first trap session in order for small mammals to become accustomed to their presence. Two days before the start of each trapping session, traps were pre-baited with a small amount of a mixture of whole oats and sunflower seeds and left open for two consecutive nights (Edalgo and Anderson 2007). After each pre-bait session, small mammals were live-trapped for three consecutive nights. Traps were baited with approximately 5 g of the same mixture of oats and sunflower seeds with a piece of apple or carrot included as a moisture source. Traps were set within two hours of sunset and checked within two hours after sunrise the following morning. Captured animals were identified to species and weighed using 60 g spring scales (PESOLA AG, Baar, Switzerland). The sexual condition of each individual was assessed using scoring techniques similar to McCravy and Rose (1992) and Moses and Boutin (2001). For males, testes position (abdominal or scrotal) was noted, and for females, teats were scored as either inactive (small and difficult to see), enlarged (teats large; pregnant), lactating (teats large and fur worn), or returning to normal (teats healing with fur re-growth). Each animal was tagged with a uniquely-numbered ear tag (Monel #1005-1, National Band and Tag, Newport, KA) and released at the point of capture. Whenever the number of animals caught at a particular site equalled or exceeded 35 on a single morning ($\geq$ 70% trap saturation), the number of traps at the site was increased by 50% for the remainder of the trapping session by adding an additional trap to every second trap station (Parmenter et al. 2003). At the end of each trap session, residual bait was removed from the traps to avoid supplemental feeding of small mammal populations between trap sessions. Traps then were locked open and left *in situ* until the following session.

Small Mammal Trapping – Winter

Small mammals were live-trapped at the two dedicated winter sites for three sessions from August through October 2007, using methods identical to those described in section above. These trapping sessions were completed in order to obtain estimates of small mammal populations prior to the winter months. Three winter trapping sessions were completed between January through March 2008 at the dedicated winter site and one regular site (i.e. a site used for the spring, summer and fall trapping sessions) in the lower grasslands, and two winter trapping sessions occurred at the dedicated winter site and one regular site in the upper grasslands between January and February 2008. One winter site and one regular site, as opposed to two regular sites, were trapped in each grassland type so as to minimize any potential negative effects such winter trapping may have on the small mammal populations at sites used for the majority of this study.

In November 2007, prior to the first snowfall of the season, each Longworth-style live trap was placed inside a plastic trap shelter, based on the designs of Pruitt (1959) and Iverson and Turner (1969), in order to prevent snow from hindering trap function. Each shelter measured 33 × 28 × 13 cm (*l* × *w* × *h*), and on each side a 5.7 cm diameter hole was cut to allow small mammal entrance. The shelters were covered with a 25.5 × 30.5 cm wooden removable top, to allow access to the trap while minimizing snow disturbance around the trap site. To prevent the shelters from being overturned by wind prior to snow cover, and to facilitate finding the traps under the snow, each shelter was pinned to the ground using a 53 cm metal surveyor stake flag (Figure 2.1).

Trapping methods and animal processing otherwise followed procedures outlined for the summer work, however, peanut butter was added to the bait and traps were set for a maximum of 10 hours in order to minimize potential trap mortality (Pruitt 1959). To access traps, snow was gently removed from the top of the shelters, and replaced once the trap set/check was completed. Snowshoes were worn at all times while on the trapping sites, and a single track was used to access all traps in an effort to minimize potential disturbance to the subnivean space.

Figure 2.1. Snow shelter used to facilitate winter trapping (A), and the snow shelter *in situ* with snow removed from the shelter's top (B).

Habitat Sampling

On each of the eight main live-trapping grids, eighteen 3 × 3 m semi-permanent plots were systematically placed between trap stations, and were used to ascertain shrub species and percent cover. Grass and forb species identification and percent cover, as well as bare ground, crust (lichens and mosses), rock, coarse woody debris (CWD: woody material ≥ 2.5 cm diameter) and litter (above ground dead vegetation) cover estimates were gauged by systematically placing three 20 × 50 cm frames in each of the semi-permanent plots, and assessing the percent cover of each metric within the frame.

To assess herbaceous litter and biomass (above ground live vegetation) levels, as well as sagebrush litter levels (un-rooted woody material < 2.5 cm diameter) at the lower grassland sites only, three randomly-placed 70 m transects were established at each site. From each transect, four litter and biomass samples were collected using 1 × 1 m frames randomly placed along each transect. All litter and biomass samples were oven-dried for 48 hours and weighed.

Vertical and horizontal visibility levels were assessed in accordance to Carlyle et al. (2010). To assess vertical visibility, four vole-sized pieces of square dowel (10 × 2.5 × 2.5 cm) were placed systematically beneath the litter within a 0.5 × 0.5 m frame. A digital photograph of the dowels was taken from 1 m above the ground directly above the dowels with the assistance of a camera tripod. To assess horizontal visibility, a digital photograph of a 50 × 50 cm board was taken at a distance of 4 m with the camera 1 m off the ground. The dowels and board were painted fluorescent orange so as to contrast with the surrounding vegetation. Using the 70 m random transects described above, photos of both the board and dowels were taken at 7 m intervals along each transect. For comparative purposes, reference photographs were taken of the board and dowels in similar manners, but with no foliar obscurity. Digital photos were assessed using an open-source photo software package called the GNU Image Manipulation Package (Kimball and Mattis 2007). For each photograph, the number of orange pixels exposed through the foliage was counted twice using the photo software and averaged. This number was divided by the number of orange pixels counted on the reference photographs to obtain a percent of the board or dowels exposed through the foliage.

Soil compaction was estimated by using a HFG-110 hand-held force gauge (Transducer Techniques, Temecula, CA). The instrument measures the force needed to push a gauge with a 12.57 mm^2 tip through the soil, and expresses that measure in units of kilogram-force (kgf). One kilogram-force is equivalent to 9.81 newtons. At each of the eight live trapping grids, 20 square holes approximately 20 cm deep were systematically dug between trap stations. Compaction was estimated by pushing the force gauge into each of the four sides of the hole at depths of 1 and 10 cm, and averaging the resulting measurements at each hole for each soil depth.

Small Mammal Abundance and Apparent Survival

Program CAPTURE (Otis et al. 1978) was used to generate closed population estimates by trap session and site for small mammal species when 11 or more individuals were captured (Moses and Boutin 2001). When 10 or fewer individuals were captured during a trap session, the total number of individuals caught during the trap session was used as a measure of abundance. When CAPTURE selected a model for which abundance was not estimable, the next best model as picked by CAPTURE was used to estimate abundance. All abundance estimates were then converted to densities (animals per hectare).

To determine if small mammal survival differed between upper and lower elevation sites, Cormack-Jolly-Seber (CJS) recapture models were developed using program MARK (White and Burnham 1999). MARK allows for the estimation of apparent survival (Φ) and recapture rate (p) parameters using the method of maximum likelihood estimation (White 2008), and can incorporate treatment (g) and time (t) effects and their interactions (Larsen et al. 2007). Within each year of study, apparent survival rates between males and females by species were first compared and then comparisons between upper and lower grasslands were made. An *a priori* set of 25 candidate models were used to compare treatments. Models ranged from the fully parameterized global model ($\Phi_{(g*t)}\ p_{(g*t)}$), to the “no effect” model for both treatment and time ($\Phi_{(.)}\ p_{(.)}$). Akaike’s Information Criterion adjusted for small sample sizes (AIC_c) was used to compare models (Burnham et al. 1995).

Prior to examining the models, the goodness-of fit of the most global model ($\Phi_{(g*t)}\ p_{(g*t)}$) was tested using bootstrapping techniques (200 simulations) available within MARK. The over-dispersion factor of the data ($\hat{c}$) was determined by dividing the observed deviance of the global model by the mean deviance of the simulated (bootstrapped) data, and was used to account for data over-dispersion by adjusting the AIC_c to the quasi-AIC_c ($QAIC_c$; Cooch and White 2008). The number of parameters for each model was hand-calculated and adjusted as necessary in order to ensure the correct ranking of models by MARK. Model selection was based on the model with the lowest $QAIC_c$ value (Lebreton et al. 1992). Overall survival estimates were derived from the model with the lowest $QAIC_c$ value. When the best model’s $QAIC_c$ differed from the next best model(s) by $\leq$ 2.00, model averaging of these models was performed to estimate survival parameters (Cooch and White 2008).

Small Mammal Demographics

A number of demographic characteristics were used to compare small mammal communities between treatments. These characteristics included sex ratios, proportion of populations composed of juveniles and the proportion of populations composed of reproductive adult females.

Weight at sexual maturity has been used to distinguish adults from juveniles in small mammal populations (Keller and Krebs 1970, Fairbairn 1977b). However, the age and weight at which some small mammal species become sexually mature can vary between years (Negus et al. 1977), can be influenced by social condition and diet (Negus and Pinter 1966), and can vary between the sexes (Hoffman 1958). In accordance with Sullivan and Sullivan (2004), mass at sexual maturity was ascertained by determining the weight at which 50% of the animals displayed signs of sexual maturity. This was accomplished by plotting the percent of males and females showing signs of sexual maturity (males = testes scrotal; females = nipples enlarged, lactating or returning to normal) in each one-gram weight category. A least squares regression was performed on the data, and the predicted weight at which 50% of the animals showed signs of sexual maturity was used as the point at which sexual maturity was reached. Female deer mice were classified as adults if they weighed $\geq$ 21 g, male deer mice if they weighed $\geq$ 19 g, and male voles if the weighed $\geq$ 26 g. Due to the highly variable nature of the female vole data, a least squares regression did not produce reliable results. For female voles, weight at sexual maturity was determined by ascertaining the lowest weight class in which $\geq$ 50% of the animals showed signs of sexual maturity; which was $\geq$ 26 g. These mass limits are consistent with those described by Sullivan and Sullivan (2004).

Statistical Considerations

Small mammal density and demographic data were analyzed separately by year, using two-way repeated-measures ANOVA tests with elevation as the independent variable and trapping session as the repeated-measure factor. For each repeated-measures ANOVA, a variety of covariance models were developed in a manner consistent with Littell et al. (2002). The model with the lowest AIC$_c$ value was used to draw conclusions from the repeated-measures data. When a significant interaction was observed, the simple effects were further analyzed using ‘slicing’ methods described by Littell et al. (2002). In addition, mean population densities of the June, July and September trapping sessions were compared between years for both the upper and lower grasslands separately using a one-way ANOVA. Paired t-tests were used to examine the differences between lower and upper elevation mean small mammal densities and demographic information per trap session over the course of the entire study.

Habitat metrics were compared between upper and lower elevation sites using a nonparametric Kruskal-Wallis test. Further, plant cover data were used to assess plant species diversity using diversity indices calculated with the Microsoft Office Excel (vers. 2007) add-in module Diversity.xla (available at: http://www.reading.ac.uk/ssc/software/diversity/diversity.html). Diversity indices generally fall into two types: those that place more emphasis on rare species in the sample (i.e. Type I) and those that put most weight on the common species (i.e. Type II; Peet 1974). As such, both the Shannon-Weiner diversity index (Pielou 1966), a Type I index, and the Simpson's diversity index (Simpson 1949), a Type II index, were calculated for the analysis.

Spearman's rank correlation analysis (Zar 1999) was used to examine the association between small mammal species densities at each site and the habitat metrics collected at those sites, including plant species richness and diversity. The mean abundances of each small mammal species across the 2007 and 2008 trapping sessions were used for the analysis, and correlations were considered strongly positive when $\rho \geq 0.50$ and strongly negative when $\rho \leq -0.50$ (Cohen 1988).

All data were analyzed using SAS 9.2 software (SAS Institute Inc. 2008). For the one-way ANOVA tests and t-tests, assumptions of normality were tested for all data and when these assumptions were not met, data were either transformed or the corresponding nonparametric analysis was performed using methods described in Schlotzhauer and Littell (1997). A significance level of $\alpha = 0.05$ was used for all tests, except that Bonferroni tests with the appropriately-adjusted α- or P-values were used for all post-hoc multiple comparisons and when the simple effects for significant interactions were examined.

RESULTS

Site Characteristics

Elevational differences between the eight main upper and lower sites were significant (lower elevation mean = 532.3 m, upper elevation mean = 906.5 m; $H = 5.33$, d.f. = 1, $P = 0.02$), and Table 2.1 summarizes the differences in habitat variables between the upper and lower grassland sites. As expected, upper elevation sites had higher amounts (kg/ha) of herbaceous litter and biomass, and higher levels of litter and grass coverage (m^2/ha).

Table 2.1. Comparison of habitat characteristics (mean ± s.e.) in the upper and lower grassland sites using the Kruskal-Wallis test (d.f. = 1).

Habitat Variable	Lower Elevation Mean	Upper Elevation Mean	*H*	*P*
Herbaceous litter (kg/ha)	457.8 (133.9)	2088.6 (604.2)	5.33	0.02
Herbaceous biomass (kg/ha)	490.3 (138.5)	1520.7 (188.7)	5.33	0.02
Shrub litter (kg/ha)	779.3 (62.1)	0.0	-	-
Bare ground (m^2/ha)	1999.3 (362.5)	169.4 (75.8)	5.33	0.02
Coarse woody debris (m^2/ha)	631.0 (72.7)	0.0	-	-
Crust (m^2/ha)	3019.7 (90.9)	756.9 (372.5)	5.33	0.02
Grass (m^2/ha)	3322.5 (537.4)	8144.9 (393.4)	5.33	0.02
Litter (m^2/ha)	5116.7 (361.9)	9251.9 (295.0)	5.33	0.02
Rock (m^2/ha)	343.8 (183.1)	80.3 (45.4)	3.00	0.08
Shrub (m^2/ha)	2765.3 (400.0)	0.7 (0.7)	5.60	0.02
Soil compaction: 1 cm depth (kgf)[A]	2.0	2.5	2.08	0.15
Soil compaction: 10 cm depth (kgf)[A]	4.8	4.7	0.08	0.77
Horizontal visibility (% visibility)[B, C]	0.5	0.6	2.08	0.15
Vertical visibility (% visibility)[B]	0.7	0.4	4.08	0.04
Plant Richness	17.8 (3.2)	24.3 (2.3)	2.08	0.15
Plant Shannon-Weiner diversity index	1.7 (0.3)	2.0 (0.1)	1.33	0.25
Plant Simpson's diversity index	0.72 (0.1)	0.79 (0.0)	0.33	0.56

[A] The means presented here are the logarithmic means back-transformed to the original measurement scale. Standard errors are not provided as per Krebs (1999).

[B] The means presented here are the arcsine means back-transformed to the original measurement scale. Standard errors are not provided as per Krebs (1999).

[C] Normality could not be obtained for this metric.

On the other hand, lower grasslands had greater levels of bare ground, crust and shrub coverage. The amount of rock coverage was not significantly different between the two habitat types, nor was soil compaction at either the 1 cm or the 10 cm depths. The lower grasslands showed lower amounts of horizontal visibility than the upper grasslands, probably due to the higher amounts of shrub coverage, whereas the upper grasslands had significantly lower amounts of vertical visibility, most likely a result of the upper grassland's higher amounts of herbaceous litter and biomass. Upper grassland sites tended to have higher plant species richness than lower grassland sites, but the differences were not significant. Sites did not differ with respect to plant species richness or diversity. Abundant species, based on percent cover estimates, at upper grassland sites included rough fescue (*Festuca campestris*), Kentucky bluegrass (*Poa pratensis*), and needle-and-thread grass (*Hesperostipa comata*). In the lower grasslands, bluebunch wheatgrass (*Pseudoroegneria spicata*), Sandberg bluegrass (*Poa secunda*) and needle-and-thread-grass commonly were the abundant species. In addition, each lower grassland site had varying amounts of big sagebrush (*Artemisia tridentata*) cover.

Small Mammal Totals

Over the course of the study 1,420 individual small mammals of three main species were captured over 21,086 trap nights. Deer mice (*Peromyscus maniculatus*) were the most numerous, with 906 animals caught (63.8% of total). Montane voles (*Microtus montanus*) were the second most abundant with an estimated 483 individuals captured (34.0% of total), followed by an estimated 31 meadow voles (*Microtus pennsylvanicus*; 2.2% of total). In addition, 15 shrews (*Sorex* spp.) were captured in the upper grasslands. Shrews were considered incidental captures, and were released at the point of capture without being identified to species. Due to the apparently low numbers of *M. pennsylvanicus* captured in this study, and the difficulty of differentiating this species from *M. montanus* in the field, data on these two species were combined for all subsequent analyses. Deer mice were captured on all sites, whereas voles were captured almost exclusively in the upper grasslands. Only 14 of the 514 voles captured in this study were found in the lower grasslands, and all were caught during the 2006 trapping season.

Small Mammal Density Estimates

The mean densities of deer mice in the upper and lower grasslands for all trap sessions are illustrated in Figure 2.2. Densities were relatively high in 2006, then followed similar patterns in 2007 and 2008 in both the upper and lower grasslands by remaining relatively low or decreasing in May through July and then steadily increasing to peak in October. A paired t-test examining the differences between lower and upper elevation mean deer mouse densities per trap session over the course of the study showed no significant differences between the two grassland types (t = 1.68, d.f. = 14, P = 0.12).

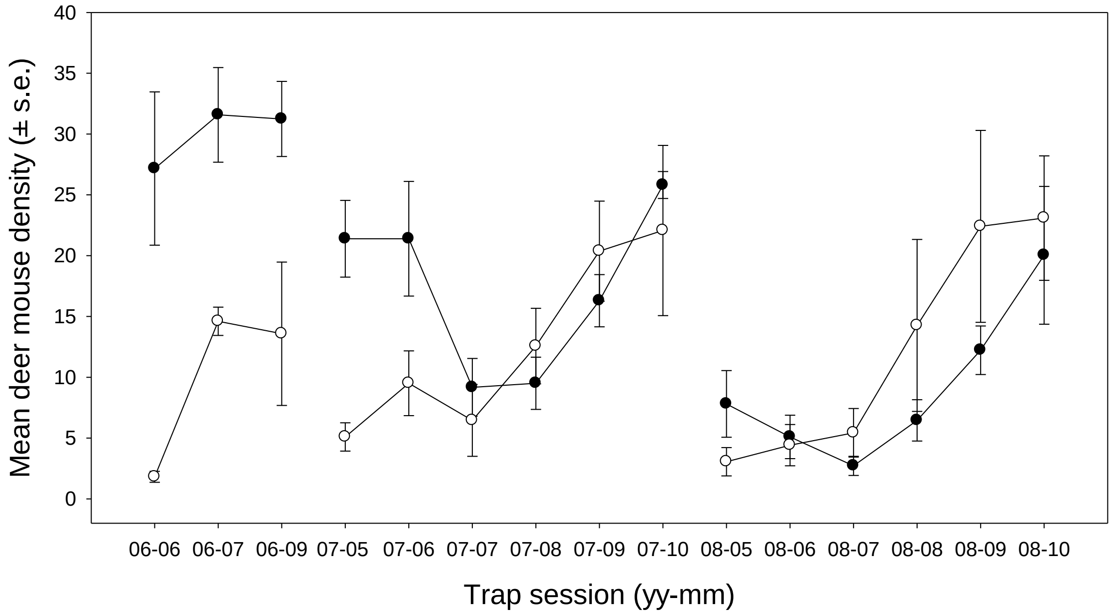

Figure 2.2. Mean population densities (animals/ha) for *P. maniculatus* in upper (○) and lower (●) grasslands across all 15 trap sessions.

Table 2.2 details the results of the repeated-measures ANOVA tests for deer mouse densities. In 2006, lower grasslands had significantly higher densities of deer mice than

Table 2.2. Comparisons of the densities of *P. maniculatus* captured by year, and between upper and lower elevation grasslands and trapping session using two-way repeated-measures ANOVA tests.

	Elevation			Session			Elevation × Session		
	F	d.f.	*P*	*F*	d.f.	*P*	*F*	d.f.	*P*
2006	22.71	1, 6	< 0.01	2.77	2, 11	0.11	0.65	2, 11	0.54
2007	1.82	1, 6	0.23	9.00	5, 30	< 0.01	4.56	5, 30	< 0.01
2008	0.57	1, 6	0.48	5.11	5, 30	< 0.01	1.99	5, 30	0.18

upper grasslands. In 2007, a significant difference between trap sessions was observed; however, a significant interaction was also observed. An examination of the simple effects showed that, when the data were sliced by trap session ($\alpha = 0.008$) only trap session 07-05 had a significant difference in densities between the two grassland types ($P < 0.01$), whereas the other trap sessions did not (07-06: $P = 0.02$; 07-07: $P = 0.58$; 07-08: $P = 0.53$; 07-09: $P = 0.41$; 07-10: $P = 0.45$). Slicing the data by elevation ($\alpha = 0.025$) revealed that both the lower and upper elevations had significant differences in deer mouse densities between trap sessions ($P < 0.01$ and $P < 0.01$, respectively). For 2008, densities differed significantly by trap session, but not by elevation. Post-hoc analyses of the trap session data showed that session 08-05 was significantly different than session 08-10, and that sessions 08-06 and 08-07 were both significantly different than sessions 08-09 and 08-10.

A one-way ANOVA comparing densities between all three years at each elevation separately showed a significant difference between years for the lower grasslands ($F = 29.36$, d.f. = 2,33, $P < 0.01$), with 2006 densities significantly higher than 2007 and 2008 densities, and 2007 densities significantly higher than those of 2008. Overall, no substantive differences were seen between years in the upper grasslands ($F = 0.23$, d.f. = 2,32, $P = 0.80$).

As voles (*Microtus* spp.) were all but absent from the lower grasslands, no comparisons between upper and lower elevations were made. Further, one-way repeated-measures ANOVA tests could not be performed due to insufficient ‘error’ degrees of freedom. Alternatively, one-way ANOVA tests or the equivalent non-parametric tests were used to examine the changes, per year, in vole densities over trap sessions.

In the upper grasslands, vole populations expressed high levels of variability in 2006, with some sites having densities as high as 118 animals per hectare, and some sites having no animals in each of the three trap sessions that year. Vole densities decreased dramatically from September 2006 to May 2007, and remained low throughout the 2007 season. Densities further declined in 2008, and voles were essentially absent from all trapping sites from May through August 2008, and then came back to an average high of 11 animals per hectare in October 2008 (Figure 2.3). In all years, there were no significant differences in densities between trapping sessions (2006: $H = 2.14$, d.f. = 2, $P = 0.37$; 2007: $F = 0.88$, d.f. = 5,18, $P = 0.51$; 2008: $H = 6.85$, d.f. = 5, $P = 0.23$). A non-parametric comparison of average vole densities between years indicated significant differences in densities between years ($H = 9.54$, d.f. = 2, $P = 0.01$), with 2006 densities probably significantly higher than either 2007 or 2008 levels.

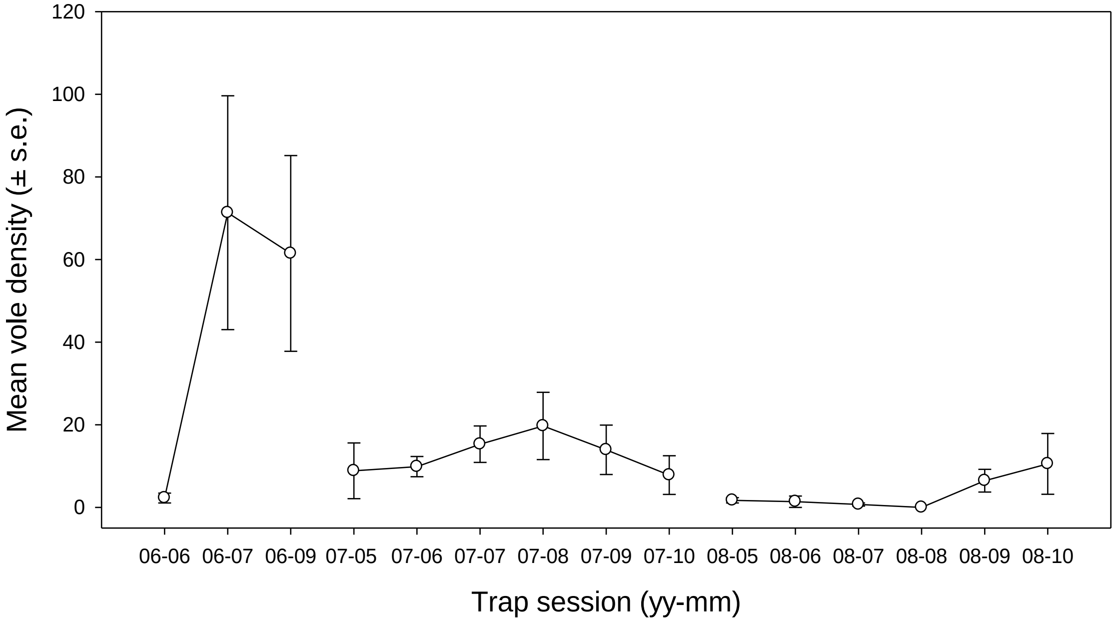

Figure 2.3. Mean population densities (animals/ha) for *Microtus* spp. in upper grasslands across all 15 trap sessions.

The densities of deer mice and voles were combined by trap session in order to compare total small mammal densities between upper and lower elevations, and between trapping sessions. Generally, small mammal densities were greater in upper grasslands than in lower grasslands (Figure 2.4). The exceptions were the first two trap sessions of 2007 and the first session of 2008, where lower grassland mean densities were marginally higher than those at the upper sites. Pooled across years, mean densities between upper and lower grasslands were just significantly different (t = -2.16, d.f. = 14, P = 0.05), with the upper grasslands having higher mean densities than the lower grasslands.

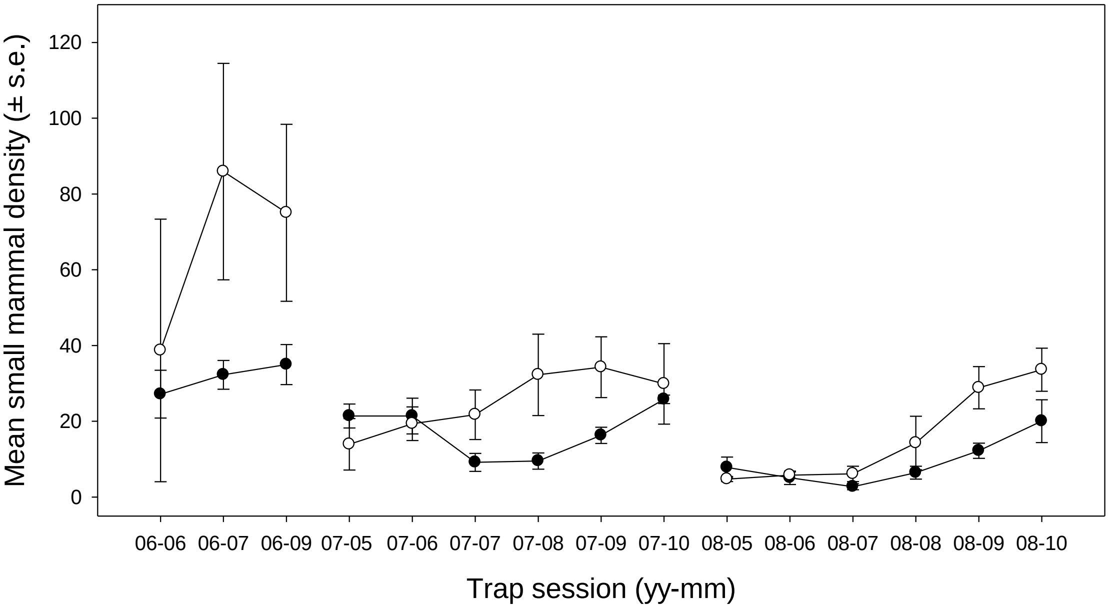

Figure 2.4. Mean population densities (animals/ha) for small mammals in upper (○) and lower (●) grasslands across all 15 trap sessions.

Table 2.3 details the results of the two-way repeated-measures ANOVA tests for total small mammal densities. In 2006, the interaction between elevation and trap session was significant. An examination of the simple effects showed that, when the data were sliced by trap session ($\alpha = 0.02$), none of the trap sessions showed a significant difference in densities between the two grassland types (06-06: P = 0.59; 06-07: P = 0.04; 06-09: P =

Table 2.3. Comparisons of the densities of small mammals captured by year, and between upper and lower elevation grasslands and trapping session using two-way repeated-measures ANOVA tests.

	Elevation			Session			Elevation × Session		
	F	d.f.	*P*	*F*	d.f.	*P*	*F*	d.f.	*P*
2006	3.09	1, 6	0.13	7.11	2, 11	0.01	6.46	2, 11	0.01
2007	1.46	1, 6	0.27	1.66	5, 30	0.17	2.50	5, 30	0.05
2008	3.80	1, 6	0.10	6.61	5, 30	< 0.01	2.04	5, 30	0.10

0.10). Slicing the data by elevation (α = 0.025) revealed that the upper elevation had significant differences in deer mouse densities between trap sessions (*P* = 0.01) whereas the lower grasslands did not (*P* = 0.95). A significant interaction was again observed in 2007, and when sliced by trap session (α = 0.008), once more none of the trap sessions showed a significant difference in densities between the two elevations (07-05: *P* = 0.40; 07-06: *P* = 0.82: 07-07: *P* = 0.16; 07-08: *P* = 0.01; 07-09: *P* = 0.05; 07-10: *P* = 0.64). Slicing the data by elevation (α = 0.025) showed that neither the lower nor upper grasslands had significant differences in densities between trap sessions (*P* = 0.05 and *P* = 0.06, respectively). For 2008, densities between trap sessions were significantly different, and the post-hoc analysis showed that sessions 08-05 through 08-08 were all significantly different than sessions 08-09 and 08-10.

A one-way ANOVA comparing small mammal densities by year in the upper and lower grasslands separately showed significant differences between years in the lower grasslands (*F* = 29.79, d.f. = 2,33, *P* < 0.01), with 2006, 2007 and 2008 densities all significantly different from each other. Densities also were significantly different by year in the upper grasslands (*F* = 3.48, d.f. = 2,32, *P* = 0.04) with 2006 densities significantly higher than 2008 levels.

Deer Mouse Demographics

As *P. maniculatus* was the only species caught in both the upper and lower grasslands, only their demographics are considered in depth here.

The percentages of female deer mice captured per trap session were highly variable, ranging from 0.00 to 1.00 (Figure 2.5). Overall, upper grassland sites had marginally significantly higher mean percentages of females in the population than lower sites, when analyzed using a paired t-test (*t* = -2.11, d.f. = 14, *P* = 0.05), yet this was not always the case for each year of study.

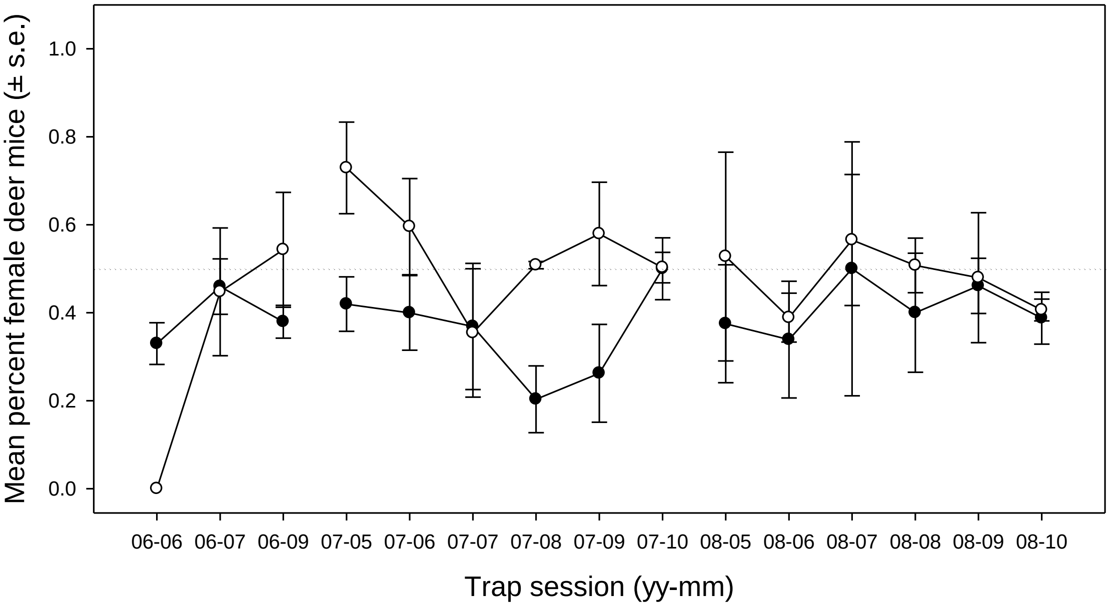

Figure 2.5. Mean percent female *P. maniculatus* in upper (○) and lower (●) grasslands across all 15 trap sessions, and including a 50% reference line.

Table 2.4 details the results of the repeated-measures ANOVA tests comparing the mean percentages of female *P. maniculatus* between upper and lower elevation grasslands and trapping session, and separated by year. In 2006, there was a significant interaction between the independent variables elevation and session, as well as a significant difference in trap session values. An evaluation of the simple effects revealed that, when sliced by trap session (α = 0.017), none of the sessions showed significant density differences between the upper and lower grasslands (06-06: *P* = 0.11; 06-07: *P* = 0.93; 06-09: *P* = 0.33). When sliced by elevation (α = 0.025), the upper grasslands

Table 2.4. Comparisons of the percentages of female *P. maniculatus* captured by year, and between upper and lower elevation grasslands and trapping session using two-way repeated-measures ANOVA tests.

	Elevation			Session			Elevation × Session		
	F	d.f.	*P*	*F*	d.f.	*P*	*F*	d.f.	*P*
2006	0.08	1, 6	0.78	76.36	2, 10	< 0.01	46.80	2, 10	< 0.01
2007	6.94	1, 6	0.04	1.26	5, 30	0.31	1.48	5, 30	0.23
2008	0.91	1, 6	0.38	0.32	5, 26	0.89	0.06	5, 26	> 0.99

showed significant differences between trap sessions ($P < 0.01$), but the lower grasslands did not ($P = 0.07$). 2007 was the only year to show a significant difference between elevation, and for 2008, the percentages of female deer mice caught did not significantly differ between either elevation or trap session, nor was the interaction significant.

The one-way ANOVA comparing small mammal densities by year in the upper and lower grasslands separately showed there were no significant differences in percentages of females caught between years in both the lower grasslands ($F = 0.48$, d.f. = 2,32, $P = 0.62$) and the upper grasslands ($F = 1.25$, d.f. = 2,31, $P = 0.30$).

The proportion of adult deer mice in the population was usually higher at lower grassland sites than at upper elevations, and comparing the mean proportions between the two grassland types using a paired t-test showed the differences to be highly significant ($t = 28.42$, d.f. = 14, $P < 0.01$). Generally, the proportion of adults increased through the summer months, and then decreased dramatically with the onset of fall (Figure 2.6).

In 2006, both a significant interaction and a significant difference between trap sessions were noted (Table 2.5). An analysis of the simple effects showed that, when sliced by trap session ($\alpha = 0.017$), session 06-06 showed significant differences between elevations ($P < 0.01$), session 06-07 a nearly significant difference ($P = 0.04$), and session 06-09 a non-significant difference ($P = 0.10$). When sliced by elevation ($\alpha = 0.025$), the upper grasslands had significant differences between trap sessions ($P < 0.01$), whereas the lower grasslands did not ($P = 0.34$). In 2007, significant differences in elevation and by trapping session were noted, with the lower grasslands having higher

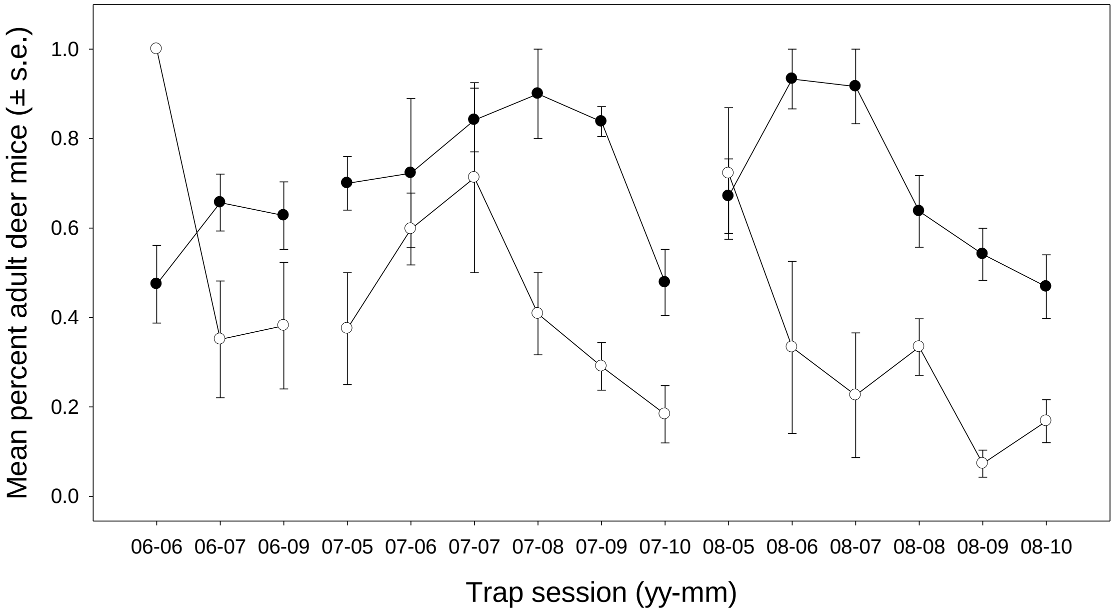

Figure 2.6. Mean percent adult *P. maniculatus* in upper (○) and lower (●) grasslands across all 15 trap sessions.

Table 2.5. Comparisons of the percentages of adult *P. maniculatus* captured by year, and between upper and lower elevation grasslands and trapping session using two-way repeated-measures ANOVA tests.

	Elevation			Session			Elevation × Session		
	F	d.f.	*P*	*F*	d.f.	*P*	*F*	d.f.	*P*
2006	0.02	1, 6	0.90	4.06	2, 10	0.05	12.10	2, 10	< 0.01
2007	18.42	1, 6	< 0.01	3.90	5, 30	< 0.01	1.39	5, 30	0.26
2008	27.4	1, 6	< 0.01	4.50	5, 26	< 0.01	5.87	5.26	< 0.01

levels of adults in the population. Post-hoc analysis of the trapping sessions showed that the 07-07 and 07-10 trapping sessions were significantly different. In 2008, a significant interaction and significant differences between elevations and trap sessions were observed. An analysis of the simple effects showed that, when sliced by trap session ($\alpha =$

0.008), sessions 08-06, 08-07 and 08-09 showed significant differences between elevations ($P < 0.01$, $P < 0.01$ and $P < 0.01$, respectively), whereas sessions 08-05, 08-08 and 08-10 did not ($P = 0.83$, $P = 0.02$ and $P = 0.02$, respectively). When sliced by elevation ($\alpha = 0.025$), the upper grasslands had significant differences between trap sessions ($P = 0.01$), as did the lower grasslands ($P < 0.01$).

Compared across years, there were significant yearly differences of proportions of adults caught in the lower grasslands ($F = 4.32$, d.f. = 2,32, $P = 0.02$) with 2006 and 2007 having significantly different proportions of adults in their populations. In the upper grasslands, the proportion of adults in the populations also were significantly different between years ($H = 8.71$, d.f. = 2, $P = 0.01$).

Due to the small numbers of adult female deer mice trapped over the course of the study, a comparison of the proportions of reproducing adult females by year and trapping session was not performed. Instead, data for the June, July and September trapping sessions for all years of study were pooled by elevation, and the proportions of reproductively active adult female deer mice compared between the upper and lower grasslands using a Kruskal-Wallis test. As well, data for all trap session in 2007 and 2008 were pooled by elevation, and the proportions of reproductively-active adult female deer mice compared between the upper and lower grasslands. Comparing the June, July and September values across all years of study showed that there was no significant difference between the two elevations ($H = 2.08$, d.f. = 1, $P = 0.15$). The comparison of the pooled 2007 and 2008 data showed similar results ($H = 3.00$, d.f. = 1, $P = 0.08$).

Deer Mouse Apparent Survival and Elevation

As *P. maniculatus* was the only the species caught in both upper and lower grasslands, only their apparent survival across the elevation gradient was compared.

The most appropriate models describing monthly *P. maniculatus* apparent survival rates in 2006, 2007 and 2008 were ones that did not include differences between males and females (Table 2.6), and as such, the sexes were combined for all subsequent analyses. The analysis showed that *P. maniculatus* survived equally well in upper and

Table 2.6. Top Cormack-Jolly-Seber apparent survival models for *P. maniculatus* by year for sex and elevation treatments. Survival, Φ; recapture, *p*; time effects, (t); no effects, (.).

Year	Treatment	Top Model
2006	Sex	$\Phi_{(.)}\, p_{(.)}$
2007	Sex	$\Phi_{(.)}\, p_{(t)}$
2008	Sex	$\Phi_{(t)}\, p_{(.)}$
2006	Elevation	$\Phi_{(.)}\, p_{(.)}$
2007	Elevation	$\Phi_{(.)}\, p_{(t)}$
2008	Elevation	$\Phi_{(t)}\, p_{(.)}$

lower grasslands in each year of study, with the top models for each year of study lacking any treatment (i.e. elevation) effect on the survival parameter (Table 2.6). There were indications of slight differences in apparent survival rates between the two elevation classes, however, as the next best models describing the data (i.e. models that had QAIC_cs which differed from the top model by ≤ 2.00) did include an elevation treatment effect (Table 2.7).

Overall apparent survival rates for *P. maniculatus* in the lower grasslands ranged from 0.28 ± 0.11 to 0.81 ± 0.10, and in the upper grasslands from 0.29 ± 0.11 to 0.82 ± 0.10 (Table 2.7). In 2006 and 2007, apparent survival rates remained relatively constant for all trap session intervals, respectively, and only slight differences in rates were observed between upper and lower elevations. In 2008, a time component was included in the top model, and for that year, apparent survival rates in both elevations began the trapping season quite low, steadily increased throughout the trapping season, and peaked in the final trap session interval.

Table 2.7. Apparent survival rates of *P. maniculatus* per trap session interval, by year and for lower and upper elevations. When > 1 model is listed, model averaging was used to infer survival rates. Survival, Φ; recapture, p; treatment effects, (g); time effects, (t); no effects, (.); additive effects (no interaction terms), (g+t).

Year	Model(s) Used	Elevation	Trap Session Interval (yy-mm to yy-mm)	Apparent Survival Rate (± s.e.)
2006	$\Phi_{(.)} p_{(.)}$, $\Phi_{(.)} p_{(g+t)}$, $\Phi_{(.)} p_{(t)}$, $\Phi_{(t)} p_{(.)}$, $\Phi_{(g)} p_{(.)}$, $\Phi_{(.)} p_{(g)}$	Lower	06-06 to 06-07	0.46 (0.15)
			06-07 to 06-09	0.44 (0.14)
		Upper	06-06 to 06-07	0.44(0.17)
			06-07 to 06-09	0.43 (0.16)
2007	$\Phi_{(.)} p_{(t)}$, $\Phi_{(g)} p_{(t)}$,	Lower	All sessions	0.52 (0.04)
		Upper	All sessions	0.53 (0.05)
2008	$\Phi_{(t)} p_{(.)}$, $\Phi_{(t)} p_{(g)}$, $\Phi_{(g+t)} p_{(.)}$	Lower	08-05 to 08-06	0.28 (0.11)
			08-06 to 08-07	0.45 (0.13)
			08-07 to 08-08	0.61 (0.14)
			08-08 to 08-09	0.60 (0.09)
			08-09 to 08-10	0.81 (0.10)
		Upper	08-05 to 08-06	0.29 (0.11)
			08-06 to 08-07	0.47 (0.13)
			08-07 to 08-08	0.63 (0.13)
			08-08 to 08-09	0.62 (0.09)
			08-09 to 08-10	0.82 (0.10)

Over-Winter Abundance and Apparent Survival

Winter appeared to be a particularly difficult time for small mammals in both the upper and lower grasslands, with all sites showing considerable declines in small mammal densities between the final 2007 trapping season and the first winter session of 2008 (Figure 2.7). The two upper grassland sites had the highest decreases, dropping from densities of 56 and 38 animals per hectare in the 07-10 trapping session, to zero animals in both the 08-01 and 08-02 sessions.

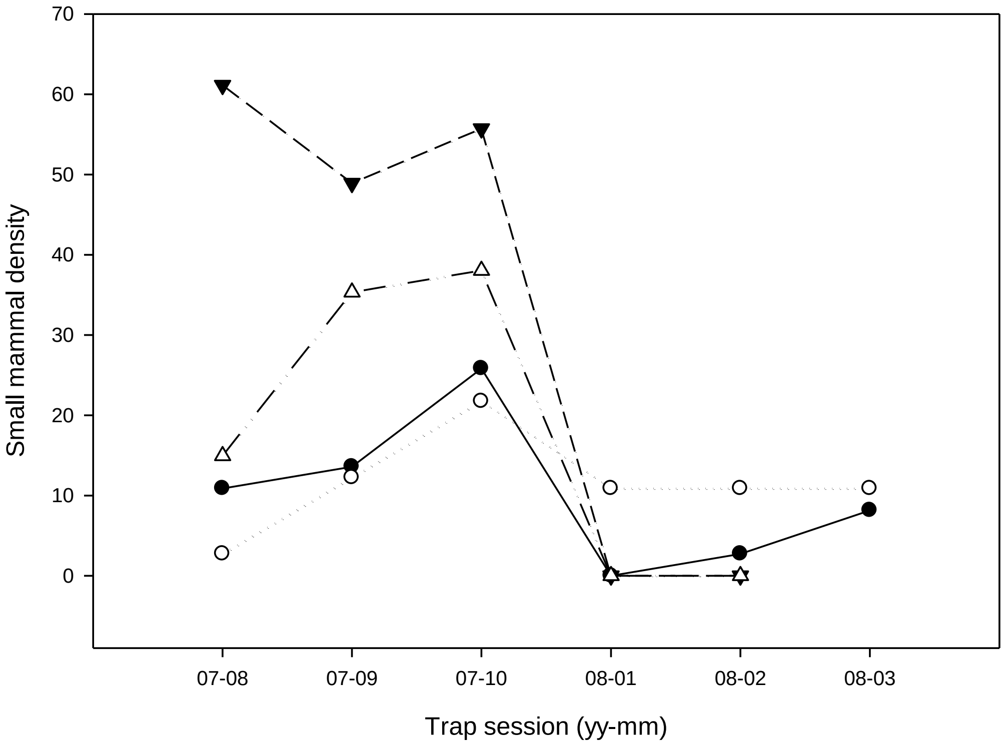

Figure 2.7. Small mammal population densities (animals/ha) the lower grassland (●) and lower grassland winter (○) sites, and the upper grassland (▼) and upper grassland winter (△) sites across the final three trapping sessions of 2007, and the three lower grassland and two upper grassland winter trapping sessions of 2008.

Over-winter apparent survival (October 2006 to May 2007, and November 2007 to May 2008) for both *P. maniculatus* and *Microtus* spp. was exceedingly low, making estimates of such unattainable; hence, only the actual numbers of recaptured individuals are presented here. In total, 11 individuals out of 434 apparently survived through either the winter of 2006/07 or the winter of 2007/08. Of those 11, seven apparently survived through the 2006/07 and four through the 2007/08 winter season (Table 2.8). No individuals were recaptured after both the 2006/07 and 2007/08 over-winter periods (i.e. no one animal survived through both over-winter periods), and all individuals that were recaptured following an over-winter period were *P. maniculatus*.

Table 2.8. Numbers of over-winter surviving individuals of *P. maniculatus* and *Microtus* spp. for the 2006/07 and 2007/08 over-winter periods in the lower and upper elevation grasslands.

Species	Over-winter period	Elevation	Total number of individuals caught in the last 2006 or 2007 trap session	Total number of individuals that survived the over-winter period	Percent of individuals trapped in the last session that survived the over-winter period
P. maniculatus	2006/07	Lower	91 (2006)	6	6.59
		Upper	39 (2006)	1	2.56
	2007/08	Lower	75 (2007)	1	1.33
		Upper	57 (2007)	3	5.26
Microtus spp.	2006/07	Lower	11 (2006)	0	0.00
		Upper	137 (2006)	0	0.00
	2007/08	Lower	0 (2007)	-	-
		Upper	24 (2007)	0	0.00

Correlation Analysis

The mean abundance of *P. maniculatus* and *Microtus* spp. across the 2007 and 2008 trapping sessions were correlated with site characteristics at each of the eight trapping sites (Table 2.9). *Peromyscus maniculatus* densities were not significantly correlated with any of the site characteristics measured, whereas *Microtus* spp. densities were correlated with most site attributes. Correlations for *Microtus* spp. generally followed habitat differences at the elevational level, showing strong correlations with herbaceous litter and biomass levels, grass cover, litter cover and plant richness, and strong negative correlations to sage litter levels, bare ground, coarse woody debris, crust, rock and shrub cover, and vertical visibility. Mean *P. maniculatus* densities and *Microtus* spp. densities were not significantly correlated (ρ= 0.30, P = 0.46). Also, *P. maniculatus* and *Microtus* spp. densities were not correlated when analyzed on a per trap session basis across all three years of study in the upper grasslands (ρ = 0.19, P = 0.15), nor were they for any individual trapping grid on a per trap session basis, across all three years of study.

Table 2.9. Spearman’s rank correlation matrix between site characteristics and mean densities of *P. maniculatus* and *Microtus* spp. Within each cell, the uppermost number equals Spearman’s correlation ρ and the lower number equals the *P*-value. Dark grey cells indicate a strong positive correlation ($\rho \geq 0.50$), and light grey cells indicate a strong negative correlation ($\rho \leq -0.50$).

Site Characteristics	*P. maniculatus*	*Microtus* spp.
Herbaceous litter levels	0.05 *0.91*	0.84 *0.01*
Herbaceous biomass levels	0.05 *0.91*	0.86 *0.01*
Sage litter levels	-0.10 *0.81*	-0.87 *0.01*
Bare ground cover	-0.14 *0.74*	-0.86 *0.01*
Coarse woody debris cover	-0.13 *0.77*	-0.87 *0.01*
Crust cover	0.38 0.35	-0.71 *0.05*
Grass cover	-0.36 *0.39*	0.71 *0.05*
Litter cover	-0.24 *0.57*	0.76 *0.03*
Rock cover	-0.07 *0.87*	-0.66 *0.08*
Shrub cover	-0.22 *0.60*	-0.86 *0.01*
Soil compaction: 1 cm depth	-0.21 *0.61*	0.34 *0.401*
Soil compaction: 10 cm depth	-0.05 *0.91*	0.01 *0.98*
Horizontal visibility	-0.18 *0.69*	0.44 *0.27*
Vertical visibility	0.02 *0.96*	-0.77 *0.02*
Plant richness	-0.29 *0.49*	0.52 *0.19*
Plant Shannon-Weiner diversity index	-0.29 *0.49*	0.43 *0.29*
Plant Simpson’s diversity index	-0.48 *0.23*	0.15 *0.72*

DISCUSSION

Total small mammal densities tended to be higher in upper grassland habitats as opposed to lower grasslands, yet this pattern did not hold for all species trapped in this study. While voles and shrews were caught almost exclusively in the upper grasslands, deer mice were caught in both habitat types, and appear to be the dominant species of the lower grasslands. This shift in species composition is likely due to the significant differences in plant communities and the associated habitat characteristics found in each grassland type.

Previous studies into small mammal community assemblages have documented similar shifts in functional groups (e.g. herbivore, omnivore, granivore) based on habitat characteristics, similar to that seen in this study. French et al. (1976) and Grant and Birney (1979) were one of the firsts to describe rodent communities across a number of North American grasslands, and demonstrated a shift in rodent assemblages based on vegetation density and composition, with microtine herbivores occurring in areas of high vegetative cover, omnivores at intermediate cover sites, and granivorous heteromyids at low cover sites. Similar findings have been reported in later studies (e.g. Pearson et al. 2001, Reed et al. 2006b), and it appears rodent communities in this study followed similar patterns.

Vegetative cover, and particularly litter, is an important habitat component for voles, and may explain why these animals were all but absent from the lower grassland sites. For rodent herbivores with relatively low digestion efficiency (French et al. 1976), who can quickly cut and consume plant matter (Howe et al. 2002, 2006), increased vegetative cover can equate to increased food availability. As semi-fossorial animals who often tunnel through plant litter, increased litter levels may reduce the risk of predation, particularly from diurnal predators, and may decrease the chances of aggressive interspecific and intraspecific interactions (Warnock 1965). Decreased levels of vegetative cover may negatively affect vole population dynamics, including recruitment and survival (Peles and Barrett 1996), and it has been hypothesized that a threshold level of cover is required for some vole populations to persist, increase, and in some instances, undergo cyclic fluctuations (Birney et al. 1976). For their study, Birney et al. (1976) suggested that cover levels between 400 and 600 g/m^2 were needed for voles at their sites to increase to the point of cycling, and on the lower grassland sites for this study, vegetative cover levels were well below those values, averaging 94.81 g/m^2. This lack of herbaceous plant cover and the biotic and abiotic benefits it provides most likely exclude voles from persisting in the lower grasslands.

Unlike voles, deer mice were found in both grassland habitats, often at higher densities in the lower grasslands, but at times higher densities in the upper grasslands. Generally, however, there were few significant differences in deer mouse densities between the two grasslands types. This observation supports previous works that document the ubiquitous nature of the species (e.g. French et al. 1976, Grant and Birney 1979, Pearson et al. 2001), given that their generalist lifestyle allows them to exploit a wide variety of habitats. Using abundance as an indicator of habitat quality has been questioned however (Van Horne 1983, Wheatley et al. 2002, Battin 2004), and looking at other population metrics such as survival and reproduction may provide deeper insights into the quality of the habitat in which wildlife persist (Schorr et al. 2007).

In this study, apparent survival rates of deer mice differed only slightly between the upper and lower grasslands, with the treatment effect (i.e. elevation) excluded from the top survival models in all years of study. The percent of reproductively active females also did not differ significantly between elevations, and although the upper grasslands did tend to have higher portions of females in their populations, on a year-by year basis these differences were seldom significant. Such results indicate that both the upper and lower grasslands may provide similar levels of habitat quality to deer mice, and yet conflict somewhat with the density results which showed that at times the lower grasslands could have significantly higher densities of deer mice. The answer to this disparity may lie in differences in over-winter survival at the two habitats.

The over-winter period appears to be a difficult time for deer mice in grassland ecosystems, as it can be for other rodent species in different habitats (e.g. Merritt and Merritt 1978, Boonstra and Krebs 2006, Larsen et al. 2007). In general, rodents living in areas with complete snow cover will persist in the subnivean space. This space protects them from external winter conditions and predators, and allows for the exploration and utilization of under-snow food resources. At the same time, the subnivean space may not be contiguous, and it has been suggested that depending on the conditions under which it is formed, snow cover can reduce the over-winter survival of rodents by encasing vegetation in ice, and significantly reducing the levels of available food resources (Korslund and Steen 2006). It has also been hypothesized that late winter/early spring thaw can produce extreme sub-snow conditions by filling much of the subnivean space with water, or by creating a layer of ice over vegetation, leading to the potential drowning and/or freezing of its rodent inhabitants, and further restricted access to food resources (Merritt and Merritt 1978, Aars and Ims 2002).

This study saw significant differences in snow depths between the upper and lower grasslands during the two over-winter trapping sessions, with the upper grasslands having continuous snow cover, and the lower grasslands remaining relatively snow-free during the course of the winter. Although the lack of snow in the lower grasslands would offer deer mice little in the way of thermal protection, it would allow them better winter foraging opportunities and protection from any adverse conditions during spring thaw. Further, although the two grassland ecosystems showed similar May through October population demographics and apparent survival rates, winter conditions in the upper grasslands may prove to be a tighter bottleneck for deer mice than in the lower grasslands. Further study into the winter dynamics of rodents in these two ecosystems is suggested.

Both 2007 and 2008 saw similar patterns of within-year deer mouse densities in both the lower and upper grasslands, with densities dropping or remaining low for the first three trapping sessions, and then significantly increasing into the fall season. Similar patterns have been reported elsewhere (Fairbairn 1977a, Gilbert and Krebs 1991, Falls et al. 2007), with the initial spring time reduction thought to be the result of increased aggressiveness and spacing behaviour of breeding males, and an increased mortality of early-breeding females (Fairbairn 1977a). The increase in densities later in the year may be the result of increased breeding success, and the presence of more juvenile individuals in the populations. This study's analysis of the percent of adult deer mice trapped per trap session lend support to this supposition, as these percentages generally decreased during fall trapping sessions while densities continued to increase.

Beyond the differences in densities at the habitat scale, vole populations in the upper grasslands showed a significant decrease in densities across the three years of study. Deer mice showed similar trends in the lower grasslands, although not to the same severity.

Studies into the nature of vole population changes are extensive (e.g. Krebs et al. 1973, Korpimäki and Krebs 1996, Krebs 1996, Boonstra et al. 1998, Oli and Dobson 2001, Korpimäki et al. 2004) and microtine species have often been used as models to examine the nature of animal population cycles. It is generally accepted that many vole populations, particularly those at northern latitudes, can undergo multi-annual cycles, generally 3-5 years, but such cycles have also been noted in grassland rodent communities (Brady and Slade 2004), and multiannual fluctuations have been observed in some populations of deer mice (Drost and Fellers 1991, Brady and Slade 2004, Bartell et al. 2008). Hypotheses to explain these cycles are extensive, with Stenseth and Ims (1993) dividing them into three broad categories: abiotic (e.g. weather), biotic extrinsic (e.g. predation, competition, food availability), and biotic intrinsic (e.g. genetic and behavioural), and the interactions between these categories. Unfortunately the current study was not long enough to determine if the observed declines from 2006 vole densities represented the onset of a low-phase of a population cycle (Boonstra et al. 1998), the short-term decline of a generally higher population, or the return of the population to a lower density steady-state after a previous population increase.

A cursory review of the historic annual rainfall levels in the area of the study showed that 2004 and 2005 precipitation levels were above the previous 30 year (1974-2003) average (281.4 mm) at 378.9 mm and 306.5 mm, respectively, while the 2006 and 2007 levels were below this historic average (268.5 mm and 230.0 mm, respectively). It is well known that precipitation levels are highly correlated to net primary productivity in arid and semi-arid systems (Sala et al. 1988, Lauenroth and Sala 1992), with small mammal densities also increasing as precipitation increases, but lagging up to a season behind (Brady and Slade 2004, Shenbrot et al. 2010, Thibault et al. 2010), and decreasing over a relatively small reduction in mean precipitation (Reed et al. 2007). The higher densities of voles in the upper grasslands and deer mice in the lower grasslands in 2006 may have been the result, in part, of higher than average precipitation levels in 2004 and 2005, with their declines in 2007 and 2008 a result of the less than average amounts of precipitation observed in 2006 and 2007. Longer-term monitoring of small mammal densities, precipitation and primary production would be needed to fully understand these interactions.

Small mammals are important components of grassland ecosystems, and this study is one of the first to provide insights into small mammal communities in the grasslands of British Columbia, Canada. It has been shown that although upper grasslands tend to have higher total small mammal densities, this relationship is not constant. Further, a shift of small mammal functional groups appears to occur, with vole species confined to the upper elevations, and deer mice found in both habitats and almost exclusively dominating the lower grasslands: a separation believed to be based on the decreased levels of plant litter at the lower grassland sites. Inspection of the apparent survival rates between deer mice in the upper and lower grasslands, however, showed no tangible differences, and so both grassland types may be of equivalent quality for this species, at least during non-winter months. And finally, this study documented the general decrease of both vole and deer mouse densities over the course of three years, a trend that may be the result, in part, of previous years' levels of precipitation. This study provides information on small mammal communities in British Columbia grasslands that was previously lacking, and offers a foundation for further research into the structure and workings of these grassland ecosystems.

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CHAPTER 3 – SELECTION OF NESTS AND DAYTIME REFUGE SITES BY DEER MICE IN A SEMI-ARID GRASSLAND IN BRITISH COLUMBIA, CANADA

INTRODUCTION

The manner in which certain organisms choose to occupy a particular habitat can be viewed as a hierarchical process in which individuals make habitat selection choices at varying spatial scales. Johnson (1980) described this hierarchy of choices as ordered selections. For example, members of a species may occupy a range of different macrohabitats (e.g. forest vs. grassland): a first order selection. Within each macrohabitat, individuals may occupy a home range (second order selection), and within each home range select areas for specific activities such as feeding or nesting (third order selection). The location where the specific activity occurs (e.g. nest site location) may be considered a fourth order selection (Johnson 1980). Small mammals have been shown to respond to habitat characteristics at both the macrohabitat and microhabitat levels (Morris 1984, 1987, Stapp 1997), and these responses can be influenced by a number of interacting factors, including food and shelter availability, levels of predation, and conspecific and inter-specific interactions (Redfield et al. 1977, Tait 1981, Dooley and Dueser 1996). Two such habitat attributes that may affect small mammal habitat selection and that have been considered potential limiting resources for small mammals are nests and daytime refuge sites (Dooley and Dueser 1990, Bright and Morris 1991).

Characteristics of nests and daytime refuge site locations (hereafter referred to collectively as refuge sites) have been described for a number of small mammal species. For example, cotton mice (*Peromyscus gossypinus*) and golden mice (*Ochrotomys nuttali*) in south-central Florida often are associated with burrows of the gopher tortoise (*Gopherus polyphemus*; Frank and Layne 1992), and for cotton mice, coarse woody debris (CWD) in some forest systems (Hinkelman and Loeb 2007). Wolff and Hurlbutt (1982) and Wolff and Durr (1986) detailed a strong affinity of deer mice (*P. maniculatus*) for arboreal nest sites in Virginia mixed-deciduous forests. Refuge sites may provide a decreased risk of predation (Klein and Layne 1978), can facilitate the coexistence of similar species (Wolff and Hurlbutt 1982, Barry et al. 1984, Harney and Dueser 1987), and may provide protection from the elements through a moderated living environment (Frank and Layne 1992); such resources may be particularly important for rodents living in xeric or semi-arid habitats.

In British Columbia, Canada, the deer mouse is a ubiquitous rodent found throughout all of the province's biogeoclimatic zones (Nagorsen 2005). In some of the province's low elevation grasslands, the deer mouse plays a significant role in the functioning of the ecosystem, including prey for a number of grassland predators like western rattlesnakes (*Crotalus oreganus*), gopher snakes (*Pituophis catenifer*), coyotes (*Canis latrans*) and raptor species. These low-elevation grassland sites are characterized by the lack of trees, but are dominated by big sagebrush (*Artemisia tridentata*) and large, bare inter-shrub areas with widely spaced bunchgrasses (van Ryswyk et al. 1966, Wikeem and Wikeem 2004). Summer daytime air temperatures can exceed 40°C, and effective refuge sites may be critical to deer mice for managing thermal stress, maximizing reproductive success, and ultimately, increasing fitness. Thus, given the relatively short season of productivity (due to latitude) and the relatively hot summer temperatures, this habitat provides an interesting backdrop for investigating potential limiting factors on deer mice, such as the selection and availability of refuge sites.

Deer mice have been shown to orient their movements towards shrubs, and to display a preference towards shrub microhabitats in grassland environments (Stapp and Van Horne 1997). Although no formal studies have examined refuge sites for deer mice in British Columbia's semi-arid grasslands, which lack trees and large quantities of CWD, they have been observed burrowing under *Artemisia* (Nagorsen 2005). Understanding where deer mice build refuge sites and how they choose refuge locations will help us understand the relationship of this dominant grassland rodent to its dry semi-arid environment, and will help assess the impacts of land management decisions, environmental change and habitat alterations.

The objective of this study was to model deer mouse refuge site selection within a low-elevation grassland macrohabitat at two scales corresponding to Johnson's (1980) third and fourth order selection scheme. To do this I used radio telemetry and examined a suite of *a priori* above-ground habitat variables. Due to the previously reported affinity of deer mice to shrubs, it was hypothesized that shrub cover would be a significant predictor of refuge sites at both scales of habitat selection.

METHODS

Study Area

Data for this study were collected from a shrub-steppe grassland near Kamloops, British Columbia, Canada (50°43’ N; 120°25’ W). The area is consistent with the “lower grasslands” described by Tisdale (1947) and van Ryswyk et al. (1966) and consists of a large expanse of *Artemisia*-dominated grassland, interspersed with bare inter-shrub areas, and grass species such as bluebunch wheatgrass (*Pseudoroegneria spicata*), needle-and-thread grass (*Hesperostipa comata*) and crested wheatgrass (*Agropyron cristatum*). The area receives infrequent grazing by foraging livestock.

Capture and Radio Telemetry

Deer mice were live-trapped at two sites between June 9, 2008 and September 3, 2008. At each site, deer mice were sampled with a 10 × 5 trapping grid (50 traps total) with 14.3 m between trap stations. A single Longworth-style live trap (Little Critter Traps, Rogers Manufacturing, Kelowna, BC) was placed within a 2 m radius of each trap station, and covered with a 15 × 30 cm board to protect it from exposure to sun and rain. Synthetic cotton bedding was added to the nesting chamber of each trap, and traps were baited with approximately 5 g of a mixture of oats and sunflower seeds with a piece of apple or carrot included as a moisture source. Traps were set within 2 hours of sunset and checked within 2 hours after sunrise the following morning. Captured deer mice were sexed and weighed using 60 g spring scales (PESOLA AG, Baar, Switzerland). As this study was part of a larger project examining small mammal communities in grassland ecosystems (see Chapter 2), most captured animals had been previously marked with a uniquely numbered ear tag (Monel #1005-1, National Band and Tag, Newport, KA), and newly captured animals were tagged thusly.

Deer mice weighing $\geq$ 20 g were considered candidates for radio telemetry, in order to keep the weight of the radio transmitter at $\leq$ 5 % of the body weight of collared individuals, and to avoid collaring transient animals attempts were made to only collar mice that had been previously tagged as part of the community study referenced above. The reproductive status of each individual was assessed using scoring techniques similar to McCravy and Rose (1992) and Moses and Boutin (2001). For males, testes position (abdominal or scrotal) was noted, and for females, teats were scored as either inactive (small and difficult to see), enlarged (teats large; pregnant), lactating (teats large and fur worn), or returning to normal (teats healing with fur re-growth). Mice were each fitted with a BD-2NC transmitter (Holohil Systems Ltd., Carp, ONT), observed for a minimum of 15 minutes to ensure the animal's welfare and to confirm the transmitter's operability, and released at the point of capture.

For the purposes of this study, "daytime" refers to the time between 2 hours after sunrise to 2 hours prior to sunset. At the onset of the study, deer mice were located twice daily at irregular intervals until it was determined they were not changing locations, after which they were located once a day. Telemetry locations were marked using a 53 cm metal surveyor stake flag and their Universal Transverse Mercator (UTM) coordinates determined using a handheld global positioning system unit. Individual deer mice were tracked for 7 to 9 consecutive days, at the end of which they were recaptured and their collars removed, and then released.

Habitat Measurements

Habitat measurements were taken after the tracking session for each particular mouse had been completed, so as not to interfere with the animal's daily movement patterns. At each telemetry location, the habitat metrics listed in Table 3.1 were estimated by centering a 1 × 1 m frame over the location and visually estimating the percent cover of each metric. To compare the habitat elements at each telemetry location with the

Table 3.1. Habitat metrics measured at telemetry locations, third order and fourth order habitat plots using a 1 × 1 m frame.

Habitat Metric	Description
Herb	Percent cover of live grasses, forbs, and cacti.
Litter	Percent cover of dead grasses, forbs and cacti, as well as downed shrub material, including leaves and woody material < 2.5 cm in diameter.
Rock	Percent cover of rocks and gravel, but excluding sand and silt.
Ground	Percent cover of sand, silt and lichen.
Shrub	Percent cover of live shrubs.
CWD	Percent cover of rooted and unrooted coarse woody debris ≥ 2.5 cm in diameter.
StemTotal	Number of shrubs rooted within the 1 × 1 m frame.
SageD	*A. tridentata* trunk diameter measured at 10 cm above the ground and recorded to the nearest 0.1 cm.
SageH	*A. tridentata* height measured vertically from the ground to the uppermost crown and recorded to the nearest 0.5 cm.
SageL	*A. tridentata* length measured from the ground along dominant branch to the uppermost crown and recorded to the nearest 0.5 cm.
RbD	*Chrysothamnus nauseosus* trunk diameter measured at 10 cm above the ground and recorded to the nearest 0.1 cm.
RbH	*C. nauseosus* height measured vertically from the ground to the uppermost crown and recorded to the nearest 0.5 cm.
RbL	*C. nauseosus* length measured from the ground along dominant branch to the uppermost crown and recorded to the nearest 0.5 cm.
Slope	Measured at telemetry location and at centre-point of the third order plots. Recorded in percent slope.

immediate surrounding area (i.e. fourth order selection), the habitat metrics in Table 3.1 were again assessed by placing the 1 × 1 m frame at a distance of 5 m at bearings of 0°, 120° and 240° from the telemetry location. To collect third order selection data, a random distance between 20 and 50 m from the telemetry location, and at a random compass bearing, was selected and marked. From that position, the 1 × 1 m frame was placed at a distance of 5 m at bearings of 0°, 120° and 240°, and the habitat metrics in Table 3.1 were again collected. This process was then repeated by going back to the telemetry location and measuring out a position the same distance from the telemetry location as the first set of third order habitat metrics, but offset by 180°. Hence, for each telemetry location, three sets of fourth order measurements and six sets of third order measurements were taken (Figure 3.1).

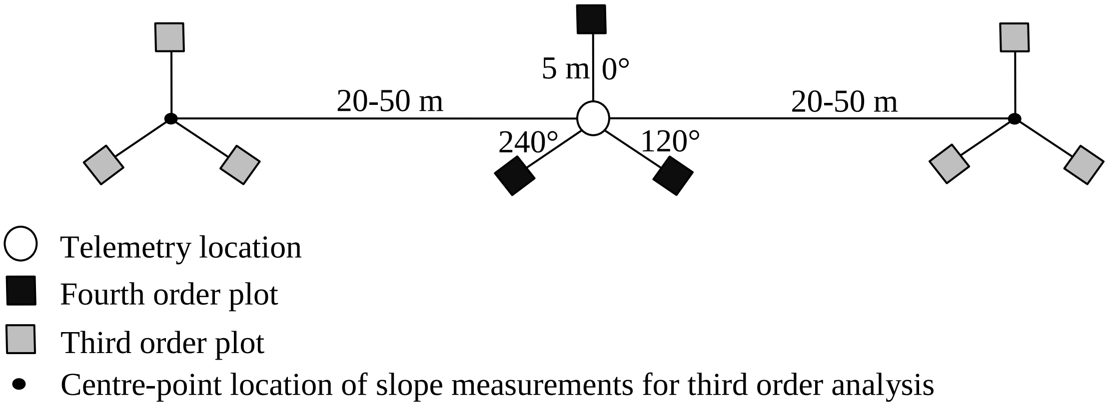

Figure 3.1. Layout of methodology for collecting habitat metrics at the third order and fourth order levels for each telemetry location.

To investigate the levels of thermal protection afforded by refuge sites, a temperature data logger (DS1921G Thermochron iButton, Maxim Integrated Products, Sunnyvale, CA) was placed within each identified refuge location. A second data logger was placed within 5 m of the telemetry location, and attached to the north side of an *Artemisia* trunk approximately 30 cm above the ground in order to measure external ambient daytime temperatures. The loggers recorded temperatures every 15 minutes, and collected data for 5 days at each location.

Data Analysis

For descriptive purposes, refuge sites were classified as: 1) underground; 2) above ground (sites where the mouse was visible on the ground’s surface); 3) arboreal (sites in shrub canopy); 4) inside shrub trunk; and 5) anthropogenic (sites in or on man-made structures). Sites were further classified according to the dominant landscape feature at the telemetry location, and included shrub, grass, rock, bare ground and anthropogenic.

To determine the minimum daily movements (i.e. the straight-line distance between consecutive telemetry locations) of deer mice, telemetry UTM coordinates were mapped and the distances determined. Telemetry locations separated by more than 36 hours were excluded from this portion of the analysis.

Conditional (i.e. case-control) logistic regression was used to analyze the selection of habitats at both the third and fourth order scales. Conditional logistic regression allows the pairing of used sites (i.e. cases) with multiple available sites (i.e. controls), which reduces autocorrelation issues often associated with spatial and temporal data (Whittington et al. 2005), and allows for a better sampling of the habitat available to the animal being tracked. Fourth order selection was analyzed using a 1:3 case:control design (i.e. predictor variables at each telemetry location compared to variable measurements taken from each of the three associated fourth order plots), and third order selection was analyzed using a 1:2 design, with the average of each predictor variable from each set of fourth order plots compared to predictor variable averages of each of the two sets of associated third order habitat plots, for every telemetry location.

Predictor variables were selected for inclusion in the model after first examining the collinearity between variables using Spearman's rank correlation analysis (Zar 1999). When variable pairs had correlations > 0.7, the variable with the lowest Akaike's Information Criterion adjusted for small sample sizes (AIC_c) using a single variable model was selected for model inclusion (Burnham and Anderson 2002). Further, the Wald statistic was calculated for each predictor variable using a single variable model, and variables with a *P*-value > 0.10 were considered uninformative, and excluded from further model development (Harrower 2007).

The goodness-of-fit of the global model (i.e. the model with all variables included) were assessed by plotting the $\Delta\chi^2$ statistic against the model's fitted values, and examining data for matched case-control sets that disproportionately affected the model's fit (Hosmer and Lemeshow 2000). Sets deemed to be outliers were removed from the dataset. Models were then developed by examining all combinations of the predictor variables. Model development was constrained by limiting the number of variables in the model to approximately 10% of the number of observations (Peduzzi et al. 1996), in this case four variables, and model selection was based on the model with the lowest AIC_c value.

As the hallmark of any good habitat selection model lies in its ability to accurately assess a species' habitat choices, the predictive success of the top models were determined using a form of *k*-fold cross validation, adapted from Boyce et al. (2002). *K*-fold cross validation generally involves splitting a dataset into three or greater subsets, and using a portion of the subsets to train the model, and the remaining subsets to test the model (Fielding and Bell 1997). For this study, a *k*-fold partition of three groups was used. Cases and their matched controls were systematically assigned to one of the three groups, and two of the three groups were used to train the model. This was repeated three times so that each partition was excluded from the training set once. For each iteration, data from the training set were used to determine the β-coefficients for each of the predictor variables in the top model, using conditional logistic regression. The β-coefficients for each variable were then averaged across all three training-set runs, and for each control (i.e. available) location, the resource selection function [RSF; w(*x*)] was determined using the averaged β-coefficients for each variable with the equation:

$$w(x) = \exp(\beta_1 x_1 + \ldots + \beta_p x_p)$$

These results were then divided into eight categories, or bins, with each bin containing approximately the same number of RSF scores (i.e. equal area bins; Boyce et al. 2002, Wiens et al. 2008). Resource selection function scores for the case (i.e. used) locations were calculated in the same manner, using the averaged β-coefficients derived from the training datasets and the equation above, and assigned to the appropriate bin. A Spearman's rank correlation analysis was then performed on the number of cases and the mid-point RSF score of each bin. A model with good predictive ability would have a strong positive correlation, as more case sites should occur in bins with higher RSF scores (Boyce et al. 2002).

Temperature data were analyzed in two ways: 1) the mean daily high external ambient temperature was compared with the corresponding mean daily temperature within the refuge site; and 2) the mean daily high external ambient temperature was compared with the mean daily high temperature within the refuge site. All comparisons were made using paired t-tests.

All data were analyzed using SAS 9.2 software (SAS Institute Inc. 2008). The goodness-of-fit for each model was examined using the SAS macro MCSTRAT, and all logistic regression models were built and analyzed using the PROC LOGISTIC procedure. The normality of the temperature data was confirmed using PROC UNIVARIATE, and the paired t-tests were performed using PROC TTEST.

RESULTS

Over the course of the study, 13 individual deer mice were collared (♂ = 8, ♀ = 5), with one male deer mouse collared and tracked twice, approximately 3 months apart. All collared males were considered reproductively-active based on testes position, and all females were considered pregnant or lactating, based on nipple morphology. In total, 42 unique daytime refuge sites were located, with 71.4% located underground, 19.1% above ground, 4.8% inside the bole of an *Artemisia*, 4.7% in an anthropogenic structure, and 0% in arboreal sites. The majority of the telemetry locations had shrubs as the dominant above-ground characteristic (76.2%), followed by grasses (16.7%), rock and bare ground (9.5% each), and finally anthropogenic structures (4.8%). These numbers exceed 100% as several sites were included in two or more categories (e.g. shrub and grass). The anthropogenic sites included one within the metal tube of a cattle guard crossing, and another under a rock and asphalt pile in a gravel quarry. These sites were removed from any further analyses. Mean male minimum daily movement was 122 m (n = 36), with a maximum daily movement of 359 m, and mean female daily movement was 69 m (n = 18), with a maximum daily movement of 262 m.

Fourth Order Selection Modelling

Of the 13 variables originally measured for inclusion in the candidate models, the variables Herb and Litter, SageD and SageH and SageL, as well as RbD and RbH and RbL were highly correlated with each other. Of these, Herb, SageD and RbD explained relatively more of the variation in the data (i.e. had the lowest AIC_c scores), and so were retained for model development, while the others were omitted. As well, the variables StemTotal and RbD both had Wald statistic P-values > 0.10 and so were removed from further model development.

Using the six remaining habitat variables, 56 models were developed to examine the fourth order selection of deer mice, with the top ten models based on AIC_c value provided in Table 3.2. An examination of the β-coefficient estimates of the parameters in the top model (SageD + Ground + CWD) indicate that the deer mice in this study were selecting refuge sites at areas with relatively larger-diameter *Artemisia*, decreased levels of bare ground and increased amounts of CWD than was typically available in the immediately surrounding microhabitats (Table 3.3). Subsequent evaluation indicated that the top model did a good job of predicting deer mouse fourth order selection. The correlation coefficient between the midpoint RSF score for each bin and the observed frequency was 0.82, with $P = 0.01$.

Table 3.2. Top 10 models used to examine refuge site selection by deer mice at the fourth order scale, and detailing the number of model variables (K), Akaike's Information Criterion adjusted for small sample sizes (AIC_c), the change in AIC_c from most parsimonious model (ΔAIC_c), and the model weight (*w*).

Model	K	AIC_c	ΔAIC_c	*w*
SageD + Ground + CWD	4	68.69	-	0.36
SageD + Ground + CWD + Rock	5	70.30	1.62	0.16
SageD + Ground + CWD + Herb	5	71.18	2.49	0.10
SageD + Ground + CWD + Shrub	5	71.36	2.67	0.10
SageD + Ground	3	71.62	2.94	0.08
SageD + Ground + Rock	4	72.89	4.21	0.04
SageD + Ground + Rock + Shrub	5	73.53	4.84	0.03
SageD + Ground + Herb	4	73.54	4.86	0.03
SageD + Ground + Shrub	4	73.59	4.90	0.03
SageD + Ground + Rock + Herb	5	75.27	6.59	0.01

Table 3.3. β-coefficients and average measurements of the habitat metrics included in the top model of the fourth order habitat analysis. Reported average measurements are taken from the telemetry locations and fourth order plots, with SageD recorded in centimetres, and Ground and CWD in percent cover of the 1 × 1 m frame.

Habitat Metric	β	Telemetry Location	Fourth Order Plots
SageD	0.31	6.97	4.25
Ground	-0.04	37.62	54.74
CWD	0.05	8.62	4.02

Third Order Selection Modelling

Fourteen predictor variables were originally measured for third order model building. Of these, all but two variables (Litter and Slope) had Wald statistic *P*-values > 0.10, and so were excluded from further model development. As a result, only three models were built to examine third order habitat selection of deer mice (Table 3.4). An examination of the β-coefficient estimates of the parameters in the top model (Slope + Litter) indicate that the deer mice in this study were selecting areas with increased slope and decreased litter (Table 3.5). Model evaluation indicated that the top model did a reasonable job of predicting deer mouse third order habitat selection. The correlation coefficient between the midpoint RSF score for each bin and the observed frequency was 0.73, with $P = 0.04$.

Table 3.4. Top three models used to examine refuge site selection by deer mice at the third order scale, and detailing the number of model variables (K), Akaike's Information Criterion adjusted for small sample sizes (AIC_c), the change in AIC_c from most parsimonious model (ΔAIC_c), and the model weight (*w*).

Model	K	AIC_c	ΔAIC_c	*w*
Slope + Litter	3	57.69	-	0.95
Slope	2	63.38	5.69	0.06
Litter	2	83.24	25.55	0.00

Table 3.5. β-coefficients and average measurements of the habitat metrics included in the top model of the third order habitat analysis. Reported average measurements are taken from the third order and fourth order plots, with Slope recorded in degrees, and Litter in percent cover of the 1 × 1 m frame.

Habitat Metric	β	Third Order Plots	Fourth Order Plots
Slope	0.11	24.29	37.10
Litter	-0.05	47.78	40.89

Temperature Analysis

In total, 35 refuge sites were included in the temperature analysis. The mean 5-day average daily high ambient temperature was 32.7°C (s.e. ± 0.9°C) with the corresponding mean 5-day average daily high temperature in refuge sites being 28.0° C (s.e. ± 0.9°C). The mean 5-day average temperature of refuge sites when the ambient temperatures were at their hottest was 26.8°C (s.e. ± 0.9°C). The ambient daily high temperatures were significantly greater than the daily high temperatures in the refuge sites ($t = 5.91$, d.f. = 34, $P = < 0.01$) and the temperatures in the refuge sites when the ambient temperature was at its peak ($t = 7.32$, d.f. = 34, $P = < 0.01$).

DISCUSSION

Nest and daytime refuge site selection by deer mice in the current study appeared to be strongly influenced at the fourth order level by the presence of *Artemisia*, and in particular, relatively large-sized *Artemisia*, as originally hypothesized. That a majority of refuge sites were found underground at or near the base of an *Artemisia* is consistent with observations by Nagorsen (2005).

Previous studies have shown the importance of shrubs to deer mice. For example, Stapp and Van Horne (1997) revealed that deer mice in shortgrass prairies oriented their movements towards shrubs, and selected shrub microhabitats in areas where shrubs were rare. A standing theory is that shrubs provide refuge sites from predators (Kotler 1984, Kotler and Brown 1988), and while deer mice may be choosing subterranean daytime rest sites beneath larger shrubs to help evade detection by avian and mammalian predators, such sites may not provide increased security from snake predation (Pierce et al. 1992). Indeed, we often were able to see the resting mouse in the refuge site, suggesting the animals would be vulnerable to snake and other ground-based predators. A more probable reason why the deer mice in this study were selecting microhabitats with relatively large *Artemisia* could be the favourable environmental conditions these shrubs provide.

Rodents living in desert and semi-arid climates are challenged with thermoregulation under exceptionally hot and dry conditions, where minimizing the loss of body water is of paramount importance (Walsberg 2000). Sagebrush are known to establish resource islands in their sub-canopies (the area below the canopy) by creating moderate microclimates when compared to inter-shrub areas (Parmenter and MacMahon 1983, Davies et al. 2009). Locating refuge sites below the canopy of large *Artemisia* may facilitate deer mice in thermoregulation as these sites have moderated maximum daily soil temperatures when compared to inter-shrub spaces (Pierson and Wight 1991, Davies et al. 2007). The current study appears to lend support to these previous findings, with average daily high temperatures at refuge sites being significantly lower than average daily high ambient temperatures. As sagebrush sub-canopies also tend to have higher soil moisture levels (Chambers 2001, Davies et al. 2007), selecting them for refuge sites may promote decreased rates of body water loss. Finally, as sub-canopy microhabitats can promote herbaceous plant growth (Chambers 2001, Davies et al. 2007) and offer retreat sites for desert insects (Parmenter et al. 1989), deer mice may orient their movements to sub-canopy areas, selecting daytime refuge locations at those areas due to the proximity to potential food sources (Parmenter and MacMahon 1983). These final benefits may be tempered somewhat by the allelopathic nature of *Artemisia* plants (Weaver and Klarich 1977, Groves and Anderson 1981).

Deer mice in this study selected sites with decreased amounts of bare ground than was typically available on the landscape: a result that was not unexpected. Bare ground may be viewed as an antonym to the microhabitat conditions provided by shrubs and their sub-canopies, with increased bare ground offering reduced amounts of protection from predators, increased exposure to extreme environmental conditions, and increased distances to potential food resources (see previous citations). An increased amount of bare ground is analogous to reduced levels of microhabitat heterogeneity, an environmental component that may be important in rodent habitat selection. Increased heterogeneity can provide more crevices and spaces to establish refuge locations, as well as multiple routes to hide and evade predator detection (Bertolino and Cordero Di Montezemolo 2007).

Increased levels of CWD was the final predictor variable for deer mouse refuge site selection at the fourth order level, and CWD has been shown to be an important habitat component for small mammals, particularly in forested habitats (e.g. Loeb 1999, Bowman et al. 2000, Butts and McComb 2000, Johnston and Anthony 2008). Studies examining the nesting and refuge site selection of rodents in forests have found small mammals using CWD as primary nest and refuge sites (e.g. McCay 2000, Hinkelman and Loeb 2007), and in this study, 2 of the 40 refuge sites were found inside the boles of dead sagebrush.

Further to CWD providing primary refuge site locations, it may provide secondary benefits to the establishment of refuge sites. In hot sagebrush habitats, CWD may act in ways similar to live shrub cover, with standing woody debris providing sites of decreased risks of predation and of moderated environmental conditions conducive to refuge site selection. Downed (i.e. horizontal) woody debris are used as silent, efficient travel routes by species of *Peromyscus* in forest settings, presumably to avoid detection by predators (Barnum et al. 1992, Roche et al. 1999, McCay 2000). Downed *Artemisia* trunks, although generally much smaller in diameter than forest CWD, may provide similar services in shrub-steppe settings by providing travel corridors that reduce the risk of predation for deer mice entering and exiting refuge locations.

At the third order level, neither the presence of large *Artemisia* nor the levels of shrub or herbaceous plant cover were included in the final models predicting deer mouse use; this was an unexpected result. At that scale, deer mice were selecting areas with increased slope and decreased levels of plant litter, a result that supports Johnson's (1980) supposition that animals can make selection choices at different spatial scales, and supports previous works that examined habitat selection of small mammals at different habitat levels (Morris 1984, 1987, Stapp 1997).

The use of steep terrain by deer mice might have its basis in the physical characteristics such slopes can provide. The fine-grained top soil at the study site appeared quite prone to erosion, with summer thunderstorms creating numerous rills and small cavities on the steeper areas of the site. The apparent increased heterogeneity of the ground surface on steeper slopes may provide greater opportunities for the establishment of refuge sites. Further, *Artemisia* boles and roots on steep slopes often were observed to create overhangs above the downhill slope, and were targeted by deer mice for burrow placement on several occasions. Deer mice may select refuge sites at the bases of large shrubs on steeper slopes, due to the increased protection such shrubs may provide.

There may be additional benefits to deer mice selecting refuge locations on steep slopes. The study site is subject to periodic grazing by cattle and it has been shown that cattle reduce their grazing on steeper slopes (Holechek 1988, Bailey 2005, Bailey et al. 2006), preferring to congregate and forage on flatter areas. Cattle observed at the study site appeared to follow these patterns, restricting their foraging and movement patterns to flat or gentle terrain in the area. Signs of recent or historic cattle use (e.g. hoof prints, feces, disturbed/flattened shrubs) were virtually absent from all areas with steep slopes. Deer mice selecting refuge sites on steep slopes may benefit from a reduced risk of livestock disturbance. The study site also receives quite a bit of human disturbance, namely from vehicle traffic (e.g. four-wheel-drive trucks, all-terrain vehicles and dirt bikes), as well as from hikers and the occasional cyclist. Human activity was generally concentrated on flatter terrain or ridgelines, and so as with livestock disturbance, selecting steep slopes for refuge sites could reduce the potential of human disturbance.

Litter was the second variable included in the top mode for third order habitat selection, with deer mice choosing areas with decreased levels of litter at this scale. This result is a bit surprising, yet previous studies have documented the preferential selection of areas with reduced litter by deer mice (Kaufman et al. 1988). A long-standing theory is that such areas allow deer mice to more easily predate on grass seeds that would otherwise be more difficult to detect in areas with increased litter (Kaufman et al. 1988, Kaufman and Kaufman 1990, Reed et al. 2004). As such, deer mouse fourth order habitat selection may be influenced by increased seed-forage opportunities at a higher spatial scale. At this stage, however, further study is required to confirm the importance of decreased litter levels of deer mouse habitat selection at the third order level.

It needs to be recognized that the top third order model did not do an exceptional job of predicting deer mouse habitat use. This indicates that deer mice may be basing refuge site area selection choices on habitat characteristics other than those measured in this study (e.g. soil compaction/friability, arthropod densities), that the third order habitats were not adequately surveyed, or that deer mice were not selecting habitats at the scale measured.

An important assumption of both paired logistic regression and the calculation of RSFs with a used-available design is that the points designated as “available” represent habitats that are actually available to the animal or individual in question (Compton et al. 2002): an assumption that is difficult not to violate with cryptic wildlife such as deer mice. The current study failed to determine the home ranges of collared individuals, and as such, ‘available’ habitat plot measurements may have fallen outside of an individual animal’s home range, and thus would not represent truly available habitat. It was assumed that fourth order plots were available to the deer mouse being tracked, due to their proximity to their paired telemetry location, but the third order habitat plots may have violated this assumption. However, because of the low deer mouse densities observed over the course of the study, averaging six individuals per hectare, it is believed that conspecific interference was minimal and that collared animals had access to optimal daytime refuge sites on the landscape (Rosenzweig 1989, Thompson 2004).

In summary, deer mice can play a significant role in semi-arid grassland ecosystems, and the selection of nests and daytime refuge sites may be one factor that affects the local distribution of the species. Shrub cover has been shown to be important to small mammals, and in the shrub-steppe grasslands of British Columbia, deer mice appear to select refuge sites at locations that not only have larger-diameter *Artemisia*, but also decreased levels of bare ground and increased amounts of CWD. These locations seem to offer mice a form of thermal protection from the extreme daytime conditions of the low-elevation grasslands, and managers wishing to keep deer mice present on the landscape should consider preserving some of these habitat attributes when making land management decisions, in a manner akin to maintaining large snags for cavity nesting animals within forest ecosystems (Carey 2000, Payer and Harrison 2003, Walter and Maguire 2005, Oaten 2007). At the third order level, deer mice may be selecting refuge sites in areas with increased slope and decreased litter, although other habitat traits may be influencing deer mouse resource selections at this scale, and further research is warranted. Despite the limitations of our study, the information presented here is the first to provide insights into the refuge site selection of deer mice in northern semi-arid grasslands. Information presented in this study can be used to direct future research into the selection habits of deer mice and other small mammal species.

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CHAPTER 4 – CONCLUSIONS

Review and Research Limitations

The overall goal of this thesis was to increase knowledge about small mammal communities in British Columbia temperate grasslands. To achieve this goal, two objectives were pursued: 1) to compare small mammal population and demographic information across markedly different upper and lower elevation grassland communities; and 2) to examine the third and fourth order resource selection of daytime refuge sites by deer mice (*Peromyscus maniculatus*) in a semi-arid grassland setting. Major results related to the first objective included: (a) total small mammal densities tended to be higher in the upper grasslands, and were significantly higher when data were pooled across years but not when analyzed on a per-year basis; (b) vole species (*Microtus* spp.) were found almost exclusively in the upper grasslands; (c) deer mice were found in both grassland habitats and densities tended to be higher in the lower grassland. These differences were not significantly different when data were pooled across years, and rarely significantly different when analyzed on a per-year basis; and (d) deer mouse apparent survival estimates did not differ between the upper and lower grasslands. Further, small mammal populations showed, at times, high levels of variability between both trapping sessions and years. For the second objective, deer mice appeared to be making third order selections based on the slope and percent cover of the landscape, and selecting daytime refuge sites (fourth order selections) at locations with large diameter big sagebrush (*Artemisia tridentata*), decreased amounts of bare ground, and increased amounts of coarse woody debris (CWD).

Small mammal populations are notorious for being highly dynamic, both spatially and temporally. Population irruptions and declines can occur over small or large scales (Korpimäki and Krebs 1996, Korpimäki et al. 2004), and although there is evidence that climatic variables may play a role in population fluctuations (Brady and Slade 2004, Korpimäki et al. 2004, Reed et al. 2007, Shenbrot et al. 2010, Thibault et al. 2010), a complete understanding of the underlying mechanisms has yet to be ascertained. The cyclic nature of some small mammal populations (Korpimäki and Krebs 1996, Brady and Slade 2004, Korpimäki et al. 2004, Bartel et al. 2008) can further complicate studies into the characteristics of their communities. Such studies require long-term data sets collected from adequately replicated research sites in order to avoid making erroneous conclusions based on interpretations of spurious results (Brady and Slade 2004). The present study collected data from eight main sites over three seasons of study, and so there is a risk that the patterns observed may not reflect the long-term structure and dynamics of small mammal communities in the areas studied. Future research efforts should endeavour to increase the number of replicate study sites in each grassland type, and attempt to collect data for 8 to 10 years, minimum. However, as always, funding avenues for this type of work will be a constraining factor.

Site selection may limit the ability to extrapolate these results to other areas of the BC grasslands, particularly those subject to invasion by alien plant species. Study sites in both the upper and lower grasslands were selected based on size (minimum one hectare) and plant community, with areas having appreciative amounts of non-native or invasive plant species avoided (Rankin unpubl.). Invasive plants are prevalent across most grasslands in British Columbia (Wikeem and Wikeem 2004), with the areas in and around Lac du Bois Grasslands Provincial Park inundated with species such as diffuse knapweed (*Centaurea diffusa*), spotted knapweed (*Centaurea stoebe*), Dalmatian toadflax (*Linaria genistifolia*) and cheatgrass (*Bromus tectorum*). The presence of these invasive species may alter the habitat characteristics (e.g. cover) of the plant community upon which small mammals rely, and so may have effects on the small mammal communities themselves (Pearson et al. 2000, 2001, Ostoja and Schupp 2009). Because the sites chosen for the current study purposely avoided areas with invasive plants, my results may not translate well to the majority of the grasslands in the area, where invasive plant species can be amply present.

With respect to the radio telemetry portion of the study, I was limited in the number of animals I could track due to logistics and resources, and a larger focused study would be able to provide a more thorough understanding of not only refuge site selection, but foraging behaviour, home range attributes, and other important life-history attributes of the animals. And although there is a belief that habitat selection at low population levels allows individuals to use the ‘best’ habitat resources (Rosenzweig 1989, Thompson 2004), the relatively small number of mice tracked for this study warrant caution when drawing conclusions from the results. A further limitation to this portion of the study was the inability to demarcate home ranges for the deer mice that were tracked. This is an important factor when attempting to determine what habitats are available to an individual when making resource selections (Compton et al. 2002), and may have been a reason for the marginal ability of the third order model to predict deer mouse habitat use.

Application of Research Findings

Land or wildlife managers rarely state that they are managing for small mammal populations, and indeed unless the small mammal in question is threatened with extinction or extirpation, rodent management normally falls very far down the list of priority actions or consideration. However, given their important roles in grassland systems (see examples in Chapter 2), land managers tasked with overseeing grasslands (particularly the endangered British Columbia grasslands) would be wise to consider maintaining rodent populations when planning management activities.

Anthropogenic activities such as grazing and prescribed burning to promote forage growth can have long-term effects on *Artemisia* and on levels of CWD (Harniss and Murray 1973, Wikeem and Strang 1983). *Artemisia*, generally the primary source of CWD in the lower grasslands, is a relatively slow-growing plant: Perryman and Olson (2000), for example, showed that in Wyoming USA, *Artemisia* could take up to 30 years to reach the average stem diameter of those used by deer mice in this study. Land managers interested in maintaining deer mouse populations should consider preserving some large-diameter *Artemisia* on the landscape to benefit this rodent species, in a manner akin to maintaining or creating large snags for cavity nesting animals within managed forest ecosystems (Carey 2000, Payer and Harrison 2003, Walter and Maguire 2005, Oaten 2007).

One of the important ecological functions of rodents is their role as sources of prey for a number of threatened and endangered grassland predators, including the western rattlesnake (*Crotalus oreganus*), gopher snake (*Pituophis catenifer*) and badger (*Taxidea taxus*). The provincial recovery strategies for both the badger and the *deserticola* subspecies of gopher snake (*P.c. deserticola*) cite the need for a better understanding of how small mammals respond to land management activities, such as grazing. The recovery strategy for badger further states that more detailed information on badger prey ecology is also necessary for the species' recovery, and Hoodicoff (2006) recommended collecting more localized information on historic, current and future prey population trends. Overall, this is a key knowledge gap that needs to be addressed to help aid in the recovery of these and other predator species in British Columbia (*jeffersonii* Badger Recovery Team 2008, Southern Interior Reptile and Amphibian Recovery Team 2008). Data presented in this study begins to fill this gap by providing local information on current small mammal populations in two grassland ecosystems.

Future Research

The constraints of this study notwithstanding, a number of recommendations can be made for future work, the first being a recommendation to establish long-term monitoring sites in the upper, middle and lower grasslands.

As discussed, long-term monitoring projects are essential to understanding small mammal populations, due to their highly dynamic nature. A long-term study should help further elucidate and confirm typical small mammal densities in the three grassland types. Any such study should endeavour to concurrently collect vegetative and climate data, as well as information on key grassland predators, particularly those threatened and endangered species listed above, that would be using rodents as prey sources. Such community-level projects are few and far between (e.g. Krebs et al. 1995, Bartel et al. 2008), but would be fundamental to understanding the factors that may be driving any observed small mammal population fluctuations.

As shown in this study and others (e.g. Merritt and Merritt 1978, Boonstra and Krebs 2006, Larsen et al. 2007), winter appears to be a difficult time for small mammals, and any long-term monitoring program should attempt to collect population and habitat data during the winter months. The snow shelters used in this study to protect the live-traps from the elements (see Figure 2.1) proved to be somewhat ineffectual. Although they were inexpensive and easy to build, their low profile made access to the traps difficult and time consuming. Future winter studies should consider using taller trap “chimneys” that allow researchers to access traps below the snow cover with minimal disturbance to the subnivean space (see for example Merritt and Merritt 1978, Korslund and Steen 2006).

Any long-term monitoring program would have the added benefit of providing data on long-term changes to the grassland community as a whole, which may be particularly relevant given the ongoing speculation with respect to the effects of climate change in British Columbia. How future changes in climate will affect provincial ecosystems remains a hotly debated topic. Hamman and Wang (2006) predicted large latitudinal and elevational expansions of the Bunchgrass and the Interior Douglas Fir biogeoclimatic ecological zones. Should this occur, the upper and middle grasslands in and around Lac du Bois may experience an ecological shift towards systems more like those found in the lower grasslands today, and accompanied by a shift in rodent functional groups, with the *Microtus* species in the upper grasslands replaced by the more xeric-tolerant deer mouse. Other studies have shown, however, that deer mouse populations may decrease significantly in times of reduced precipitation (Reed et al. 2007), so if future climate change results in an overall decrease in precipitation levels, deer mouse populations in both the lower or upper grasslands may suffer. A long-term monitoring program could catalogue these trends and provide useful information for predicting future impacts of climate change on grassland rodent communities.

Habitat and resource selection studies are gaining popularity with wildlife researchers, and the tools to analyze selection data are becoming more elegant and advanced (Boyce et al. 2002, Compton et al. 2002, Whittington et al. 2005, Wiens et al. 2008). The current study focussed on one narrow aspect of deer mouse resource selection (i.e. the selection of daytime refuge sites in the lower grasslands), and there is still much to learn about the selection habits of both deer mice and species of *Microtus*. With lessons learned from this study, future researchers may want to undertake more fulsome habitat selection projects to determine other potential resources that may be influencing the densities and distributions of small mammals in grassland ecosystems. Such studies will provide valuable information on rodent ecology and social structures, such as home range sizes, that can be lacking for several grassland small mammal species in the interior of British Columbia (Nagorsen 2005).

Concluding Remarks

Rodent species occupy pivotal positions in grassland ecosystems, both as primary consumers and modifiers of grassland resources, and as prey for a variety of grassland predators. And although their roles may be particularly acute in rare British Columbia grasslands, where they serve as sources of prey for a number of imperilled grassland species, little work has been done to asses and monitor rodent populations in these ecosystems. The current study is one of the first to offer information to begin filling this knowledge gap, and its results provide valuable insights into the densities and composition, survival rates and demographics of local rodent communities in two grassland types. Further, the telemetry portion of the study provided new information on habitat resources that may be important to a particular rodent species within a semi-arid grassland system. Wildlife and land managers can use this information to help inform species-specific recovery plans as well as anthropogenic-related activities in grasslands so as to maintain rodent populations on the landscape. Finally, this study has laid some of the groundwork needed to guide future studies in the intricacies of rodent communities and resource selection in grassland ecosystems, including those in British Columbia.

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