WEATHER, CLIMATE, AND SMALL MAMMAL POPULATION DYNAMICS IN A NORTHERN GRASSLAND

BY

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ABSTRACT

Rising temperatures of anthropogenic origin are affecting ecosystems around the world, heightening the importance of understanding how climate and weather affect wildlife populations. In semi-arid grasslands, small mammals are considered keystone species due to their role as ecosystem engineers and as prey for meso-predators. Their essential role in the food web and the rich history of small mammal population research makes them ideal indicator species to study the effects of climate on globally threatened grassland ecosystems.

My thesis explores weather and climate effects on the population dynamics of a small mammal community monitored in autumn, from 1997 to 2024, in a semi-arid grassland on the Thompson-Okanagan Plateau in British Columbia, Canada. Specifically, I detail population cyclicity and trends in the two most dominant species, the Western Deer Mouse (*Peromyscus sonoriensis*), a habitat generalist, and the Montane Vole (*Microtus montanus*), a grassland specialist. Mouse and vole densities were correlated, and thus provided no evidence of interspecies competition. Both species followed 3–4-year cycles, although the Deer Mouse was much more regular in its oscillations, showing synchronous cyclicity across the landscape. The Montane Vole had more dramatic swings in density and many sites had only sporadic captures, though peak years saw up to 50 individuals/ha. With these data, I investigated the relationship between the two populations and seasonal temperature and precipitation. Deer Mouse density was found to be significantly lower in years with warm summer temperature. No relationship was found between Deer Mice and precipitation, nor Montane Voles and either weather variable. Community structure may shift should warming temperature continue for the region, as Deer Mouse carrying capacity in semi-arid grasslands may decrease with warming temperatures.

To explore the relationship between habitat and weather across the landscape, I focused the second part of my thesis on the effects of summer heat on Western Deer Mouse populations during one specific year (2024). I compared mice occupying grassland and higher elevation forest habitat, with the assumption that forests were more moderate in heat exposure and aridity and could therefore serve as a buffer against the effects of heat. Grassland densities of Deer Mice remained stable from spring to summer, where the density of the animals in the forests increased significantly. Of note was a two-week heat wave in July that occurred between trapping events, when daytime temperatures exceeded 37°C. The proportion of reproductively active males and females decreased marginally in both habitats after the heat wave, though low capture numbers

increase the uncertainty of these conclusions. Like density, the proportion of juveniles remained stable in the grasslands but increased dramatically between spring and summer. I postulate that increased heat affected mouse pup survival in the grasslands for this generalist species.

Overall, my thesis documents long-term population trends in a northern grassland small mammal community, and provides insight into how climate change, especially heat, may affect both generalist and specialist species in semi-arid grasslands. Protection of habitat diversity, such as grassland-forest ecotones and intact grassland habitats, in this threatened ecosystem may increase resilience to continued aridification.

Keywords: climate change, population dynamics, small mammal, cycle, grassland, heat, *Peromyscus sonoriensis*, *Peromyscus maniculatus*, *Microtus montanus*, British Columbia

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Acknowledgments

I would first like to pay my respect to the Tk̓emlúps te Secwépemc. All field work for this thesis took place within Secwepemcúl̓ecw, the ancestral and unceded territory of the Secwépemc Nation.

To Karl Larsen, who guided me over beers and blackened turkey: thank you for your patience and mentorship as I learned to turn data into science, and for the many excellent conversations. Thank you to both Karl and Sheri Watson for establishing this long-term project and devoting decades of fastidious effort to maintaining it, and to the cohorts of undergraduate students at Thompson Rivers University (TRU) who did the bulk of the trapping and made the decades of field work possible. Finally, I couldn't have done this without my exemplary field assistants Hannah Kroeker, Siya Markel, Veronica McKelvey, and Erin Blythe. Thank you for getting up before the crack of dawn to get bitten by rodents, and not even complaining about it.

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The methods and trapping protocols used in this study were approved by the Thompson Rivers University Animal Care Committee, protocol no. 100857.

NOTE: While I have used singular pronouns for Chapters 1 and 4, I have chosen to use plural pronouns for Chapters 2 and 3 to acknowledge the contributions of those above and the many others, without whom this work would not have been possible.

Western Deer Mouse. Illustration by author.

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CHAPTER 1

INTRODUCTION

CLIMATE CHANGE

Ecological systems are in a state of constant flux, with regular patterns intertwined with continual change (L. Xu et al. 2021). Species are adapted to the historical baselines of their ecosystem, yet are capable of evolving alongside slow shifts in their environment and habitat, such as through climate (Davis and Shaw 2001; Johansson 2008). In recent years, however, rapid shifts in weather averages and the increasing frequency of extreme climactic events such as heat waves and drought have upset the stability of ecological communities worldwide (Smith 2011; Smith et al. 2013; Qu et al. 2016; Rosenblatt and Schmitz 2016; Krebs et al. 2019; Avotins et al. 2023), leading to worldwide declines in biodiversity (Gibbons et al. 2000; Barnosky et al. 2011). According to the International Union for Conservation of Nature and Natural Resources (IUCN), 26% of mammal, 12% of bird, 21% of reptile, and 41% of amphibian species are threatened (IUCN 2024). While other threats such as habitat fragmentation, invasive species introduction, and disease all are significant contributors, climate change is omnipresent and escalating.

Climate change can impact animal species both directly, through events such as heat waves that induce heat stress, dehydration, and length of active or breeding season (Yaeram et al. 2006; Bozinovic et al. 2011; Jacobs et al. 2020), or indirectly, through phenological mismatch and changes in plant productivity and food availability across trophic levels (Rosenblatt and Schmitz 2016; Kudo and Cooper 2019; Visser and Gienapp 2019; Morin et al. 2021; Avotins et al. 2023). Changes to a habitat's carrying capacity may benefit some species by increasing their range and distribution or decreasing inter-species competition (Long 1996; Jiang et al. 2013; Prugh et al. 2018), but often lead to a reduction and fragmentation of suitable habitat and consequent population declines (McDonald and Brown 1992; Atwood et al. 2021). This trend is especially evident in habitat "islands", where discontinuous ecosystems create isolated habitats that often are genetically and spatially distinct from neighbouring 'islands' (McDonald and Brown 1992; Robson et al. 2016). For example, increasing average temperature causes an upward shift in the elevational ranges of montane species and prevents animals from migrating to more suitable habitats, effectively "trapping" them on a mountaintop (Wilkening et al. 2015).

Grasslands and Climatic Extremes

Grasslands are a threatened habitat worldwide, and unfortunately, one of the most sensitive ecosystems to climate change. Grasslands occur on every continent except Antarctica, with North American prairies and shrubland, South American pampas, Eurasian steppes, and African savannas (Wikeem and Wikeem 2004) covering approximately 40% of Earth's land surface (Squires et al. 2018). Of this large distribution, 49% is estimated to have been degraded by climate change, agricultural development, grazing, and urbanization (Gang et al. 2014). In Canada, less that 30% of native grasslands remain (Roch and Jaeger 2014). As such, they are considered a priority focus for many research and conservation groups (GCC 2004; Squires et al. 2018).

Characterized by graminoid vegetation, grasslands tend to be semi-arid, with low levels of rainfall preventing widespread tree growth (Dixon et al. 2014) while permitting shrubs and forbs to be interspersed with grasses. Grassland plants have deep root systems that help with water uptake (Oliveira et al. 2005), fire resistance (Retallack 2001), and carbon sequestration (Lei et al. 2016; Squires et al. 2018). Seasonal droughts are common, especially in summer. Temperate grasslands recharge the moisture reservoir during winter or spring, when precipitation and snowmelt is at its highest (Wikeem and Wikeem 2004). This buffers against typical hot, dry summers. Disruptions to normal precipitation averages result in up to a 50% reduction in aboveground annual net primary production in grassland plants (Cherwin and Knapp 2012). Paradoxically, this heavy reliance on rainfall events makes arid grasslands one of the most sensitive ecosystems to drought (Cherwin and Knapp 2012; Gang et al. 2014; Lei et al. 2016). This condition is predicted to increase in frequency and severity in coming years (Prugh et al. 2018; C. Xu et al. 2021), and may eventually overcome the adaptations of some plant and animal species to hot and dry climates.

Small Mammal Communities

Small mammals play an important role in a wide variety of ecosystems due to their ubiquitous nature and strong influence on bottom-up processes (Laundre 1993; Hollander and Vander Wall 2004; Merritt 2010; Delibes-Mateos et al. 2011; Schickmann et al. 2012; Flowerdew et al. 2017; Nicod et al. 2020). As a taxa, they often increase moisture retention and plant

diversity in arid environments through burrow building (Hollander and Vander Wall 2004; Davidson and Lightfoot 2008) and help regenerate landscapes post-disturbance by spreading seeds and fungal spores (Schickmann et al. 2012; McCaffery et al. 2020; Stephens et al. 2021). As primary consumers, they are directly affected by changes in plant productivity, showing large population fluctuations in response to environmental variables (Andreassen et al. 2021; Sullivan and Sullivan 2022). Small mammals also act as the primary prey for many meso-predators (Krebs et al. 2001; Majchrzak et al. 2022). This tight connection to both higher and lower tropic levels makes small mammals an ideal study species for understanding community-level responses to climate change.

Small mammal communities have been the focus of many long-term population studies. From Charles Elton's work on the hare cycles of the Canadian Arctic in the early 1900s (Elton 1924) to long-term monitoring of small mammal communities in Europe (Korpimäki et al. 2005), these studies have offered insights into population dynamics difficult to uncover in longer-lived species. Dramatic oscillations in small mammal populations are common and often erratic, though in some cases they resolve into regular cycles of both the small mammals and their predators (Chitty 1996, Krebs 2013; Andreassen et al. 2021). Many experimental studies have used wild small mammal populations and manipulated variables such as predation, competition, or food availability to understand the factors that control population dynamics (Chitty et al. 1968, Grant 1971; Crowell and Pimm 1976, Krebs et al. 1986, Chitty 1996, Korpimäki and Norrdahl 1998; Nie and Liu 2005, Prevedello et al. 2013).

With anthropogenic threats impacting most ecosystems, small mammals often are used as indicator species (Ayodele 2025). Climate change monitoring in the arctic (Ehrich et al. 2020), forest succession after harvest and wildfire (Larsen et al. 2007; Zwolak 2009), and habitat fragmentation (Umetsu and Pardini 2007; Byrom et al. 2015) all have been studied through the lens of small mammal communities. Small mammal models illustrate competing theories as to how generalist and specialist species will respond to a changing world. For example, Fontúrbel et al. (2021) found that climate change decreases interactions between fruit-bearing plants, seed-dispersing generalist small mammals, and pollinators. Another study by Martínez et al. (2014) found that specialist small mammals were more likely to have phenotypic adaptations to their climate and environment than generalist species. Finally, many studies have investigated the effects that habitat fragmentation and microhabitat changes have on communities of generalist

and specialist small mammals (Morris 1996, Seamon and Adler 1996, Schlinkert et al. 2016). Through the vast body of knowledge on this ubiquitous group, it becomes easier to monitor changes in trophic structures and ecosystem diversity.

SEMI-ARID GRASSLAND SMALL MAMMALS

Semi-arid grassland small mammals have contributed to our understanding of anthropogenic climate change. Studies on decreasing desert specialists (Phillips 2018) and long-term trends across geologic time (Terry and Rowe 2015) suggest there is reason for concern from rising temperatures, even in species adapted to hot, dry environments. Many of these studies take place in the centre of the range, unless they are specifically investigating peripheral population dynamics. This was highlighted by Caissy et al. (2020), where the majority of at-risk plant species in Canada reached their northern range limit there, yet had only been studied outside of Canada. Peripheral populations are of particular importance in conservation initiatives due to unique environmental resilience and genetic diversity (Lesica and Allendorf 1995; Channell 2004) and research in these areas is merited.

In this thesis, I focus on a community of small mammals occupying the semi-arid grasslands of the Thompson valley in south-central British Columbia (BC), Canada. Known collectively as kwéḱwtne[1] by the local Secwepemc First Nation, the small mammal community here is largely composed of two main rodents in the Family Cricetidae, namely the Western Deer Mouse[2] (*Peromyscus sonoriensis*) and the Montane Vole (*Microtus montanus*) (Nagorsen 2005). The Deer Mouse is a generalist, consuming seeds, insects, fruit, and fungi, depending on the season and availability. They are widespread, with a range stretching across western North America, from the Yukon in northern Canada to the northern reaches of Mexico (Figure 1.1) (Greenbaum et al. 2019). The Montane Vole is a grassland specialist residing in the western United States and southern interior of British Columbia, Canada (Figure 1.1), whose diet consists almost entirely of graminoid vegetation (Pinter et al. 1992). Microtus species have the largest caecum and colon (the vegetation fermentation chambers used by non-ruminant herbivores such

[1] Pronounced “kwow-kh-na” and translates roughly as “mouse”, it can be used to refer to mice and voles generally.

[2] Previously known as the North American Deer Mouse (*Peromyscus maniculatus*).

as horses) of any rodent proportional to their size (Vorontsov and Vorontsov 1962) and have been known to practice coprophagy (Ouellette and Heisinger 1980). These adaptations for specialised vegetation digestion reflect the importance of vegetation to the microtine diet. Though sympatric through much of their range, the level of competition existing between the *Peromyscus* and *Microtus* species is controversial, and conflicting studies leave the dominant species unclear (Crowell 1973; Crowell and Pimm 1976). Elsewhere in BC, the Columbia Plateau Pocket Mouse (*Perognathus parvus*, F. Heteromyidae) outcompetes other cricetid rodents in hot, dry valley bottoms (Maida et al. 2020, Atkinson et al. in preparation). Pocket Mice and other heteromyids are desert specialists and an important part of the small mammal community in many arid ecosystems of North American (Iverson 1967; Sullivan and Sullivan 2008; Phillips 2018). In BC, however, pocket mice have been in severe decline and were considered extirpated in this study site's valley until very recently (Atkinson and Larsen 2025, see Appendix A). This observation notwithstanding, Deer Mice and Montane Voles remain the dominant small mammal in the Thompson Valley (Hales 2011) and the focus of this study.

The long-term trends of this grassland small mammal community give important clues for understanding the effects of climate change on food webs. Though the diet niche of the Deer Mouse and the Montane Vole differ, both support the disproportionate numbers of threatened meso-predators in the semi-arid grasslands such as the Burrowing Owl (*Athene cunicularia*), Western Rattlesnakes (*Crotalus oreganus*), American Badger (*Taxidea taxus*), and Ferruginous Hawk (*Buteo regalis*). Insights about trophic shifts and community structure can be gleaned from this relatively depauperate food web. Many studies focus on specific threatened species, which, though important, may overlook the impacts which non-listed species can have on those species. As ecosystem engineers and essential prey items for threatened grassland predators, this small mammal community links many facets of this ecosystem and adds to a holistic understanding of ecosystem-level changes.

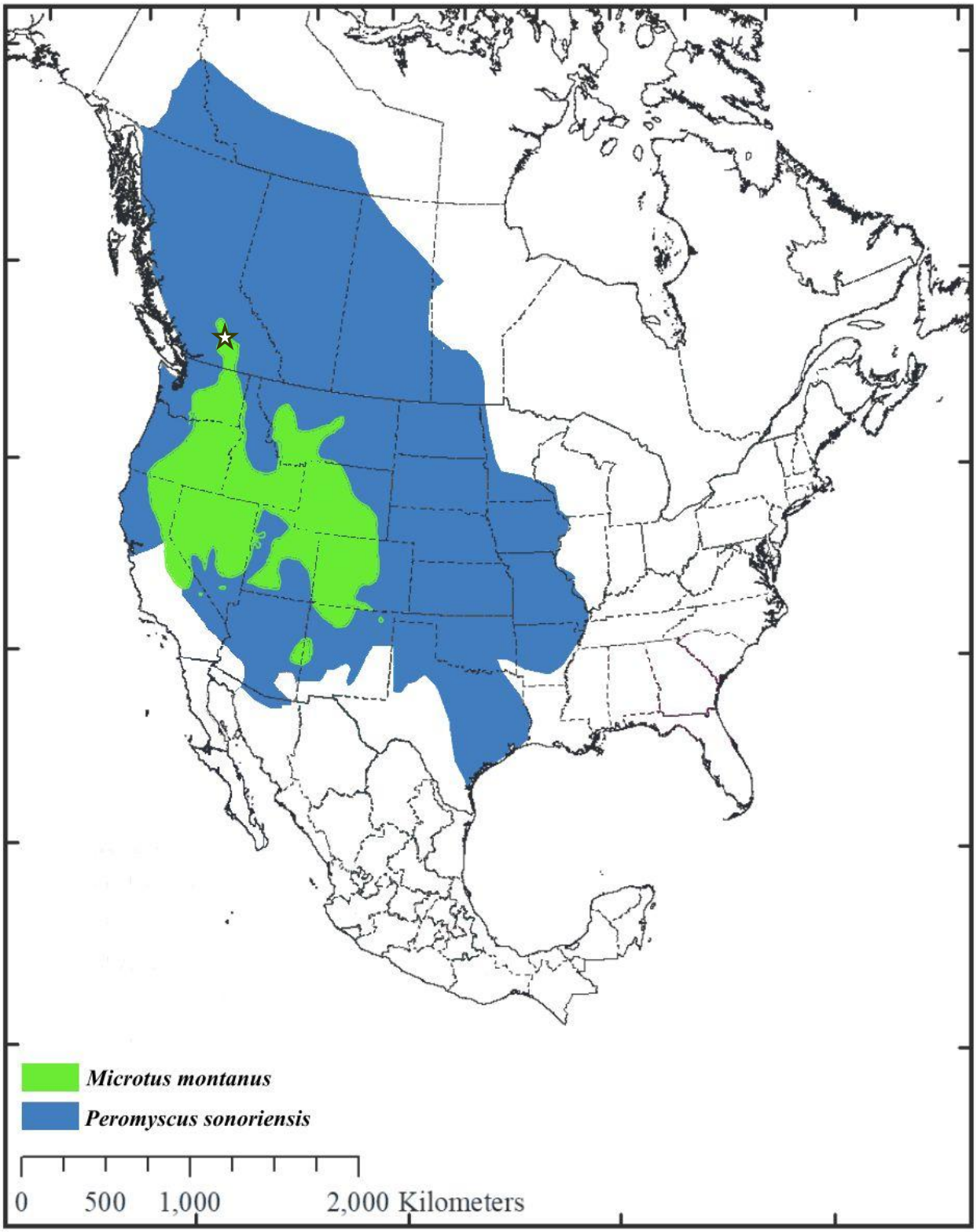

Figure 1.1 Range map of the Western Deer Mouse (*Peromyscus sonoriensis*) and Montane Vole (*Microtus montanus*) in North America. The Montane Vole is sympatric with the Western Deer Mouse across its entire range. Adapted from Greenbaum et al. (2019) range map of *Peromyscus* spp. The present study's location in southern British Columbia is indicated by the star.

THESIS OBJECTIVES

The broad overarching goal of my thesis was to investigate long term trends in a semi-arid grassland community of small mammals, focusing on the Western Deer Mouse and the Montane Vole, while also providing insight into how increasing heat may affect this community. Below I conclude the current chapter with details on the ecosystem where I conducted my work (see below).

In Chapter 2, I focus on the population dynamics of the two species to answer whether the populations are cyclic and how density has changed over time. Using 24 years of annual autumn trapping data, I identify trends and patterns in the density of each species. I use local weather records for temperature and precipitation to compare to the density for each year and identify key predictors for population density. To understand how the population may respond to future climate under anthropogenic climate change, I use climactic predictions from general circulation models (Wang et al. 2016) and combine them with the population models from this chapter to obtain small mammal density predictions for the next 50 years.

In Chapter 3, I delve into the effects of heat and seasonality on density and demographic structure of the Western Deer Mouse across two different but closely associated habitats. My objective in this chapter was to understand if extreme heat is a limiting factor to population growth and suggest a mechanism by which it could do so. Specifically, I trapped Deer Mouse populations in the spring and again in the summer at grassland sites across the valley and recorded age class and reproductive status. A forest site nearby each grassland site was trapped simultaneously, to provide reference data from Deer Mouse populations with lower heat exposure. During this specific study window, the Deer Mouse populations experienced a heat wave that exposed the animals on the landscape to extreme heat beyond that of normal seasonal temperatures.

In the fourth and final chapter of my thesis, I summarise key findings from my two main data chapters and connect them to the broader implications of climate change and habitat degradation on keystone species and trophic structure. Together, these chapters provide clarity on the small mammal community structure through time and evidence for how climate change may affect this ecosystem.

STUDY SITE

My research was conducted in Tk'emlúps[3] (the Thompson Valley) in British Columbia, Canada (Figure 1.2), a semi-arid grassland at the northern extent of the Great Basin Desert. Sitting in the rain shadow of the Coastal Mountains, summers regularly reach daytime highs of 35-40°C with a moisture deficit of 100-150 mm (Hargreaves climatic moisture deficit, Wang et al. 2016). Winters are mild for Canada and hover around 0-(-5) °C, though cold snaps may go below -20°C. Animals living in these regions must be adapted to extreme heat, but also must be able to tolerate extreme cold. Historic averages can be seen in Figure 1.3, with the most recent quarter-century having significantly warmer summers than previous quarters, a trend that is expected to continue (Smith et al. 2013).

A range of ecosystems is seen across the elevational gradient (Figure 1.4) (Meidinger and Pojar 1991). Valley bottoms are hot and dry with widely spaced bunchgrass such as Bluebunch Wheatgrass (*Agropyron spicatum*). Big Sagebrush (*Artemisia tridentata*) is common, with high densities occurring in over-grazed areas. Other common species include Kentucky Bluegrass (*Poa pratensis*), Crested Wheatgrass (*Agropyron cristatum*), Cheatgrass (*Bromus tectorum*), Common Yarrow (*Achillea millefolium*), and Prickly-pear Cactus (*Opuntia fragilis*). Bare ground between vegetation is covered with a robust cryptogam crust (Meidinger and Pojar 1991). Higher elevations have increasing canopy cover of Ponderosa Pine (*Pinus ponderosa*) or Douglas-fir (*Pseudotsuga menziesii*) and forbs such as Wild Prairie Rose (*Rosa arkansana*) interspersed by bunchgrass species as named above.

Historic trapping was conducted as part of a senior-year Wildlife Management course at Thompson Rivers University in Kamloops (Figure 1.2), led by Karl Larsen and Sheri Watson. Each autumn from 1997 to 2024, students assisted experienced trappers with trapping 3 grids (Figure 1.2). A fourth grid was trapped in 2017 and 2021 and, as of the completion of this thesis, data collection continues. Along with field assistants, I trapped these same 4 grids in spring and summer in 2023 and 2024, as well as an additional 6 new grids established across the valley in 2024 – 3 in typical grasslands and 3 in higher elevation forest.

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[3] Tk'emlúps is the Secwepemc First Nation's name for this area, meaning "meeting of the waters", referring to the confluence of the North Thompson and South Thompson Rivers.

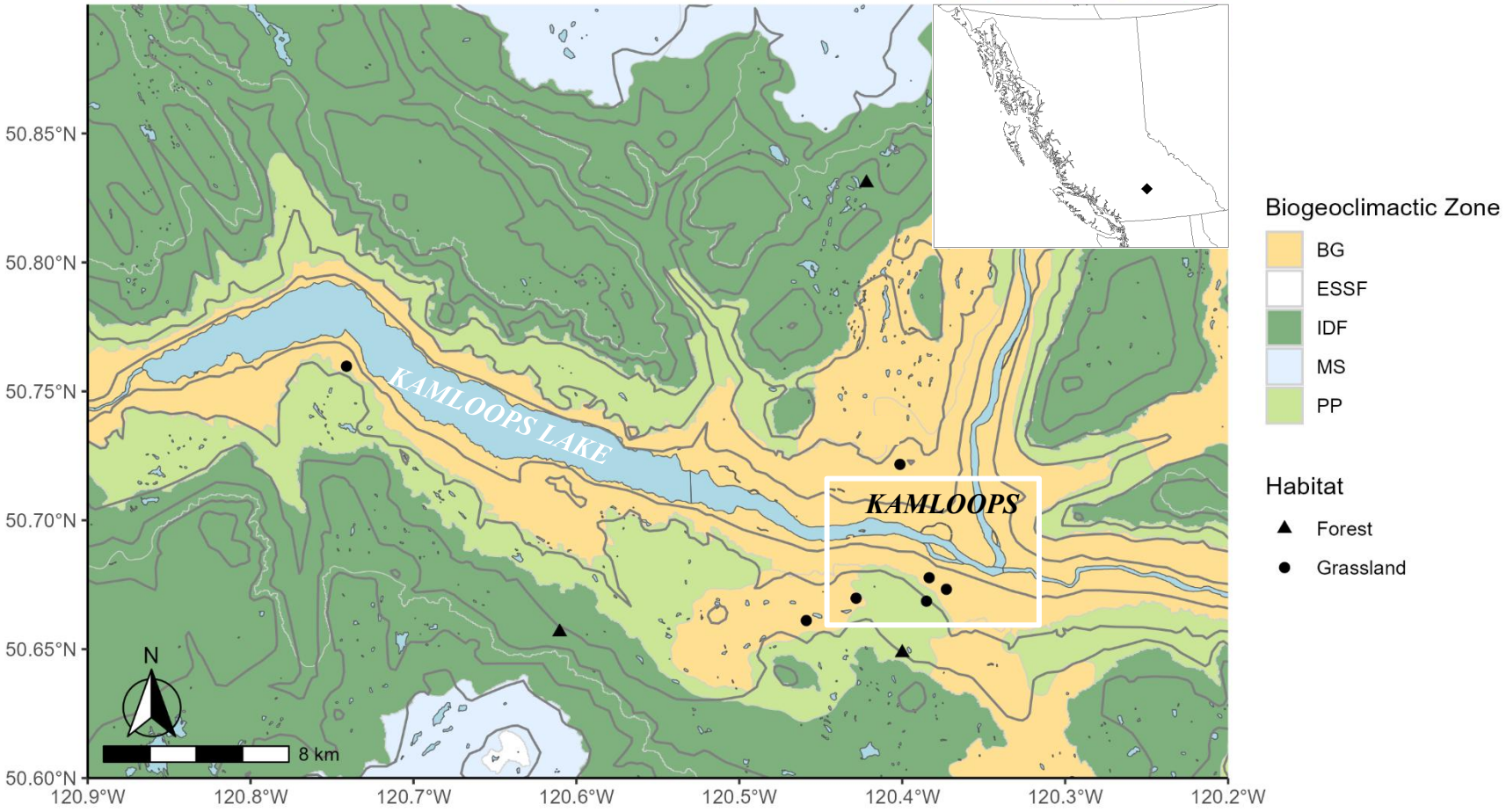

Figure 1.2 Map showing study sites (points) around the city of Kamloops (rectangle) used for small mammal trapping in the Thompson River Valley, BC, Canada (50°40'05"N 120°23'08"W). Chapter 2 used only the sites within the white rectangle (trapped 1997-2024), while Chapter 3 used all other sites (trapped 2024). Grid type is designated by a circle for grassland and a triangle for forest. The biogeoclimactic zone is the ecosystem classification system used by the British Columbia Government, with Bunchgrass (BG), Engelmann Spruce-Subalpine Fir (ESSF), Interior Douglas-fir (IDF), Montane Spruce (MS), and Ponderosa Pine (PP) zones represented in this area. Information of biogeoclimactic zones can be found in Meidinger and Pojar (1991). Elevation lines are spaced at 100 m.

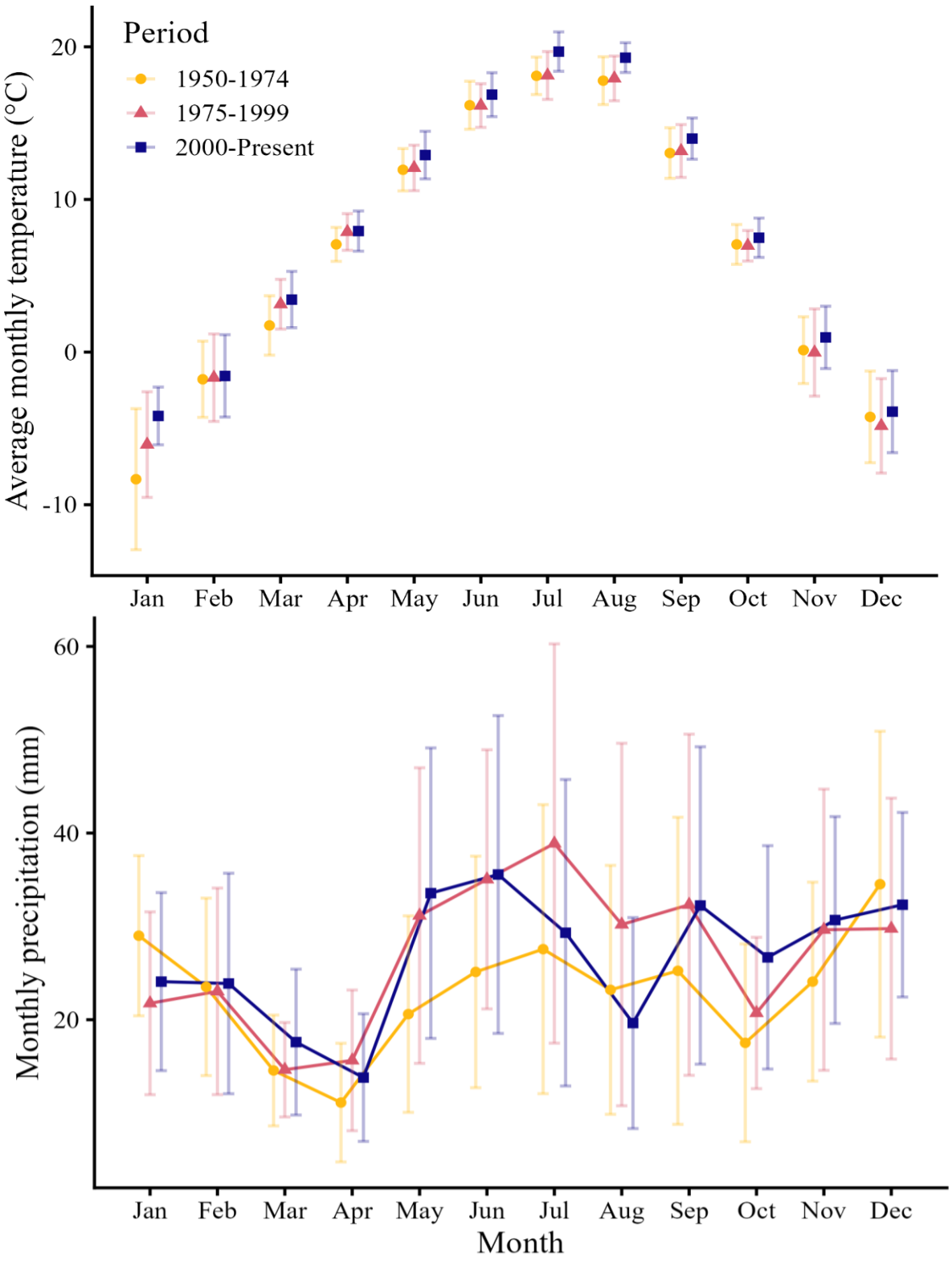

Figure 1.3 Temperature (top) and precipitation (bottom) 25-year averages for the City of Kamloops in the Thompson region of British Columbia. Error bars show standard deviation in values. Plot A demonstrates the increase in average temperature in July and August in the years 2000-2024. Data from Climate BC (Wang et al. 2016).

Figure 1.4 Typical grasslands in the Thompson Valley showing a range of shrubland and dispersed trees. Photos by author.

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CHAPTER 2

GRASSLAND SMALL MAMMAL POPULATION DYNAMICS AND CLIMATE – A 28 YEAR STUDY

INTRODUCTION

Animal populations are in constant flux, and the drivers of these population changes have fascinated researchers for over 100 years (Elton 1924). Dramatic eruptions in animal populations, such as the "Nevada Mouse Plague" of 1909 (Piper 1909; Elton 1942), have been characterised as "plagues" due to their abrupt and economically significant consequences. In some cases, the combination of climate, reproduction, predation, and behaviour may create a regularly oscillating population dynamic (Myers 2018), with populations cycling through low, increase, peak, and crash phases (Krebs et al. 2001; Andreassen et al. 2021). These oscillating dynamics are a driving force for the trophic food webs in the areas where they occur, and as a result have been extensively studied across the globe (Elton 1924; Hanski et al. 1991; Boonstra et al. 1998; Krebs et al. 2001; Krebs 2013; Bennison et al. 2018; Sullivan and Sullivan 2021; Avotins et al. 2023). The mechanisms of cyclic population dynamics are complex, but generally include a combination of weather conditions that control food availability and survival (Meslow and Keith 1971; Choquenot and Ruscoe 2000; Burt et al. 2017; Dhawan et al. 2018), phase-dependent breeding condition and behaviour (Jannett 1981; Boonstra et al. 1998; Sullivan et al. 2021), and predator interactions (Krebs et al. 2001; White and King 2006; Ylönen et al. 2019; Majchrzak et al. 2022).

Given the role that climate change is likely to play in reshaping trophic structures of ecosystems, understanding long-term population changes and their relationship to weather has taken on a new significance. Range shifts, phenological mismatch, and severe natural disasters caused by climate change have been increasingly observed in recent times (Bumbaco et al. 2013; Kudo and Cooper 2019; Visser and Gienapp 2019; Wilson et al. 2020). Rainfall, or lack thereof, may cause population eruptions (Greenville et al. 2012) or crashes (Stewart 1995; Sperry and Weatherhead 2008), while warming temperatures may increase plant productivity, leading to increased body condition (Tveraa et al. 2013; Albon et al. 2017), or cause heat stress and subsequently impaired reproduction and survival (McKechnie and Wolf 2009; Takahashi 2012; Rollins-Smith and Le Sage 2023). Mild winters have been

associated with lower amplitude peak phases in vole-weasel and lynx-hare systems (Hörnfeldt et al. 2005; Hone et al. 2011) and longer breeding seasons have been shown to cause shorter cycles in voles (Taylor et al. 2013). Some areas have seen a collapse of population cyclicity due to climate change, leading to consistently low-density populations (Hörnfeldt et al. 2005; Ims et al. 2008; Cornulier et al. 2013; Avotins et al. 2023). This can lead to cascading trophic effects, as many predators rely on the high amplitude phases of prey species for reproduction and persistence (Hanski et al. 1991; Jędrzejewski et al. 1995; Shine and Madsen 1997; Reading 2004; Avotins et al. 2023); indeed, prey-switching as a result of small mammal population crashes has been shown to impact the alternate prey species (McKinnon et al. 2014; Bowler et al. 2020; Pakanen et al. 2022).

Which species will survive rapid shifts brought on by climate change is difficult to predict. The generalist theory posits that generalists have the advantage in novel environments, as climactic changes reshape the ecosystem (Davies et al. 2004; Sweeney and Jarzyna 2022). Even within a species, peripheral populations experiencing more marginal conditions have showed greater plasticity and more "generalist" behaviour than populations at the centre of their range (Latimer et al. 2018). However, other evidence shows that rare species may benefit from extreme weather events, when more abundant and competitive species are disadvantaged (Prugh et al. 2018). Intuitively, the impact of these community shifts may be more consequential when keystone species are significantly affected, a concern raised across many ecosystems and latitudes (Harley 2011; Peers et al. 2020; Bombi et al. 2021).

Small mammals may be considered keystone species in many arid ecosystems (Delibes-Mateos et al. 2011, Sullivan and Sullivan 2021). Acting as ecosystem engineers, their burrows aerate the soil and allow water to penetrate more deeply (Laundre 1993), and they disperse seeds and fungal spores, facilitating habitat restoration post-disturbance (Hollander and Vander Wall 2004; Schickmann et al. 2012; Stephens et al. 2021). Perhaps most relevant is their trophic position, where they serve as the main prey item for a host of mesopredators (Whitford and Kay 1999; Howe et al. 2006; Johnson et al. 2011; Beca et al. 2022). Their ecological importance, relative ease of study, and large body of knowledge on their natural history makes small mammals an ideal indicator species for understanding the effects of disturbance on ecological communities.

Small mammal communities in arid and semi-arid grasslands may be predicted to change with trends towards hotter and drier climates. In southcentral British Columbia (BC), Canada, the North American shrub-steppe ecosystem reaches its northern limit. This region hosts peripheral populations of desert specialists such as the Columbia Plateau Pocket Mouse (*Perognathus parvus*), which inhabits the hot and dry valley bottoms in this region, with a shift to species such as the Western Deer Mouse (*Peromyscus sonoriensis*), Montane Vole (*Microtus montanus*), and Meadow Vole (*Microtus pennsylvanicus*) in higher elevation grasslands (Kritzman 1974; Nagorsen 2005; Maida et al. 2020). The pocket mouse is sensitive to human disturbance (Sullivan and Sullivan 2008), and may be absent in some regions due to population decline (Ramsay and Nagorsen 2024). In these areas, such as our study site, the Deer Mouse is the dominant grassland small mammal.

Increased heat waves and continued aridification of this region is expected under climate-change forecasts (Smith 2011; Smith et al. 2013), and while the generalist Deer Mice living in arid environments may tolerate increasingly hot conditions, though they do not possess the desert-specific adaptations in osmoregulation and metabolism identified in desert specialist *Peromyscus* species such as the Canyon Mouse (*Peromyscus crinitus*) (Colella et al. 2021). This, along with the limited species diversity, suggests that climate change has the potential to cause large restructuring of this grassland's food web.

This study explores the long-term (28 years) population dynamics of the two most abundant small mammal species in a northern semi-arid grassland. Firstly, we characterize population oscillations and spatial distributions of the two main species, the Western Deer Mouse and the Montane Vole, specifically the wavelength and amplitude of these oscillations and the correlation between the two species' densities through time. Secondly, we investigated the correlation between species abundance and seasonal temperature and precipitation and discuss how the small mammal community may shift under forecasted climate change scenarios.

METHODS

Study Area

This study was situated in the semi-arid interior of British Columbia. Our long-term study grids were located in low to mid-elevation grasslands in and around Kenna Cartwright Nature Park (LAT 50.7°, LONG -120.4°), a municipal park in Kamloops, BC, Canada.

The sites were located within 10 km of each other, and varied from 500 m - 700 m of elevation (Figure 1.2). Dominant vegetation includes xeric plants such as Big Sagebrush (*Artemisia tridentata*), Prickly Pear Cactus (*Opuntia fragilis*), Common Yarrow (*Achillea millefolium*), Bluebunch Wheatgrass (*Pseudorogenaria spicata*), Alkali Bluegrass (*Poa secunda*), and Ponderosa Pine (*Pinus ponderosa*) (Figure 2.1). Further details on the ecosystem are given under Study Site in Chapter 1 of this thesis.

Live Trapping

From 1997 to 2024 small mammals were live-trapped each autumn in the last week of September or first week of October. Autumn was chosen for this annual trapping event due to higher numbers of small mammals generally occurring in the post-breeding season (Andreassen et al. 2021). Three grids (hereafter referred to as A, B, C) were live-trapped simultaneously using methods similar to Larsen et al. (2007) and by incorporating the project into the curriculum of a senior wildlife class. A fourth grid (D) was opportunistically trapped in 2017 and 2021 when more students/trappers were available. Site locations can be seen in Figure 1.2. Effects of encroachment by residential sprawl on some sites were not specifically tested.

Longworth-style traps (Little Critter Live Traps, Rogers Manufacturing, West Kelowna, B.C., Canada) were used to conduct trapping. Each grid consisted of 60 traps arranged in a 4 ×15 arrangement with 15 m spacing, for a total area of 45m by 225m (approximately 1 ha). Each trap was covered with a plastic coverboard in light neutral colours as protection from sun and rain. As temperatures near 0°C were possible during each trapping session, each trap was outfitted with synthetic bedding material that was replaced if overly damp or soiled.

For each trapping session, traps were locked open and baited with sunflower seeds and whole oats, for three nights prior to trapping. Traps then were set for three consecutive

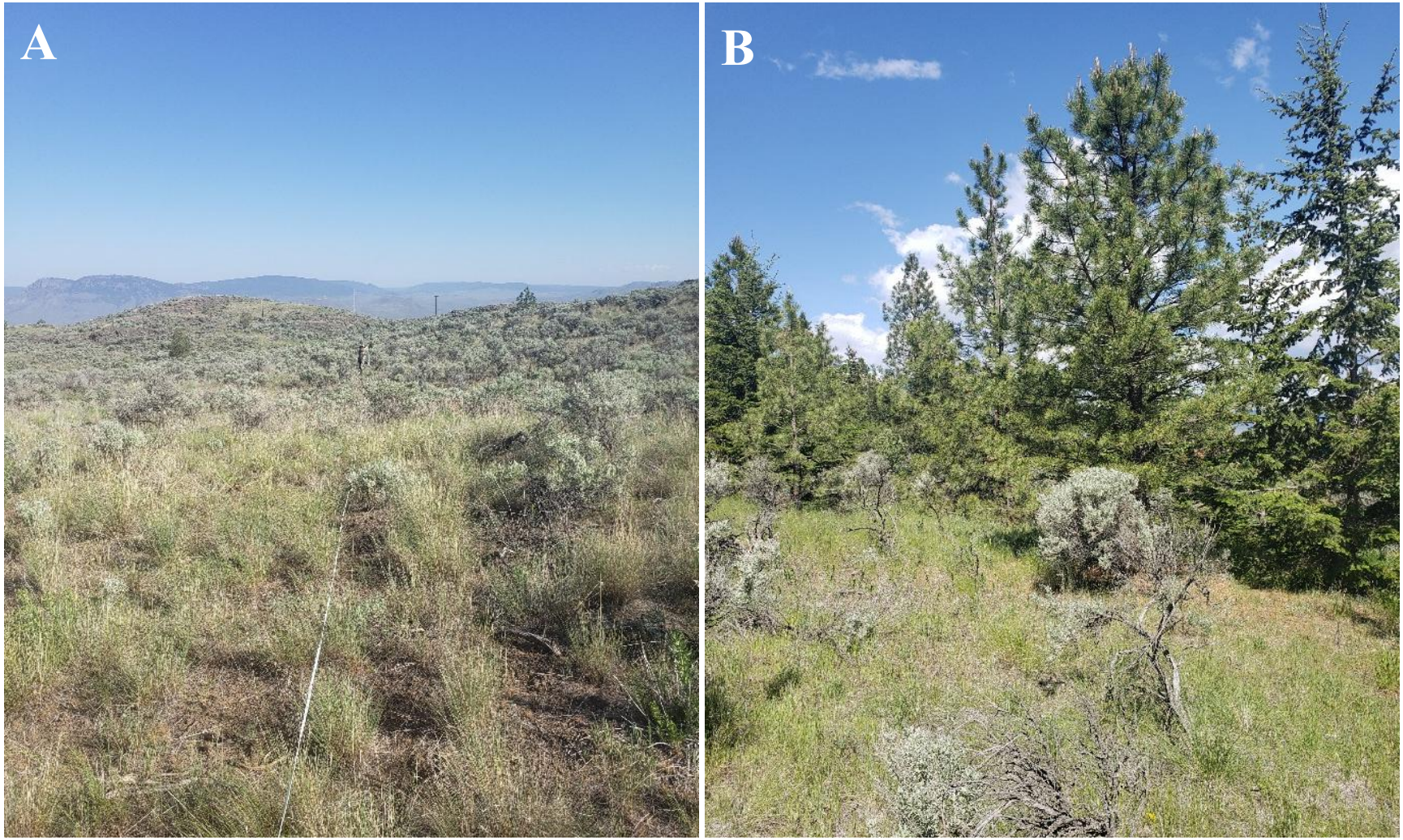

Figure 2.1 Study site depicting grasslands with shrubland (A) and widely spaced trees (B). Photos by author.

nights within 2 hours of sunset and checked each morning within 2 hours of dawn. During trap nights, chunks of apple were added to the bait mixture to provide water to captured animals. Traps were locked open during the day. At the end of each yearly session, traps were removed from the grids, disinfected with bleach, and stored until the next trapping event.

Captured animals were eartagged with National Band and Tag Company® mouse tags (model 1005-1) in the cartilage of the right ear. Species, sex, weight, reproductive status and trap location were recorded before release of the animal. Mass was taken using spring scales (PESOLA AG, Baar, Switzerland) with the animal placed in a small plastic bag. Following Sullivan and Sullivan (2021), female reproductive status was assigned to one of four categories: not evident, pregnant, lactating (nipples evident), or hair regrowth (around nipples). Males were scored by testes location (scrotal or abdominal). Testes location in males and pregnancy in females were determined by gentle palpation of the scrotal area and abdomen, respectively.

Weather

Weather variables were taken from ClimateNA ((Wang et al. 2016), a software package that combines historical weather data (1901 to present) from across North America with elevation data and satellite imagery to calculate scale-free point estimates of climate values for any location on the continent. This approach significantly improves accuracy for ecological modelling when compared to traditional weather station data (Wang et al. 2012).

Data Analysis

All analysis was performed using R (Version 4.5.2, https://www.r-project.org/). Density for each species in each grid was estimated using spatially explicit capture-recapture (SECR) models (Efford 2004; Borchers and Efford 2008; Efford and Fewster 2013), where each grid was allowed to share estimation parameters across years and species. This approach allowed us to generate density estimates even in years with very low capture numbers. We were not able to estimate density in the years 1997, 1998, 1999, and 2001 as the spatial capture data was not available. In these cases, minimum number alive was used for plotting

purposes, however we excluded these values from the modelling as they were not comparable to the SECR density estimates.

Cyclicity and periodicity of the populations were evaluated by wavelet analysis using the 'WaveletComp' package in R with a Morlet wavelet as the mother wavelet, a common approach for this type of analysis (Roesch and Schmidbauer 2018). We tested potential cycle lengths between 1 and 12 years against the density data. This analysis calculates the probability of a cycle of the tested length occurring at each point in time, and produces a 'heatmap' plot of these values. Probabilities with a significance below $\alpha = 0.05$ were accepted as cyclic at that period, and lighter pixels on the plots represent smaller *P*-values.

We used a sliding window analysis (Bailey and van de Pol 2016, van de Pol et al. 2016) to identify biologically relevant seasonal windows of mean temperature and cumulative precipitation on Deer Mouse and Montane Vole densities. This approach increases the ability of a model to detect important weather periods, as weather links often are weak. The base model used was a generalized linear model (GLM) with a gamma distribution and log link. A gamma distribution was chosen for the GLM to limit density predictions to positive values only (Dennis and Patil 1984; Diserud and Engen 2000). Models of this nature that did not converge were replaced with a linear mixed effects model (Pinheiro et al. 2024) with grid as a random effect. As trapping only occurred once per year, weather for the 12 months preceding a trapping session were used in the models. Top climate windows were ranked using AICc (Hurvich and Tsai 1989). Model significance was determined by comparing the top model to models with a random climate signal. This was accomplished by re-running the sliding window analysis (n=1000 iterations) using the original data with randomly rearranged dates (Bailey and van de Pol 2016). As there is uncertainty in exact windows, for significant windows, the 95% confidence set (the cumulative set of top models that adds to 95% of the AICc weight) was averaged to determine a more conservative window estimate (Bailey and van de Pol 2016).

RESULTS

Population Dynamics

Over 28 trapping sessions at 3 grids (252 trap nights), the most common species captured was the Western Deer Mouse (*Peromyscus sonoriensis*, 4471 individuals) followed by the Montane Vole (*Microtus montanus*, 612 individuals). Meadow Voles (*Microtus pennsylvanicus*) are known to be sympatric with Montane Voles in British Columbia in lower elevation grasslands, with the two species being very difficult to separate in the field (Nagorsen 2005); however, 16 vole mortalities found on grid sites or nearby trails during the study years all were confirmed to be *M. montanus* through dental analysis (Larsen, *unpublished*). Consequently, all voles captured during this study were assumed to be *M. montanus*. Other small mammals captured included Yellow Pine Chipmunks (*Neotamias amoenus*, 193 captures), shrews (*Sorex spp*., 6 captures), House Mice (*Mus musculus*, 2 individuals), and one Western Jumping Mouse (*Zapus princeps)*. No Northern Pocket Gophers (*Thomomys talpoides*) were captured; however, fresh burrow mounds were present on grids throughout the study.

In general, mouse densities were higher than those for voles over the course of the trapping years. Density differences between species (Kruskal-Wallis $\chi^2 = 70.20$, DF = 1, $P < 0.001$), between grids (Kruskal-Wallis $\chi^2 = 15.9$, DF = 3, $P < 0.001$), and between sessions (Kruskal-Wallis $\chi^2 = 52.7$, DF = 27, $P < 0.001$) were statistically significant. Vole and mouse yearly density estimates were found to be significantly correlated (Pearson's R = 0.49, D.F. = 72, $P < 0.01$). Though numbers fluctuated greatly, one grid produced significantly higher small mammal numbers than the other grids year over year (Figure 2.2). This pattern of relative carrying capacity was present in both low and high animal years.

Regular population oscillations were present for both mice and voles, though some periods showed stronger cyclicity than others. Deer Mouse cyclicity was consistent across all grids (Figure 2.3 A-C). A longer, initial cycle with a 5-year period was detected between 2003 and 2012, following by a shift to a 3-year cycle for the remainder of the study. All three grids showed significance for both cycle lengths. Montane voles showed moderate cyclicity with 3- and 6-8-year periods (Figure 2.3 D-F), although only in the later years of the study.

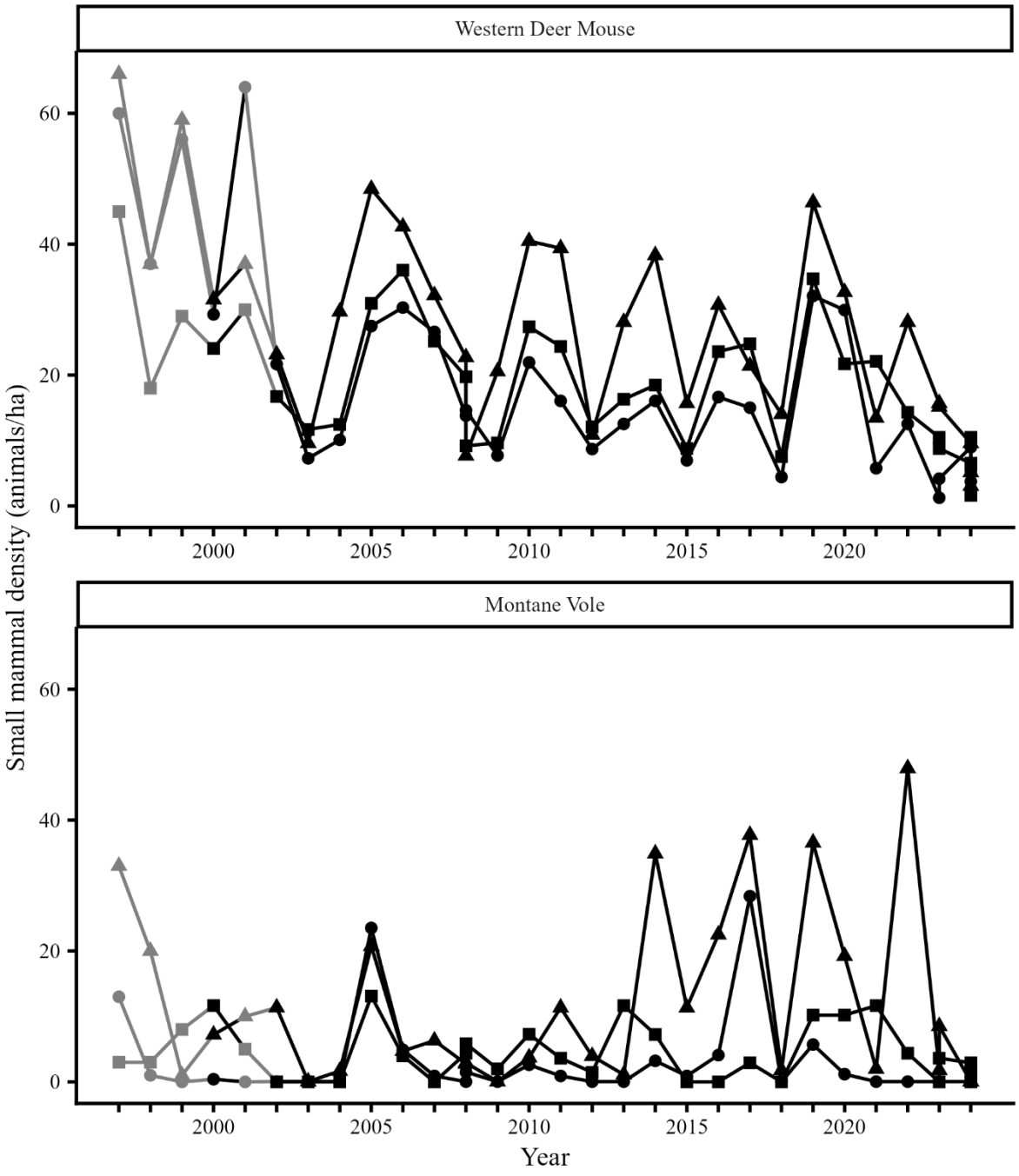

Figure 2.2 Time series for Western Deer Mouse (*Peromyscus sonoriensis*) and Montane Vole (*Microtus montanus*) density estimates across three grassland grids in the Thompson Valley, BC, Canada. Grids were located 1-3 km apart and trapped in late September to early October each year from 2000 to 2024. Grids on graph are A (●), B (▲), and C (■). Minimum number alive was used for 1997-1999 and 2001, as trap location was not available for these years to complete a SECR estimate. Black points denote spatially explicit capture-recapture density estimates, while grey points denote minimum number alive, which can overestimate density due to edge effects.

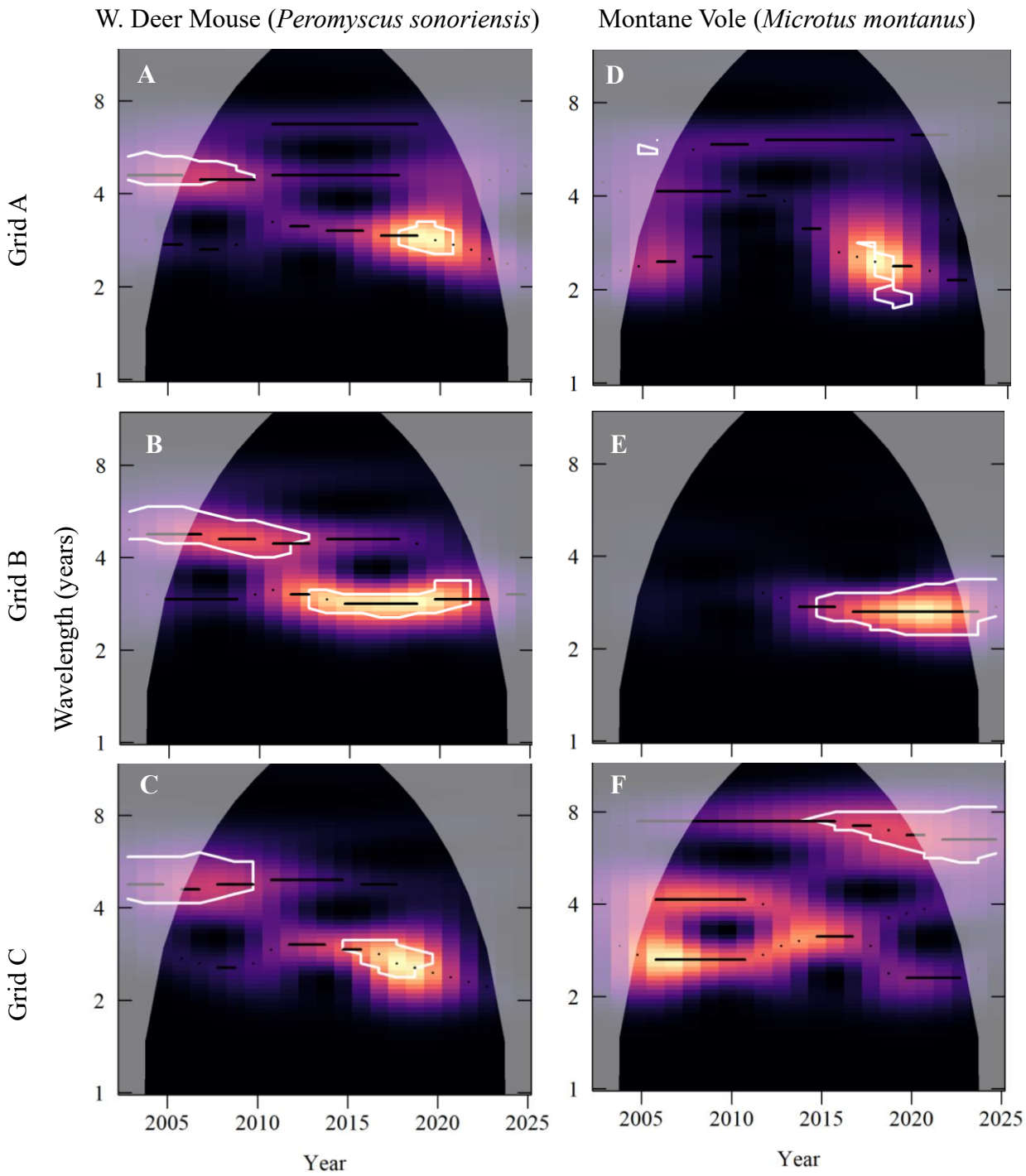

Figure 2.3 Wavelet power analysis of Deer Mouse (*P. maniculatus*) (A-C) and Montane Vole (*M. montanus*) (D-F) autumn population density over 25 years (2000-2024) on three live-trapping grids near Kamloops, British Columbia, Canada. Lighter colours on the heatmap indicate when a tested cycle length (y-axis) provides a strong match for the data. On each graph, the polygon(s) outlined in white encompasses cycle lengths that are significant at $\alpha = 0.05$.

Weather Effects on Density

Only one relationship between small mammal density and weather was found to be significant: that of the Deer Mouse and average summer temperature (Table 2.1). The significant temperature window for Deer Mice was July to August, but all top models for temperature windows were centred around the summer and generally fell within a broader window of June to September (Figure 2.4), solidifying the importance of summer as a significant variable, but indicating some variability in the exact months. Overall, higher summer temperature was significantly associated with lower Deer Mouse densities the following autumn (Figure 2.5).

No significant relationships were seen between Deer Mice and precipitation, nor with Montane Voles and either weather variable (Table 2.1).

DISCUSSION

Community Structure and Population Dynamics

This semi-arid grassland small mammal community was found to be composed of predominantly Western Deer Mice and Montane Voles, consistent with previous trapping projects occurring in the region (Sullivan and Sullivan 2006; Hales 2011; Sullivan et al. 2021; Sullivan et al. 2023). Other species were detected in low numbers, though this may be partially attributed to trapping methods. Fresh mound throws for pocket gopher were present all grids, but catching this animal typically requires placing traps in an excavated burrow (Witmer et al. 1999). Yellow Pine Chipmunks were regularly sighted and trapped in low numbers; however, these animals are largely diurnal (Cade 1963), and our night trapping would not effectively target them. Shrews, jumping mice, and house mice were trapped very rarely, and are likely not present in great numbers at this site.

The cycle length of the Deer Mouse and Montane Vole sheds more light on observed distribution and population dynamics. Both species were found to be cyclic, though the vole cycle length was not consistent across all cites. Cycle lengths of 3-5 years were seen in both the Western Deer Mouse and the Montane Vole, which is consistent with studies on voles and other cricetid species in the northern hemisphere (Korpimäki and Krebs 1996; Elmhagen et al. 2011; Krebs 2013; Myers 2018; Andreassen et al. 2021) as well as with Deer Mouse and Montane Vole studies in the area (Sullivan et al. 2023). The oscillations of the Deer Mouse in this study were very regular and synchronous until the peak in 2019, after which a marked decrease and lull in

Table 2.1 Top temperature and precipitation windows for predicting small mammal autumn densities in a sliding window analysis. Mouse models are generalised linear models with a gamma distribution and log-link. Vole models are mixed-effects models controlling for grid effect. Top windows are indicated by both month names and months before trapping date (October) in the brackets, where September is 1 month prior to October, August is 2 months prior, and November is 11 months prior. The 95% confidence set (the average window for top models that collectively add up to 95% of the AICc weight) is shown for significant model(s).

Species	Climate variable	Statistic used	Top window	ΔAICc	Model β	Model SE	Model weight	95% window set	Model *P* (n=1000)	Model R^2
Mouse	Temperature	Mean (°C)	Jul-Aug (3-2)	-15.14	-0.27	0.06	0.19	Jun-Sep (4.3-1.3)	**< 0.01**	0.35
Mouse	Precipitation	Sum (mm)	Dec-Apr (10-6)	-6.57	-0.01	<0.01	0.17	—	0.79	—
Vole	Temperature	Mean (°C)	Jan-Feb (9-8)	-3.02	-1.54	0.67	0.07	—	0.81	—
Vole	Precipitation	Sum (mm)	Oct-Nov (12-11)	-3.98	0.15	0.06	0.09	—	0.78	—

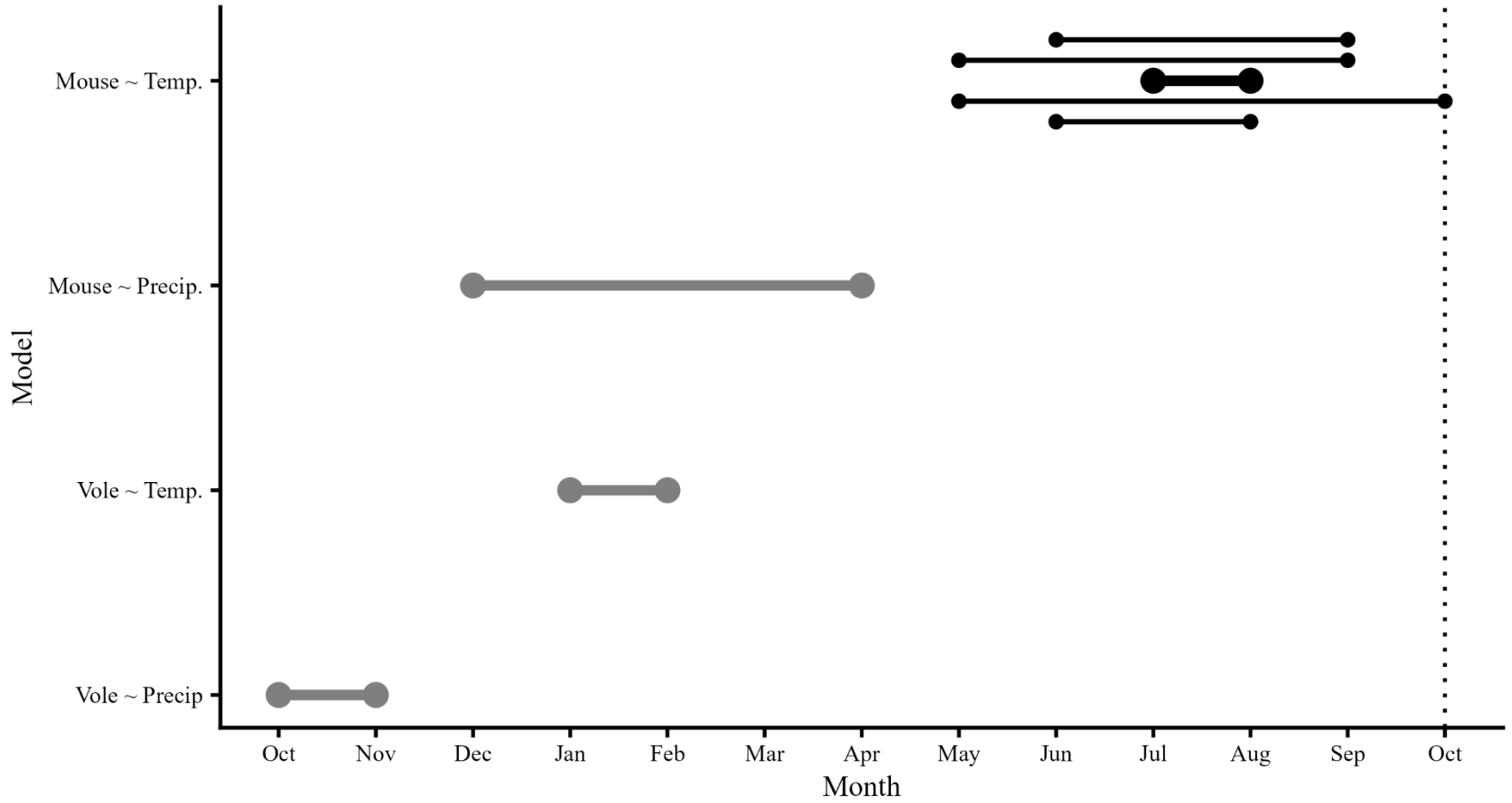

Figure 2.4 Top temperature and precipitation windows in predicting autumn Western Deer Mouse and Montane Vole density. Significant windows are shown in black and non-significant windows are in grey. The dotted line indicates the trapping date where autumn animal densities are drawn (first week of October). Top windows for each relationship are indicated by heavy lines. Runner-up models (within AICc of 2 of the top model) are only shown for significant windows and are indicated by thin lines.

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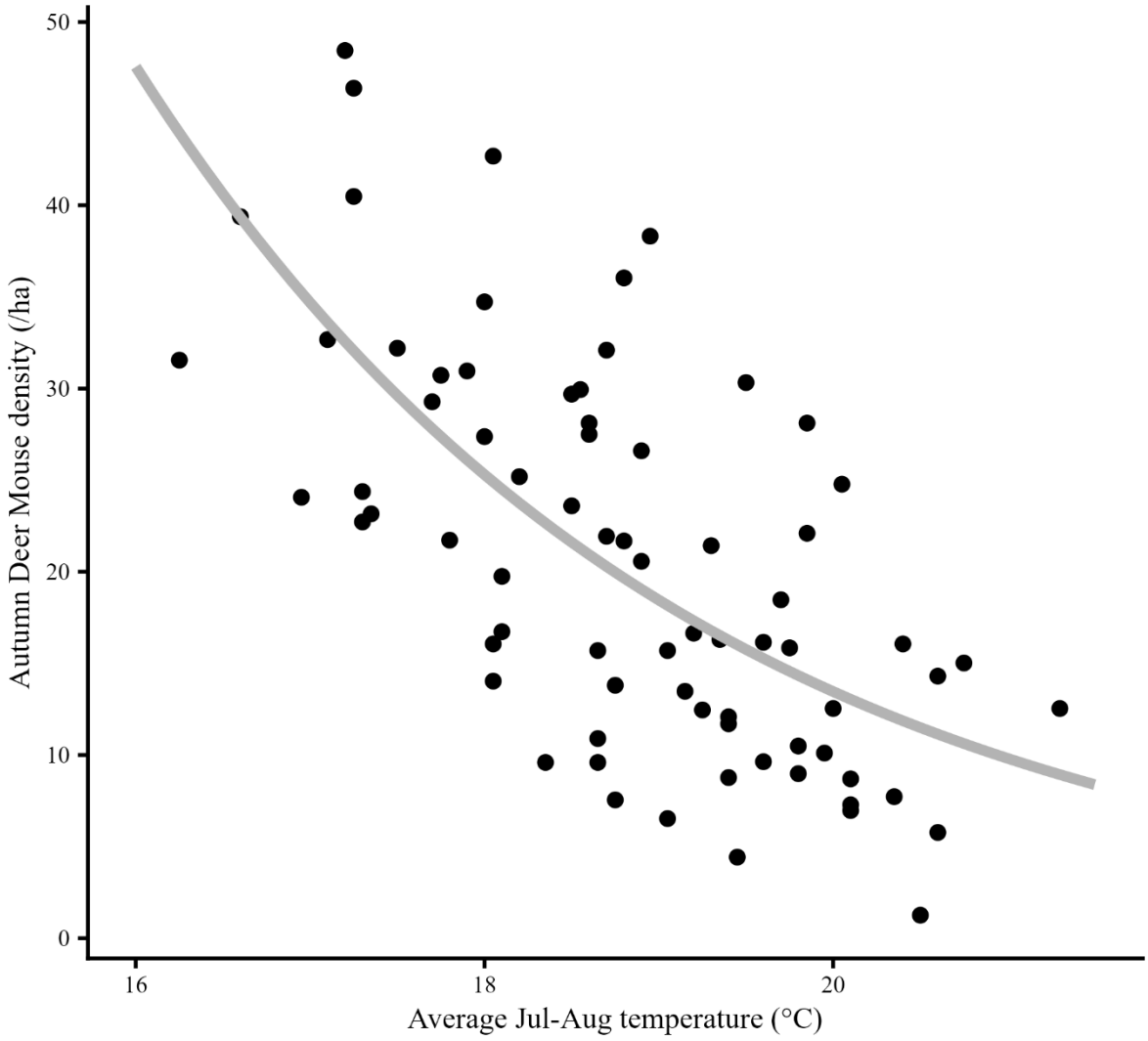

Figure 2.5 Relationship between autumn Western Deer Mouse density and the top temperature window of average July-August temperature. Model output can be found in Appendix B.

regular cyclicity was apparent. Interestingly, a 2019 peak in mouse numbers was seen in surveys more than 200 km away (Sullivan and Sullivan 2022, Atkinson et al. *in preparation*), suggesting oscillations for this species may be synchronous across a large spatial scale.The following lull may be due to a series of record-breaking heat waves in the subsequent years, given the apparent sensitivity of sensitivity of Deer Mice to warm summers found in this chapter (also see Chapter 3). Vole oscillations, on the other hand, were dramatic and irregular. Relative lows, interrupted by a single peak across all grids in 2005, were seen from 1997 to 2013. A distinct change in the vole dynamics occurred on Grid B from 2014 onwards, with dramatic density swings every other year, while the proximate grids remained in a relative low. Our study did not measure any variables that seemed to be responsible for this change in population dynamic; however, there is some evidence of a source-sink dynamic at this site. While all sites are typical grasslands for this region, Grids A and C are slightly lower in elevation and contain more sagebrush and bare ground than Grid B, whereas Grid B has more continuous cover of grasses and forbs (Atkinson and Larsen *unpublished*). Given the specialist nature of Montane Voles to grasslands (Klenner and Sullivan 2025), they may be more successful in the continuous grasses of Grid B than the brushy habitats of Grids A and C. The cycle lengths seen across the grids supports this, with Grid B showing clear 3-4-year cycles, while the other grids have less frequent and lower peaks, generally every 6-8 years. If the threshold for this “spill-over” dynamic only occurs every other cycle in a 3-4-year dynamic, this would explain the 6–8-year cycle observed in voles on the more “marginal” grids. Additionally, opportunistic trapping in the forests adjacent to the grids in 2024 (Atkinson *unpublished*) did not produce any voles, which suggests that they are in fact grassland specialists, and not occurring on our grassland grids due to forest immigrants. This preference for meadows and grasslands is well documented, with Montane Voles being much more abundant in grassy habitats than forested or shrub-dominated habitats (Sera and Early 2003, Anich and Hadly 2013). Similarly, Harrower (2017) observed an increase in Montane Vole abundance with an increase in grassland moisture and subsequent plant productivity. Cyclic species are considered at higher risk of extirpation due to the very low densities seen in low years (Myers and Cory 2013), and therefore both Deer Mice and Montane Voles appear to have a more tenuous grasp on these grassland habitats given their cyclic nature than

other species with more stable populations, as seen in the Columbia Plateau Pocket Mouse (Atkinson et al. *in prep.*).

Competition between Deer Mice and Montane Voles was not visible in this study, as the density of the two species were found to be correlated, and population peaks of mice or voles at one grid did not rule out a peak of the other species on the same grid that year. Previous research on *Peromyscus* and *Microtus* species suggests that the generalist Deer Mouse is often competitively excluded from the habitats of specialist species like the vole (M'Closkey and Fieldwick 1975). However, elsewhere in this region Deer Mouse and Montane Vole populations were found to be correlated (Sullivan and Sullivan 2023), which suggests that these species occupy sufficiently distinct niches that precludes competition in semi-arid grasslands. As mentioned above, Montane Voles may have a source-sink dynamic across microhabitats in this grassland, and as such represent a grassland specialist. Deer Mice, however, were present in numbers at each grid across the study period, which was expected for this generalist species. The microhabitat limitations likely play a stronger role in the occupation and abundance of mice and voles in semi-arid grasslands than inter-species competition. This has been seen in other *Microtus* and *Peromyscus* systems, with very little diet overlap between the two groups and occupancy mainly determined by microhabitat difference in vegetation (M'Closkey and Fieldwick 1975).

Present and Future Effects of Climate

In our study community, Western Deer Mice and Montane Voles had very different relationships to weather and their differences have implications for how the two populations may respond to climate change. Only Deer Mouse density showed any regulation by weather variables, while Montane Vole density was highly variable but not correlated to temperature nor precipitation.

Temperature and not precipitation showed a significant relationship with Deer Mouse density. This is contrary to many studies on arid small mammal populations, that are often associated with precipitation-driven eruptions (Krebs and Singleton 1993; Bennison et al. 2018; Andreassen et al. 2021). Specifically, our study showed higher summer temperature was significantly associated with low mouse density. Potential causes for this include increased juvenile mortality or reduced reproductive output from heat stress (Chapter 3).

Other studies have found links between weather and *Peromyscus* species in semi-arid environments (Tietje et al. 2018; Srivathsa et al. 2019), with lower mouse densities associated with increasing temperature and higher densities associated with increasing precipitation, though others have not found any significant relationships with weather (Loehman et al. 2012).

Montane Vole population dynamics in our study were not found to be driven by weather variability. Sullivan et al. (2021) found a lack of correlation between Montane Vole density and weather variables, while other studies on European and Japanese vole species have found links to both temperature and precipitation (Selas et al 2019; Li et al. 2021; Samia et al. 2024; de la Huerta-Schliemann et al. 2025). Generally, *Microtus* population changes are thought to be predominantly driven by demographic shifts and predation levels (Jannett 1981; Korpimäki and Krebs 1996; Elmhagen et al. 2011; Korpela et al. 2014; Sullivan et al. 2021), which were not measured during the course of this study. Demographic changes may have been apparent had the trapping session taken place during the breeding season, however, in autumn the vast majority of animals caught were adults in non-breeding condition. Predation has been suggested to have a stronger effect on Montane Voles than on Deer Mice from an experimental study by Maron et al. (2010) where predator exclusion, specifically weasel exclusion, changed population dynamics for voles but not mice. This may be a strong component at play, given the high amplitude seen in our vole cycles but lack of obvious correlates.

The links we detected between weather patterns and small mammal populations in the past several decades could foreseeably shift the community structure due to the long-term effects of climate change. The predicted increase in extreme heat events and average summer temperature may lead to a lower carrying capacity of the Western Deer Mouse in semi-arid grasslands. Montane Vole populations likely will be less affected, with source-sink dynamics or predation pressure plausibly playing a stronger role in their occupation of these grasslands, though additional study would be necessary to confirm these claims. The lack of observed competition between the species makes it unlikely that the Montane Vole would fill any niche left by the Deer Mouse, though reduced competition may benefit species such as the Columbia Plateau Pocket Mouse (Atkinson and Larsen 2025, Appendix A), which occupy low-elevation grasslands in several nearby valleys. This species would likely be more

resilient to the aridification from climate change, and may even benefit from a hotter and drier habitat (Iverson 1967). Due to the sensitivity to human disturbance and the extremely limited (known) distribution in the Thompson Valley, however, this seems unlikely without management intervention. The dampening of Deer Mouse numbers in warm summers and the changes in oscillation patterns in both Deer Mice and Montane Voles is indicative of a shifting community structure. As climate change continues to affect semi-arid grasslands, potential shifts in small mammal populations may lead to larger trophic restructuring.

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CHAPTER 3

HABITAT TRADE-OFFS FOR DEER MICE DURING EXCEPTIONAL SUMMER HEAT

INTRODUCTION

As average temperatures rise due to the effects of climate change, ecological communities face increasing pressure to conform and adapt to new normals. Rising mean temperatures and their negative effects on wildlife, including seasonal phenological mismatch, (Kudo and Cooper 2019; Visser and Gienapp 2019, Andriuzzi 2025) or habitat-level changes (Gonzalez et al. 2010; Constable et al. 2014) are well documented. Sustained high temperatures, or heat waves, while creating the conditions for natural disasters wildfires and floods, also act as an acute stressor for organisms and may directly cause impaired reproductive success (Dang-Cong et al. 2021) or mortality (McKechnie and Wolf 2009). This has the potential to cascade through food webs, as even animals more tolerant of heat may experience decreased food availability should plant communities or prey species be affected.

Mammals have a variety of thermoregulatory adaptations to evade heat. Behaviourally, they may change microhabitat use to avoid direct sun exposure (Adolph 1990) or move activity periods to cooler times to avoid heat and maintain optimal body temperature (Perea-Rodríguez et al. 2022). Burrowing mammals in desert environments employ both of these behaviours by increasing nocturnal activity during the summer while taking cover underground during the day (Rowsemitt 1991; Walsberg 2000). Physiological adaptations include increased appendage surface area for heat dissipation (Hill and Veghte 1976; Weissenböck et al. 2010), sweat glands (Smith and Johnson 2016), and the ability to induce torpor (Reher and Dausmann 2021), among others. When temperatures exceed thermoregulatory capabilities, decreased fitness or death is expected. For example, sperm production and viability in male mammals such as mice and monkeys has been shown to decrease after heat treatments (Chen et al 2008, Liu 2010; Dang-Cong et al. 2021; Jacobs et al. 2024). Similarly, in females, heat exposure during pregnancy impedes uterine development, decreases the number of viable embryos, and even changes epigenetic gene expression in offspring (Silva et al. 2024). Milk production and litter size in heat-exposed animals, from mice to pigs, also was has shown to be lower than in control groups (Black et al. 1993; Yaeram et al. 2006; van der Vinne et al. 2014). Most dramatically, large mortality

events in wildlife have been linked to heat waves (O'Shea et al. 2016; Piatt et al. 2020), potentially limiting food availability across trophic levels and increasing pressure on at-risk species. (Scheffers et al. 2014)

Habitat characteristics can play a large role in providing refuge from heat in a region. As mentioned above, many species use microhabitats or ecotones as a habitat refuge when the environmental conditions are unfavourable (Harabiš 2016, McCann 2016). These refuges may be as simple as large rocks that act as a thermal mass and maintain cool temperatures underneath or wetter substrate in low-lying areas, or larger scale ecotone use such as a forest on the edge of a hotter grassland. This habitat complexity can create the foundation for a source-sink dynamic, with a flow of individuals immigrating to more marginal habitats. Individuals persisting in these marginal habitats may be less successful under normal circumstances than those in the centre of the range, but are more resilient under atypical conditions. Yuan et al. (2018) highlighted the difference that habitat can play on the thermal tolerance of a species, showing that rainforest skinks (*Trachylepis affinis*) were less heat tolerant than skinks living in the drier forests at the edge of the savanna. When warming periods occurred, models showed that the ecotone skinks could take refuge in nearby forest, while forest skinks lacked a cooler habitat to use as refuge. The persistence of a species under climate regimes may depend on its ability to shift habitat use within a landscape. Generalist species may have the advantage here, however, peripheral populations of specialist species tend to be more generalist and therefore more resilient to variable weather and unfavourable conditions than populations in typical habitat (Lesica and Allendorf 1995, Lomolino and Channell 1995).

Small mammals are keystone species in many arid environments (Laundre 1993; Davidson and Lightfoot 2008; Delibes-Mateos et al. 2011; Sullivan and Sullivan 2021) and many species are well-adapted to heat (Randall 1978; Tracy and Walsberg 2002; Colella et al. 2021; Eizenga et al. 2023). They generally employ heat avoidance through the use of underground burrows and nocturnal activity periods (Walsberg 2000; Ramirez et al. 2022). However, even desert specialists such as Ord's Kangaroo Rat (*Dipodomys ordii*) have a low tolerance to temperatures above 35°C (Wunder 1974; Walsberg 2000), and diurnal species such as the antelope squirrel (*Ammospermophilus leucurus*) limit their exposure to the extreme daytime desert temperatures to very short periods of time (Chappell and

Bartholomew 1981). For desert species, increased heat from climate change can mean trade-offs in time spent foraging (Eizenga et al. 2023; Flewwelling et al. 2023), leading to unexpected sensitivity to heat waves and drought even in relatively hot ecosystems (Cherwin and Knapp 2012; Prugh et al. 2018).

In western North America, the most ubiquitous small mammal species is the Western Deer Mouse (*Peromyscus sonoriensis*). This species is a generalist omnivore and colonizer of disturbed habitats (Halvorson 1982; Shonfield and Bayne 2019) They are capable of inhabiting a range of environments from semi-arid grasslands to more mesic forests in interior British Columbia, with the exception of extreme arid conditions that may be shared or dominated by the Columbia Plateau Pocket Mouse (*Perognathus parvus*, O'Farrell 1975, Maida et al. 2020). Eizenga et al. (2023) raised concerns that the Deer Mouse may be incapable of adapting to the elevated temperatures and more frequent heat waves predicted under climate change scenarios in North America. The declines of other keystone small mammal species in arid habitats have been documented (Phillips 2018), with potential for trophic cascades and changes in habitat structure, as these ecosystem engineers play an important role in moisture retention, vegetation structure, and fire regimes (Laundre 1993; Martin 2003; Ryan et al. 2020). In the southern semi-arid grasslands of British Columbia, Canada, the Western Deer Mouse is arguably exposed to warmer summer temperatures than any other habitat in Canada. Thus, these ecosystems provide an opportune situation for understanding the ability of the species to persist on the landscape in the face of extreme summer heat.

In Chapter 2, we used long-term trapping data from 2000 to 2024 in the semi-arid grasslands of British Columbia, Canada, to show that Western Deer Mouse abundance decreases substantially in years with very hot summers. In this chapter, we explore in greater depth the resiliency of Western Deer Mouse populations to summer heat in the same ecosystem. We tackle this by comparing Deer Mouse demographics in grasslands to populations of the animal that exist in juxtaposed forests; forests were expected to be wetter and cooler than adjacent grasslands (Meidinger and Pojar 1991) and therefore were treated as a buffer for the effects of heat. To accomplish this comparison, we live trapped subpopulations of Deer Mice in both of these habitats over the course of spring and summer. Serendipitously, our study sites experienced a heat wave between the spring and summer

trapping sessions, with sustained daytime temperatures of 37-42°C between July 5 and July 21, 2024, enabling us to record changes in density, body condition, and reproduction under extreme heat. As trees are known to shield against extreme temperatures (Speak et al. 2020; Petit and Frazer 2023), we expected density to remain stable or increase in the forest stands while declining in the open grasslands. Body condition also was expected to be lower in the grassland versus forest populations, and proportion of reproductive condition adults and of juveniles were expected to decrease in the grassland group.

METHODS

Study Area

The Thompson Valley, where this work was conducted, is a dry valley in the rain-shadow of the Coastal Mountains of British Columbia, Canada, near the city of Kamloops (LAT 50.7°, LONG -120.4°). This valley represents one of the northernmost extensions of the shrub-steppe ecosystems emanating from the Great Basin Desert in the United States. It is generally warm and dry, with average daytime highs of 30°C and average nighttime lows of 15°C in the summer, and average highs and lows of 1°C and -5°C in the winter (Meidinger and Pojar 1991, Wang et al. 2016). Annual precipitation averages 295 mm, with much of the precipitation occurring during the winter and spring (Figure 1.3). The habitats exist on an elevational gradient, with shrubby low-elevation grassland transitioning to grass- and forb-dominated high-elevation grassland, and eventually forest with Douglas-fir and Ponderosa Pine. The ecotone of these habitats is a mosaic of small forest stands that become increasingly dense as elevation increases.

Sites were chosen on accessible land of each habitat type, at least 2 km from the ecotone to avoid potential source-sink dynamics from adjacent habitats. Grassland grids consisted of low to mid elevation grassland, with native bunchgrass such as Bluebunch Wheatgrass (*Agropyron spicatum*) and Rough Fescue (*Festuca altaica*), and forbs such as Big Sagebrush (*Artemisia tridentata*) and Common Rabbitbrush (*Ericameria nauseosa*). Forest grids contained predominantly Ponderosa Pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) with a mixed understory of grass and moss (Figure 3.1). See Chapter 1 for more detailed description of the ecosystem and study site. Three grassland grids and three forest grids were established and trapped, with each grassland grid being paired to a nearby forest grid 4-15 km distant, and trapped simultaneously to ensure similar

weather conditions affected both treatments. These grids were independent of those used in Chapter 2.

Weather

Soil moisture was measured at four locations per grid on each of the trapping days to verify differences in aridity between the forest and grassland habitats. Measurements were taken upon arrival to the site, generally between 5:00 am and 7:00 am, using a Hydrosense II (Campbell Scientific Incorporated, Logan, UT, USA) moisture reader with a 13 cm probe. Temperatures on the grids were monitored using 42 thermal dataloggers (iButton DS1921G-F5# Thermochron, iButton Link Technology, Whitewater, WI, USA) from June to August 2024. The dataloggers were encased in protective capsules (iButton DS9107 iButton® Capsule, iButton Link Technology, Whitewater, WI, USA) and placed in three different location types: taped underneath branches and shaded for the air measurements, placed in the soil at the base of brush for ground measurements, and buried 10 cm underneath the soil at the base of brush for underground measurements. Each grid was set up with two dataloggers for each location type, in case one logger failed. The depth of 10 cm was selected to represent the approximate depth of Deer Mouse burrows (Weber and Hoekstra 2009; Weber et al. 2013) and previous telemetry work in the area showed that Deer Mouse in this ecosystem use sagebrush as daytime refuge sites (Hales 2011, Atkinson unpubl.). Each logger recorded a measurement every hour for the duration of the study. Loggers that recorded extreme, mismatching readings (greater than 85 °C or lower than -40 °C) were considered faulty and removed from the analysis. Diurnal temperature ranges, from sunrise to sunset, were calculated for each logger from the difference between the maximum and minimum temperature readings for each 24 h period.

Live Trapping

Two live-trapping sessions were undertaken between June and August 2024. Spring trapping occurred between June 18-26, 2024, and summer trapping between August 19-25, 2024. Trapping protocol was identical to that described in Chapter 2, with traps locked open and pre-baited with sunflower seeds, whole oats, and apple chunks for 3 nights prior to three nights of trapping. Forty traps were places in a 4 by 10 grid, spaced 15 m apart. In the event

Figure 3.1 Study sites showing (A) grassland and (B) forest habitats in the spring. Photos by author.

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more than 50% of traps were triggered on any one night, we added an additional trap at each station (80 traps/grid). Traps were set within two hours of dusk and checked within 2 hours of dawn before being locked open for the day.

Each captured animal was weighed in a 150 mL pill bottle placed on an electronic field scale (Triton T3, My Weigh, Mendota Heights, MN, USA), providing weights to the nearest 0.01 g. Reproductive status of captured animals was characterized as not evident, pregnant, lactating (nipples evident), or hair regrowth (around nipples) for females, and by testes location (scrotal or abdominal) for males. Testes location in males and pregnancy in females were determined by gentle palpation of the scrotal area and flanks, respectively. To estimate body condition, we measured zygomatic width (mm) of captured animals using calipers placed posterior to the eyes, as well as measuring pes length (mm) using a ruler hooked on the hind foot toenail (Aplin et al. 2003).

Logistics enabled a maximum of four grids to be trapped simultaneously: after the first set of two (one grassland and one-forest) were trapped simultaneously, baiting the remaining two sets (also 2 grassland + 2 forest) was immediately begun, starting on the same day as first set was completed. The identical sequence was repeated in August.

Data Analysis

All data were analysed in R (Version 4.5.2, https://www.r-project.org/). Daily average temperature was calculated as the mean of all logger readings for each day and habitat. Temperature and moisture comparisons between habitats were tested on proximate grassland-forest site pairs using a paired t-test or Wilcoxon-signed ranks paired test, depending on normality. Daily average (average temperature for each 24h period, beginning and ending at midnight), daily maximum, and daily minimum temperatures were compared across each exposure group (air, ground, underground).

Density was estimated using a spatially explicit capture-recapture (SECR) model (Efford 2004; Borchers and Efford 2008; Efford and Fewster 2013) parallel to that used in Chapter 2. Body condition was estimated using the scaled-mass index described by Peig and Green (2009, 2010) to control for growth effects on body size by using a standardised major-axis regression. The measurements we used to compare weight to skeletal size was log-

transformed weight in grams and log-transformed zygomatic width in mm, which was computed as follows:

$$\widehat{M_i} = M_i \left[\frac{L_0}{L_i}\right]^{b_{SMA}}$$

where M_i is the body mass, L_i is the length of the individual, L_0 is the mean mass of the sample population, b_{SMA} is the scaling exponent calculated by the standardised major axis regression of mass and length of the sample population, and $\widehat{M_i}$ is the expected mass at the given length. Therefore our M_i is a mouse's log transformed mass and our L_i is a mouse's log transformed zygomatic width. Preferentially we would have used body length as the skeletal size measurement, however these data could not be measured consistently by a single person in the field. Habitat and seasonal comparisons for density and body condition were done using an ANOVA or H test (non-parametric ANOVA/Kruskal-Wallis), depending on normality. Differences in the proportions of animals across our reproductive categories were modelled using a generalised linear model (GLM) with a binomial distribution (logistic regression) and an interaction term for habitat and season.

RESULTS

Site Seasonal Changes

Temperature

Data from eight of 42 deployed loggers were unusable, but at least one datalogger was functional on each grid. Functional data loggers from the same grid tended to produce very similar temperature data, so one logger per grid was considered acceptable. As expected, grassland habitats showed significantly higher temperatures than forest habitats across the landscape (Figure 3.2). Daily maximum air temperature was especially disparate (paired Kruskal-Wallis between grassland-forest pairs; $\chi^2 = 193.12$, DF = 1, $P < 0.001$), with an average high of 35.8°C ±7.5 in the grassland and 28.2°C ±7.4 in the forest. Underground temperature ranges were moderated more, though still significantly different (H= 326.44, DF = 1, $P < 0.001$), with an average high of 31.0°C ±7.4 in the grasslands and 18.8°C ±4.7 in the forests. Daily minimum air temperature was comparable between habitats, with an average

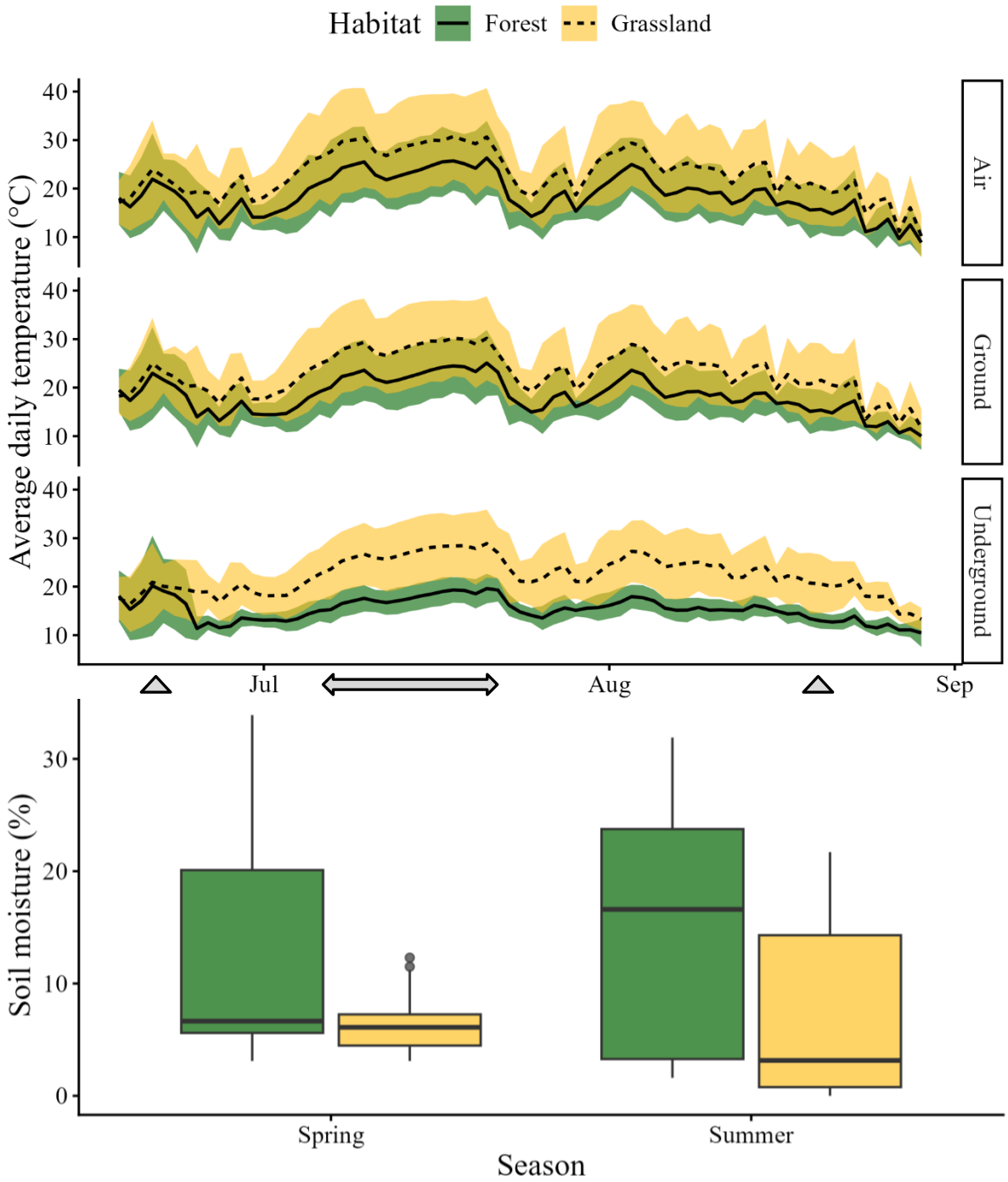

Figure 3.2 Temperature (top) and soil moisture (bottom) measured at each of 6 grid sites across the Thompson Valley between June and September 2024. In the top graph, daily averages are shown with grassland average daily temperature indicated by the dotted line and forest average by the solid line. The daily temperature range (highest and lowest temperature in the 24h period) is indicated by the shaded areas, with the overlap of forest and grassland temperatures indicated by the yellow-green colour. Trapping events are indicated by the grey triangles. An extreme heat event can be observed in the two-week window mid-July (double-sided arrow). Soil moisture was measured using a soil probe at 4 locations on each grid each morning of trapping for both spring and summer sessions (n = 144).

low of 12.5°C ±3.6 in the grassland and 11.8°C ±3.4 in the forest. On average, air temperature in the grasslands was 4.3°C higher (Wilcoxon $W = 2700$, $P < 0.001$), ground temperature was 4.7°C higher ($W = 2700$, $P < 0.001$), and underground temperature was 7.5°C higher ($W = 2700$, $P < 0.001$) than measured forest temperatures, confirming the greater heat experienced by grassland animals regardless of exposure.

The study area experienced a period of extreme heat from July 5 to 21, 2024, with daytime highs reaching 41.1°C (recorded at the Kamloops Airport). This heat wave occurred between the June and July trapping sessions, as indicated by the arrows in Figure 3.2 (top).

Moisture

The grassland sites experienced greater aridity in summer months than adjacent forests, as per our predictions. Spring soil moisture was not significantly different between the grassland and forest habitats ($H = 3.44$, DF = 1, $P = 0.064$, Figure 3.2). Summer soil moisture, however, had a significant difference with significantly higher moisture levels in forests than grasslands ($H^2 = 18.87$, DF = 1, $P < 0.001$).

Habitat Comparison

Abundance and Body Condition

Deer Mice were the most abundant small mammal in this area by a significant margin, though one grid was highly productive and was responsible for 139 of the 283 deer mice captured in the grasslands. Other animals captured were the Yellow-Pine Chipmunk (*Neotamias amoenus*, n = 5) and the Southern Red-backed Vole (*Clethrionomys gapperi*, n = 2). Of significance was the capture of a single Columbia Basin Pocket Mouse (*Perognathus parvus*) in June 2024, a threatened species in BC not detected in this valley since 1949 (Atkinson and Larsen 2025, see Appendix A).

Interestingly, Western Deer Mouse density was significantly higher in the grassland than the forest in springtime ($H^2 = 4.69$, DF = 1, $P = 0.030$), however this difference was not observed in the summer ($H^2 = 0.60$, DF = 1, $P = 0.439$, Figure 3.3). No significant difference between spring and summer abundance in the grasslands was detected ($H^2 = 0.51$, DF = 1, $P = 0.475$) but a significant increase in density occurred in the forest between our spring and summer trapping sessions ($H^2 = 3.86$, DF = 1, $P = 0.049$).

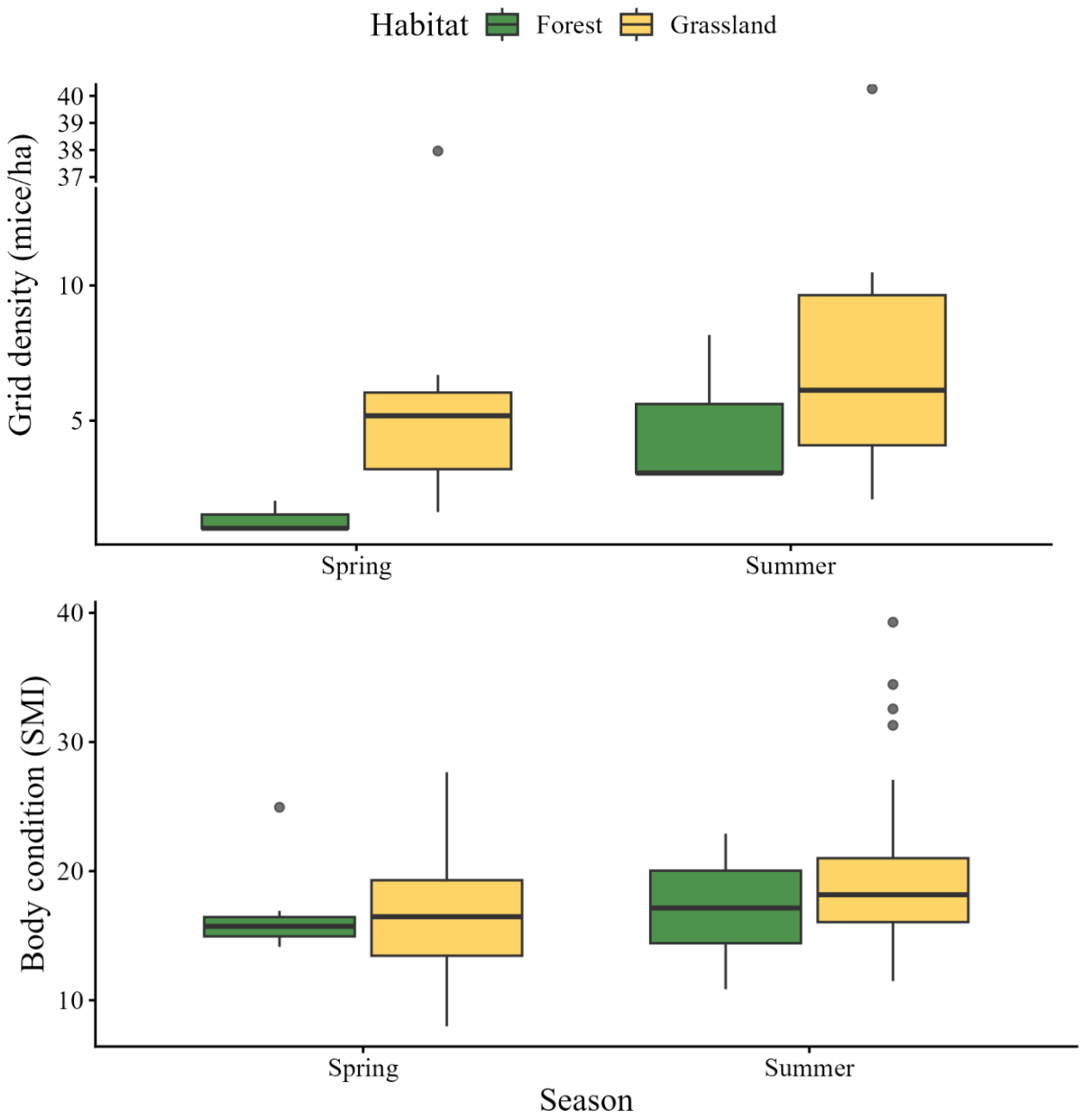

Figure 3.3 Box plot comparison of Western Deer Mouse densities (top) and body condition (bottom) differences according to season and habitat type. For density, each grid density was estimated using a spatially explicit capture-recapture model (see Chapter 2 for methods) and classified by habitat type. In the spring, grassland mouse density was significantly higher ($P = 0.030$) and forest density increased significantly between spring and summer ($P = 0.049$). One grassland grid had considerably higher density than the other grids, and can be seen above the break as an outlier. Mouse body condition was estimated using the scaled-mass index (SMI) method to control for differences in scaling. The metrics used were zygomatic width (mm) and weight (g). Mouse body condition increased between spring and summer in the grasslands ($P = < 0.001$). Pregnant females and individuals with external parasites were excluded from this calculation. No other comparisons were significant. Please see text (Habitat Comparison) for additional comparisons and *P*-values.

Deer Mouse body condition was not significantly different between grasslands and forests in spring (n = 141, $H^2 < 0.01$, DF = 1, $P = 0.98$) or summer (n = 150, $H^2 = 0.60$, DF = 1, $P = 0.44$, Figure 3.3). When pooled across seasons, grassland mice had higher body condition in the summer than the spring (n = 261, $H^2 = 18.37$, DF = 1, $P < 0.001$). This difference in body condition between seasons was not observed in forest mice (n = 30, $H^2 = 0.14$, DF = 1, $P = 0.713$). Density was not found to have a strong effect on the body condition of Deer Mice (Pearson's correlation = -0.11, $t = -0.36$, DF = 10, $P = 0.729$, Figure 3.4).

Demographics

Significant correlations between habitat, season, and reproductive status or age class were found (Figure 3.5). Predicted probabilities from the logistic regression indicated higher levels of pregnancy and lactation in spring than summer for female mice in both habitats, though this result was not significant. Grasslands showed consistently higher probabilities of females in reproductive condition than forests; however, confidence intervals overlapped substantially and again no effects were statistically significant (Figure 3.5 left). For males, reproductive activity was similar between habitats in spring, with approximately half of individuals presenting with scrotal testes in both forest and grassland. In summer, the probability of scrotal testes declined in forests but remained higher in grasslands (Figure 3.5 middle). These results must be interpreted with caution, as the power to detect habitat differences in this study were underpowered due to very low male captures in the forest (spring n = 2, summer n = 6, power test for habitat differences < 0.01). There may still be an effect of summer heat on male reproduction, as five of the six adult males captured in the forest had undescended testes, but the sample size is small. Juveniles were absent from forest sites in spring but were common in summer, whereas grasslands supported moderate juvenile proportions in both seasons (Figure 3.5 right). Again, large confidence intervals due to zero captures in spring forest grids created uncertainty, but the marked increase in juvenile probability was strongly significant.

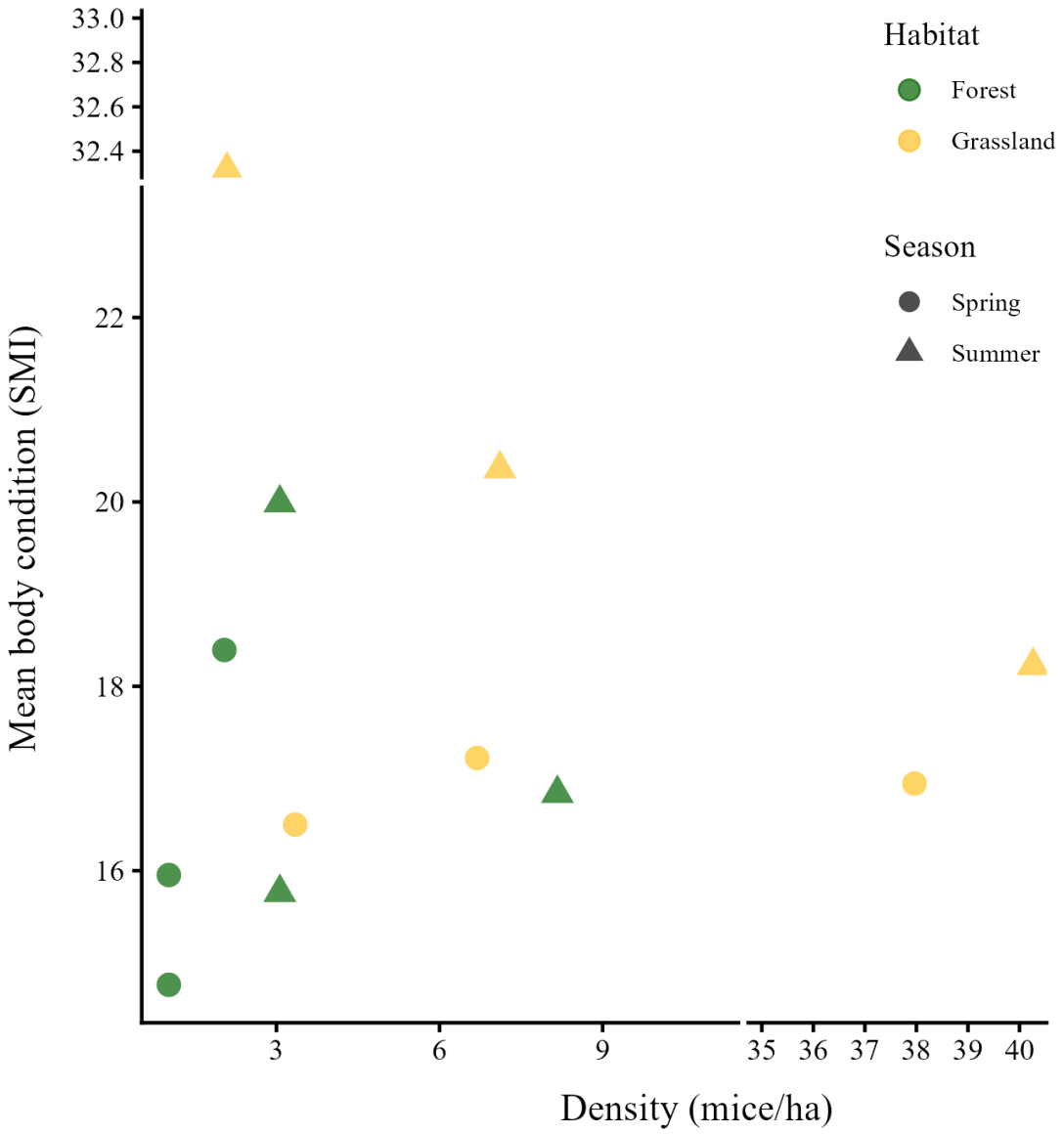

Figure 3.4 Plot of Western Deer Mouse density (animals/ ha) versus mean body condition for each grid. Density was estimated using a spatially explicit capture-recapture model, and body condition was estimated using scaled-mass index (SMI) [see text for details]. The Pearson's correlation between density and body condition was -0.11 and not significant (t = -0.36, DF = 10, P = 0.73).

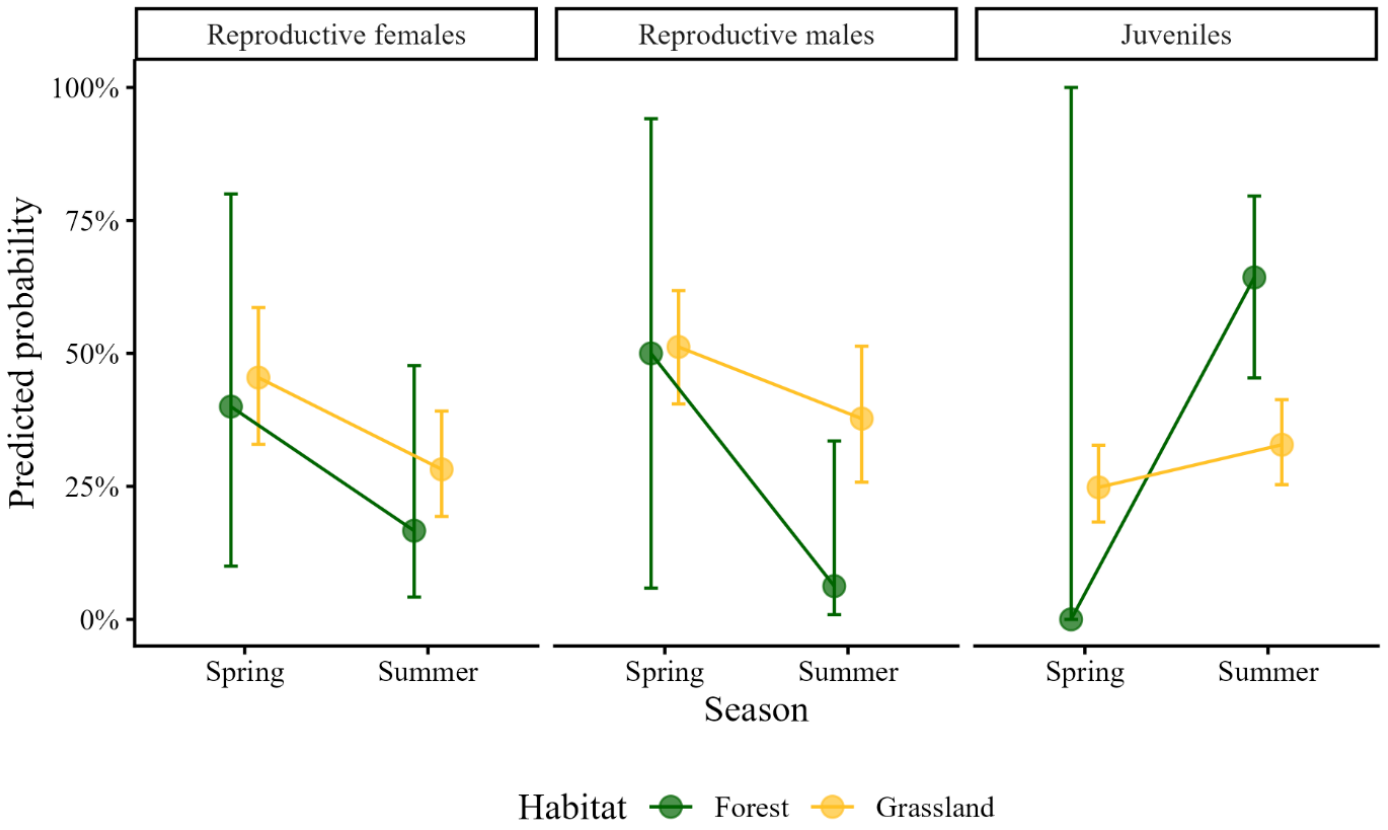

Figure 3.5 Predicted probability with 95% CI of the reproductive condition and juvenile occurrence of Western Deer Mice in the Thompson Valley between spring and summer and forest and grassland. Probability was modelled from a binomial GLM of the capture data from 2024. Reproductive females (adults only) were classified as lactating or pregnant, reproductive males (adults only) as possessing scrotal rather than inguinal testes; juveniles classified as those individuals weighing less than 15.0 g, the lowest weight of mouse captured at this location that was found to be reproductively active (Atkinson, *unpubl*. from 2023-2024 trapping data). Large confidence intervals in the forest were due to low capture numbers; therefore, caution with interpretation is warranted. Captures within a habitat were pooled across grids.

Discussion

As anticipated, open grassland habitat was verified to be hotter and drier in the summer months than the proximate forest habitats, although both had Western Deer Mice as the dominant small mammal species. The largest temperature discrepancy between habitats occurred on measurements collected underground, likely due to the forest canopy providing more of a moderating effect than the sparse brush found on the grassland sites. This suggests that mice taking refuge in grassland burrows during the day likely experience greater temperatures than those in nearby forested habitats.

Forests appear to be marginal habitat for the Deer Mouse, given the consistently lower densities of Deer Mice produced on forest grids than grassland grids. This was contrary to our expectations, as the generalist Deer Mouse is known to successfully inhabit a range of ecosystems. A pattern of low Deer Mouse abundance in forests was noted by Sullivan and Sullivan (2023), who cited several studies across western Canada with peak Deer Mouse densities of 8-15 mice/ha (Gilbert and Krebs 1991, Millar 2001, Sullivan et al. 2023). This is consistently lower than the grassland densities observed both in this chapter (40 mice/ha), as well as in Chapter 2 (48 mice/ha). This density discrepancy could be due to a number of factors. Grasshopper irruptions could act as a pulse for grassland Deer Mice, so perhaps high grasshopper numbers the year before lead to the high density seen on some of our grassland grids (Jameson 1952, Langley 1994). Cone masting from conifers can act as a regulatory mechanism for forest Deer Mice (Ostfeld et al. 1996; Schnurr et al. 2002, Sullivan et al. 2023; Sullivan et al. 2025), so a non-masting year could result in a low population density. Competition from other species could drive Deer Mice out of the habitat, however, we only caught two Southern Red-backed Voles (*Clethrionomys gapperi*) at one forest grid, which is likely too low a density to competitively exclude Deer Mice. Yellow-pine Chipmunks were also trapped in our forests, but again, only in very low numbers (n = 3). Most likely, forests present unfavourable habitat for the generalist Deer Mouse. While they can persist there, they seem unlikely to thrive, as has been suggested in Sullivan and Sullivan (2023) and Sullivan et al. (2023).

Small mammal populations in temperate zones generally are expected to increase throughout the spring and summer as reproduction swells their numbers (Andreassen et al. 2021; Sullivan et al. 2023). In our study, however, increases were muted in the grassland

populations between our two sampling periods, suggesting a lack of recruitment or immigration in that habitat type. Populations of forest mice, however, increased substantially. This may have been due to successful reproduction, or immigration from the higher-density grasslands to cooler forested habitats. The significantly greater density of Deer Mice observed in the grasslands suggest that grasslands may be able to support higher numbers of animals than dry forests, though lack of protection from extreme heat may counteract some of that benefit.

Both males and female Deer Mouse were less likely to be in reproductive condition after the heat wave, though reproductive-condition individuals continued to be present at all sites. This was in line with our predictions, though the larger decrease in the forest suggests grassland populations may have some local adaptation to heat and subsequently are less likely to experience heat-mediated declines in fertility (Colella et al. 2021; Bautista et al. 2024). Acclimation to heat also is supported by the increase in body condition seen after the heat wave in grassland mice, though another explanation for this apparent increase is the reallocation of energy normally used for reproduction (Caldwell and Connell 1968). An increase in body condition could be explained by diet, as Deer Mice are omnivores and insect abundance could have increased in the grasslands, however, we did not measure this variable. Though present, the effect of heat on reproduction in adults was slight, and likely not responsible for any observable declines in population.

We suggest that the elevated underground temperatures during the heat wave may be responsible for the low proportion of juveniles detected in the grasslands in the summer, and subsequently the stagnation in grassland density while forest populations increased. In Chapter 2, we showed that summer heat was temporally correlated to low Deer Mouse abundance in grasslands over a 27-year span. Mouse pups have limited thermoregulation capabilities for the first 1-2 weeks of their life, and depend on burrow conditions and maternal care (Weber and Olsson 2008; Pineros Schuster 2025). Additionally, female mice have been shown to prioritize their own thermal comfort over caring for their litter (Hoffman et al. 2023). These behaviours could result in decreased juvenile survival under sustained extreme heat, and may explain our observations in seasonal density changes, or lack thereof.

Deer Mice are known to live in very hot environments, however, behavioural avoidance of heat through burrowing and nocturnality means that they largely are able to

avoid such conditions (Hales 2011). Concern for small mammal species living in arid environments has been raised, as climate change may cause sustained heat waves where overnight temperatures do not drop sufficiently to allow foraging activity (Eizenga et al. 2023). Of the small mammal species that live in deserts, 95% are nocturnal (Walsberg 2000), and there is substantial evidence that even desert specialists cannot maintain activity in temperatures above 35°C (Wunder 1974; Walsberg 2000; Tracy and Walsberg 2002; Colella et al. 2021; Ramirez et al. 2022; Eizenga et al. 2023). While we did not observe extreme overnight temperatures during this study, continued rising temperatures may cause even overnight temperatures to be above the thermoregulatory abilities of this species.

Through this study, we detected a Great Basin Pocket Mouse in the valley (approx. 30 km from Kamloops), a species unreported for over 70 years (Atkinson and Larsen 2025). This species could potentially replace the Deer Mouse if the latter becomes unable to sustain grassland populations under hotter, drier conditions. Pocket mice inhabit more arid valleys to the south, including near-desert conditions, where they outcompete the Deer Mouse and maintain stable populations even in years of record heat (Atkinson et al. *in preparation*). Aside from this lone detection, pocket mice have not been detected in the immediate area around Kamloops despite intense fall trapping for the last 30 years (Chapter 2, and also see Hales 2011); still, their recent detection suggests this species may be capable of expanding its range further into the current strongholds of the Deer Mouse.

Our study, although only one summer in length, provides an example of where animals known to inhabit hot environments may still be at risk due to climate warming. Also, a multi-year study may have failed to include an extreme heatwave event that provided a good test of resiliency in the study population. While adult Deer Mice showed marginal effects from the heat wave, the lower proportion of juveniles and overall density changes suggest that Deer Mouse populations are vulnerable to sustained heat. Clearly, they can persist during short temperature extremes, but less clear is how sustained exposure to high temperatures will affect populations of this generalist in semi-arid grasslands and forests. Higher densities of mice were present in the grasslands, however, this and other studies suggest that forests do not have high carrying capacities for this species. The benefits of ecotones between forested and grassland habitats would allow the Deer Mouse to benefit from both the higher quality habitat in the grasslands, as shown by the dramatically higher

densities, as well as the heat refuge the forested habitat provides. Human development tends to increase habitat fragmentation and decrease habitat complexity, both of which are detrimental to the species that may benefit from naturally occurring habitat mosaics. Protecting complex, natural habitats would increase the resiliency of Deer Mice to climate change by maintaining access to ecotones as refugia from heat and allowing a repopulation of grassland habitats from forest mouse populations.

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CHAPTER 4

CONCLUSION

SUMMARY OF THESIS

The underlying focus of this thesis is the long-term patterns of semi-arid grassland wildlife communities under anthropogenic climate change. I used long-term density of two keystone grassland species, the Western Deer Mouse and the Montane Vole, to document the patterns and changes in a small mammal community over the course of 25 years and their relationships to seasonal weather patterns. In the second part of this research, I delved deeper into the effects of heat on the Western Deer Mouse, documenting the density, demography, and body conditions of Deer Mice before and after a heat wave.

The principal findings of my thesis were the following:

- The dominant small mammal species in the semi-arid grasslands of the Thompson Valley are the omnivorous Western Deer Mouse and the herbivorous Montane Vole.
- Populations of these two species fluctuated drastically year-to-year, exhibiting a cyclic dynamic with a period of 3-5 years. The spatial distribution of cyclicity suggests a source-sink dynamic for voles, from upper to lower grasslands.
- Western Deer Mouse density was significantly lower in years with warmer summers.
- Montane Vole density was not found to be linked to temperature nor precipitation.
- Grasslands were found to support a greater density of mice than forests during a one-year investigation. Forest Deer Mouse populations increased substantially after a heat wave, while grassland populations stagnated, which indicates that while the carrying capacity of Deer Mice may be higher in the grasslands, they may be less buffered from the effects of heat waves.
- The probability of both male and female adult mice showing evidence of lactation (females) or descended testicles (males) decreased marginally after a heat wave in both grasslands and forests, though more so in forests. The body condition of grassland mice increased slightly after the heat wave. Together, these findings may indicate that grassland mice are more resilient to extreme heat.

- The proportion of juveniles in the forest rose substantially after the heat wave, while the proportion of juveniles in the grasslands did not. High underground temperatures at Deer Mouse burrow depth may have decreased the survival rate of grassland mouse pups during the heat wave. Alternatively, weaned juveniles my have dispersed from this area following the heat wave.

MANAGEMENT IMPLICATIONS

Small mammals, such as the Deer Mouse and Montane Vole, rarely are managed for their own sake, despite their role as keystone herbivores and the existence of many threatened species (Turvey et al. 2017; Kennerley et al. 2021). In fact, many native species are commonly persecuted as pests (Delibes-Mateos et al. 2011; Baudrot et al. 2020; Sullivan and Sullivan 2021). This likely stems from the vast success of a select few opportunistic species, such as the House Mouse (*Mus musculus*) and the Black Rat (*Rattus rattus*), which have colonized most continents on Earth and can harbour zoonotic disease (Han et al. 2015). Unfortunately, though only 7% of rodent species are considered pests (Capizzi et al. 2014), the vast majority of small mammals across many families share the prejudiced public opinion. This is reflected in the disproportionate research focus on more charismatic species: carnivores and ungulates receive the vast majority of research attention, while small mammal orders such as insectivores, rodents, and bats received little attention, despite containing very large proportions of endangered species (Amori and Gippoliti 2000). Wildlife management in British Columbia is no exception, with over 60% of the at-risk land mammal species being small mammals (Appendix C).

This thesis highlights the threat that climate change mediated aridification and increasingly severe heat waves may have on the current grassland small mammal community in the study region. While this is a significant threat, the degraded state of grasslands and subsequent decrease in species diversity likely diminishes the overall resilience of this ecosystem to climate change. The focal species of this study, the generalist Western Deer Mouse, may not have had such overwhelming dominance at the study sites had the Columbia Plateau Pocket Mouse not experienced historical declines (Nagorsen 2005). The resilience of this habitat's trophic structure is now reliant on a less diverse small mammal community than historically, at least among the most abundantly-trapped species, and my work raises

concerns for the ability of the Western Deer Mouse to continue to fill these roles under climate change scenarios.

I recommend continued small mammal trapping in the Thompson Valley to continue to identify key trends as climate change continues to shape the region. Overall, Western Deer Mouse density has been declining at our site since a peak in 2019 (Figure 2.2). Given the continued record-breaking heat seen across North America each year (Fischer et al. 2025), continued monitoring is needed to see if this is a regular low, or a more permanent shift in carrying capacity. Additionally, while it would require a much greater effort, predator monitoring at the site, potentially through camera-trapping or hair snags, would greatly increase our knowledge of the actual trophic consequences of climate change on this ecosystem, and potentially shed light on the driving factors of vole population dynamics. Long-term monitoring is extremely informative in understanding shifting baselines and slow but inexorable trends due to unmitigated climate change. Maintaining monitoring programs through short-term hypothesis testing provides the largest return on investment for research, creating both short- and long-term information, as the pursuit of specific hypothesis-testing questions created the basis for long-term monitoring if repeated at the same site.

To maintain a healthy and diverse small mammal community in the semi-arid grasslands of British Columbia, I suggest creating a management plan for the Columbia Plateau Pocket Mouse, as it is not currently protected (Ramsay and Nagorsen 2024). The capture of a pocket mouse in this study for the first time in 70 years opens the possibility that Deer Mice may be replaced by pocket mice if climate-related declines continue and pocket mouse conservation is undertaken. Thus, prey for the plethora of grassland predators that hunt small mammals may be buffered over time by the gradual (or not-so-gradual) replacement of the Deer Mouse by the pocket mouse. However, pocket mice are not disturbance specialists, and require more pristine grasslands (Sullivan and Sullivan 2008; COSEWIC 2019), suggesting high-quality grassland habitat should be conserved. Additionally, there are many areas in the province where the pocket mouse may persist undetected. Extensive inventory would be required to determine the true range and abundance of this species, which is a costly and labour-intensive undertaking. Camera-trapping of small mammals has proven to be a reliable indicator of presence, and even density in some cases (Littlewood et al. 2021; Parsons et al. 2021; Hopkins et al. 2024;

Verhees et al. 2024). I suggest that arrays of cameras in suitable habitats be used to determine the presence of rare species, and select target areas for live-trapping.

To summarise, the work in this thesis gives rise to the following management suggestions:

- Continue small mammal community monitoring in these British Columbia grasslands to determine if the decrease seen in Deer Mouse density is a temporary low or more permanent change.
- Monitor small mammal predators at this site to better understand trophic cascades from climate effects.
- Evaluate the Columbia Plateau Pocket Mouse, and enact a management plan. This supports diversity in the small mammal community should the Western Deer Mouse experience climate-mediated declines.

CONCLUSION

Small mammals are an essential and often overlooked group of species. Their roles in supporting trophic structures and shaping their environment through bioturbation and seed or spore dispersal cement their importance in ecosystems. My research highlights the impact that climate change can have on small mammal communities, with generalists such as the Deer Mouse showing low tolerance to increased summer heat regimes. Maintaining habitat mosaics and native grasslands in this situation is key to resilience at this trophic level, and the protection of species such as the pocket mouse should be considered. Negative public perception should not diminish our responsibility to this taxon. I hope that this thesis provides an argument to broaden small mammal research and to approach wildlife management holistically.

"Is it not a maimed and imperfect nature I am conversing with?... I should not like to think that some demigod had come before me and picked out some of the best of the stars. I wish to know an entire heaven and an entire earth."

— Henry David Thoreau

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APPENDIX A

REDISCOVERY OF THE COLUMBIA PLATEAU POCKET MOUSE (*PEROGNATHUS PARVUS*) AT THE NORTHERN EXTENT OF THE RANGE OF THE SPECIES

This note was previously published and is reprinted here with permission:

Atkinson K, Larsen KW. 2025. Rediscovery of the Columbia Plateau Pocket Mouse (*Perognathus parvus*) at the northern extent of the range of the species. Western Wildlife. 12:1–5.

The Columbia Plateau Pocket Mouse (*Perognathus parvus*; previously the Great Basin Pocket Mouse) ranges from southeastern California northwards through Nevada, Utah, Idaho, Oregon, and Washington, USA, before reaching its northern limit in southern British Columbia, Canada (Nagorsen 2005). At the northern limits, these mice are restricted to threatened arid grassland habitats (Ramsay and Nagorsen 2024). They require dry, sandy soils for burrowing and sandbathing (Kritzman 1974) and tend to be replaced by Western Deer Mice (*Peromyscus sonoriensis,* previously *P. maniculatus*) at higher altitudes (O'Farrell 1975). In British Columbia, the species is considered Special Concern (Ramsay and Nagorsen 2024) although it has not yet been assessed at the federal level. Historic records show *P. parvus* in three principal areas in the province (Figure A.1): (1) in the south Okanagan Valley, which continues east to the Kettle Valley and west to the Similkameen Valley; (2) in the north Okanagan Valley; and (3) in the Thompson River Valley.

The arid grasslands in southern British Columbia are contiguous with grasslands in Washington, and some species associated with this ecosystem have been shown to have gene flow across the U.S.-Canada border (Schmidt 2019). The north Okanagan and Thompson regions, however, are more isolated. The arid grassland habitat in the north Okanagan is bordered to the south by the urban sprawl of Kelowna, which is suspected to segregate this population from those of the south Okanagan (Nagorsen 2005). To the west of the Okanagan lies the Thompson Valley that also contains arid grasslands. The two valleys are geographically isolated from one another, and the Thompson Valley ecosystem likely has existed as a habitat island since the Holocene Climate Optimum (about 5,500 years before present), when mid to high elevation grasslands transitioned to forest, blocking habitat corridors in the region (Mathewes and King 1989). Many of the species in the Thompson

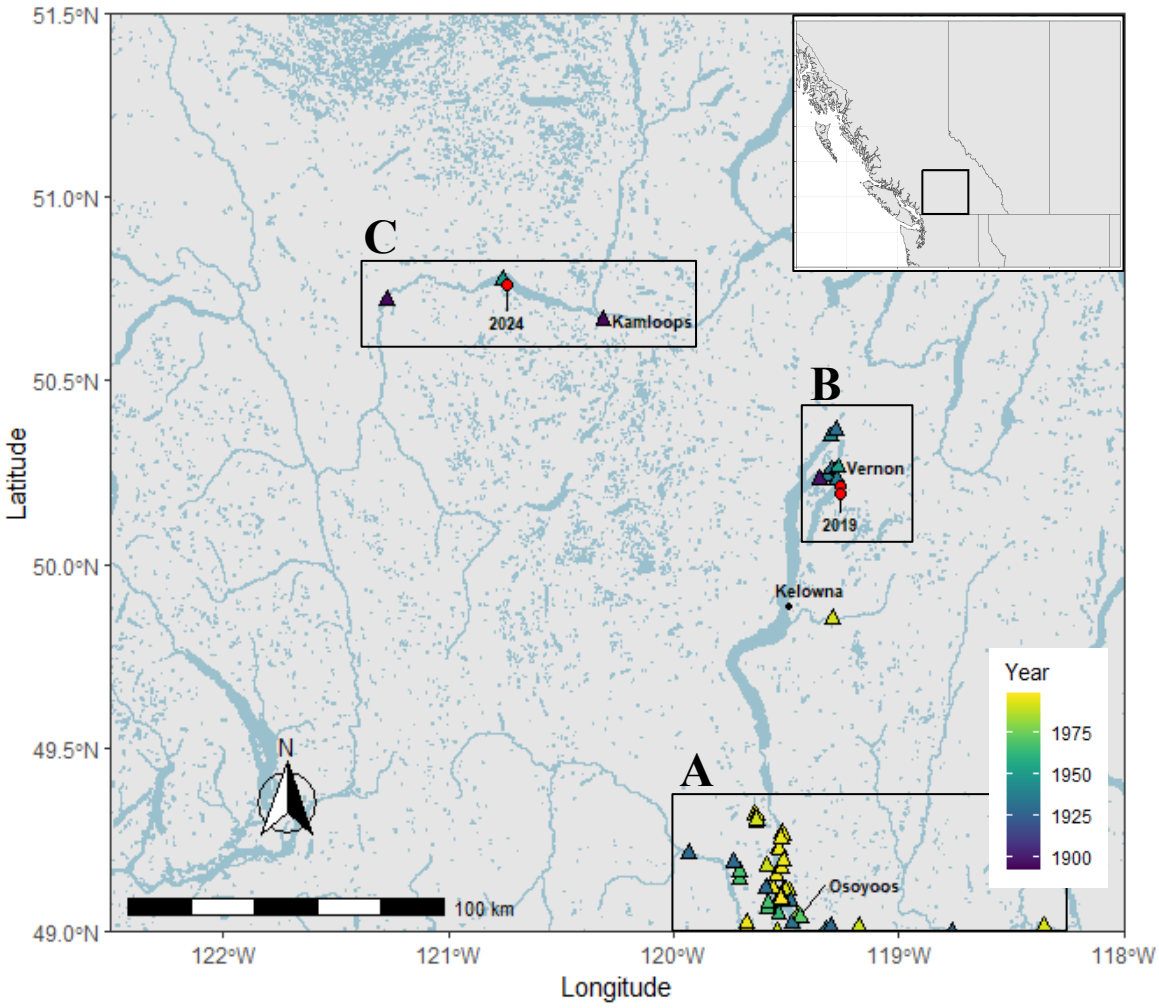

Figure A.1 Known locations of the Columbia Plateau Pocket mouse (*Perognathus parvus*) in British Columbia, Canada. Populations are defined by three primary areas: (A) the south Okanagan Valley, near the town of Osoyoos, (B) the north Okanagan Valley, near the town of Vernon, and (C) the Thompson Valley, near the city of Kamloops. Until recently, P. parvus had remained undetected in the Thompson and north Okanagan Valleys since 1949. Recent trapping (red points) in the north Okanagan (2019) and the Thompson Valley (2024) re-establishes the presence of the animal in these historic locations.

Valley reach their northern limit here and so are more limited by marginal climatic conditions than populations in more southern habitats. This combination of genetic isolation and marginal conditions leaves fringe populations with increased risk of extirpation from these areas (McDonald and Brown 1992; Williams et al. 2010). The conservation value of these populations, however, often is high due to their strong contribution to the overall genetic diversity of a species, as fringe populations tend to have experienced differing selection pressures than central populations within the range of a species (Lesica and Allendorf 1995; Williams et al. 2010).

Until our study, the last records of pocket mice in the Thompson Valley and the north Okanagan were 1949 and 1951, respectively (Nagorsen 2005; Ramsay and Nagorsen 2024). A small mammal live-trapping program in the grasslands surrounding the city of Kamloops (1997-present) has failed to detect pocket mice, along with several other short-term studies overlaid on the long-term sites (unpubl. data). Additional trapping in the valley also has been undertaken in communities outside of Kamloops with similar results (Whittington and Harestad 1992; Hales 2011).

In the summer of 2019, a small mammal live-trapping inventory (Pereira 2019) captured 20 individual Columbia Plateau Pocket Mice in Kalamalka Lake Provincial Park, in the North Okanagan just outside the city of Vernon (Latitude 50.207895, Longitude -119.256038) within grassland and dry, open forest habitat. These captures were 4.2 km from the nearest known capture location (1937) and 7.7 km from a specimen caught in 1951. One of these two historic capture locations has since been developed and now consists of residential and commercial developments (pers. obs.).

On 28 August 2024, we caught a single Columbia Plateau Pocket Mouse during a short-term live trapping study within an isolated habitat patch near Kamloops Lake, close to the community of Savona (Latitude 50.751280, Longitude -120.840732). The individual was a non-reproductive adult female (Figure A.2) with a mass of 19.02 g, a zygomatic width of 12.45 mm, a pes length of 22.5 mm, and an ear length of 7 mm. The trapping session consisted of three nights of pre-baiting with sunflower seeds, whole oats, and apple pieces followed by three consecutive nights of trapping. The trapping grid consisted of 40 Longworth-style traps spaced 15 m apart in a 4 × 10 grid. Earlier in the same summer (18–20 June), an identical trapping session that we conducted at the exact same location failed to

Figure A.2 Photographs displaying (A and B) the cheek pouches and body and (C) tail shape of the individual Columbia Basin Pocket Mouse (*Perognathus parvus*) caught south of Kamloops Lake, British Columbia, Canada, on 29 August 2024. (Photographed by Kara Atkinson).

produce any captures of pocket mice. Other animals we caught in the same trapping session as the pocket mouse at this location were 18 Western Deer Mice and four Yellow Pine Chipmunks (*Neotamias amoenus*).

Our 2024 capture location was within 2 km of the 1949 pocket mouse observation (specimen CM 46420 in the Carnegie Museum of Natural History Collection, Pittsburgh, Pennsylvania). The trap location was on a south-facing slope, situated in a shrub-grassland ecosystem with an historic average annual precipitation of 320 mm (Wang et al. 2016).

Common plant species at the site included Bluebunch Wheatgrass (*Pseudoroegneria spicata*), Needle-and-Thread Grass (*Hesperostipa comata*), Big Sagebrush (*Artemisia tridentata*), Rubber Rabbitbrush (*Ericameria nauseosa*), and Prickly Pear Cactus (*Opuntia fragilis*). Bluebunch Wheatgrass has been noted as a dominant species in Columbia Plateau Pocket Mouse habitat in the Okanagan (Sullivan and Sullivan 2008).

The southern interior of British Columbia is expected to become hotter and drier in coming years (Smith 2011; Prugh et al. 2018; Xu et al. 2021). Research has shown that the ubiquitous Western Deer Mouse tends to be outcompeted in hot, dry valley bottoms by pocket mice (O'Farrell 1975; Maida 2020; Melaschenko and Hodges 2020). As a result, pocket mice may benefit from both the climatic shifts and the reduced competition from the Western Deer Mouse. This pattern is supported by several studies suggesting that rare species may benefit from climate change, as they become more competitive against current dominant generalists (Jiang et al. 2013; Prugh et al. 2018).

The persistence of the pocket mouse in a *Peromyscus*-dominated community at the periphery of its range suggests the potential for range expansion into the arid valley bottoms in the Thompson Valley, mirroring their distribution in the South Okanagan and Washington (O'Farrell 1975; Maida et al. 2020; Melaschenko and Hodges 2020). Previous inventory work in the south Okanagan indicates that pocket mice reach much higher density in natural arid grassland/sagebrush habitat than in dry forests (e.g., Ponderosa Pine, *Pinus ponderosa*) or abandoned fields and tends not to be present in agricultural land, such as orchards (Sullivan and Sullivan 2006, 2008). These authors also observed that pocket mice have poor dispersal success and highly specific habitat requirements (Sullivan and Sullivan 2008), suggesting that disturbed habitat could present significant barriers for the conservation and success of this species, as it has for other species within this genus (Brehme 2023).

The site of our recent observation re-establishes and verifies the presence of the Columbia Plateau Pocket Mouse in the Thompson Valley. This now represents the most northern known location of this species, 180 km north of the nearest published observation records. Our observation, along with the recent detections of the species in the North Okanagan, will significantly change the estimated range of these animals in Canada, a metric important to the assessment of a species at risk (Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2015; IUCN Standards and Petitions Committee. 2024. Guidelines for Using the IUCN Red List Categories and Criteria. Version 16. Available from: https://www.iucnredlist.org/ [Accessed 27 November 2024]). Additional inventory work is required in southern British Columbia to determine whether connectivity exists between the Thompson Valley population and the known locations of the animal in the south and north Okanagan. The arid grassland ecosystem of southern British Columbia is itself considered threatened (Austin et al. 2008, Williams 2015), and with increased pressure through human development, obtaining a clearer picture of the distribution of the Columbia Plateau Pocket Mouse is warranted.

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APPENDIX B

MODEL SPECIFICATIONS AND OUTPUT FOR TEMPERATURE WINDOWS CORRELATED WITH WESTERN DEER MOUSE DENSITY IN CHAPTER 2

Table B.0.1 Top temperature windows in the sliding window analysis predicting Western Deer Mouse density with a cumulative AICc model weight adding to 95% of model support. The weighted mean open-close date of the top 12 models is 4.3–1.3 months before the trapping event (October).

Rank	Window (open-close)*	ΔAICc	Model Weight	Cumulative
1	3–2	-15.14	0.1885	0.1885
2	5–0	-14.71	0.1518	0.3404
3	5–1	-14.24	0.1200	0.4604
4	4–2	-14.21	0.1187	0.5791
5	4–1	-13.30	0.0753	0.6544
6	5–2	-12.98	0.0642	0.7185
7	3–3	-12.82	0.0590	0.7776
8	6–0	-12.73	0.0565	0.8341
9	4–0	-12.44	0.0489	0.8829
10	6–1	-11.51	0.0307	0.9137
11	4–3	-10.73	0.0208	0.9345
12	5–3	-10.18	0.0158	0.9503

* Months before trapping date (October), where September is 1 month prior, August is 2, and July is 3.

Model Output: model significance is 0.0074

	Estimate	**S.E.**	**t-value**	***P***	**Null deviance**	**Residual deviance**	**AIC**	**R^2**
Intercept	8.91	0.88	10.16	**< 0.001**	24.21 on 73 D.F.	15.68 on 72 D.F	526.95	0.35
Av. Jul-Aug temperature	-0.32	0.05	-6.79	**< 0.001**	—	—	—	—

APPENDIX C

AT-RISK WILDLIFE SPECIES IN BRITISH COLUMBIA, CANADA

Table C.0.1 Blue (threatened) and red (endangered) mammals in British Columbia, Canada. Accessed on January 13, 2026 from BC Species & Ecosystems Explorer [https://a100.gov.bc.ca/pub/eswp/]. Species group determined by taxonomic lineage. Groups represented are: SMAM (small mammal), CARN (carnivore), RUM (ruminant).

Scientific Name	English Name	Group	Provincial	BC List
Enhydra lutris	Sea Otter	CARN	S3S4 (2022)	Blue
Gulo gulo	Wolverine	CARN	S3 (2025)	Blue
Mustela haidarum	Haida Ermine	CARN	S3 (2010)	Blue
Mustela richardsonii anguinae	Ermine, *anguinae* subspecies	CARN	S3 (2010)	Blue
Neogale frenata altifrontalis	Long-tailed weasel, *altifrontalis* subspecies	CARN	SH (2024)	Red
Pekania pennanti pop. 4	Fisher - Boreal Population	CARN	S3 (2025)	Blue
Pekania pennanti pop. 5	Fisher - Columbian Population	CARN	S1S2 (2025)	Red
Spilogale gracilis	Western Spotted Skunk	CARN	S2S3 (2023)	Blue
Taxidea taxus	American Badger	CARN	S2 (2015)	Red
Ursus arctos	Grizzly Bear	CARN	S3? (2015)	Blue
Bos bison athabascae	Wood Bison	RUM	S2 (2024)	Red
Bos bison bison	Plains Bison	RUM	SX (2024)	Red
Cervus canadensis roosevelti	Roosevelt Elk	RUM	S3S4 (2017)	Blue
Oreamnos americanus	Mountain Goat	RUM	S3 (2024)	Blue
Ovis canadensis	Bighorn Sheep	RUM	S3? (2015)	Blue
Ovis dalli dalli	Dall's Sheep	RUM	S3 (2023)	Blue
Ovis dalli stonei	Stone's Sheep	RUM	S3S4 (2017)	Blue

Rangifer tarandus pop. 1	Caribou (Southern Mountain Population)	RUM	S1 (2017)	Red
Rangifer tarandus pop. 14	Caribou (Boreal Population)	RUM	S2? (2017)	Red
Rangifer tarandus pop. 15	Caribou (Northern Mountain Population)	RUM	S2S3 (2017)	Blue
Rangifer tarandus pop. 18	Caribou (Central Mountain Population)	RUM	S1S2 (2017)	Red
Antrozous pallidus	Pallid Bat	SMAM	S2 (2022)	Red
Aplodontia rufa	Mountain Beaver	SMAM	S3 (2024)	Blue
Callospermophilus saturatus	Cascade Golden-mantled Ground Squirrel	SMAM	S3? (2024)	Blue
Corynorhinus townsendii	Townsend's Big-eared Bat	SMAM	S3 (2022)	Blue
Euderma maculatum	Spotted Bat	SMAM	S3S4 (2022)	Blue
Lasiurus cinereus	Hoary Bat	SMAM	S3S4 (2022)	Blue
Lepus americanus washingtonii	Snowshoe Hare, *washingtonii* subspecies	SMAM	S1S2 (2024)	Red
Lepus townsendii	White-tailed Jackrabbit	SMAM	SX (2022)	Red
Marmota vancouverensis	Vancouver Island Marmot	SMAM	S1 (2024)	Red
Microtus townsendii cowani	Townsend's Vole, *cowani* subspecies	SMAM	S1 (2024)	Red
Myotis ciliolabrum	Western Small-footed Myotis	SMAM	S3S4 (2022)	Blue
Myotis lucifugus	Little Brown Myotis	SMAM	S3S4 (2022)	Blue
Myotis septentrionalis	Northern Myotis	SMAM	S2S3 (2022)	Blue
Myotis thysanodes	Fringed Myotis	SMAM	S2S3 (2022)	Blue
Myotis yumanensis	Yuma Myotis	SMAM	S3 (2022)	Blue

Neotamias minimus oreocetes	Least Chipmunk, *oreocetes* subspecies	SMAM	S3 (2020)	Blue
Neotamias minimus selkirki	Least Chipmunk, *selkirki* subspecies	SMAM	S2 (2024)	Red
Neotamias ruficaudus ruficaudus	Red-tailed Chipmunk, *ruficaudus* subspecies	SMAM	S2 (2021)	Red
Neotamias ruficaudus simulans	Red-tailed Chipmunk, *simulans* subspecies	SMAM	S3 (2021)	Blue
Ochotona collaris	Collared Pika	SMAM	S3 (2024)	Blue
Perognathus parvus	Columbia Plateau Pocket Mouse	SMAM	S3 (2024)	Blue
Reithrodontomys megalotis	Western Harvest Mouse	SMAM	S3 (2024)	Blue
Scapanus townsendii	Townsend's Mole	SMAM	S1 (2024)	Red
Sorex bendirii	Pacific Water Shrew	SMAM	S2 (2024)	Red
Sorex merriami	Merriam's Shrew	SMAM	S1 (2024)	Red
Sorex navigator brooksi	Western Water Shrew, *brooksi* subspecies	SMAM	S3 (2024)	Blue
Sorex preblei	Preble's Shrew	SMAM	S1S2 (2024)	Red
Sorex rohweri	Olympic Shrew	SMAM	S2 (2024)	Red
Sorex trowbridgii	Trowbridge's Shrew	SMAM	S3 (2024)	Blue
Sorex tundrensis	Tundra Shrew	SMAM	S1S2 (2024)	Red
Sylvilagus nuttallii	Nuttall's Cottontail	SMAM	S3S4 (2024)	Blue
Synaptomys borealis artemisiae	Northern Bog Lemming, *artemisiae* subspecies	SMAM	S2S3 (2024)	Blue
Thomomys talpoides segregatus	Northern Pocket Gopher, *segregatus* subspecies	SMAM	S1S3 (2020)	Red
Zapus hudsonius alascensis	Meadow Jumping Mouse, *alascensis* subspecies	SMAM	S3 (2020)	Blue

Table C.0.2 Provincial conservation status ranks from British Columbia, Canada.

Type of Rank	**Meaning**
S	Subnational ranks assigned and maintained by the B.C. Conservation Data Centre
N	National ranks assigned by national and international conservation authorities
G	Global ranks assigned by national and international conservation authorities
Modifier Code	**Meaning**
X	Presumed extirpated
H	Historical (species) / possibly extirpated (ecological communities)
1	Critically imperiled
2	Imperiled
3	Special concern, vulnerable to extirpation or extinction
4	Apparently secure, with some cause for concern
5	Demonstrably widespread, abundant and secure
NA	Not applicable
NR	Not yet assessed
U	Unrankable
##	Range Rank—Used to indicate the range of uncertainty about conservation status (e.g. S2S3)
?	Inexact or Uncertain—Denotes inexact or uncertain numeric rank

Table C.0.3 Count of at-risk mammals in British Columbia Canada. Data from Table C.0.1.

Group	**Count of Species**	**Percentage**
CARNIVORE	10	18.18%
RUMINANT	11	20.00%
SMALL MAMMAL	34	61.82%
Total	**55**	**100.00%**