SMALL MAMMAL ABUNDANCE, HABITAT SELECTION, AND MOVEMENT PATTERNS IN SHRUB-STEPPE HABITAT IN BRITISH COLUMBIA'S OKANAGAN VALLEY

by

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ABSTRACT

This study determines the role of vegetation in shaping individual habitat use, tortuosity of movement patterns and patterns of population density of western harvest mice (*Reithrodontomys megalotis*), Great Basin pocket mice (*Perognathus parvus*) and deer mice (*Peromyscus maniculatus*) in British Columbia's Okanagan Valley. The former two mice are considered at risk in British Columbia due to loss or alteration of native habitat by human development and invasive species such as cheatgrass (*Bromus tectorum*). The objectives of this study were: 1) to determine the effects of cheatgrass on small mammal abundance and habitat use; 2) to use fractal analyses of path tortuosity to assess the spatial scales at which mice perceive their environment and; 3) to determine the role of vegetation and population density in shaping movement patterns. Trapping and tracking were conducted in 2008 in the Okanagan Valley of British Columbia at the northern reaches of the Great Basin ecosystem on 12 sites spanning a gradient of cheatgrass cover. Habitat use and movement patterns were delineated by powdering mice with fluorescent pigment and following their trails.

In the fall, the average population density per 1-hectare site was 18.0 ± 4.5 Great Basin pocket mice, 0.21 ± 0.08 deer mice and 0.08 ± 0.02 western harvest mice, while in the summer only Great Basin pocket mice were trapped (8.71 ± 3.20). Cheatgrass invasion ranged from 1 to 18 % cover. Cheatgrass abundance was not correlated with the population density of any small mammal species. In the summer, bare ground and shrub cover best-predicted Great Basin pocket mouse density, while in the fall bare ground alone was the best predictor. Great Basin pocket mice selected bare, open habitat. Vegetation was avoided with the exception of annual grasses, mainly comprised of

cheatgrass, which Great Basin pocket mice selected. Bare ground in combination with cheatgrass may have provided optimal habitat for movement. Great Basin pocket mouse path tortuosity increased with vegetation cover and population density and decreased with open habitat. The fractal dimension of movement pathways was consistent over the spatial scales measured in this study.

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DEDICATION

To my parents, who instilled in me a love of learning
and a thirst for knowledge

CO-AUTHORSHIP STATEMENT

I designed this research project and selected all of the study sites. I was responsible for all aspects of fieldwork, data analyses, and manuscript preparation. Dr. Karen Hodges provided guidance throughout my thesis and with the preparation of manuscripts.

CHAPTER 1: Introduction

Vegetation can have a large influence on the fitness of animals. From insects to birds, habitat plays a crucial role in the success of individuals by providing foraging grounds, nest sites, cover from predation, and preferred microclimates (Lagos et al. 1995, Molina-Montinegro et al. 2006, Mullican et al. 2005, Newton 1994). Altering vegetation can make an area more or less suitable for individuals of a species. The question then arises, how does one measure habitat quality in relation to vegetation?

One of the most common methods of measuring habitat quality is to measure population density responses to changes in vegetation. Higher densities indicate better quality habitat while lower densities indicate lower quality habitat (Corbalan et al. 2006). For example, the eradication of prairie dogs (*Cynomys ludovicianus*) has been linked to the encroachment of woody plants on grasslands in Texas (Weltzin et al. 1997), while in Colorado, increases in deer mouse (*Peromyscus maniculatus*) density in shortgrass prairie were correlated with higher shrub abundance (Stapp and Van Horne 1997). Density is not always a good indicator of habitat quality; if good quality habitat becomes overpopulated, sink populations with high densities can form in adjacent areas where habitat quality is lower (Van Horne 1983).

Habitat selection by individual mice can also be a measure of habitat quality. Habitat characteristics would be considered high quality if they were used more frequently than habitat characteristics selected at random from the environment. Habitat quality as inferred by individual habitat selection can be linked to population densities; densities increase in areas in which selected habitat characteristics are abundant (Price

1978, Waser and Ayers 2003).   For example, banner-tailed kangaroo rats (*Dipodomys spectabilis*), a keystone species in southern Arizona, preferentially select open, bare ground and population densities declined with woody plant encroachment (Waser and Ayers 2003). Other studies have demonstrated similar trends: variation in the abundance of a species can be predicted by the prevalence of the preferred habitat characteristic (Price 1978, Stapp and Van Horne 1997). Individual habitat use does not always predict population density responses to vegetation, thus generalizations among species or habitat types cannot be made and must be explicitly tested (Jorgensen 2004).

Energy spent in an environment is another predictor of habitat quality. Animals expend more energy in high quality habitat and less energy in low quality habitat (Nams and Bourgeois 2004). Energy expenditure can be measured by quantifying the tortuosity of movement pathways; animals moving linearly would expend less energy than animals moving tortuously through a habitat. For example, Stapp and Van Horne (1997) found that deer mouse paths were more tortuous under shrubs, a preferred habitat characteristic.

Finally, to determine the influence of vegetation on habitat quality, it is important to assess the spatial scale at which animals respond to their environment. The tortuosity of movement patterns, as measured by fractal analysis, provides a means to determine the spatial scale at which animals perceive their environment (Doerr and Doerr 2004, Mayor et al. 2009, Nams and Bourgeois 2004, Webb et al. 2009). The appropriate spatial scale depends on the animal in question: 1 km might be a small spatial scale for a migrating bird, but a large spatial scale for a mouse. A study in which the inappropriate spatial scale is used may lead to erroneous conclusions.

1.1 Small mammals and cheatgrass

Invasive species, such as cheatgrass (*Bromus tectorum*), play a key role in altering vegetation. Cheatgrass, a winter annual, is particularly prominent throughout the Great Basin ecosystem where it has invaded approximately 40,000,000 hectares of land (Mack 1981). Its encroachment on native shrub-steppe habitat may alter vegetation by decreasing shrub canopy cover, altering timing, quantity and diversity of seed production, and increasing litter production (Clark and Clark 1991; Kaufman and Kaufman 1990, Knapp 1996, Link et al. 2006). If shifts in vegetation caused by cheatgrass have an impact on habitat quality, one would expect subsequent changes in small mammal density, habitat use and movement patterns (Hanley and Page 1982, Lagos et al. 1995, Nams and Bourgeois 2004).

The Great Basin ecosystem reaches its northern boundary in the Okanagan Valley located in the southern interior of British Columbia. This semi-arid region exists nowhere else in Canada. Only 40 % of the natural shrub-steppe ecosystem of the south Okanagan Valley remains intact due to loss of native habitat by human development, cattle grazing and invasive species, such as cheatgrass (Cannings 1999, Harper et al. 1993). Many of the unique plant and animal species living in the Okanagan are found nowhere else in Canada, and over 250 species are identified as at risk (Bezener et al. 2004).

In the Okanagan Valley, deer mice are the most common mouse species, whereas Great Basin pocket mice (*Perognathus parvus*) and western harvest mice (*Reithrodontomys megalotis*) are considered to be at risk. The former is red-listed in British Columbia (threatened or endangered) while the latter is blue-listed in British

Columbia (species of special concern) (B.C. Conservation Data Centre 2007) and is federally listed as a Species of Special Concern (COSEWIC 2007). This study focuses on determining how changes in vegetation, such as those brought about by cheatgrass invasion, influence these three mouse species.

1.2 Focal species

1.2.1 Western harvest mouse

Western harvest mice are found in arid regions in western North America, ranging from central Mexico to just north of the Canadian border (Banfield 1974). Western harvest mice are omnivorous, mainly feeding on grains (McGee 1982) and supplementing their diet with moth and butterfly larva as well as plant tissue (Meserve 1976, Whitaker and Mumford 1972). Western harvest mice do not cache food in their nests (Nagorsen 2005). Their preferred habitat is grassy and weedy sites such as meadows, pastures and riparian areas, as well as habitats with high grasses and shrub cover and linear fencerows (Nagorsen 2005, Webster and Jones 1982). Western harvest mice in the Okanagan Valley are mainly found in old field and sagebrush (*Artemisia sp.*) habitats (Sullivan and Sullivan 2006).

Western harvest mice are nocturnal (Pearson 1960) and their peak activity is in the earliest part of the night (Banfield 1974). They are active year round and breed from early spring until late fall (Sullivan and Sullivan 2009, Webster and Jones 1982). Runways made by voles (*Microtus* sp.) are exploited by western harvest mice for aboveground movement (Banfield 1974). Spherical nests (12.5 cm in diameter) are located above ground, either under vegetation or in shrubs up to 1 m above the ground

(Banfield 1974, Webster and Jones 1982). Western harvest mice do not construct burrows, but will make use of burrows created by other animals (Nagorsen 2005). Home range size of western harvest mice in the southwestern United States ranges from 0.95 hectares to 1.12 hectares (Nagorsen 2005).

1.2.2 Great Basin pocket mouse

The range of the Great Basin pocket mouse extends from northern Arizona to southern British Columbia, including most of the Great Basin ecosystem (Verts and Kirkland 1988). Great Basin pocket mice are nocturnal semi-fossorial granivores (Gano et al. 1983, Schreiber 1979) and nests are located belowground in permanent burrows (Verts and Kirkland 1988). Great Basin pocket mice are able to eat cheatgrass seeds (O'Farrell et al. 1975) and can therefore tolerate disturbed sites that have been invaded by cheatgrass (Nagorsen 2005). In the Okanagan Valley, Great Basin pocket mice have been trapped most consistently in old fields, sagebrush and ponderosa pine (*Pinus ponderosa*) forests (Sullivan and Sullivan 2006).

Great Basin pocket mice use grassland and shrub-steppe habitat with sandy soils (Verts and Kirkland 1988). Digging burrow systems in sandy soils requires less energy than in other soil types, such as clay, and sandy soils provide a medium for dust bathing, an activity used to delineate territory and maintain pelage (Blaustein and Risser 1974). Great Basin pocket mice enter torpor throughout the year (Verts and Kirkland 1988) and are generally inactive between December and February (Hedlund and Rickard 1981; O'Farrell et al. 1975). In British Columbia, home range size averaged 0.07 hectares for females and 0.09 hectares for males (Nagorsen 2005, Verts and Kirkland 1988).

1.2.3 Deer mouse

Deer mice are relatively ubiquitous throughout North America and their range extends from Mexico to the treeline in the Yukon (Banfield 1974). Deer mice are the most abundant small mammal species trapped in the Okanagan Valley (Sullivan and Sullivan 2006). Deer mice favour habitats with tall grasses, including old fields, sagebrush and riparian areas, although populations are found in a variety of different environments (Kaufman and Fleharty 1974, Sullivan and Sullivan 2006). They are omnivorous, and eat invertebrates, seeds, berries and plant tissue (Kritzman 1974, Meserve 1976).

Deer mice are good climbers and dens can be located in tree cavities meters above the ground, or under shrubs in shrub-steppe habitat (Nagorsen 2005). Territoriality varies in deer mice by population; in polygamous populations, adult males defend territories while in other populations male territories overlap (Nagorsen 2005). Home ranges vary from an average of 0.9-1.0 hectares for males to 0.5-0.6 hectares for females (Banfield 1974).

1.3 Objectives

In this thesis I investigate the role of vegetation in shaping the habitat use, patterns of population density and tortuosity of movement patterns of Great Basin pocket mice, western harvest mice and deer mice in shrub-steppe habitat in British Columbia's Okanagan Valley. In Chapter 2, I focus on the impacts of cheatgrass, a pervasive invasive grass species, on both small mammal population density and individual habitat use. I examine differences in habitat use among species, and determine whether

individual habitat use predicts population density. Individual habitat use as well as population density responses to habitat provide insight into habitat types that are important to each species. In Chapter 3, I focus on the impact of habitat on the tortuosity of movement patterns of mice. I first use path tortuosity to determine the spatial scales at which mice perceive their environment and potentially respond to vegetation. I then examine the impacts of vegetation (both on pathways and at sites) and population density on path tortuosity.

I hypothesize that 1) cheatgrass cover is lower quality habitat for mice 2) path tortuosity will increase in higher quality habitat. I specifically predict that 1) cheatgrass cover will negatively affect mouse density; 2) individual mice will avoid cheatgrass in favour of other vegetation; 3) mouse path tortuosity will be positively correlated with vegetation cover and mouse population density and; 4) mouse paths will be more tortuous at smaller spatial scales and less tortuous at larger spatial scales.

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CHAPTER 2: Small mammal abundance and habitat selection on cheatgrass-invaded sites in British Columbia's Okanagan Valley[1]

2.1 Introduction

Cheatgrass (*Bromus tectorum*) is an exotic winter annual that was introduced to North America as a seed contaminant in the late 1800s and has proliferated throughout the continent (Knapp 1996). It is particularly problematic in the Intermountain West, a region delineated by the Rocky Mountains and the Cascade Range. Shrub-steppe landscapes are a major component of the desert ecosystems of the Intermountain West and are currently threatened by degradation of native habitat (Dobkin and Sauder 2004). Cheatgrass has invaded approximately 40,000,000 hectares of land in this region and is a dominant component of the grassland and shrub-steppe ecosystems (Mack 1981).

Cheatgrass populations have exploded in shrub-steppe habitat as a result of the absence of a native annual grass, growth patterns, and altered fire regimes. There are no native annual grasses in the Great Basin, thus cheatgrass proliferated in a habitat with little competition (Knick 1999). Cheatgrass germination in both the spring and fall is dependent on cool, moist conditions (Hull and Pechanec 1947). Plants that germinate in the fall overwinter in a dormant state and resume growth early in the spring (Hull and Pechanec 1947), completing their lifecycle by the onset of summer (Cline et al. 1977, Stewart and Hull 1949). The early growth pattern of cheatgrass allows it to out-compete native perennial grasses by sequestering water, which is limited in arid regions, before perennials start their growth cycle (Knapp 1996). By the time native perennial seedlings

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[1] A version of this chapter will be submitted for publication

have begun growing, cheatgrass has depleted the available water in the upper soil layers (Knapp 1996).

Cheatgrass dominance in shrub-steppe increases fuel load by producing more litter than native perennial grasses (D'Antonio and Vitousek 1992). The interspaces between cheatgrass plants are also relatively small when compared to the spatial distribution of native shrubs and bunchgrasses, allowing fires to spread rapidly. The presence of cheatgrass in the Intermountain West has altered fire cycles by increasing the frequency of fires in grassland and shrub-steppe communities, thereby altering vegetation structure and decreasing native plant diversity (Link et al. 2006). Unlike cheatgrass, whose fast growth promotes immediate re-establishment, most shrubs in the Great Basin ecosystem regenerate from seed and require several years to recover after a fire (Knapp 1996). Cheatgrass depletes water resources in the upper layers of the soil profile, slowing regeneration of shrubs and perennial bunchgrasses whose growing seasons start later in the year (Knapp 1996).

Research has focused on understanding mechanisms by which cheatgrass invades grasslands, as well as its effects on native plant communities (e.g. Beckstead and Augspurger 2004, Hempy-Mayer and Pyke 2008, Roundy et al. 2007). Comparatively few studies have concentrated on the impacts of cheatgrass on populations of terrestrial vertebrates or invertebrates (Gano and Rickard 1982, Hall et al. 2009, Newbold 2005, Ostaja et al. 2009). Understanding the links between cheatgrass and small mammal abundance and composition is particularly important, as rodents play a large role in ecosystem processes. Burrowing small mammals increase water infiltration and soil aeration (Laundre 1993), while soil disturbances and selective seed consumption by

granivores can affect germination rates, the spatial distribution of seeds, and plant community composition (McMurrray et al. 1997). Small mammals are also a source of food for a variety of predators including owls, snakes and coyotes (*Canis latrans*) (Gano and Rickard 1982).

Changes in plant species composition and vegetation structure, such as those brought about by cheatgrass invasion, can affect rodents by altering both food availability and susceptibility to predation (Lagos et al. 1995, Mullican et al. 2005). Cheatgrass provides less canopy cover than shrubs, and their stems are more dispersed than perennial grasses, potentially altering mice susceptibility to predation. Cheatgrass monocultures could also affect rodent foraging by altering the timing, quantity and diversity of seed availability in comparison to native shrub-steppe habitat. Additionally, cheatgrass would be a less reliable food source; native perennial grass growth is relatively stable, but cheatgrass germination depends on cool, moist conditions and can vary significantly from year to year (Hull and Pechanec 1947). Increased amounts of litter, such as that produced by cheatgrass, could also decrease the ability of small mammals to detect seeds (Clark and Clark 1991; Kaufman and Kaufman 1990).

Drastic changes in vegetation cover might alter small mammal habitat use and population densities (for the purposes of this paper, habitat is defined as categories of vegetation: bunchgrass, annual grass, lichens or mosses, litter, or areas devoid of any ground cover; Hanley and Page 1982, Lagos et al. 1995). In southern Arizona, kangaroo rats (*Dypodomys spectabilis*) preferentially select open bare habitat; when woody plants encroached on study sites, there was a subsequent decline in population size (Waser and Ayers 2003). Other small mammal studies have demonstrated similar trends: variations in

abundance of a species can be predicted by available habitat at a site relative to the habitat preferences of a species (Price 1978). Individual habitat use does not always predict population density responses, thus generalizations among species or habitat types cannot be made and must be explicitly tested (Jorgensen 2004).

Trends have emerged from studies assessing the impact of cheatgrass on small mammals for three species of rodents typical of shrub-steppe habitats, Great Basin pocket mice (*Perognathus parvus* Peale 1848), western harvest mice (*Reithrodontomys megalotis* Baird 1858) and deer mice (*Peromyscus maniculatus* Wagner 1845). Both deer mice and Great Basin pocket mice are more abundant in native shrub-steppe habitat compared to those dominated by cheatgrass (Brandt and Rickard 1994, Gano et al. 1983, Gitzen et al. 2001, Hanser and Huntly 2006). The pattern for western harvest mice is less clear due mainly to low sample sizes (Gano et al. 1983, Gano and Rickard 1982, Gitzen et al. 2001).

Understanding the effect that cheatgrass has on small mammal communities has been confounded by experimental design problems including recent fires that eliminated shrubs from control sites, thereby changing multiple vegetation variables at one time (Brandt and Rickard 1994, Gano and Rickard 1982), and small sample sizes (Gano and Rickard 1982, Gano et al. 1983). Most study sites were located in Washington, thus research in a broader geographic area of the Great Basin would be beneficial to gaining a better understanding of the impacts of cheatgrass invasion on mice (Brandt and Rickard 1994, Gano and Rickard 1982, Gano et al. 1983, Gitzen et al. 2001).

The Great Basin ecosystem reaches its northern boundary in the Okanagan Valley in the southern interior of British Columbia, Canada. Only a small portion of the natural

shrub-steppe ecosystem of the south Okanagan Valley remains intact due to loss of native habitat from human development, cattle grazing and invasive species, such as cheatgrass (Harper et al. 1993). The Government of British Columbia has identified two small mammal species living in the Okanagan Valley as species at risk: the Great Basin pocket mouse is red-listed (endangered or threatened), and the western harvest mouse is blue-listed (species of special concern) (B.C. Conservation Data Centre 2007). Additionally the western harvest mouse is nationally listed as a species of special concern (COSEWIC 2007) with the only remaining Canadian populations located in the Okanagan Valley and a small population (*R. megalotis dychei*) in Alberta (COSEWIC 2007, Webster and Jones 1982).

The current study assesses the effects of habitat characteristics, including cheatgrass, on population densities and habitat choice of three native mouse species in British Columbia's Okanagan Valley: Great Basin pocket mice, western harvest mice and deer mice. No previous research has examined habitat use of rodents as a possible mechanism to explain population density responses to cheatgrass. This study will also broaden the geographic area over which small mammal cheatgrass studies have been conducted, and will be the first to assess the impact of cheatgrass on small mammals in British Columbia's Okanagan Valley. I hypothesize that cheatgrass is lower quality habitat for mice. I predict that: 1) cheatgrass cover will negatively affect the density of deer mice, western harvest mice and Great Basin pocket mice; 2) individual Great Basin pocket mice, western harvest mice and deer mice will avoid cheatgrass in favor of other vegetation.

2.2 Methodology

2.2.1 Study sites

This study was conducted in the South Okanagan Valley in British Columbia between May and November 2008. Twelve study grids were established: three at White Lake, three at the Vaseux-Bighorn National Wildlife Area and six at the Haynes Lease Ecological Reserve (Table 2.1). White Lake study sites consist of shrub-steppe habitat dominated by sagebrush (*Artemisia tridentata*), needle-and-thread grass (*Stipa comata*), bluebunch wheatgrass (*Pseudoroegneria spicata*), cheatgrass and Japanese brome (*Bromus japonicus*). The Vaseux-Bighorn National Wildlife Area and the Haynes Lease Ecological Reserve are grasslands.   Vaseux-Bighorn National Wildlife area consists of needle-and-thread grass, bluebunch wheatgrass, red three-awn (*Aristida longiseta*), cheatgrass, Japanese brome, and shrubs killed by a fire in 2003. The dominant vegetation at the Haynes Lease Ecological Reserve is sand dropseed (*Sporobolus cryptandrus*), red three-awn, needle-and-thread grass and cheatgrass. Shrubs are intermittent at both grassland sites and are primarily antelope brush (*Purshia tridentata*). No sites were grazed by cattle or burned within the last 5 years (2003-2008).

Each study site was 0.81 hectares, consisting of a 7 × 7 trapping grid with 15 m spacing. Small mammals were trapped to assess population densities, and to mark animals for tracking to determine habitat use. Two Sherman live traps were placed at each station: one on the ground, and one on an elevated platform (20 cm x 30 cm) positioned approximately 20 cm above the ground. Platforms consisted of a rectangular piece of plywood supported by an oval piece of wire fencing (appendix II). Elevated

traps were used because western harvest mice are scansorial, and higher trapping success

has been found in elevated traps (Cummins and Slade 2007).

2.2.2 Trapping

No trapping or tracking occurred for two days prior to the full moon and two days

after the full moon, as moonlight affects small mammal behaviour, generally resulting in

a decrease in activity (Price et al. 1984). Each site was trapped for five consecutive days

in both the summer (June-July) and fall (September-October). Traps were baited with

unrolled oats and sunflower seeds before sunset and traps were checked at sunrise. Cotton

batting was provided as a nesting material. Each mouse was identified to species, ear-

tagged with a unique number (Monel #1, National Band and Tag Co., Lexington, KY),

weighed to the nearest 0.5 g (Pesola spring balance), aged as a juvenile or adult based on

pelage characteristics and weight, sexed, and reproductive status determined (scrotal or

non-scrotal for males; perforate, non-perforate, pregnant or lactating for females). Great

Basin pocket mice are difficult to ear tag effectively, and thus were also marked using

permanent coloured sharpie markers (ventral, lateral and dorsal surface of neck) to

provide a unique color combination for identification upon recapture. Sharpie markers

lasted for the duration of one trapping session but did not persist from summer to fall.

Each animal was released at its capture site. Mass was used to determine the age class of

Great Basin pocket mice and western harvest mice. Sullivan and Sullivan (2009)

determined mass at sexual maturity for Great Basin pocket mice and western harvest

mice in the Okanagan Valley. Great Basin pocket mice weighing 1-18.5 g were classified

as juveniles, and adults were ≥ 19 g. Western harvest mice weighing 1-10.5 g were classified as juveniles, and those weighing ≥ 11g as adults.

Field data were collected under University of British Columbia animal care committee permit A08-0146, British Columbia Ministry of the Environment permit PE08-42228, Environment Canada permit 59-08-0341 and British Columbia Provincial Parks permit OK08116425.

The Lincoln-Peterson estimator for closed populations was used to determine the population size of each species of small mammal as outlined in Williams et al. (2001). Trapping days 1-3 were used as the first capture period and days 4-5 were the second period of capture. Density was estimated by dividing the number of individuals captured by the effective trapping area. Half the mean maximum distance moved was used to determine the effective trapping area (Wilson and Anderson 1985). Variance of the boundary strip was calculated according to Karanth and Nichols (1998) and density variance was calculated following Williams et al. (2001). Summer Great Basin pocket mouse and fall western harvest mouse and deer mouse capture rates were low and therefore only one effective trapping area was calculated for each species among all sites. For the fall, effective trapping area of Great Basin pocket mice was calculated individually for six sites (three at the Haynes Lease Ecological Reserve, three at White Lake) where capture rates were high. Due to low rodent densities a single value was determined for Vaseux-Bighorn National Wildlife Area (three sites) and a single value was determined for the Haynes Lease Ecological Reserve (three sites).

2.2.3 Tracking

At each study site, I used fluorescent powder to track small mammals (Lemen and Freeman 1985) for a minimum of two nights each season. Mice were tracked to estimate habitat selection, avoidance, or use in proportion to availability of vegetation. Traps were baited just before dusk with unrolled oats and sunflower seeds, and checked approximately three hours later. If there were fewer than four animals in the traps, traps were left open, and closed traps with animals were left unprocessed. The site was then checked again at about 2:00 a.m. at which time animals were processed regardless of number caught. For any animals that had not been previously captured, measurements were taken as outlined in the trapping procedure. Recaptured animals were weighed, sexed and identified to species.

Animals were placed in a plastic sandwich bag with non-toxic fluorescent powder (Radiant Color Corp., Richmond CA) until coated, then released at the capture site. Three colors of fluorescent powder were used (magenta, orange, blue). To use the same color of fluorescent powder on two animals, trapping locations had to be separated by a minimum of three trapping stations (45 m) to reduce the possibility of tracks of the same color crossing. A maximum of eight small mammals were powdered per plot per night.

The night after rodents were coated in fluorescent powder, we used a handheld fluorescent light (UVP, Inc., Upland, California) to follow pathways. Rodents were not tracked the night of powdering so that observers would not bias focal animal behavior. The fluorescent powder was followed either as long as it was possible to see the fluorescent pigment, or for as long as time allowed. Each path was demarcated with a distinct color of pin flag or flagging tape at 0.5 m intervals. If a pathway looped onto

itself the most likely movement pattern of the rodent was estimated. A minimum of 25 m of each pathway was followed unless the path was no longer visible or the rodent entered a burrow and did not reemerge.

2.2.4 Vegetation sampling: pathway analysis

The vegetation characteristics of each rodent pathway were measured to determine whether vegetation types were being avoided, selected or used in proportion to availability. The first 5 m of each pathway was discarded to reduce the bias of a flight response. If the pathway was ≤25 m long, the remaining 20 m of the pathway was sampled in 0.5 m increments. If the pathway was >25 m, 0.5 m sampling sections were randomly distributed throughout the pathway to avoid the possibility of sampling vegetation patterns that repeat at regular intervals. A maximum of 20 m of each pathway was sampled. Pathways <10 m were not included in the analysis.

At each 0.5 m sampling station I recorded three different height classes of cover: ground level (0 cm), intermediate vegetation (1-50 cm) and shrub vegetation (≥ 50 cm). Ground level cover consisted of lichens and mosses, litter, bare ground (including rocks), and vegetation. Intermediate vegetation ranging from 1-50 cm in height was categorized as cheatgrass, other annuals, perennial grasses or forbs. Shrub vegetation was >50 cm and consisted only of shrubs. The length over which each habitat characteristic covered the pathway was measured to the nearest 5 cm. Multiple levels of vegetation could be present at a specific point. Sampling provided a measure of percent cover of each vegetation variable.

2.2.5 Vegetation sampling: available habitat

Habitat along rodent pathways was compared to available vegetation at each site. I conducted vegetation surveys at each site once per season. At each site I randomly selected the location of five 25 m line transects that did not overlap. Over each meter I estimated percent composition of vegetation as described for pathway analysis.

2.2.6 Statistical analyses

Statistical analyses were performed using JMP statistical analysis software (v. 7.0.2, SAS Institute Inc. 2007). Data are presented as mean $\pm$ 1 standard error and the statistical significance for all tests was $p < 0.05$ unless otherwise specified.

Vegetation along individual pathways was compared to available habitat at each site using Manly's alpha as a selection index (Krebs 1989) to determine the habitat use patterns of each individual. Great Basin pocket mice were the only species tracked in the summer because no other species was trapped, while in the fall habitat use data were obtained for all three species (Table 2.2). To avoid pseudoreplication for animals that were tracked more than once per season, only one Manly's alpha value per habitat characteristic per animal was calculated using average habitat use over all pathways recorded. To use Manly's alpha as a selection index, the habitat characteristic had to be present at all sites. Annuals (other than cheatgrass) were not present at every site, therefore cheatgrass and annuals were grouped together as annual grasses for this analysis.

Analysis of Variance (ANOVA) was used to determine differences in habitat use across the three mice species. The Tukey-Kramer HSD post-hoc test was used to

determine significant differences among means. Student's t-tests (parametric data) and

Wilcoxon signed-rank tests (non-parametric data) were used to determine differences

between calculated Manly's alpha values and Manly's alpha threshold values (habitat use

in proportion to availability). Selection or avoidance of vegetation types was determined

if calculated values were significantly higher or lower than Manly's alpha threshold

values. P values were Bonferonni corrected by species per season to 0.005.

Linear regression was used to assess the relationship between small mammal

population density and cheatgrass cover. The results from the Manly's alpha habitat use

analysis were used to select the best habitat predictor variables for small mammal

population density. Habitat characteristics that were either selected or avoided by the

mice were included as predictor variables in a multiple linear regression model for each

season. Akaike's Information Criterion for small sample sizes (AIC_c) was determined

using least square regression statistics and Akaike weights (w_i) were calculated to select

the best model for each season (Burnham and Anderson 1998). AIC_c is an information

criterion that penalizes models for extra predictor variables; the model with the lowest

AIC_c value and highest weight is the best-fit model.

2.3 Results

Only three species of small mammals were caught in this study: Great Basin

pocket mice, western harvest mice and deer mice. Great Basin pocket mice dominated

captures during both seasons; the average density per site in the summer (8.7 ± 3.2) was

lower than in the fall (18.0 ± 4.5) (Table 2.2, Z=-2.1, p=0.0349, n=12). Deer mice and

western harvest mice were present only in the fall and population sizes were relatively

low (Table 2.2). Great Basin pocket mouse sex ratios were relatively even while age ratios were slightly skewed towards juveniles (Table 2.2). Ninety percent of western harvest mice, 50% of deer mice and 20% of Great Basin pocket mice were captured in elevated traps.

Percent cover of cheatgrass and annual grasses ranged from 1-18%, bare ground 1-38%, and shrubs 0-25% across all sites (Table 2.3). Total percent cover of living plant material ranged from 33-54% among all sites. Annual grasses were comprised solely of cheatgrass at six of the study sites, and ranged from 36 to 95% cheatgrass at the remaining six sites. Annual grasses other than cheatgrass were dominated by Japanese brome, another invasive species that has a similar phenology to cheatgrass.

In the summer, Great Basin pocket mouse population densities were positively correlated with cheatgrass (Fig. 2.1, r^2=0.43, p=0.020, n=12). However, there was a large gap in cheatgrass cover between a site at the Haynes Lease Ecological Reserve that had relatively high cheatgrass (18 % cover cheatgrass) and all other sites (1-8 % cover cheatgrass) that decreased the predictive ability of the regression analysis. When this site was omitted from the analysis, Great Basin pocket mouse populations were marginally negatively, but marginally correlated with cheatgrass (Fig. 2.1, r^2=0.31. p=0.072, n=11).

During both seasons and over all vegetation height classes, Great Basin pocket mice selected bare, open habitat, although the intermediate level of open habitat was used in proportion to availability in the summer (Fig. 2.2). Vegetation was avoided in every height class with the notable exception of annual grasses comprised mainly of cheatgrass, which Great Basin pocket mice selected in the fall (Fig. 2.2B). Selection of annual grasses in the summer was marginally not significant (t= 2.95, p=0.0051, n=44), but may

be due to the smaller summer sample size. Biological soil crusts were also avoided in the fall (Fig. 2.2A).

The most striking difference in fall habitat use between species was at the shrub level; both western harvest mice and deer mice selected shrubs significantly more than Great Basin pocket mice, while Great Basin pocket mice selected open habitat more often (Fig. 2.2C, $F_{2,87}$=9.3, p=0.0002). At the ground and intermediate levels in the fall (Fig. 2.2A and B), deer mice and western harvest mice used similar habitat to Great Basin pocket mice although selection was not generally statistically significant due to low sample sizes.

In both the summer and fall there was little variation in Great Basin pocket mouse habitat use between sexes, age classes or seasons. The sole differences occurred at the intermediate level in the fall; adults used significantly more open habitat than juveniles ($F_{1,70}$=8.1, p=0.0059, adults: 0.44 ± 0.03, juveniles: 0.36 ± 0.02) and overall more open habitat ($F_{1,114}$=21.2, p<0.0001) and fewer forbs ($F_{1,114}$=11.3, p=0.0010) were selected when compared to the summer (Fig. 2.2B).

Bare ground, annual grasses and shrubs were selected as the predictor variables to model Great Basin pocket mouse density, as each of these habitat characteristics was either avoided or selected. The best-fit model to explain habitat use in the summer included bare ground and shrubs with an Akaike weight of 0.43 (Table 2.5A). Mouse density was positively associated with bare ground and negatively correlated with shrubs:

Density = -0.39 + 1.21 bare ground - 0.70 shrub

The global model was the second best model, with an Akaike weight of 0.30 and separated from the best model by less than 1 AIC_c value (Table 2.5A). The global model included one more predictor variable and thus was considered an inferior model, although it could not be ruled out as it was within 2 AIC_c values of the best-fit model (Burnham and Anderson 1998). Deer mouse and western harvest mouse captures were too infrequent to model densities (Table 2.2).

In the fall, the bare ground model was the strongest predictor of Great Basin pocket mouse density; the Akaike weight was 0.67 with over 2 AIC_c values separating it from the next best model (bare ground and annual grasses) (Table 2.5B). Great Basin pocket mouse density was positively correlated with bare ground:

Density = -9.57 + 1.77 bare ground

2.4 Discussion

2.4.1 Cheatgrass and population density

Cheatgrass cover did not consistently predict Great Basin pocket mouse density in contradiction to the first prediction that mouse density would be negatively related to cheatgrass cover. In the summer, Great Basin pocket mouse populations were positively correlated with cheatgrass cover, while in the fall densities were not related to cheatgrass. If an outlier was removed from the summer data set, Great Basin pocket mouse density and cheatgrass cover were negatively, but marginally correlated, and only over a very narrow range of cheatgrass invasion (1-8% cover). The lack of a consistent significant relationship between cheatgrass cover and mouse density suggests that at the lower

ranges of cover observed in this study, cheatgrass does not drive Great Basin pocket mouse population density.

These results conflict with other research that has measured the densities of rodents in cheatgrass-invaded habitat. Previous studies in communities dominated by Great Basin pocket mice observed fewer mice in areas predominantly composed of cheatgrass when compared to native shrub-steppe habitat (Brandt and Rickard 1994, Gano and Rickard 1982, Gano et al. 1983, Gitzen et al. 2001, Ostaja and Schupp 2009). It is possible that cheatgrass affects mouse density at high but not low levels of invasion.

2.4.2 Cheatgrass and habitat use

Contrary to my second prediction, Great Basin pocket mice did preferentially select annuals, mainly comprised of cheatgrass, when moving through shrub-steppe vegetation. At low densities and compared to other vegetation types (perennial grasses, shrubs or forbs) cheatgrass may facilitate movement through shrub-steppe habitat. Perennial bunchgrasses, shrubs and forbs provide stronger barriers to mouse movement than annual grasses that grow individually and do not have thick vegetation bases. Thus, it is possible that low-density cheatgrass habitat is relatively easy for Great Basin pocket mice to move through when compared to high-density cheatgrass, while still providing more cover than bare ground.

Primarily granivorous Great Basin pocket mice might use cheatgrass habitat for foraging, and could benefit from the early seed production of cheatgrass when native bunchgrasses have not yet set seeded (Kritzman 1974). This notion is reinforced by Beatly (1969) and O'Farell et al. (1975), whose results indicated that Great Basin pocket

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mouse reproductive success was positively associated with winter annuals such as cheatgrass. Cheatgrass seeds were also the dominant component of the diet of Great Basin pocket mice in northern Washington, in a study in which cheatgrass was the dominant species of grass (Schreiber 1973). Great Basin pocket mice may have therefore been selecting cheatgrass habitat because it was profitable for foraging.

2.4.3 Open Habitat: Great Basin pocket mouse density and habitat use

Great Basin pocket mice selected bare ground in the summer at a time when no other species of small mammals were present to compete for habitat, which suggests a strong preference for open, bare ground. The same trend in habitat use was observed in the fall. Bare ground was also a component of both best-fit habitat models predicting Great Basin pocket mouse density.

Bare ground facilitates movement for rodents; any dense vegetation or thick litter decreases the ability of small mammals to move quickly and efficiently through their environment. Kritzman (1974) noted that Great Basin pocket mice in eastern Washington moved through open habitat using very little vegetation as protective cover. In contrast, previous studies in desert communities with large numbers of co-existing heteromyid rodents have concluded that bipedal heteromyids (*Dipodomys* sp.) mainly forage in open habitat while quadrupedal forms, such as pocket mice (*Perognathus* sp.), forage under shrubs to avoid exposed areas (Rosenzweig 1973, Thompson 1982). My results suggest that this trend does not hold true in shrub-steppe habitat devoid of competing heteromyid rodents.

2.4.4 Habitat selection by deer mice and western harvest mice

The only differences in habitat use among species occurred at the shrub level. Deer mice and western harvest mice selected shrubs and avoided open habitat, whereas Great Basin pocket mice avoided shrubs and selected open habitat. These results are similar to other studies in which deer mice were predominantly located near shrubs, a pattern that might be explained by availability of food (Harris 1984, 1986). Although all three focal species are omnivorous to a degree, both western harvest mice and deer mice rely more on arthropods, which are predominantly found near shrubs (Harris 1986). Arthropods may provide an important source of water in the summer months for both deer mice and western harvest mice, which, unlike Great Basin pocket mice, cannot subsist on a diet of seeds alone (MacMillen 1964).

Deer mouse and western harvest mouse selection of shrub habitat may have also relaxed interspecies competition with the numerically dominant Great Basin pocket mouse. Shrubs were the only measured habitat characteristic for which selection was different among species. Thus, any dietary competition occurring between species in the fall months might have been reduced by differential selection of shrubs as foraging habitat.

2.4.5 Habitat use as a predictor of population density

Great Basin pocket mice were the dominant species captured in this study and the only one for which both habitat use and population density relationships were modeled. Habitat selection was an accurate predictor of the habitat characteristics important in predicting population density. Bare, open habitat was strongly selected both seasons,

while shrubs were avoided. Great Basin pocket mouse densities were best explained in the summer by shrubs and bare ground while in the fall bare ground alone was the best predictor of mouse density. Bare ground was positively correlated with Great Basin pocket mouse density and shrubs were negatively associated.

These results contrast with other small mammal research in which individual habitat use was not always a good predictor of habitat characteristics that explained variation in rodent population density (Jorgensen 2004, Morris 1987). Morris (1987) used live trap locations to assess habitat use and found that macrohabitat in combination with yearly fluctuations in density better explained white-footed mouse (*Peromyscus leucopus*) and meadow vole (*Microtus pensilvanicus*) densities than microhabitat use. Due to the time-intensive nature of tracking small mammals, many studies use rodent trap locations as a proxy for habitat use (e.g. Simonetti 1989). Results of such studies are difficult to interpret as animals might be baited away from habitat normally used to forage, and habitats used for non-foraging activities (e.g. mating, escape from predation, grooming) would not be represented. Thompson's (1982) findings support this idea; microhabitat use when directly observing animals was different than habitat use data derived from live-trapping locations. The habitat use of individual mice in the current experiment was obtained by direct and continuous measurements of individuals, providing better estimates of habitat use than studies conducted using live-trap locations.

2.4.6 Conclusions

Previous studies have demonstrated that small mammal species density is generally lower on cheatgrass-invaded sites than native vegetation (Brandt and Rickard

1994, Gano et al. 1983, Gano and Rickard 1982, Gitzen et al. 2001, Ostaja and Schupp 2009). These results do not apply to sites with lower ranges of cheatgrass cover in the Okanagan Valley in British Columbia; cheatgrass did not consistently predict Great Basin pocket mouse density. Instead, bare habitat was the most constant habitat predictor for density and habitat use of Great basin pocket mice. Cheatgrass may be an important resource for Great Basin pocket mice; individuals in this study selected annual grass habitat, generally dominated by cheatgrass, while avoiding all other vegetation. Habitat assessments were conducted by tracking rodents and not based on trapping data, providing accurate habitat use data that reflected the relationship between site habitat and population densities. Future work assessing the impacts of cheatgrass on small mammals over a broader range of cheatgrass cover and geographic locations within the Intermountain West would provide better insight into the impacts of this invasive species on mice communities.

Table 2.1. Locations for all study sites used in this research. UTM coordinates are in Zone 11, NAD 27. Study sites are located in the Okanagan Valley in British Columbia.

Study area	UTM East (m)	UTM North (m)	Number of sites	Elevation (m)	Dominant vegetation
Haynes Lease Ecological Reserve	316189	5440403	6	300-317	Grassland
Vaseux-Bighorn National Wildlife Area	316420	5463029	3	330-475	Grassland
White Lake	308396	5465607	3	561-572	Shrub

Table 2.2. Small mammal population densities in the South Okanagan Valley, British Columbia, averaged over all 12 field sites in summer (June - July) and fall (September - October) 2008. Means are provided ± 1 SE. The number of sites on which each species was captured is in parentheses and the trapping grid on each site was 0.81 hectares. See Appendix I for population density by site.

Season	Species	% Males/site	% Adults/site	Density (animals/hectare)
Summer	Great Basin pocket mouse	47 ± 6	34 ± 7	8.71 ± 3.20 (10)
Fall	Great Basin pocket mouse	46 ± 6	34 ± 7	17.96 ± 4.52 (12)
Fall	Deer mouse	64 ± 13	71 ± 14	0.21 ± 0.08 (7)
Fall	Western harvest mouse	100	0	0.08 ± 0.02 (5)

Table 2.3. Habitat characteristics of study sites in the Okanagan Valley in British Columbia in the summer and fall 2008. The values reported are the mean percent cover ± 1 SE of each habitat type over all study sites during each season. Annual grasses do not include cheatgrass. Shrubs consist of both live and dead shrubs. Open habitat refers to areas devoid of any vegetation.

Vegetation height class	Habitat type	Summer		Fall	
		Mean (% cover)	Range (% cover)	Mean (% cover)	Range (% cover)
Ground (0 cm)	Bare ground	11.3 ± 2.0	3.1 - 23.3	15.6 ± 2.3	5.4 - 20.9
	Lichens and mosses	14.7 ± 3.8	0.7 - 36.0	12.8 ± 3.3	0.1 - 37.3
	Litter	50.3 ± 5.7	25.2 - 77.8	55.4 ± 5.1	22.0 - 76.6
	Vegetation	23.7 ± 3.4	7.5 - 41.5	16.2 ± 2.2	6.2 - 22.4
Intermediate (1-50 cm)	Cheatgrass	4.7 ± 1.0	1.8-14.6	5.3 ± 1.4	0.7 - 18.0
	Annual grasses	0.8 ± 0.4	0 - 4.5	0.6 ± 0.2	0 - 2.4
	Perennial grasses	20.3 ± 2.1	8.3 - 30.1	19.8 ± 1.9	10.2 - 31.5
	Forbs	7.8 ± 0.9	2.6 - 13.5	9.6 ± 1.6	2.7 - 17.3
	Open	66.3 ± 2.2	53.6 - 79.1	64.7 ± 2.2	49.4 - 77.6
Shrub (≥ 50 cm)	Shrubs	6.5 ± 2.3	0 - 24.9	6.3 ± 2.1	0.1 - 20.42
	Open	93.5 ± 2.3	75.1 - 100	93.7 ± 2.1	79.6 - 99.9

Table 2.4. Small mammals tracked for habitat use analysis during the summer and fall 2008 in the south Okanagan Valley in British Columbia.

Season	Species	Number tracked	Sex ratio (M:F) of mice tracked	Age ratio (A:J) of mice tracked
Summer	Great Basin pocket mouse	44	18:26	20:24
Fall	Great Basin pocket mouse	71	37:34	24:47
Fall	Deer mouse	12	7:5	11:1
Fall	Western harvest mouse	5	4:1	1:4

Table 2.5. Linear regression models describing Great Basin pocket mouse population density from 12 shrub-steppe sites in the Okanagan valley in British Columbia in summer (A) and fall (B). Habitat types include bare ground (bare ground and rocks), shrubs (live and dead), and annual grasses. The Akaike Information Criterion metrics are the number of model parameters (K), AIC_c scores and differences (Δ_i), Akaike weights (w_i) and the coefficient of determination (r^2).

A. Summer

Model	K	AIC_c	Δ_i	w_i	r^2
Bare ground + shrubs	4	55.13	0	0.43	0.60
Bare ground + shrubs + annual grasses	5	55.81	0.68	0.30	0.79
Bare ground	3	57.19	2.05	0.15	0.42
Bare ground + annual grasses	4	59.76	4.63	0.04	0.51
Annual grasses	3	59.79	4.65	0.04	0.28
Shrubs + annual grasses	4	60.99	5.85	0.02	0.46
Shrubs	3	62.25	7.11	0.01	0.11

B. Fall

Model	K	AIC_c	Δ_i	w_i	r^2
Bare ground	3	50.63	0	0.67	0.83
Bare ground + annual grasses	4	52.90	2.28	0.21	0.86
Bare ground + shrubs	4	54.45	3.82	0.10	0.84
Bare ground + shrubs + annual grasses	5	57.65	7.02	0.02	0.88
Shrubs	3	71.81	21.18	<0.01	0.02
Annual grasses	3	72.00	21.37	<0.01	0.00
Shrubs + annual grasses	4	76.50	25.87	<0.01	0.02
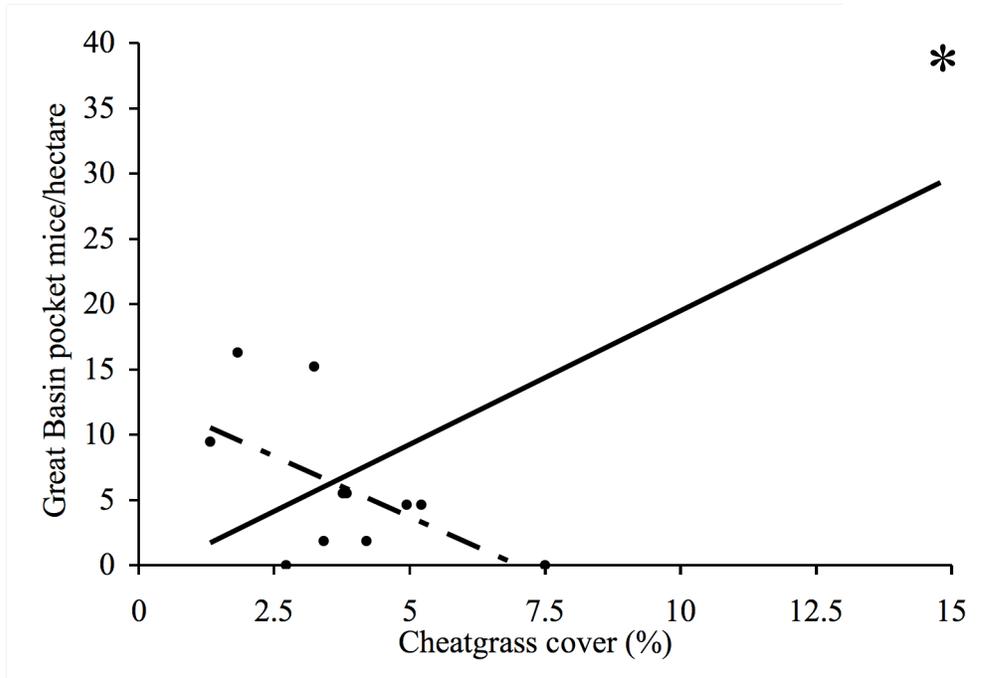
Figure 2.1. The density of Great Basin pocket mice during the summer 2008 in the Okanagan Valley in British Columbia described by variation in percent cheatgrass cover (A. $Y= -0.981 + 2.047 X$; n = 12; solid line, p=0.020). When the outlier (*) was excluded from the data set, Great Basin pocket mouse density was negatively, but marginally related to cheatgrass cover (A. $Y= 12.97-1.85 X$; n = 11, broken line, p=0.072).

Figure 2.2. Habitat selection by three small mammals in the Okanagan Valley in British Columbia's shrub-steppe habitat at (A) ground, (B) intermediate and (C) shrub levels: Great Basin pocket mice (summer n=71, fall n=44), deer mice (n=12) and western harvest mice (n=5). Habitat selection values are reported as mean value ± 1SE. Manly's alpha threshold values are indicated by the solid line. Habitat use values above the threshold indicate selection for a habitat type, whereas values below indicate avoidance. Values further away from the threshold value indicate a greater degree of selection or avoidance. Habitat selection values that differ significantly ($p<0.005$) from the threshold are indicated by an asterisk (*). For a specific habitat characteristic, the same letter (A) indicates mean habitat use among species is not statistically different, while different letters (A and B) indicate mean habitat use that is statistically different among species. There were no differences in habitat selection among species at the ground and intermediate levels.

A. Ground level
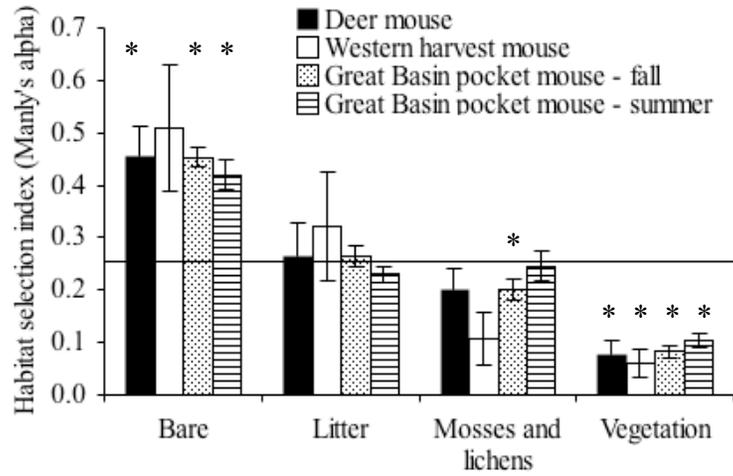
B. Intermediate level
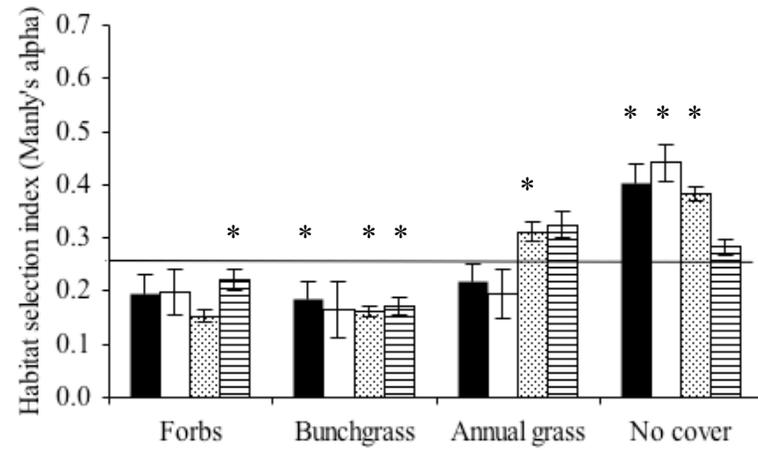
C. Shrub level
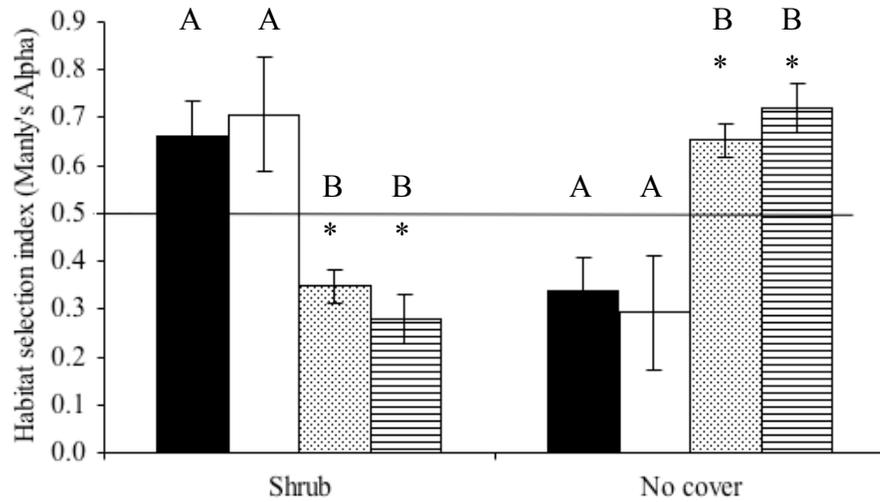
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CHAPTER 3: Do vegetation and population density predict path tortuosity of Great Basin pocket mice in shrub-steppe habitat?[1]

3.1 Introduction

Movements of animals are shaped by many features of their environment: spatial distribution of vegetation and food, structural features of the habitat, perceived risk of predation, territoriality, location of conspecifics or heterospecifics, and individual condition (Crist et al. 1992, Dick and Burrough 1988). Although time spent in a habitat can be a good measure of habitat quality, pathway tortuosity provides a proxy for energy spent searching or foraging, and thus is a better measure of habitat quality (Nams and Bourgeois 2004).

Changes in plant cover, vegetation structure and species composition can affect habitat quality for small mammals by altering both food availability (Mullican et al. 2005) and susceptibility to predation (Lagos et al. 1995), thus causing shifts in movement patterns (Hanley and Page 1982, Lagos et al. 1995, Stapp and Van Horne 1997). Understanding the impacts of vegetation on mouse pathway tortuosity provides a means to identify habitat that is important for the focal species while not relying on population density data, which can sometimes be misleading (Van Horne 1983).

Both the distribution and quantity of resources can alter path tortuosity. Animals are expected to travel more tortuously in habitat where the availability of resources is high. More tortuous paths in an area of known clumped resources (Nelson and Chew 1977), followed by more linear pathways in habitat devoid of resources would be

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[1] A version of this chapter will be submitted for publication

economical; in contrast, a linear search pattern would increase the likelihood of success when resources are evenly distributed (Etzenhouser et al. 1998, Wiens et al. 1995).

Given similar structural complexity, movement pathways in habitats that are beneficial for foraging and have low perceived predation risk are expected to be more tortuous, as animals would spend more time searching for food (Benhamou and Bovet 1989). Conversely, a habitat in which perceived predation risk is high and the abundance of food is low would be traversed quickly, in a straighter line, to access higher quality habitat elsewhere. Thus movement patterns are likely to vary if environmental differences have an impact on habitat quality. For example, path tortuosity of American martens (*Martes americana*) increased in coniferous vegetation that was beneficial for foraging (Nams and Bourgeois 2004).

Population density can also impact path tortuosity; deer mouse (*Peromyscus maniculatus*) density and path tortuosity were positively correlated in shortgrass prairie (Stapp and Van Horne 1997). Habitat quality may be higher in habitats that support more animals, and thus tortuosity may increase with increases in population density. Factors such as social interactions can weaken the link between habitat quality and density (Van Horne 1983). In species that are intolerant of conspecifics, such as Great Basin pocket mice (*Perognathus parvus*) (O'Farrell et al. 1975), territoriality causes movements to be spatially constrained, independent of habitat quality; as population density increases, territory size decreases and movements become more tortuous because mice are restricted to a smaller area, and not because habitat quality is higher (Bascompte and Vila 1997, Webb et al. 2009).

The majority of mouse movement data stems from mark-recapture studies where distance traveled is inferred by recapture location, and movement path characteristics are not quantified (e.g. Garland and Bradley 1984, Kozel and Fleharty 1979, Rehmeier et al. 2004, Root et al. 1999). Comparatively few studies have directly analyzed mouse pathways and they have focused on the impacts of vegetation on movement patterns (Benhamou 1990, McDonald and St. Clair 2004, Stapp and Van Horne 1997, Wells et al. 2006). Deer mice, meadow voles (*Microtus pennsylvanicus*) and red-backed voles (*Clethrionomys gapperi*) had more tortuous movement pathways under canopy cover than when moving in open habitat (McDonald and St. Clair 2004). Deer mouse tortuosity increased with increases in low-density shrub cover, a habitat feature commonly preferred by this species (Chapter 2, Stapp and Van Horne 1997). These studies have not tested the impacts of specific habitat characteristics other than shrubs on pathway tortuosity, but they have demonstrated that habitat features alter movement patterns of mice.

Fractals are one of a number of metrics (e.g. sinuosity, straightness index, random walk models) used to quantify the tortuosity of movement pathways and are arguably the most intuitive to understand (Benhamou 2004, Turchin 1996). The more space-filling a path, the higher the fractal value as the movement pattern fills an area approaching two-dimensional space and has a fractal dimension of 2.0, i.e. Brownian motion (Mandelbrodt 1967). The more linear the pathway, the lower the fractal value as the movement pattern approaches a one-dimensional line, and the closer the fractal dimension to 1.0 (Mandelbrot 1967). Animal movement pathways generally lie between these two extremes (Webb et al. 2009).

Although it was originally assumed that natural processes quantified using fractals are scale-independent (Mandelbrot 1967), this notion must be explicitly tested (Nams 2004). On a small spatial scale, the movement pattern of a foraging animal would be more tortuous than on a larger spatial scale, such as during migration, when movement is more directed (Laidre et al. 2004); therefore, the fractal dimension of movement pathways measured over a large enough range of spatial scales may decrease with increases in spatial scale. Spatial scale depends on the focal animal in question; 500 m would be a large spatial scale for a mouse, but a small spatial scale for a caribou. Recent movement papers have suggested that the fractal dimension of movement pathways is scale-dependent (Doeer and Doeer 2004, Mayor et al. 2009, Nams and Bourgeois 2004, Webb et al. 2009, With 1994). The fractal value(s) of movement pathways should therefore be quantified only for the spatial scale(s) at which the data are collected, and patterns cannot be extrapolated to scales beyond the scope of the experiment (Nams 2005).

Within the spatial scales of a study, discontinuities in fractal dimension can indicate domains of spatial scale at which animals perceive their environment (Nams 2005). A constant fractal value over spatial scales implies a domain over which the causal factor or factors for the movement pattern observed do not change (Wiens 1989). Fractals therefore provide a method for determining the spatial scales at which mice respond to their environment, and for testing the impacts of predictor variables at these scales (Doerr and Doerr 2004, Mayor et al. 2009, Nams and Bourgeois 2004, Webb et al. 2009)

The current study uses fractal analysis to determine the domains of spatial scale at which three mouse species native to British Columbia's Okanagan Valley perceive their environment, while also measuring the impacts of movement path vegetation, site habitat, and population density on path tortuosity. In the Okanagan Valley, deer mice are a numerically dominant mouse, whereas Great Basin pocket mice and western harvest mice (*Reithrodontomys megaloti*s) are considered species at risk (B.C. Conservation Data Centre 2007, COSEWIC 2007). Great Basin pocket mice are red-listed in British Columbia (threatened or endangered) while western harvest mice are blue-listed in British Columbia (species of special concern) (B.C. Conservation Data Centre 2007) and are federally listed as a Species of Special Concern (COSEWIC 2007). Both species live in shrub-steppe habitat in the south Okanagan Valley and only 40% of the native shrub-steppe habitat remains intact (Cannings 1999, Harper et al. 1993). Quantifying path tortuosity for at-risk species provides a means to assess habitat quality at the appropriate scales at which these mice perceive their environment.

I hypothesize that path tortuosity will increase in higher quality habitat. I specifically predict that: 1) mouse path tortuosity will be positively correlated with vegetation cover; 2) mouse path tortuosity will be positively correlated with population density of conspecifics; 3) mouse paths will be more tortuous at small spatial scales and more linear at large spatial scales.

3.2 Methodology

3.2.1 Study sites

This study was conducted in the South Okanagan Valley in British Columbia between May and November 2008. Twelve study grids of 0.81 hectares were established: three at White Lake, three at the Vaseux-Bighorn National Wildlife Area and six at the Haynes Lease Ecological Reserve (Table 2.1). White Lake study sites consisted of shrub-steppe habitat dominated by sagebrush (*Artemisia tridentata*), needle-and-thread grass (*Stipa comata*), bluebunch wheatgrass (*Pseudoroegneria spicata*), cheatgrass (*Bromus tectorum*) and Japanese brome (*Bromus japonicus*). The Vaseux-Bighorn National Wildlife Area and the Haynes Lease Ecological Reserve were grasslands. The Vaseux-Bighorn National Wildlife area consisted of needle-and-thread grass, bluebunch wheatgrass, red three-awn (*Aristida longiseta*), cheatgrass, Japanese brome, and dead sagebrush and antelope brush (*Purshia tridentata*) killed by a fire in 2003. The dominant vegetation at the Haynes Lease Ecological Reserve was sand dropseed (*Sporobolus cryptandrus*), red three-awn, needle-and-thread grass and cheatgrass. Shrubs were intermittent at both grassland sites and were primarily antelope brush. No sites were grazed by cattle or burned within the last 5 years.

Ninety-eight Sherman live traps were used for population estimates at each site (methodology described in Chapter 2). Traps were placed in two positions: on the ground, and on elevated platforms (20 cm x 30 cm) positioned approximately 20 cm above the ground (appendix II). Platforms consisted of a rectangular piece of plywood supported by an oval piece of wire fencing. Elevated traps were used because western

harvest mice are scansorial, and higher trapping success has been found in elevated traps (Cummins and Slade 2007).

Field data were collected under University of British Columbia animal care committee permit A08-0146, British Columbia Ministry of the Environment permit PE08-42228, Environment Canada permit 59-08-0341 and British Columbia Provincial Parks permit OK08116425.

3.2.2 Tracking

At each study site, I used fluorescent powder to track small mammals (Lemen and Freeman 1985) for a minimum of two nights during the summer (June – July) and fall (September – October) seasons. No tracking occurred for two days prior to the full moon and two days after the full moon, as moonlight affects small mammal behaviour, generally resulting in a decrease in activity (Price et al. 1984). Traps were baited just before dusk with unrolled oats and sunflower seeds. Traps were checked approximately 3 hours after being set. If there were fewer than four animals in the traps, traps were left open and closed traps with animals were left unprocessed. The site was then checked again at 2:00 a.m., at which time all animals were processed regardless of number caught.

Each new mouse was identified to species, ear-tagged with a unique number (Monel #1, National Band and Tag Co., Lexington, KY), weighed to the nearest 0.5 g (Pesola spring balance), aged as a juvenile or adult based on pelage characteristics, and sexed. Recaptured animals were weighed, sexed, and identified to species to ensure proper identification. Each animal was released at its capture site. Mass was used to determine the age class of Great Basin pocket mice and western harvest mice. Sullivan

and Sullivan (2009) determined mass at sexual maturity for Great Basin pocket mice and western harvest mice in the Okanagan Valley: Great Basin pocket mice weighing 1-18.5 g were classified as juveniles, and adults were ≥ 19 g; western harvest mice weighing 1-10.5 g were classified as juveniles, and those weighing ≥ 11g as adults (Sullivan and Sullivan 2009). Great Basin pocket mice are difficult to ear tag effectively, and they were also marked using permanent coloured sharpie markers (ventral, lateral and dorsal surface of neck) to provide a unique colour combination for identification upon recapture. These marks lasted for the duration of one trapping session but did not persist from summer to fall.

Animals were placed in a plastic sandwich bag with non-toxic fluorescent powder (Radiant Color Corp., Richmond CA) until coated, then released at the capture site. Three colours of fluorescent powder were used (magenta, orange, blue). To use the same colour of fluorescent powder on two animals, trapping locations had to be separated by a minimum of three trapping stations (45 m) to reduce the possibility of tracks of the same colour crossing. A maximum of eight mice were powdered per plot per night.

The night after mice were coated in fluorescent powder, pathways were followed with a handheld fluorescent light (UVP, Inc., Upland, California). Mice were not tracked the night of powdering so that observers would not bias animal behaviour. The first 5 m of each pathway were not used to measure tortuosity or vegetation characteristics to reduce the bias of a flight response. The fluorescent powder was followed either as long as it was possible to see the pigment, or for as long as time allowed. Each path was demarcated with a distinct colour of pin flag or flagging tape at 0.5 m intervals. If a pathway looped onto itself, the most likely movement pattern of the mouse was

determined. A minimum of 25 m of each pathway was followed unless the path was no longer visible or the mouse entered a burrow and did not reemerge.

When fluorescent powder trails were followed with a UV light, trails were sometimes difficult to see, especially along bare ground. Occasionally, powder traces were > 0.5 m apart from each other on a pathway (the distance between pin flags). If fluorescent powder traces were < 2 m apart, a straight-line distance was recorded between points. If the powder traces along a trail were > 2 m apart, the two path segments were treated as individual pathways. Fluorescent powder trails sometimes had offshoots that never returned to the main pathway. These offshoots were also treated as separate paths. Any pathways < 5 m long were not used in the fractal analyses.

3.2.3 Tortuosity

To measure the tortuosity of the mouse pathways, the azimuth between pin flags was recorded to the nearest degree (Stapp and Van Horne 1997). Data were then converted to Cartesian coordinates and pathways were rediscretized (larger and larger ruler sizes were used to measure path length) at a variety of spatial scales for further analysis.

3.2.4 Vegetation sampling: pathway analysis

The vegetation characteristics of each mouse pathway were recorded to determine whether pathway vegetation predicts tortuosity. The first 5 m of each pathway was discarded to reduce the bias of a flight response. If the pathway was ≤ 25 m, it was

sampled in 0.5 m increments. If the pathway was > 25 m, 0.5 m sampling sections were randomly distributed throughout the pathway to avoid the possibility of sampling vegetation patterns that repeat at regular intervals. A maximum of 20 m of each pathway was sampled. Pathways < 10 m were not included in this analysis.

At each 0.5 m sampling station, I recorded three different height classes of cover: ground level (0 cm), intermediate (1-50 cm) and shrub ($\geq$ 50 cm). The length over which each habitat characteristic covered the pathway was measured to the nearest 5 cm. Ground level habitat consisted of bare ground and vegetation. Vegetation ranging from 1-50 cm in height consisted of annual grasses, perennial grasses and forbs. Vegetation that was taller than 50 cm consisted of shrubs. Multiple levels of vegetation could be present at a specific point. Sampling provided a measure of percent cover of each vegetation type.

3.2.5 Vegetation sampling: available habitat

The available vegetation at each study site was measured to determine whether it was a good predictor of the pathway fractal value at each site. I conducted vegetation surveys at each site once per season, randomly selecting five 25 m line transects that did not overlap. Over each meter segment I estimated percent composition as described for pathway analysis.

3.2.6 Data analyses

3.2.6.1 Correlated random walks

Prior to calculating the fractal dimension of paths, I tested the data to determine whether they fit a correlated random walk model (Turchin 1996). Pathways that can be described as correlated random walks cannot be analyzed with fractals, as fractal dimension (D) increases continually with spatial scale. In such cases, Fractal D is a function of the scale at which the data are collected and is not biologically relevant (Nams and Bourgeois 2004, Turchin 1996).

Following Nams and Bourgeois (2004), all mouse pathways were grouped to determine whether patterns differed significantly from that of a correlated random walk model. The movement pathways were significantly longer than what would be expected by a correlated random walk, indicated by a positive value for R_{diff} (df=151, R_{diff}=0.218, p<0.01). Fractal D thus could thus be used to calculate pathway tortuosity for further analysis.

3.2.6.2 Fractal D

The original fractal D estimator derived by Mandelbrot (1967) inaccurately estimates fractal D at large ruler sizes (spatial scales), because the length of the pathway is underestimated and path length varies with the point at which the measurements begin. Nams (2006) proposed the Fractal Mean estimator to better estimate fractal D. This metric estimates the straight-line distance between the end of the ruler length and the end of the pathway to measure path length more precisely. The ruler is also walked up and down each path to calculate two fractal values that are subsequently averaged, providing

a more accurate estimate of fractal D as the length of the pathway depends on the point at which the measurement begins. The Fractal Mean estimator was used to determine the fractal dimension of each path >5 m because it is a more accurate metric than the original fractal D estimator (Nams 2006).

3.2.6.3 Domains of spatial scale

To determine domains of spatial scale (Wiens 1989), all movement pathways were grouped by species. Gross distance is the distance traveled by the focal animal along the pathway, as opposed to the net displacement, or net distance between the start and end of the path. The slope of log spatial scale (independent variable) versus log gross distance (dependent variable) (Fractal D =1-slope) was analyzed with both linear regression and piecewise regression (Fig. 3.1). If piecewise regression fit the data significantly better than linear regression (here defined as an increase in r^2 value >0.05), then domains of spatial scale were delineated as the spatial scales at which the slope of the piecewise regression was constant, and further analysis was carried out at these scales. If linear regression best-fit the data, then pathways were truly fractal and self-similar at all scales measured in this study; analyses were conducted over only one spatial scale.

To maximize the range of scales at which domains of spatial scale were identified, a subset of long paths was selected for this portion of the analysis. Eight Great Basin pocket mouse pathways were analyzed over a spatial scale of 0.5-20 m, four deer mouse pathways at a spatial scale of 0.5-37.5 m, and three western harvest mouse pathways at a spatial scale of 0.5-30 m. Linear regressions best-fit all the data (Great Basin pocket

mouse: $r^2=0.974$, p<0.001; deer mouse: $r^2= 0.984$, p<0.001; western harvest mouse: $r^2=0.980$, p<0.001).

To ensure that small sample sizes were not driving these results, analyses were conducted at successively smaller spatial scales (minimum = 0.5-5 m), including more pathways at each scale, thereby increasing the sample size. Results were similar at all spatial scales of analysis; fractal values did not change significantly and a linear regression was always the best-fit model. Fractal *D* was scale invariant at the spatial scales measured in this study.

Fractal values calculated over a small spatial scale (0.5-5m) were subsequently selected to maximize sample size. Because pathways are self-similar at the scales measured in this study, results could be extrapolated to a spatial scale of 20 m for Great Basin pocket mice, 37.5 m for deer mice, and 30 m for western harvest mice. To determine fractal *D* for each pathway, 30 dividers were equally spaced between 0.5 and 5 m. Before any further analysis, fractal values were normalized by transforming data using log (*D*-1).

3.2.7 Statistical analyses

Statistical analyses were performed using JMP statistical analysis software (v. 7.0.2, SAS Institute Inc. 2007). Fractal values and tests for correlated random walks were calculated in Fractal 5.0 (V.O. Nams, Nova Scotia Agriculture College, Truro, Nova Scotia, Canada). Data are presented as mean $\pm$ 1 SE and the statistical significance for all tests is p < 0.05 unless otherwise specified. To avoid pseudoreplication for animals that

were tracked more than once per season, only one Fractal *D* value was calculated per individual using average path tortuosity weighted by path length.

Analysis of Variance (ANOVA) was used to compare seasonal differences in path tortuosity between species. A three-way ANOVA was used to assess seasonal differences in Great Basin pocket mouse path tortuosity by sex and age. Linear regression was used to assess the impact of site habitat characteristics and population density on path tortuosity of Great Basin pocket mice, and the relationship between path vegetation characteristics and path tortuosity for Great Basin pocket mice and deer mice. Site vegetation was not used to predict deer mouse density because individuals were captured on only four sites. Linear regression was also used to determine the impact of mass, a proxy for individual condition, on path tortuosity. A t-test was used to assess differences in path tortuosity between male and female deer mice.

Any vegetation characteristics or population densities that were significantly correlated with tortuosity ($p < 0.10$) were included as predictor variables in a multiple linear regression model for each season and for both path and site vegetation characteristics. Akaike's Information Criterion for small sample sizes (AIC_c) was determined using least square regression statistics, and Akaike weights (w_i) were calculated to select the best model for each season (Burnham and Anderson 1998).

3.3 Results

Only three species of small mammals were trapped in this study: Great Basin pocket mice, western harvest mice and deer mice. Great Basin pocket mice dominated

captures during both seasons while deer mice and western harvest mice were present only in the fall and population sizes were relatively low (Table 2.2, Table 3.1).

Great Basin pocket mouse pathway tortuosity was significantly higher in the summer than in the fall (Table 3.2, Figure 3.2, $F_{1,90}=0.408$, $p < 0.0264$). There was no difference in pathway tortuosity between sexes or age classes of Great Basin pocket mice either season (Table 3.2), nor did body mass predict tortuosity in summer ($r^2=0.06$, $p=0.173$, n=35) or fall ($r^2=0.0006$, $p=0.861$, n=58). There was no difference in pathway tortuosity between species in the fall ($F_{2,73}=0.39$, $p=0.678$).

There was no difference in pathway tortuosity between male and female deer mice ($t=-0.91$ $df=10$, $p=0.384$) nor did mass predict path tortuosity ($r^2=0.03$, $p=0.598$, n=12). Age differences could not be determined for deer mice because captures were highly skewed towards adults (Table 3.1). Sample sizes were too low to determine differences in path tortuosity between sexes and age classes of western harvest mice or to use mass to predict tortuosity (n=4, Table 3.1).

3.3.1 Habitat characteristics

Site population density, shrubs, and intermediate vegetation predicted Great Basin pocket mouse path tortuosity in the fall ($p<0.10$, n=58, Table 3.3A, Table 3.4). The best-fit model for the fall included population density and open habitat 1-50 cm in height as predictors with an Akaike weight of 0.23 and explained 11.3% of the variation in tortuosity (Table 3.4):

Log (1-fractal D) = -1.78 + 0.005 • density - 0.01• open habitat (1-50 cm)

The shrubs model was the second-best model with an Akaike weight of 0.17, followed by open vegetation at an intermediate height of 1-50 cm, and the population density and shrubs model (Table 3.4). The latter two had Akaike weights of 0.16, but all models were within 2 AIC$_c$ values of each other and therefore none could be ruled out (Table 3.4). In the summer, neither density nor site vegetation predicted Great Basin pocket mouse pathway tortuosity.

The same vegetation characteristics were sampled along pathways (Table 3.3 B) and used to predict path tortuosity. In the fall, no vegetation variables predicted Great Basin pocket mouse path tortuosity. In the summer, bare ground along pathways was negatively correlated with path tortuosity (Fig 3.3; r^2=0.11, p=0.0486, n=35). Pathway vegetation did not significantly predict deer mouse path tortuosity in the fall, but the power was low due to the small sample size (n=12).

3.4 Discussion

3.4.1 Habitat characteristics

Great Basin pocket mouse path tortuosity was positively correlated with vegetation cover and negatively correlated with open habitat at each height class (0 cm, 1-50 cm, > 50 cm), confirming the first prediction. There was no relationship between habitat and path tortuosity of deer mice or western harvest mice, but these results may be attributed to the small sample size of each species (Table 3.1).   Bare open habitat, or conversely all vegetation, were the only habitat variables that predicted Great Basin pocket mouse path tortuosity whether at a site or on a pathway. Individual vegetation characteristics did not explain variation in path tortuosity. Intermediate bare habitat (1-

50 cm) available at sites was negatively correlated with Great Basin pocket mouse path tortuosity in the fall, while pathway bare ground (0 cm) was negatively correlated with summer tortuosity. Tortuosity in the fall also increased with increasing site shrub cover (> 50 cm).

Path tortuosity might increase under vegetation cover because of the structural features of vegetation or because habitat quality is higher under vegetation cover than in open habitat. It is energetically costly for mice to move through grass, forbs or shrub stems (Simonetti 1989), therefore mice might move around vegetation bases, resulting in increased tortuosity. Vegetation may also be a more profitable habitat than bare, open ground for primarily granivorous Great Basin pocket mice (Kritzman 1974). Seed density in North American deserts is positively associated with shrub cover and decreases in shrub interspaces (Guo et al. 1998). The most efficient method of foraging would be to move more tortuously under shrubs or vegetation where resources are clumped and more linearly in interspaces between resources patches (Etzenhouser et al.1998, Wiens et al. 1995).

Habitat predicted very little of the variation in movement tortuosity in this study. The ability to detect the impacts of specific habitat types on path tortuosity would have increased had pathways been stratified and tortuosity calculated for each habitat type separately (Nams 2005). If habitat characteristics had opposite effects on tortuosity, calculating one overall fractal value for a pathway would result in an intermediate path tortuosity that is not relevant to any individual habitat characteristic.

Stapp and Van Horne (1997) found thresholds in the relationship between vegetation characteristics and tortuosity; at higher vegetation cover values there was no

relationship. In this study, each pathway vegetation characteristic covered no more than 37% of any one pathway (Table 3.2). A relationship between a single vegetation type and movement tortuosity may exist, but not over the range of cover measured in this study.

3.4.2 Population density

Great Basin pocket mouse density was positively correlated with path tortuosity in the fall, supporting the second prediction. Similarly to the habitat variables measured in this study, density accounted for little variation in path tortuosity. The relationship between density and tortuosity may be explained by the social structure of Great Basin pocket mice; individuals live solitarily in nests and are intolerant of conspecifics and heterospecifics (O'Farrell et al. 1975, Verts and Kirkland 1988). An increase in mice in a given area, such as that observed in the fall, should decrease the area available per individual and movement would be similar to an animal constrained by fences; tortuosity would increase (Bascompte and Vila 1997, Webb et al. 2009).

There was no relationship between mouse pathway tortuosity and density in the summer, most likely due to low population sizes in the summer. Great Basin pocket mice were only present on 10 of the 12 sites in the summer, decreasing the probability of detecting a relationship between density and tortuosity if one exists.

Finally, both habitat and population density explained very little of the variation in movement path tortuosity of Great Basin pocket mice within each season. Possible predictors of path tortuosity not measured in this study include the spatial distribution of

vegetation and food, physical features of the habitat, perceived risk of predation, and location of conspecifics or heterospecifics (Crist et al. 1992, Dick and Burrough 1988).

3.4.3 Spatial scale

In contradiction to the third prediction, mouse movement pathways appeared to be truly fractal; there was no change in fractal D over the scales measured in this study. Some previous studies have observed changes in tortuosity over spatial scales (Nams and Bourgeois 2004, Webb et al. 2009), while in other research path tortuosity has remained constant (Crist et al. 1992, Wiens 1989). The range of spatial scales measured in this study represent only one domain in which the mechanism responsible for variation in tortuosity remained constant, but was neither amount of vegetation cover nor population density. Thus, over a spatial scale equivalent to two-thirds of the diameter of the home range size of a Great Basin pocket mouse (Verts and Kirkland 1988), pathways are scale invariant.

It is possible that the grain size of this study, 0.5 m, was too large to measure the impacts of vegetation on movement patterns, although in a study on deer mice with a grain size of 1 m, vegetation did affect tortuosity (Stapp and Van Horne 1997). Tortuous paths under shrubs could be detected as the average shrub diameter was greater than 0.5 m, but foraging bouts under forbs or bunchgrasses may not have been measured because the grain size was too large. Nams and Bourgeois (2004) found that American martens (*Martes americana*) pathways were driven by vegetation characteristics at a spatial scale of 1.0-3.5 m. American martens are much larger animals and their home ranges are at minimum 59 hectares (Buskirk and McDonald 1989). Thus one might

expect a mouse, whose home range is less than 1 hectare, to forage at a smaller grain size than 0.5 m.

3.4.4 Seasonal differences

Path tortuosity of Great Basin pocket mice was higher in the summer than in fall, which suggests a change in mouse behaviour between seasons (Laidre et al. 2004). It is most likely that the increased summer path tortuosity was due to increased foraging. Great Basin pocket mice are predominantly in torpor in the winter and accumulate seeds throughout the year to have enough food stores to last the winter months (O'Farrell 1975). The majority of food is gathered during the summer when seed production in shrub-steppe habitat is at its highest (O'Farrell 1975). Females had marginally higher path tortuosity in the summer than in the fall, while male path tortuosity did not change. Greater female path tortuosity in the summer may have been due to higher energy requirements during pregnancy and lactation, resulting in more foraging and more tortuous paths (O'Farrell 1975).

The difference in fractal dimension between the two seasons is relatively small ($\Delta D = 0.035$), but small changes in fractal value can have considerable impacts on path length because fractal D is measured as an exponent in logarithmic scaling (Milne 1997). Small differences are therefore biologically relevant because they represent relatively large changes in energy expenditure over time (Nams and Bourgeois 2004).

3.4.5 Conclusions

Unlike previous research on mice and other animals, only a small portion of the within-season variation in path tortuosity of Great Basin pocket mice could be explained by changes in vegetation or population density. The grain size may not have been small enough to encompass the scale at which tortuosity is impacted by vegetation. The tortuosity of mouse movement paths did not change over spatial scales, which indicates that mouse movement pathways are truly fractal at the scales measured in this study. Domains of spatial scale where fractal values do not change have never been measured in mice and these results suggest that future studies should focus on a broader range of scales, perhaps including a smaller grain size and a spatial scale the size of the home range of the focal animal. Finally, path tortuosity in the summer was higher than in the fall; higher energy expenditure in summer months may be due to increased foraging because of greater availability of food.

Table 3.1. Characteristics of individual small mammals tracked with pathways long enough for fractal and habitat use analysis during the summer and fall 2008. The age ratio refers to adult (A) and juvenile (J) mice.

Season	Species	Number tracked	Sex Ratio (M:F) of mice tracked	Age Ratio (A:J) of mice tracked	Fractal D
Summer	Great Basin pocket mouse	35	14:21	19:16	1.0453-1.3269
Fall	Great Basin pocket mouse	58	32:26	21:37	1.0174-1.3612
Fall	Deer mouse	12	6:6	11:1	1.0444-1.1506
Fall	Western harvest mouse	4	4:0	4:0	1.0458-1.2440

Table 3.2. Three-way ANOVA comparing seasonal differences in Great Basin pocket mouse path tortuosity by sex and age in British Columbia's Okanagan Valley.

Term	df	Sum of Squares	F	p
Season	1, 90	0.4077	5.103	0.0264
Sex	1, 90	0.213	0.266	0.6071
Age	1, 90	0.157	0.196	0.6589
Sex*age	1, 89	0.01	0.129	0.7208
Season*sex	1, 89	0.247	3.094	0.0822
Season*age	1, 89	0.005	0.066	0.7977
Season*sex*age	1, 88	0.0178	0.223	0.6383

Table 3.3. Habitat characteristics of study sites (A) and movement pathways (B) of mice in the Okanagan valley in British Columbia in the summer and fall 2008. The values reported are the mean percent cover ± 1 SE of each habitat characteristic relevant to Great Basin pocket mice over all study sites during each season.

A. Site Vegetation

Vegetation Class	Habitat Characteristic	Summer		Fall	
		Mean (% cover)	Range (% cover)	Mean (% cover)	Range (% cover)
Ground (0 cm)	Bare ground	76.3 ± 3.4	58.5 - 92.5	83.8 ± 2.2	71.1 - 93.8
	Vegetation	23.7 ± 3.4	7.5 - 41.5	16.2 ± 2.2	6.2 - 22.4
Intermediate (1- 50 cm)	Annual grasses	5.6 ± 1.0	1.8 -14.8	5.9 ± 1.3	0.7 - 18.2
	Perennial grasses	20.3 ± 2.1	8.3 - 30.1	19.8 ± 1.9	10.2 - 31.5
	Forbs	7.8 ± 0.9	2.6 - 13.5	9.6 ± 1.6	2.7 - 17.3
	Open	66.3 ± 2.2	53.6 - 79.1	64.7 ± 2.2	49.4 - 77.6
Shrub (>50 cm)	Shrubs	6.5 ± 2.3	0 - 24.9	6.3 ± 2.1	0.1 - 20.42
	Open	93.5 ± 2.3	75.1 - 100	93.7 ± 2.1	79.6 - 99.9

B. Pathway Vegetation

Vegetation Class	Habitat Characteristic	Summer		Fall	
		Mean (% cover)	Range (% cover)	Mean (% cover)	Range (% cover)
Ground (0 cm)	Bare ground	91.7 ± 0.8	78.6 - 98.6	93.8 ± 1.0	72.7 - 100
	Vegetation	8.3 ± 0.8	1.4 - 21.4	6.2 ± 1.0	0 - 27.3
Intermediate (1- 50 cm)	Annual grasses	5.7 ± 0.6	0.5 - 14.7	5.3 ± 0.5	0 - 22.9
	Perennial grasses	12.3 ± 1.2	1.3 - 29.1	10.8 ± 0.7	1.5 - 26.0
	Forbs	6.0 ± 0.7	1.2 - 16.0	4.9 ± 0.4	0.3 - 13.8
	Open	76.4 ± 1.3	62 - 91	79.0 ± 0.8	66.1 - 90.6
Shrub (>50 cm)	Shrubs	9.2 ± 2.3	0 - 37.1	5.3 ± 0.9	0 - 30
	Open	90.7 ± 2.3	62.9 - 100	94.7 ± 0.9	70 - 100

Table 3.4. Linear regression models describing Great Basin pocket mouse path tortuosity from 11 shrub-steppe sites in the Okanagan Valley in British Columbia in the fall of 2008. Vegetation characteristics describe available vegetation at each of 11 study sites (one of the 12 sites had no Great Basin pocket mouse pathways). Model variables included: Great basin pocket mouse population density (density), live and dead shrubs (shrubs), areas devoid of vegetation 1-50 cm in height (intermediate open). The values are the number of model parameters (K), AIC_c scores and differences (Δ_i), Akaike weights (w_i) and the coefficient of determination (r^2).

Model Name	K	AIC_c	Δ_i	w_i	r^2
Density + intermediate open	4	-143.29	0.00	0.23	0.11
Shrubs	3	-142.67	0.61	0.17	0.07
Intermediate open	3	-142.54	0.74	0.16	0.07
Density + shrubs	4	-142.52	0.77	0.16	0.10
Density	3	-141.46	1.82	0.09	0.05
Density + shrubs + intermediate open	5	-141.39	1.89	0.09	0.12
Shrubs + intermediate open	4	-141.23	2.06	0.08	0.08

A. Movement Path

10 m
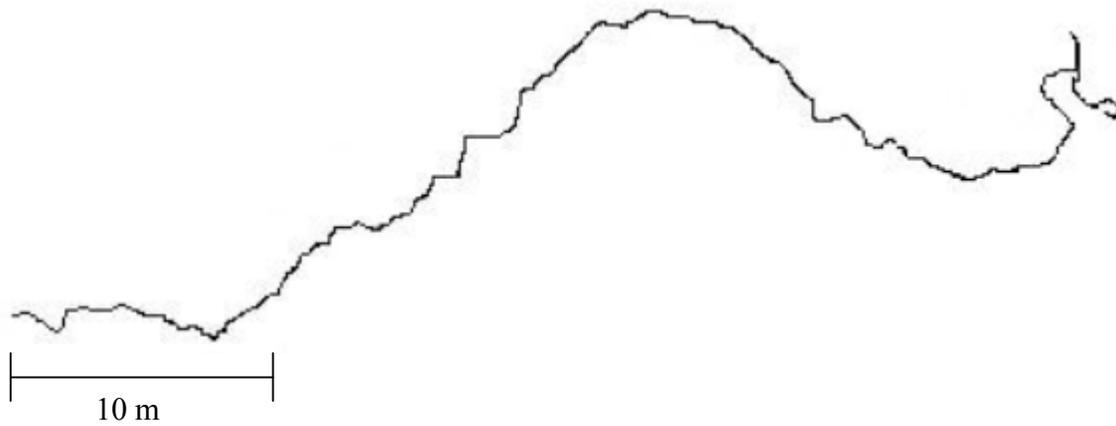
B. Fractal Dimension
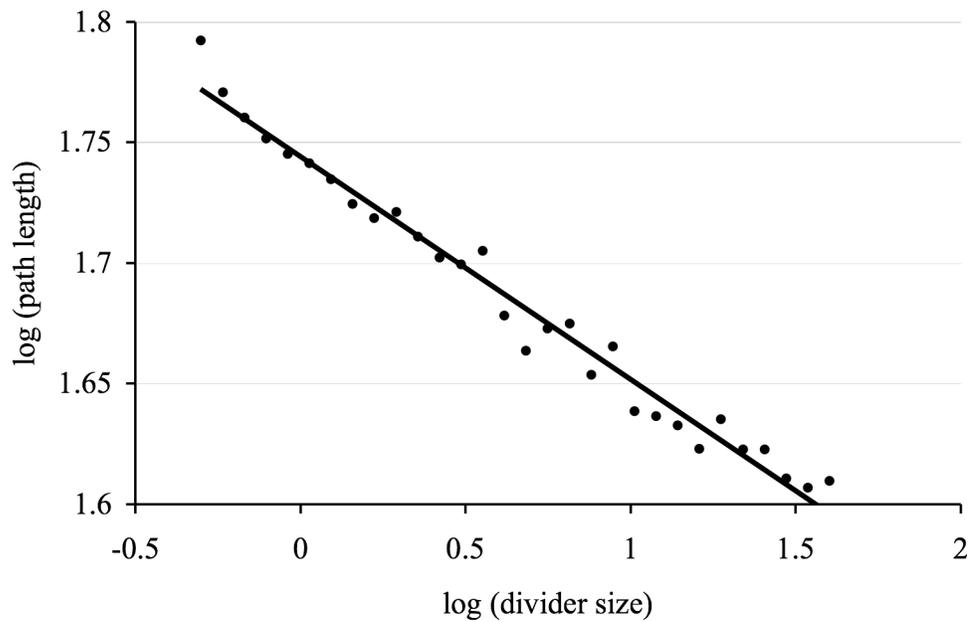
Figure 3.1. (A) A sample movement pathway of a juvenile female Great Basin pocket mouse in shrub-steppe habitat in British Columbia's Okanagan Valley in the fall of 2008. (B) This graph represents path length (y-axis) as a function of divider size (x-axis). Divider size is synonymous with spatial scale. Fractal D is calculated by subtracting the slope of the regression line from 1 (y=1.7444 - 0.0924x), therefore D=1.0924.
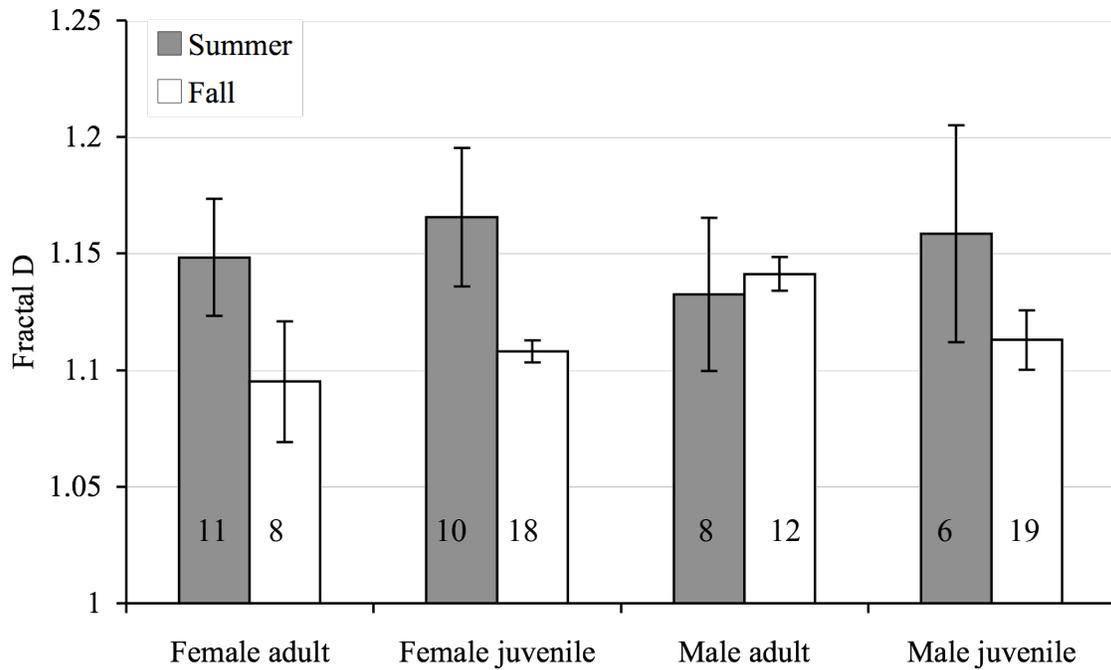
Figure 3.2. Average pathway tortuosity of Great Basin pocket mice was higher in the summer than in the fall in British Columbia's Okanagan Valley (p=0.0264, Table 3.2). The sex by season interaction in the three-way ANOVA was marginally significant (p=0.08, Table 3.2). Fractal D values are not normally distributed and were log transformed prior to analyses, but the values presented in the figure are not log transformed. Higher fractal D values represent more tortuous paths, while lower fractal values represent more linear paths. Error bars represent $\pm$ 1 SE. The sample size is written within each bar.
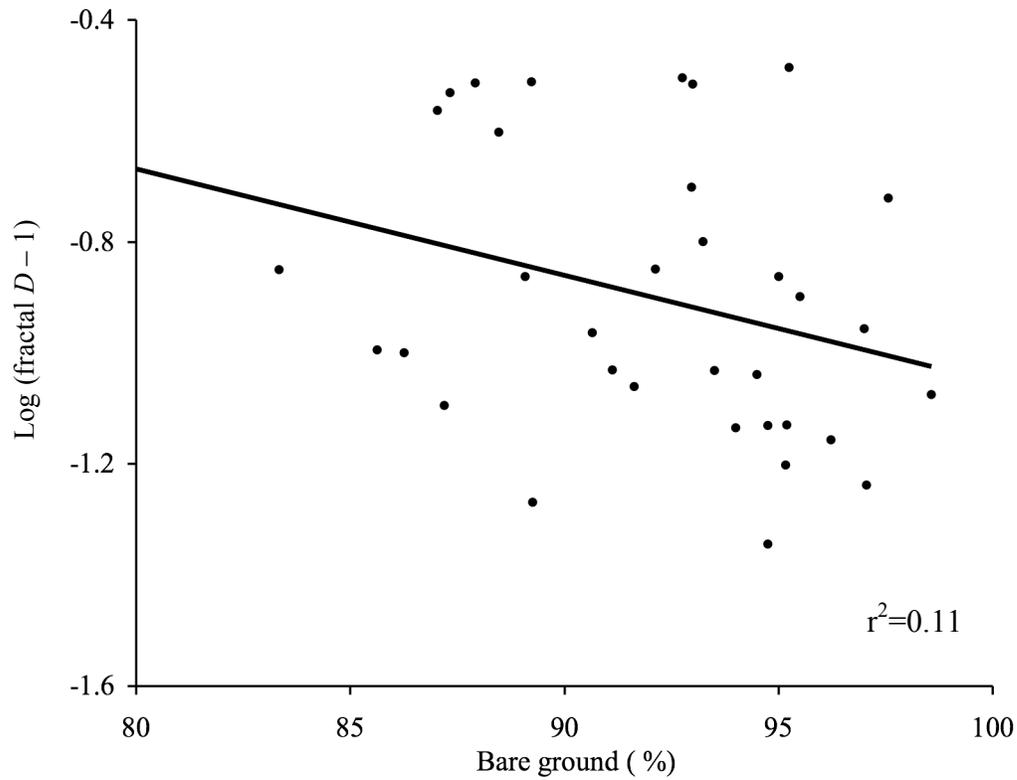
Figure 3.3. The tortuosity of movement paths of Great Basin pocket mice during the summer 2008 in British Columbia's Okanagan Valley described by variation in pathway bare ground (y=-0.865 - 0.019 x; n = 35, p=0.0486). Fractal D values are not normally distributed and were log transformed for statistical analysis. Tortuosity is described by Log (fractal D-1); higher values represent more tortuous paths, and lower values represent more linear pathways.

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CHAPTER 4: Conclusions

The Great Basin desert ecosystem reaches its northern extreme in British Columbia's Okanagan Valley. In this shrub-steppe region, over 250 species are listed as at risk, including two species of mice: Great Basin pocket mice (*Perognathus parvus*) and western harvest mice (*Reithrodontomys megalotis*) (B.C. Conservation Data Centre 2007, Bezener et al. 2004, COSEWIC 2007). In contrast, deer mice (*Peromyscus maniculatus*) are generally abundant in the region. This study focused on the role of vegetation, including cheatgrass (*Bromus tectorum*) a pervasive invasive species, in shaping the movement patterns, habitat use, and population densities of these mouse species. Trapping grids were established on 12 sites to quantify mouse population densities, and fluorescent powder was used to track mice to measure habitat use and path tortuosity.

Great Basin pocket mice were the most abundant small mammal on trapping grids in both the summer and the fall. In the summer they were the only nocturnal small mammal species on any of the study sites (8.7 ± 3.2 animals per hectare), and in the fall they represented over 95 % of all captures (18.0 ± 4.5 animals per hectare). There were low densities of deer mice (0.21 ± 0.08 animals per hectare) and western harvest mice (0.08 ± 0.02 animals per hectare).

Cheatgrass, an invasive grass prevalent throughout the Great Basin, did not drive Great Basin pocket mouse populations in the South Okanagan Valley contrary to my first prediction. Over the low range of cheatgrass cover measured in this study (1-18%), cheatgrass did not consistently predict Great Basin pocket mouse density in either the summer or the fall (Fig. 2.3). These results contrast with previous research in Washington

and Utah in which small mammal communities, mainly comprised of Great Basin pocket mice, had lower densities on cheatgrass-dominated sites than in native shrub-steppe habitat (Brandt and Rickard 1994, Gano and Rickard 1982, Gano et al. 1983, Gitzen 2001, Ostaja and Schupp 2009). There may be a threshold below which cheatgrass does not have a strong impact on mouse population density and above which populations decline.

Unlike any previous research assessing the relationship between mice and cheatgrass (Brandt and Rickard 1994, Gano et al. 1983, Gano and Rickard 1982, Gitzen 2001, Ostaja and Schupp 2009), I specifically addressed mouse habitat use in relation to cheatgrass cover. Contrary to my second prediction, Great Basin pocket mice selected cheatgrass while all other vegetation was avoided (Fig. 2.2). Cheatgrass may offer optimal movement and foraging ground for granivorous rodents because stems are dispersed, providing bare ground for ease of movement and cover against predation, while also supplying seeds as food source (Beatly 1969, Kritzman 1974, O'Farell et al. 1975, Schreiber 1973).

During both seasons and over all vegetation height classes, Great Basin pocket mice selected bare, open habitat (Fig 2.2). The selection of bare, open habitat and the general avoidance of vegetation by Great Basin pocket mice contrasts with previous research in desert communities with large numbers of co-existing heteromyid rodents (Rosenzweig 1973, Thompson 1982). In these studies, pocket mice (*Perognathus* sp.) avoided bare ground in favour of the cover provided by vegetation. In the current study, Great Basin pocket mice were the only nocturnal mouse species trapped on study sites in the summer and accounted for over 95% of trapped mice in the fall. Thus, in the absence

of competition, Great Basin pocket mice use open habitats for movement in the Okanagan Valley.

Habitat use patterns of individual Great Basin pocket mice accurately reflected population density responses to site vegetation (Table 2.5). Bare ground was the main driver for both habitat use and population density: mice selected it for movement, and densities were higher at sites with more bare ground. In several previous small mammal studies, habitat use did not predict population density, most likely because these studies did not track mice, but instead inferred habitat use by quantifying vegetation at trap locations (Jorgensen 2004, Morris 1987, Thompson 1982). The method used to quantify habitat use is important, and any technique that directly measures movement, such as fluorescent powder, would be superior to a method that records only fragments of mouse behaviour, such as data obtained from trapping records. Using trap locations as a proxy for habitat use likely biases results as animals might be baited away from habitat normally used for foraging, and habitats used for non-foraging activities would not be represented. In this study, the habitat use patterns of individual mice were obtained by direct and continuous measurements, which provide better estimates of habitat use than studies inferring usage from trap locations.

Confirming my third prediction, Great Basin pocket mouse pathway tortuosity increased slightly as vegetation cover increased and decreased slightly with increases in bare ground (Table 3.4, Fig. 3.3). These results are consistent with previous research on other mouse species in which pathways were more tortuous under vegetation than in open habitat (McDonald and St. Clair 2004, Stapp and Van Horne 1997).

If increased habitat use and higher tortuosity are measures of high quality habitat, my results are contradictory; movement paths were straighter in habitats that were used, and more tortuous in habitats that were avoided. Which metric is then a better indicator of habitat quality? Because habitat use and population density responses to vegetation are similar, and vegetation explained very little of the variation in movement tortuosity, my data would suggest that habitat use may better predict habitat quality than movement path tortuosity in this system.

In the fall, tortuosity increased with increases in Great Basin pocket mouse density, supporting my fourth prediction, but accounted for little of the variation in path tortuosity. Great Basin pocket mice live solitarily, and therefore an increase in density would limit the area available to each individual. Movement would be similar to that of an animal constrained by a fence - tortuosity would increase (Bascompte and Vila 1997, Webb et al. 2009). The small amount of variation explained by Great Basin pocket mouse population density may be attributed to low population densities; densities may not have been high enough to have an impact on path tortuosity, or perhaps density does not drive movement tortuosity over the spatial scales measured in this study.

In contrast to my last prediction, the tortuosities of movement patterns of Great Basin pocket mice, western harvest mice and deer mice were consistent over a spatial scale equivalent to two-thirds of the diameter of the home range of a Great Basin pocket mouse. Thus, over the spatial scale in which Great Basin pocket mice conduct most of their daily activities, there is no change in the tortuosity of their movement patterns; tortuosity is the same when foraging at a small spatial scale as it is at a larger scale when movement is directed towards a nest site. These results are similar to studies of smaller

organisms such as insects, but inconsistent with studies of small mammals and larger-bodied animals in which tortuosity changed with spatial scale (Crist et al. 1992, Nams and Bourgeois 2004, Webb et al. 2009, Wiens 1989). It is possible that the spatial grain and extent of this study are not broad enough to identify different domains of spatial scale.

The spatial scales measured in this study represent one domain over which the causal factor or factors that predict changes in movement do not vary. Only small amounts of the variation in Great Basin pocket mouse path tortuosity could be explained by path vegetation, site vegetation and mouse density, while individual weight did not explain any of the variation in path tortuosity. The spatial grain (0.5 m) may have been too large for Great Basin pocket mice; mechanisms that were used as predictors for pathway tortuosity may operate at a finer scale than 0.5 m. It is also possible that movement tortuosity of Great Basin pocket mice is dependent on factors that I did not measure, such as the spatial distribution of vegetation and food, location of conspecifics and heterospecifics, or predation risk (Crist et al. 1992, Dick and Burrough 1988).

4.1 Final conclusions

In recent years there has been a dearth of small mammal habitat use studies, even though the relationship between individual habitat use and population density responses to vegetation remains unclear (Jorgensen 2004). Although measuring density responses to vegetation change is a commonly used method of assessing habitat quality, this metric can lead to erroneous conclusions. Thus studies, such as this one, that incorporate more

than one method of measuring habitat quality may provide more insight into the relationship between habitat and individual fitness.

Mouse movement patterns did not change over a spatial scale equivalent to two-thirds of the diameter of the home range size of a Great Basin pocket mouse. Great Basin pocket mice selected bare open habitat for movement, and bare open habitat was positively correlated with population density. Individual habitat use was a good predictor for population density responses of Great Basin pocket mice to vegetation. Paths were slightly more linear in bare open habitat when compared to movement under vegetation cover, but overall, little of the variation in path tortuosity could be attributed to either vegetation or population density.

The response of Great Basin pocket mice to cheatgrass may depend on the degree of cheatgrass invasion, but at the low range measured in this study ($\leq 18\%$ cheatgrass cover) there was no consistent relationship between cheatgrass cover and population density. Great Basin pocket mice did select cheatgrass cover while avoiding all native vegetation.

The degree to which cheatgrass affects small mammal habitat quality still remains unclear. Future work assessing the response of small mammals to cheatgrass over a greater range of cheatgrass cover would be beneficial. It is possible that cheatgrass may not be the ultimate factor driving lower densities of small mammals in cheatgrass-dominated sites; future research should focus on the mechanism responsible for changes in small mammal abundance on cheatgrass-dominated sites. Ultimately, the cause may be an indirect effect of cheatgrass invasion, such as loss of bare ground, a habitat characteristic that is seemingly important to Great Basin pocket mice.

4.2 References

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APPENDICES

Appendix I: Mouse densities and site locations

Table A1.1 Study site locations and population density by mouse species in both the summer (June-July) and fall (September October). Population densities are listed ± 1standard deviation. UTM coordinates are in Zone 11, NAD 27. Study sites are located in the Okanagan Valley in British Columbia: three were at the Vaseux-Bighorn National Wildlife Area, three were at the Haynes Lease Ecological Reserve and three were at White Lake.

Site	UTM East	UTM North	Summer Great Basin pocket mouse density (animals/hectare)	Fall Great Basin pocket mouse density (animals/hectare)	Fall Deer mouse density (animals/hectare)	Fall Western harvest mouse density (animals/hectare)
Vaseux-Bighorn National Wildlife Area	316420	5463029	0	0.82 ± 0.21	3.64 ± 0.86	2.05 ± 0.37
	317302	5462180	9.45 ± 2.97	9.84 ± 2.56	0	0
	316166	5463480	0	2.46 ± 0.64	1.93 ± 0.28	0
Haynes Lease Ecological Reserve	316189	5440403	4.61 ± 1.24	7.27 ± 2.08	0.64 ± 0.09	0.68 ± 0.12
	316403	5440425	5.53 ± 1.49	9.62 ± 2.83	0	0.68 ± 0.12
	316401	5440151	4.61 ± 2.58	15.95 ± 4.38	0.64 ± 0.09	0
	316396	5439943	16.28 ± 5.02	17.81 ± 5.85	0.64 ± 0.09	0
	316266	5439695	15.21 ± 5.49	34.30 ± 7.92	0	0.68 ± 0.12
	316298	5439508	39.56 ± 12.12	58.38 ± 14.64	3.21 ± 0.47	1.37 ± 0.25
White Lake	308531	5465812	1.84 ± 0.50	21.88 ± 6.60	3.37 ± 0.61	0
	308396	5465607	5.53 ± 1.49	18.60 ± 3.87	0	0
	308886	5464175	1.84 ± 0.50	18.64 ± 3.51	0	0

Appendix II: Elevated platform

Figure A2.1 Elevated platform on which traps were placed. Ninety percent of western harvest mice were trapped on elevated platforms.

Appendix III: Animal care certificate

THE UNIVERSITY OF BRITISH COLUMBIA

ANIMAL CARE CERTIFICATE

Application Number: A08-0146

Investigator or Course Director: Karen E. Hodges

Department: UBCO Admin Unit 2 Arts & Sci

Animals:

Wild Rodents Western harvest mouse (Reithrodontomys megalotis); Great Basin pocket mouse (Perognathus parvus), deer mouse (Peromyscus maniculatus) 1440

Start Date:	April 1, 2008	**Approval Date:**	July 23, 2009

Funding Sources:

Funding Agency: Environment Canada
Funding Title: Conservation Biology Research in the South Okanagan

Funding Agency: British Columbia Ministry of Water, Land and Air Protection
Funding Title: Chair of Conservation Biology/Specifies at Risk (Bert Brink)

Unfunded title: Responding to cheatgrass at a range periphery: movement and population dynamics of two rodents of conservation concern

The Animal Care Committee has examined and approved the use of animals for the above experimental project.

This certificate is valid for one year from the above start or approval date (whichever is later) provided there is no change in the experimental procedures. Annual review is required by the CCAC and some granting agencies.

A copy of this certificate must be displayed in your animal facility.

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