GRANIVORY AND GRANIVORES IN NATIVE GRASSLANDS AND AGROPYRON CRISTATUM STANDS IN THE NORTHERN GREAT PLAINS

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by
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Troy Mark Radtke, candidate for the degree of Doctor of Philosophy in Biology, has presented a thesis titled, *Granivory and Granivores in Native Grasslands and Agropyron Cristatum Stands in the Northern Great Plains*, in an oral examination held on April 10, 2012. The following committee members have found the thesis acceptable in form and content, and that the candidate demonstrated satisfactory knowledge of the subject material.

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ABSTRACT

*Agropyron cristatum* (crested wheatgrass) is a management concern in the northern Great Plains because of the low plant biodiversity and high stability in *A. cristatum* stands. Small consumers have the potential to contribute to *A. cristatum* invasion and stability through granivory and herbivory. Little is known about ant species composition in the Northern Great Plains. I quantified seed removal rates, granivore seed preferences, and ant communities in paired native grasslands and *A. cristatum* stands.

I examined temporal variation in vegetation factors that influence granivory rates. Finally, I determined the relationship between seed size and vertebrate granivore preferences in herbaceous and woody communities, and I sampled ants to determine species composition and how vegetation parameters influence ant communities.

Granivory rates did not differ between native grasslands and *A. cristatum* stands. Forb cover and season were important predictors of granivory rates in 2009, with higher granivory later in the growing season and at sites with greater cover of forbs. In 2010, there were no important predictors of granivory rates. Granivory rates in *A. cristatum* stands were similar to those in native
grasslands, possibly because the vegetative cover and litter depth of *A. cristatum* stands was similar to that of native grasslands. Granivores did not prefer native seeds to exotic ones and showed little seed preference.

A review of vertebrate granivore seed size preferences revealed that granivores often prefer relatively small seeds in forests and relatively large seeds in herbaceous communities. However, the absolute size of preferred seeds in each community is often similar.

Ant species richness was similar between native grasslands and *A. cristatum* stands, while ant species composition differed between the two vegetation types. However, there were no differences in total ant abundance or the abundance of functional groups between native grasslands and *A. cristatum* stands. Ant abundance increased with the covers of bare ground and litter.

Granivory was related to variables such as forb cover and bare ground, which varied within both vegetation types. Yet, in spite of differences in plant species dominance and plant diversity between native grasslands and *A. cristatum* stands, there were few differences between the vegetation types in terms of granivory rates, granivore seed preferences or total ant abundance.
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To my wife, Brenda.

For your unselfishness and unlimited love and support.
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1. GENERAL INTRODUCTION TO THE THESIS

1.1 INTRODUCTION

The grasslands of the northern Great Plains of North America have undergone dramatic changes since European settlement. One of the greatest changes is the widespread introduction and spread of exotic plants such as *A. cristatum* (crested wheatgrass, hereafter *A. cristatum*). Widespread planting of *A. cristatum* occurred in the Great Plains during and after the drought of the 1920s and 1930s when many crop fields were abandoned. *A. cristatum* was sown because it establishes easily, is cold- and drought-tolerant, and grazing of *A. cristatum* by livestock results in increased weight gain compared with native grasses (Smoliak 1968, Smoliak and Slen 1974). *Bromus inermis* (smooth brome) is another exotic grass that was extensively planted in the northern Great Plains for forage and soil stabilization. Both of these grasses commonly form near-monocultures that are often persistent for decades (Looman and Heinrichs 1973, Heidinga and Wilson 2002). Both species continue to be planted on the northern Great Plains. These grasses invade native prairie, reducing plant and vertebrate diversity (Heidinga and Wilson 2002, Poulin 2003, Henderson and Naeth 2005). However, their effects on
invertebrate diversity have not been determined.

The effects of cattle grazing on A. cristatum biomass and water status have received much attention (Smoliak and Slen 1974, Balph and Malecheck 1985, Wraith et al. 1987), but no research has focused on the effects of native consumers on A. cristatum. Although research has been conducted on the effects of A. cristatum on bird (Wiens and Rotenberry 1985, Sutter and Brigham 1998) and small mammal (Reynolds and Trost 1980, Groves and Keller 1983) community composition, the effects of A. cristatum on invertebrate species composition are also unknown. I consider the role that small native consumers have on seed predation, plant biomass and plant species composition in native grasslands and A. cristatum stands of the northern Great Plains.

Small consumers have important effects on many herbaceous communities. In experimental grasslands in Illinois, Microtus pennsylvanicus (meadow voles) reduced plant biomass and caused changes in plant species composition (Howe et al. 2006). Plants that were preferred forage for Microtus pennsylvanicus declined while species avoided by Microtus pennsylvanicus increased. In Arizona grasslands, removal of seed specialist rodents, Dipodomys spp. (kangaroo rats), resulted in a shift in vegetation type, from shrub- to grass-dominated (Brown and Heske
In general, *Dipodomys* spp. preferred large seeds to small ones, which caused an increase in large-seeded plants and a decrease in small-seeded plants following *Dipodomys* spp. exclusion. Whether small mammals and insects have similar effects on *A. cristatum* is not known.

While seed predation of *A. cristatum* has not been examined, many other aspects of *A. cristatum* biology have received attention. *A. cristatum* competitively suppresses adult plants of native species, as well as suppressing the establishment of new individuals (Bakker and Wilson 2001, Bakker et al. 2003). The negative effects of *A. cristatum* on native plants occur both above- and below-ground (Bakker and Wilson 2001). *A. cristatum* begins growth earlier in the year and has higher growth rates than native grasses (Smoliak and Johnston 1968), leading to light limitation and reduced photosynthesis in neighboring plants (e.g., Tilman 1993). However, belowground competition can be a more important factor than aboveground competition in determining grassland species composition (Wilson and Tilman 1991). Belowground competition affects seedling emergence and performance in grasslands (Aguilera and Laurenroth 1993, Aguilera and Laurenroth 1995, Dyer and Rice 1999), and competition is often identified as the main
factor limiting the establishment and persistence of native plants in *A. cristatum* stands (Bakker and Wilson 2001).

In addition to competition, the paucity of native plants in *A. cristatum* stands may be related to abundant seed production by *A. cristatum* and the lack of seeds of native plants. Seed production of *A. cristatum* is often more than double that of native grasses (Pyke 1990, Heidinga and Wilson 2002) and *A. cristatum* produces seed even during years when drought precludes native seed production (Pyke 1990). *A. cristatum* seeds dominate seedbanks in *A. cristatum* stands and often make up a significant proportion of seeds in adjacent native stands (Marlette and Anderson 1986). The low number of native seeds in *A. cristatum* stands is to be expected because seed banks closely resemble the mature vegetation in the immediately vicinity (Marlette and Anderson 1986, Peart 1989). Adding seeds of species which are rare or absent from a site often results in significant seedling emergence of those species, suggesting seed limitation (Turnbull et al. 2000, Martin and Wilsey 2006). Adding *Bouteloua gracilis* (blue grama) seeds to an *A. cristatum* stand in which very few native grasses existed previously resulted in the emergence of *Bouteloua gracilis* seedlings (Ambrose and Wilson 2003). Other studies have also shown that adding
native seeds to *A. cristatum* stands can result in native plant emergence (Bakker et al. 1997, Bakker et al. 2003). Marlette and Anderson (1986) suggested that the stability of *A. cristatum* stands might be a consequence of dominance of the seed bank by *A. cristatum*, and considered this to have a greater affect on stability than competition.

Seed addition for native species does not always result in establishment in *A. cristatum* stands. While *Bouteloua gracilis* establishes through seed addition (Bakker et al. 1997, MacDougall et al. 2008), *Hesperostipa comata* (needle and thread grass) and *Koeleria macrantha* (junegrass) do not establish (Bakker et al. 1997, Ambrose and Wilson 2003). Of the *Bouteloua gracilis* plants that did establish, few did so without water addition, herbicide application to *A. cristatum*, or disturbance prior to seeding. These results suggest that seed addition alone may not result in establishment (Bakker et al. 1997). In fact, in many seed addition studies the species with added seeds failed to establish (Tilman 1997, Symstad 2000, Fraser and Madson 2008). This may be due to a lack of suitable sites for the germination and establishment of those species.

The lack of native plant establishment in *A. cristatum* stands may also be explained by apparent competition caused by small consumers (Callaway and Aschehoug 2000). Apparent
competition differs from direct resource competition in that apparent competition does not involve any direct negative interaction between species competing for resources (Holt 1977). In contrast, resource competition occurs when one species has a negative effect on another through use of the same resources. Many studies that claim to have demonstrated resource competition have not determined whether any indirect interactions have occurred (Connell 1990). While these studies provide empirical evidence that seems to support direct competition, they often fail to provide strong causal links. Apparent competition could contribute to *A. crista*atum dominance and invasion of native plant communities if the presence of *A. crista*atum results in greater granivory or herbivory of native plants. Experiments that manipulate resources and other factors potentially responsible for direct and apparent competition are often necessary to determine the cause of the observed effect.

In summary, understanding the mechanisms through which *A. crista*atum exclude native plants and maintain stable populations may be helpful for managing this species. While seed limitation and resource competition have received support as explanations for invasive plant stability (Callaway and Aschehoug 2000, Seabloom et al. 2003a,
Agrawal et al. 2005), they have recently been complemented by explanations related to apparent competition, i.e., granivory or herbivory in the cases of some invasive species (Pearson and Callaway 2008).

1.2 EFFECTS OF SMALL CONSUMERS ON GRASSLAND SPECIES COMPOSITION

1.2.1 Granivory

Granivory-driven apparent competition has been demonstrated for some invasive plant species. For example, exotic annuals have invaded California grasslands, which were likely once composed of native forbs and perennial grasses (Seabloom et al. 2003b). The persistence of the exotic annuals was attributed to superior competitive ability (Dyer and Rice 1999). However, recent research has shown that native species are strong competitors, but are seed- and establishment-limited (Seabloom et al. 2003a, 2003b). Exotic plants displace natives indirectly via higher granivory and herbivory by small mammals on native plants (Orrock et al. 2008). Small mammal consumption of native plants is facilitated by exotics, which cause either a change in the foraging activities of small mammals or an increase in their abundance, probably because the greater height of the exotic plants results in lower predation risk
Another example of granivory contributing to invasive plant stability comes from grasslands dominated by the invasive forb *Centaurea maculosa* (spotted knapweed). Biocontrol insects were introduced into this system to control *Centaurea maculosa*. These insects caused an increase in *Peromyscus maniculatus* (deer mouse) abundance because their larvae are eaten by mice (Pearson and Fletcher Jr. 2008). *Peromyscus maniculatus* populations increased and preferentially consumed the seeds of native plants, while avoiding those of the exotic forbs (Pearson and Callaway 2008). Therefore, through a food-web interaction, biocontrol insects caused second-order apparent competition, which negatively impacted native plants. Because plant invasions often cause changes in the abundance and composition of consumers (Onsager 2000), and consumers can exert strong effects on plant communities (Olff and Ritchie 1998, Maron and Kauffman 2006, Pearson and Callaway 2008), it seems plausible that consumers may play a role in the establishment and stability of invasive plants through apparent competition. However, this type of interaction has been tested for only a few invasive plant species to date.

Granivores in grasslands are primarily rodents,
insects and birds. Heteromyid rodents (e.g. kangaroo rats, *Dipodomys* spp.) are seed specialists that have received much attention because they often have significant effects on plant communities (Brown and Heske 1990, Howe and Brown 1999, Howe et al. 2002). Heteromyids typically prefer larger seeds, thus causing a decrease in large-seeded species (Inouye et al. 1980, Brown and Heske 1990, Samson et al. 1992).

Few heteromyid rodents exist in my study area (southern Saskatchewan and northeastern Montana) and the commonest rodents in this region (e.g. *Peromyscus maniculatus* and *Spermophilus* spp.) are largely herbivorous or omnivorous (Flake 1973). These rodents could have significant impacts on plant species composition through granivory. For example, in North American tallgrass prairies, *Microtus pennsylvanicus* (meadow vole) choose larger seeds, causing reductions in larger seeded plants and releasing plant species with small seeds (Howe and Brown 1999). *Peromyscus* spp. can be influential granivores in old fields in eastern North America (Mittlebach and Gross 1984, Myster and Pickett 1993, Manson and Stiles 1998) and can cause declines in seed densities of seed banks (Anderson and MacMahon 2001). *Spermophilus* spp. (ground squirrels) are known to eat significant quantities
of seeds (Flake 1973, Dyni and Yensen 1996), yet little research has implicated them in changes in plant species composition.

Among insects, ants are the most common granivores, although other insects can also cause seed loss (Andersen 1989). Ants can harvest large numbers of seeds and have affected plant species abundance and composition in deserts, (Brown et al. 1979, Davidson et al. 1985, Samson et al. 1992) and dry forests (Andersen 1989). However, specialized seed harvester ants common in North American deserts are absent from most of the northern Great Plains and existing ants may harvest few seeds (Mittlebach and Gross 1984, Clark and Wilson 2003) and thus have minimal effect on overall plant community dynamics in grasslands (Brown and Human 1997).

While many species of birds eat seeds, the total consumption of seeds by birds is relatively low (Risser et al. 1981). Birds are relatively unsuccessful at finding seeds where there is dense vegetative cover (Brown and Heske 1990) and their effect in grasslands with high vegetative cover may be negligible (Mittlebach and Gross 1984, Howe and Brown 1999). However, in grasslands where more bare ground exists, birds may consume large quantities of seeds (Nelson et al. 1970, Pulliam and Brand 1975) and
can partially determine plant species composition (Howe and Brown 1999).

Few granivory studies have been conducted in the northern Great Plains. A Colorado grassland restoration experiment demonstrated that rodents foraged more intensively where larger seeds were present (Hoffman et al. 1995). This caused a decrease in a large-seeded grass, *Bouteloua dactyloides* (buffalograss), and an increase in a small-seeded grass *Bouteloua gracilis* (blue grama), in rodent-accessible plots compared with exclosures. Diet analysis of *Peromyscus maniculatus* and *Spermophilus* spp. in Idaho demonstrated that seeds occurred in stomachs of > 43% of individuals of *Peromyscus maniculatus* (Johnson 1961) and > 67% of *Spermophilus* spp. (Dyni and Yensen 1996), although their effect on plant communities was unknown. Granivory by *Peromyscus maniculatus* in Montana limited the establishment of native plants in a former grassland dominated by exotic forbs (Pearson and Callaway 2008).

Plant species that are seed-limited because of granivory are commonly those with relatively large seeds (Brown et al. 1979, Bricker et al. 2010). Vertebrate granivores are often assumed to prefer larger-seeded species (Blate et al. 1998, Kollmann et al. 1998). However, many studies have found no seed size preferences (Kollmann...
et al. 1998, Hau 1997, Holl and Lulow 1997, Munoz and Cavieres 2006), and some have found preferences for smaller-seeded species (Osunkoya 1994, Nepstad et al. 1996, Blate et al. 1998, Mendoza and Dirzo 2007). Additionally, because seeds often vary in size by five or more orders of magnitude within a plant community (Moles et al. 2007), and researchers only offer a small subset of available seed sizes in each study, it is uncertain whether vertebrate granivores will always prefer the larger seeds offered. A review of granivory studies is needed to determine general patterns of vertebrate granivore seed size preferences.

The effect of granivory on plant communities depends not only on the granivores present and the number of seeds consumed, but also on the location from which seeds are removed. Differential seed removal among microsites can affect the composition and distribution of plant communities because many plant species have specific microsite requirements for germination and seedling survival. Some research has demonstrated greater seed removal in open or gap microsites (Reed et al. 2004, 2006), some has found greater granivory under litter or plant canopies (Mittlebach and Gross 1984, Reader 1991), and some found no differential seed removal among microsites (Abramsky 1983, Barberá et al. 2006). Thus, the few studies
that have attempted to determine if differential levels of seed removal occur at various microsites have found no consistent pattern.

1.2.2 Herbivory

Most studies of herbivory in grasslands have focused on large grazers, but small mammals can also be important (Keesing 2000). There is growing evidence that small mammals shape plant communities by consuming plants that are palatable and lack chemical and physical defenses (Howe et al. 2002, Burt-Smith et al. 2003, MacDougall and Wilson 2007). In tallgrass prairies, meadow voles can cut > 30% of vegetation (Howe et al. 2006), decreasing plant diversity (Howe and Lane 2004) and reducing plant biomass (Howe and Brown 1999). The effect of small mammal herbivory is likely disproportionately high on seedlings because of their greater palatability and smaller reserves. Similar to granivory, the effects of herbivory may be small if herbivore consumption is no greater than other sources of mortality. However, because exclosures are commonly used to determine the effects of small mammals on plant communities, it can be difficult to distinguish between granivory and herbivory as causes of vegetation change.

The understanding of the degrees and causes of top-
down (e.g., consumer) and bottom-up (e.g., resource) regulation in plant communities is important for identifying mechanisms of invasive plant success. The effect of herbivores on grassland plant diversity typically varies along gradients of grassland productivity, herbivore size and relative palatability of seeds and seedlings (Bakker et al. 2006). Herbivores have greater effects on productive grasslands than on unproductive ones, and larger herbivores have greater effects than smaller ones (Olff and Ritchie 1998). Plant species with higher palatability suffer greater losses than those with lower palatability (Howe et al. 2002). *A. cristatum* stands are more productive than native prairie, which may cause an increase in consumer populations and activity (Birney et al. 1976). *A. cristatum* stands supports higher densities of grasshoppers than native prairie (Onsager 2000). Grasshoppers have direct negative effects on species diversity (Branson and Sword 2007), but they may provide an additional food source for small mammals like deer mice (Pearson and Fletcher Jr. 2008), thereby increasing their abundance and potential effects on vegetation (Orrock et al. 2008a, Pearson and Callaway 2008). Although palatability of *A. cristatum* to small consumers is unknown, because *A. cristatum* is more tolerant of herbivory than native prairie plants (Caldwell
et al. 1981), the increased consumers may disproportionately affect native plant establishment and persistence. This apparent competition through native consumers in A. cristatum stands deserves further investigation.

1.3 ANT COMMUNITIES

Knowledge of species composition and abundance of ants in native grasslands and A. cristatum stands is needed in order to address their role as consumers. Ants influence the composition of many plant communities (Beattie and Culver 1977, Brown and Human 1997). In grasslands, Formica obscuripes alters soil conditions in the vicinity of their nest mounds, which increases the heterogeneity of the plant community (Beattie and Culver 1977). Ants can also indirectly affect vegetation via their mutualisms with aphids. For example, beetle defoliation of immature Populus spp. (cottonwood) trees can reach 25% (Floate and Witham 1994). Aphids on Populus spp. trees attract aphid-tending ants, which subsequently reduce beetle herbivory (Floate and Whitham 1994). Furthermore, ants are considered good bioindicators, particularly for disturbance (Stephens and Wagner 2006) and restoration (Andersen 1993, Andersen et al. 2003), because variation in ant species composition
often reflects variation in other invertebrate groups (Majer 1983).

Invertebrate communities are frequently altered by invasive plant species (Gratton and Denno 2005, Gerber et al. 2008), but it is unknown whether A. cristatum stands contain different ant assemblages from native grasslands. A. cristatum stands differ from native grassland in plant species composition and vegetation structure, both of which affect ant assemblages (Majer 1985, Andersen 1983, 1986). Because of their ability to affect plant communities, ants may contribute to A. cristatum success. However, too little is currently known about ant species composition or their impact on the diversity and structure of plant communities in the northern Great Plains to develop any hypotheses related to A. cristatum invasion or stability. The first step in understanding the potential roles ants have in structuring native- and A. cristatum-dominated plant communities of the northern Great Plains is documenting ant species distributions in these communities.

1.4 CHAPTER SUMMARIES

A. cristatum has become a management concern in the northern Great Plains (Vaness and Wilson 2007). The causes of its stability and invasion as well as its potential
effect on native plants and animals are unclear. *A. cristatum* invasion potentially affects and is affected by small consumers. However, small consumers have received little attention, even though studies show them to have important effects in other grassland communities (Brown and Heske 1990, Howe et al. 2002). Furthermore, differences in ant species composition between native grasslands and *A. cristatum* stands have not been determined. Here I address relationships among small native consumers and native grasslands as well as *A. cristatum* stands in the northern Great Plains.

Chapter Two examines relative granivory rates in native grasslands and *A. cristatum* stands, and how granivory rates vary with season and vegetation characteristics. Because granivory rates vary by seed species and granivore species, Chapter Three examines granivory rates of seven common grasslands species by three granivore taxa: small mammals, birds and invertebrates. Chapter Four investigates vertebrate granivore seed size preferences. Chapter Five explores ant species composition, abundance and species richness in native grasslands and *A. cristatum* stands. Chapter Six is a summary to the thesis.
2. GRANIVORY IN NATIVE AND EXOTIC GRASSLANDS OF THE NORTHERN GREAT PLAINS

2.1 ABSTRACT

Granivores have the potential to contribute to the stability and spread of invasive grasses in the northern Great Plains. Plant invasions often result in a change in granivore species composition and abundance. Altered granivore populations can limit the establishment of native plants. On the other hand, vegetation characteristics can also influence granivory rates. I measured granivory rates (quantified as the removal of seeds of the grass *Panicum miliaceum*) at six sites in native grasslands and invasive *A. cristatum* or *Bromus inermis* stands. I also determined how vegetation factors and season influence granivory rates in native grasslands and *A. cristatum* stands. Granivory rates did not differ significantly between native grasslands and *A. cristatum* stands, but a *Bromus inermis* stand had granivory rates three times higher than those in a native grassland. The most important determinant of granivory rates in native grasslands and *A. cristatum* stands was forb cover, with higher granivory at sites with greater cover of forbs. Greater granivory with increasing forb cover may be due to the positive impact forbs have on
Peromyscus maniculatus and Microtus pennsylvanicus abundance. Season was also important, with greater granivory later in the growing season. The change in vegetative structure with Bromus inermis invasion resulted in a shift in small mammal species composition from Spermophilus tridecemlineatus in native grassland to Microtus pennsylvanicus and Poliocitellus franklinii in Bromus inermis stands, which may be the cause of the higher granivory rate in Bromus inermis. Granivory rates in northern Great Plains grasslands appear to be influenced more by vegetation structure and season than by plant species identity.

2.2 INTRODUCTION

Agropyron cristatum is an introduced perennial bunchgrass from Eurasia that was commonly used to revegetate abandoned crop fields in the northern Great Plains during and following severe drought in the 1930s (Dillman 1946). A. cristatum invades native grasslands, so it is now a major concern in managed grasslands in the northern Great Plains where attempts to restore native grasslands are underway.

Understanding the mechanisms responsible for A. cristatum stability and invasion is vital to its
management. Some invasive plants benefit from apparent competition with native plants (Orrock et al. 2008, Pearson and Callaway 2008). Apparent competition occurs when one species has an indirect negative effect on another species (Holt 1977). Invasive plants can affect native plants through apparent competition via granivory when invasive plants result in changes in granivore species composition and abundance, leading to higher granivory levels and suppression of native plants (Orrock et al. 2008). Changes in granivore species composition and abundance are often the result of a change in food resources (Williams et al. 1992, Pearson et al. 2000, Gosper et al. 2006) or predation risk, typically caused by changes in vegetative structure (Orrock et al. 2008, Mattos and Orrock 2010).

Invasive plants affect and are affected by small consumers. Thus, a positive feedback loop between *A. cristatum* and small consumers may exist if *A. cristatum* invasion results in greater consumer pressure on native plants, which benefits *A. cristatum* and results in further invasion. The potential for *A. cristatum* to cause increased consumer pressure exists because *A. cristatum* produces more seeds (Koehler and Anderson 1991, Heidinga and Wilson 2002) and harbors more insects (Onsager 2000) than native grasslands, and both seeds and insects are food for
consumers. If an increase in granivory results from plant invasion, it could contribute to invasive plant success by limiting native plant establishment.

In addition to plant invasion, granivory rates may also be affected by vegetation characteristics (Hay and Fuller 1981, Bowers and Dooley 1993). Vegetation characteristics influence granivore composition and abundance, as well as behaviour. Vegetative cover and biomass often have the greatest influence on granivore species composition, but vegetation structure (Rosenzweig and Winakur 1969), such as the presence of shrubs, can also influence species composition. Vegetation characteristics also affect where a granivore forages within its home range and can therefore influence a seed’s probability of being eaten (Bowers 1990). For example, seeds covered with litter may be more (Reed et al. 2006) or less (Reader 1991) likely to be eaten than seeds on bare ground. Knowledge of the effect of vegetation characteristics on seed removal in the northern Great Plains is lacking.

Differential granivory among microsites may determine the impact that seed removal has on plant communities. Microsites refer to the topographical features of a soil surface that are relevant to the spatial scale of seeds (Harper et al. 1965). If granivory occurs primarily on
seeds located in microsites that are unsuitable for seedling establishment, it will have little impact on plant recruitment (Calvino-Cancela 2007). However, even low granivory rates can influence community composition if granivores selectively remove seeds from the most suitable microsites for seedling establishment (Hulme 1997). It is unclear whether differential seed removal by microsite occurs in the northern Great Plains.

I examined granivory related to the presence of exotic grasses. I measured granivory levels in both native and exotic grasslands to determine if granivory rates are higher in exotic grasslands than in native grasslands. I also determined the effect of among and within-site vegetation characteristics and season on granivory rates. This research will help us better understand the role that granivores may play in A. cristatum invasion and stability.

2.3 STUDY AREA

I worked at six sites, located in southern Saskatchewan and northeast Montana: White Butte Recreation Site (50°28’ N, 104°22’ W), 18 km east of Regina, Saskatchewan; Gap Community Pasture (49°17’ N, 104°38’ W), 18 km southwest of Ceylon, Saskatchewan; Shamrock Community Pasture (50°14’ N, 106°31’ W), 11 km northeast of Shamrock,
Saskatchewan; Auvergne-Wise Creek Community Pasture (49°39’ N, 107°47’ W), 9 km south west of Cadillac, Saskatchewan; Grasslands National Park (49°22’ N, 107°53’ W), 7 km south of Val Marie, Saskatchewan; and Medicine Lake National Wildlife Refuge (48°28’ N, 104°22’ W), 5 km southeast of Medicine Lake, Montana. Average annual precipitation ranges from 35 cm at Grasslands National Park to 38 cm at White Butte Recreation site, with roughly half of precipitation falling during May-July (Environment Canada, National Climate Data and Information Archive). Average July temperatures range from 19.9 °C at Medicine Lake National Wildlife Refuge (Western Regional Climate Center) to 18.3 °C at Grasslands National Park. Average January temperatures range from -12.4 °C at Grasslands National Park to -15.8 °C at White Butte Recreation Site (Western Regional Climate Center). These sites were chosen because they are representative of most publically-owned managed grasslands in the northern Great Plains.

Within each site, I chose a pair of grasslands, one dominated by native grasses and one dominated by introduced grasses (*Bromus inermis* at White Butte and *A. cristatum* at other sites). The *Bromus inermis* stand was roughly 13 ha, while all other grasslands used for this study were > 32 ha. Paired grasslands had similar topography, soils, and
climate. Native grassland vegetation was dominated by *Hesperostipa comata*, *Koeleria macrantha*, and *Bouteloua gracilis* at all sites.

White Butte Recreation Site and Grasslands National Park had not been grazed for several decades before this study and were not grazed during this study. At Medicine Lake National Wildlife Refuge, the site was burned in 2005, heavy grazing occurred in the *A. cristatum* stand in 2007 and moderate grazing occurred in the native stand in 2006, but no grazing or burning occurred during this study. At the three community pastures, grazing had occurred most years prior to the study and continued during the study. Native grassland in Shamrock and Auvergne-Wise Creek Community Pastures were grazed in late summer through fall and while *A. cristatum* pastures were grazed in spring. At Gap Community Pasture, both native and *A. cristatum* pastures were grazed in spring.

### 2.4 METHODS

#### 2.4.1 Seed removal trials

To determine if seed removal rates varied between native and exotic grasslands, I conducted seed removal trials using *Panicum miliaceum* seeds. I used *Panicum miliaceum* seeds because they are similar in size to seeds
naturally occurring in the study area. Further, they are highly palatable, have little chemical or physical defense, and are often preferred to native seeds (Parmenter et al. 1984, Kelrick et al. 1986). Therefore, when *Panicum miliaceum* seeds are encountered by granivores, they are likely to be eaten.

I conducted three seed removal trials in 2009 and two in 2010 at each site, with each trial lasting two days. In 2009, seed removal trials were conducted in May, June through early July, and August, and in 2010 trials were conducted in June through early July, and August. I set up transects of 50–75 seed depots each in the native and exotic grassland at each site. I used the same transect locations during every seed removal trial. Depots were spaced 10 m apart. Each depot consisted of a 3.8-cm-long roofing nail pushed through a piece (2.5 X 2.5 cm) of masking tape with four *Panicum miliaceum* seeds stuck to the tape. The nail and tape were pushed into the ground with the seeds on top of the tape at ground level. The masking tape was strong enough that seeds were not easily removed by wind or water. In contrast, it appeared that rodents and birds could easily remove seeds from masking tape because nearly all seed depots that had any seed removed had all four seeds removed. Flagging tape was placed roughly 50 cm
from the depot to mark its location. Depots were checked after two nights and the number of depots that received granivory was recorded. Since vertebrate granivores typically eat all seeds upon discovering a seed depot (Brown et al. 1975, Hay and Fuller 1981, Mittlebach and Gross 1984), nearly all depots had either four or zero depredated seeds. I assumed that granivory had occurred if at least two seeds were missing. Because one site contained *Bromus inermis* as the exotic grassland instead of *A. cristatum*, it was not pooled with the other five sites for analyses.

At two sites, Medicine Lake and Grasslands National Park, I also used seeds of seven locally-abundant species: *A. cristatum, Bouteloua gracilis, Bromus inermis, Koeleria macrantha, Petalostemon purpurea, Pascopyron smithii* and *Hesperostipa comata*. This was done to determine relative removal rates by birds and mammals among the eight species so generalizations about natural seed removal could be made. Seeds of *Bouteloua gracilis, Koeleria macrantha, Petalostemon purpurea, Pascopyron smithii* and *Hesperostipa comata* were hand-collected from Medicine Lake National Wildlife Refuge. Seeds of *A. cristatum* and *Bromus inermis* were purchased from Big Sky Seeds (Shelby, MT). Each plot allowed access by all granivores and had eight seed depots,
one for each seed species. Each depot was constructed similarly to the depots used for the *Panicum miliaceum* seed removal trials, with four seeds placed on masking tape that was pinned to the ground with a roofing nail. There were 20 plots in each native grassland and *A. cristatum* stand at each site. Seed depots were installed in mid July, 2010 and granivory rates were determined in mid August, 2010 after seeds had been available to granivores for approximately one month.

I determined the effect of vegetation characteristics on seed removal rates at two scales. Vegetation data for analysis of among-site (among geographic locations) vegetation characteristics were pooled within each combination of sampling period, site and vegetation type to determine the effects of vegetation characteristics on seed removal rates across the study area. Data for analysis of the within-site vegetation characteristics were used to make comparisons between the vegetation of used and available seed depots within each site.

2.4.2 Among-site vegetation characteristics

To determine how vegetation characteristics affected granivory rates among sites, I sampled 10 randomly located 50 X 50 cm vegetation plots for each sampling period at all
six sites and both vegetation types (native grassland and \textit{A. cristatum}). I recorded litter depth and percent cover of total vegetation, litter, graminoids, forbs, dicots, \textit{Selaginella densa} and bare ground (Daubenmire 1959). For litter depth, two measurements per plot were taken.

2.4.3 \textit{Within-site vegetation characteristics}

To determine the effect of vegetation characteristics on granivory rates within each of the six sites, I sampled 50 X 50 cm and 10-cm diameter vegetation plots of depredated and random depots for each sampling period at all sites and vegetation types. I used a use-availability design (Garton et al. 2005) and considered depredated depots to be used and random depots to be available. Random depots were chosen from all depots, regardless of whether or not they were depredated. I compared vegetation characteristics of depredated depots with vegetation of the previously described ten randomly located 50 X 50 cm plots for each site and season. I recorded litter depth and cover data of the same vegetation characteristics at each depredated depot. Finally, centered on all depredated depots and at 10 randomly selected depots, I recorded vegetation data from one 10-cm diameter plot for each location and sampling period to determine if microsite
characteristics affected seed removal rates. In the 10-cm diameter plots, I recorded percent cover of live plants, *Selaginella densa*, and bare ground. I determined litter depth by averaging two values taken 2.5 cm from the center of each plot and opposite to each other.

2.4.4 *Data analysis*

To standardize granivory data because of unequal sampling, I used \(100 \times (1 + (-((\text{undepredated depots}/\text{total depots})^{-2}))\)) which gives the percent of depots depredated per night. This granivory rate assumes equal granivory each night, which was necessary because the number of replicates and duration of seed removal trials was variable due to weather. All granivory rates were arcsine-square root transformed to improve normality. For among-sites analysis of sites containing native grasslands and *A. cristatum* stands, I used least squares regression to determine effects of grassland type, season (sampling period) and all vegetation characteristics from random plots on granivory rate. Site was treated as a random effects variable and was included in all models. Model selection was based on Akaike’s Information Criterion for small sample sizes (\(\text{AIC}_{c}\)) where \(w_i\) indicates the likelihood of the candidate model having the best fit among the whole set of models. To
determine relative importance of variables, I computed predictor weights for any variable that was included in a model with $w_i > 0.01$. Predictor weights of a variable represent the sum of the three best models that contain that variable. Post-hoc analyses were conducted using Student’s t-tests and Tukey’s HSD tests.

For within-site vegetation analysis, I used case-control (i.e., conditional or paired) logistic regression to compare vegetation between depredated (used) and available depots. I combined data from both years but analyzed native grasslands and A. cristatum stands separately. Vegetation data for each plot in which granivory occurred were paired (1-m matching, Hosmer and Lemeshow 2000) with the ten random vegetation plots for that site and season.

I compared granivory rates between seeds of Panicum miliaceum and seven locally abundant species using ANOVA. I also compared granivory rates between paired native grasslands and Bromus inermis stands using ANOVA with sampling period included as a random effect.

Least squares regression and ANOVA analyses were performed using JMP (version 8.0.2, SAS Institute, Cary, North Carolina, USA). Logistic regression analyses were performed using R statistical software version 2.11.1
2.4.5 Small mammal trapping

Species composition of small mammals was determined using Sherman live traps. I placed traps in the same grassland and at the same time as the seed removal experiments. To avoid affecting the seed removal experiments, trapping transects were at least 50 m away from the nearest depot, and > 200 m away from most depots. Although trapping could have reduced predation for the nearest depots, any effect was expected to be minor. I chose locations for trapping transects that appeared to have similar vegetation and structure to locations used for seed removal transects. Each grassland had one transect, which consisted of 25 traps, each separated by 11 m. I baited traps with peanut butter and Panicum miliaceum seeds and set them as lightly as possible to avoid a bias toward catching heavier rodents (Schowalter, 2005). Cotton was placed in each trap to provide insulation to trapped animals during cold or wet periods. I checked traps each morning and evening for two days. When weather was hot, I checked traps three times a day, or closed them during the day to avoid mortality. Small mammals were marked by clipping fur at the tip of the tail with a scissors to
avoid duplicate counts of individuals, except for
*Spermophilus tridecemlineatus, Spermophilus richardsonii*
and *Poliocitellus franklinii*, which were not marked because
their larger size made handling them difficult.

2.5 RESULTS

2.5.1 Among-site vegetation characteristics

Grassland type was not an important determinant of
granivory rate in either 2009 (native, 2.6% ± 1.2 seeds
removed per/day; *A. cristatum*, 5.7% ± 2.6 seeds removed/day
[\( \bar{x} ± SE \) throughout] or 2010 (native, 7.5% ± 4.9 seeds
removed per/day; *A. cristatum*, 7.9% ± 1.3 seeds removed
per/day). For 2009, the model that included only percent
cover of forbs best explained granivory rates (Table 2.1).
The model that included both cover of forbs and season also
received considerable support (Table 2.1). Based on
predictor weights (Table 2.2), percent cover of forbs was
the most important variable and was positively related to
granivory. Season was also relatively important with higher
granivory rates in late summer (9.9% ± 3.8 seeds
removed/day) than in spring (0.87% ± 0.29 seeds
removed/day, \( P < 0.001 \)) or early summer (1.74% ± 0.43 seeds
removed/day, \( P = 0.006 \)). For 2010, the intercept-only model
performed best, indicating little support for any other
Table 2.1 Least squares regression models explaining among-site granivory rates at five sites dominated by native grasses or *Agropyron cristatum* in the northern Great Plains during 2009 and 2010. Models with uninformative parameters are not shown.

<table>
<thead>
<tr>
<th>Model</th>
<th>-2LL</th>
<th>K</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>Δ&lt;sub&gt;i&lt;/sub&gt;</th>
<th>w&lt;sub&gt;i&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>2009</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% Forbs</td>
<td>-35.14</td>
<td>3</td>
<td>-22.64</td>
<td>0.00</td>
<td>0.47</td>
</tr>
<tr>
<td>% Forbs, season</td>
<td>-40.19</td>
<td>5</td>
<td>-21.69</td>
<td>0.96</td>
<td>0.29</td>
</tr>
<tr>
<td>% Dicots</td>
<td>-32.78</td>
<td>3</td>
<td>-20.28</td>
<td>2.36</td>
<td>0.14</td>
</tr>
<tr>
<td>Intercept</td>
<td>-27.45</td>
<td>2</td>
<td>-18.25</td>
<td>4.39</td>
<td>0.05</td>
</tr>
<tr>
<td>Season</td>
<td>-32.68</td>
<td>4</td>
<td>-17.08</td>
<td>5.57</td>
<td>0.03</td>
</tr>
<tr>
<td><strong>2010</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-9.82</td>
<td>2</td>
<td>-0.62</td>
<td>0.00</td>
<td>0.83</td>
</tr>
<tr>
<td>Litter depth</td>
<td>-8.02</td>
<td>3</td>
<td>4.48</td>
<td>5.11</td>
<td>0.06</td>
</tr>
<tr>
<td>Season</td>
<td>-7.27</td>
<td>3</td>
<td>5.23</td>
<td>5.85</td>
<td>0.04</td>
</tr>
<tr>
<td>Grassland type</td>
<td>-6.15</td>
<td>3</td>
<td>6.35</td>
<td>6.97</td>
<td>0.03</td>
</tr>
</tbody>
</table>

**Notes:** -2LL: -2 Log likelihood; K: number of parameters; AIC<sub>c</sub> scores are used to rank models. A lower AIC<sub>c</sub> indicates more support for that model. Δ<sub>i</sub> indicates the difference in model support relative to the best performing model. w<sub>i</sub> indicates the likelihood of the candidate model having the best fit among the whole set of models.
Table 2.2 Predictor weights of important individual among-site parameters computed using the top three least squares regression models, which explain seed removal rates at five sites dominated by native grasses or *Agropyron cristatum* in the northern Great Plains during 2009 and 2010 (Table 2.1).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Predictor weight</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>2009</strong></td>
<td></td>
</tr>
<tr>
<td>% Forbs</td>
<td>0.76</td>
</tr>
<tr>
<td>Season</td>
<td>0.32</td>
</tr>
<tr>
<td>% Dicots</td>
<td>0.15</td>
</tr>
<tr>
<td><strong>2010</strong></td>
<td></td>
</tr>
<tr>
<td>Litter depth</td>
<td>0.07</td>
</tr>
<tr>
<td>Season</td>
<td>0.05</td>
</tr>
<tr>
<td>Grassland type</td>
<td>0.03</td>
</tr>
</tbody>
</table>
model. Granivory rates were higher in late summer (10.6% ± 4.7) than in early summer (4.7% ± 1.3), but not significantly so (P = 0.077). Despite the importance of forbs in 2009, the forbs model received virtually no support in 2010 (w_i < 0.01). Percent cover of forbs was lower at most sites in 2009 than in 2010 (Table 2.3). Models that included litter depth in 2009 also received little support (w_i < 0.02) despite being relatively important in 2010.

*Panicum miliaceum* seed removal rates did not differ from those of seven locally abundant species (Fig. 2.1). Granivory rates were higher in *Bromus inermis* stands than in paired native grasslands (F_1,9 = 10.65, P = 0.0310, Fig. 2.2).

### 2.5.2 **Within-site vegetation characteristics**

Vegetation characteristics at locations where granivory occurred were different than those at random locations. At vegetation plots at the 50-cm-scale, percent cover of dicots was greater at depredated plots than at random plots in *A. cristatum* stands (odds ratio (OR) = 1.013, 95% confidence interval (CI) = 1.001 - 1.025, P = 0.037) and percent cover of bare ground was greater at depredated plots than at random plots in native stands (OR
Table 2.3 Summary of vegetative characteristics and predation rates by site and season in 2009 and 2010. Sites: AW—Auvergne-Wise Creek Community Pasture, SHAM—Shamrock Community Pasture, GAP—Gap Community Pasture, ML—Medicine Lake National Wildlife Refuge, GNP—Grasslands National Park, WB—White Butte Recreation Site. Predation rate is mean percent millet seed removed per day. Litter depth is the mean depth of litter (cm) from 10 random locations measured using a ruler. All other categories are mean percent cover from 10 random locations.

<table>
<thead>
<tr>
<th>Site</th>
<th>Predation rate</th>
<th>Total Litter vegetation</th>
<th>Depth</th>
<th>Graminoids</th>
<th>Forbs</th>
<th>Dicots</th>
<th>Litter</th>
<th>Selaginella densa</th>
<th>Bare</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td><strong>2009 Spring</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Native</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AW</td>
<td>0</td>
<td>68</td>
<td>0.40</td>
<td>30</td>
<td>1.1</td>
<td>6.0</td>
<td>46</td>
<td>29</td>
<td>12.5</td>
</tr>
<tr>
<td>SHAM</td>
<td>0.67</td>
<td>82</td>
<td>0.75</td>
<td>30</td>
<td>0.9</td>
<td>10.3</td>
<td>72</td>
<td>16</td>
<td>11.1</td>
</tr>
<tr>
<td>GAP</td>
<td>0</td>
<td>85</td>
<td>1.21</td>
<td>21</td>
<td>3.4</td>
<td>7.3</td>
<td>78</td>
<td>13</td>
<td>7.6</td>
</tr>
<tr>
<td>ML</td>
<td>0</td>
<td>69</td>
<td>0.10</td>
<td>33</td>
<td>11.1</td>
<td>14.7</td>
<td>46</td>
<td>0</td>
<td>46.9</td>
</tr>
<tr>
<td>GNP</td>
<td>1.34</td>
<td>74</td>
<td>1.12</td>
<td>36</td>
<td>1.6</td>
<td>6.2</td>
<td>64</td>
<td>72</td>
<td>0.8</td>
</tr>
<tr>
<td>WB</td>
<td>1.01</td>
<td>72</td>
<td>0.22</td>
<td>27</td>
<td>6.1</td>
<td>7.5</td>
<td>53</td>
<td>31</td>
<td>10.2</td>
</tr>
<tr>
<td>Agropyron cristatum</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>AW</td>
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<td>66</td>
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<td>11.8</td>
<td>64</td>
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<td>13.7</td>
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<td>GAP</td>
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<td>75</td>
<td>0.02</td>
<td>38</td>
<td>5.1</td>
<td>5.5</td>
<td>52</td>
<td>1</td>
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<tr>
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<td>4.0</td>
<td>6.3</td>
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<td>5.2</td>
<td>70</td>
<td>12</td>
<td>4.0</td>
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<td>2.7</td>
<td>5.7</td>
<td>99</td>
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<tr>
<td><strong>Early summer</strong></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<td></td>
<td></td>
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Figure 2.1 Granivory rate of *Panicum miliaceum* seeds and seeds of seven common grassland species of the northern Great Plains (n = 40; error bars indicate SE).
Figure 2.2 Granivory rates of *Panicum miliaceum* seeds in native grasslands and *Bromus inermis* stands during 2009 (lower panel) and 2010 (upper panel).
= 1.045, CI = 1.019 – 1.072, \( P < 0.001 \)). At the 10-cm-scale within sites, the cover of Selaginella densa was lower at depredated plots than at random plots in A. cristatum stands (OR = 0.983, CI = 0.969 – 0.997, \( P = 0.016 \)) while no vegetation characteristics were different between depredated and random plots in native stands.

2.5.3 Vertebrate granivores

Peromyscus maniculatus was the most commonly captured granivorous mammal at all sites (Table 2.3) except at White Butte, where Spermophilus tridecemlineatus was most commonly captured in the native grassland and Poliocitellus franklinii and Microtus pennsylvanicus were most commonly captured in Bromus inermis in 2009 and 2010 respectively. Total trap nights for each site ranged from 330 to 495.5.

Commonly observed granivorous birds included Sturnella neglecta (Western Meadowlark), Eremophila alpestris (Horned Lark), Calcarius ornatus (Chestnut-collared Longspur), Anthus spragueii (Sprague’s Pipit), Poecetes gramineus Vesper Sparrow), Passerculus sandwichensis (Savannah Sparrow), Ammodramus bairdii (Baird’s Sparrow) and Spizella pallida (Clay-colored Sparrow).
Table 2.4 Number of small mammals captured per trap-night in 2009 and 2010 in the two grassland types in the northern Great Plains.

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2.6 DISCUSSION

Forb cover and season had the greatest influence on seed removal rates in native grasslands and *A. cristatum* stands. Any differences in removal rates between native grasslands and *A. cristatum* stands appeared to be masked by the larger influence of forb cover and season. Other exotic species have resulted in elevated consumer pressure, negatively affecting native plant establishment (Orrock et al. 2008, Pearson and Callaway 2008), but I found no evidence for granivore-mediated apparent competition in *A. cristatum* stands.

The only habitat characteristic that appeared to affect granivory rates was forb cover, although this relationship only occurred in 2009, suggesting that the importance of forbs is variable. The relationship between forb cover and granivory rate in 2009 could be due to the positive effect of forbs on small mammal abundance. Despite having different preferences for vegetative biomass, both *Microtus pennsylvanicus* (Huntly and Inouye 1987) and *Peromyscus maniculatus* (Hingtgen and Clark 1984, Stapp 2007) often show associations with forbs, which they preferentially consume over grasses (Neal et al. 1973, Hingtgen and Clark 1984). However, forbs are rarely a determinant of abundance or habitat use by grassland birds.
(Dieni and Jones 2003, Davis 2004) or *Spermophilus tridecemilneatus* (Stapp 2007).

The general lack of overall vegetation effects on among-site granivory rates may result from the large spatial distribution of sites as well as the large number of potential granivores. This study was conducted over a larger geographic region than most granivory studies. Because of the large geographic area, vegetation characteristics varied considerably among the sites, which may have made it difficult to identify common among-sites relationships between vegetation characteristics and seed removal. Any effect of vegetation on granivory rates is likely due to vegetation affecting granivore density (Huntly and Inouye 1987) or foraging activity (Bowers 1990). Granivores in this study included several species of birds and mammals, whose habitat preferences and foraging strategies differ from each other (Snyder and Best 1988). The various habitat preferences and foraging strategies among all granivores may have obscured any vegetation effects related to single species of granivores.

In addition to greater seed removal with greater cover of forbs in 2009, seed removal also increased as the growing season proceeded. Bird and small mammal populations typically have a birth pulse in spring and small mammals
can have multiple litters each growing season under suitable conditions (Blair 1940). Therefore, I expected granivore populations and thus granivory to increase throughout the growing season, and this pattern held true. Granivory rates that parallel granivore abundance occur in many plant communities including European forests (Kollmann et al. 1998) and South American deserts (Lopez de Casenave et al. 1998) and grasslands (Murillo et al. 2007). Additionally, seeds often make up a much greater proportion of diet in *Peromyscus maniculatus* and *Spermophilus tridecemlineatus* in July-August than in May-June (Flake 1973) and the greater granivory levels could reflect the development of a search image or foraging that focuses on seeds at this time of year (Tinbergen 1960, Murton 1971).

To accurately determine relative granivory rates, studies must use seeds that are representative of those granivores may encounter in nature. *Panicum miliaceum* seed removal was similar to seven locally abundant species (Figure 2.1), making it a suitable choice.

Unlike *A. cristatum* stands, the *Bromus inermis* stand exhibited greater vegetative cover than the nearby native stand. *Bromus inermis* invasion also appeared to have resulted in a shift in small mammal composition with *Microtus pennsylvanicus* and *Poliocitellus franklinii* being
the dominant small mammals in *Bromus inermis* and *Spermophilus tridecemlineatus* being the dominant small mammal in the native stand. Granivory rates were higher in the *Bromus inermis* stand than in the paired native grassland (Fig. 2.2). Recruitment limitation in *Bromus inermis* stands by small consumers has been demonstrated (MacDougall and Wilson 2007) and the possibility that *Bromus inermis* invasion results in changes in granivore composition and higher granivory rates which limit native plant establishment deserves more research.

Effects of within-sites (within 10- and 50-cm plots) vegetation characteristics on seed removal, determined by comparing vegetation between depredated and random depots at each site, varied by grassland type and scale. Greater seed removal in A. cristatum stands was positively associated with cover of dicots (shrubs and forbs). Most of the cover of dicots in this study comes from forbs, an important source of food for small mammals, yet cover of forbs was not a significant ($P = 0.86$) within-site determinant of seed removal despite its importance among sites. This suggests that the shrub component of dicots, such as *Symphoricarpos occidentalis*, is important in determining seed removal, possibly because it reduces predation risk (Bowers 1988). Seed removal by rodents can
be higher under shrubs than in open microsites (Hay and Fuller 1981, Hulme 1997). However, the opposite pattern can also be true with granivores removing more seed in open microsites than under microsites with vegetative cover (Reed et al. 2006). Despite the higher seed removal rates associated with dicot cover in A. cristatum stands, seed removal in native grasslands was higher in open microsites. These seemingly contradictory results may be explained by the method of vegetation sampling (Daubenmire 1959), which does not distinguish between ground cover and canopy cover. The Daubenmire (1959) method estimates vegetation layers separately so that the area covered by shrubs is recorded, as well as the area of bare ground underneath the shrub. Therefore, seeds removed from bare ground underneath a shrub canopy will be positively associated with both vegetative characteristics. Fine-scale vegetation use by small mammals and birds is usually determined by food and predation risk (Kolter 1984, Longland and Price 1991, Orrock et al. 2004). Rodents respond to perceived predation risk by removing less seed in open microsites than sheltered ones (Bowers 1990, Orrock et al. 2004) as well as removing less seed during nights without cloud cover and with greater moon illumination (Bowers 1990, Orrock et al. 2004). Owls capture North American desert rodents more
frequently in the open than under shrub canopies (Longland and Price 1991). The positive association of bare ground with seed removal in the 50-cm plots in native grasslands may be caused by the greater detection of seeds on bare ground than seeds obscured by litter or vegetation (Vander Wall 1994, Clark et al. 1991, Clark and Kaufman 1991, Reed et al. 2006). In contrast, seed detection did not appear to be the reason for the greater probability of seed removal with higher bare ground in native stands at the 50-cm plots. Bare ground was not important at the 10-cm plots, a more appropriate scale for detection of seeds. The importance of bare ground may be simply due to preferences of granivores like Peromyscus maniculatus and Eremophila alpestris for foraging in relatively more open habitats. This could be a function of species-specific differences in perceived predation risk (Bakker et al. 2009), as some granivore species feel more secure in open areas where predators (e.g., weasels) are more likely to be seen, whereas other granivore species prefer dense cover to hide from other kinds of predators (e.g., raptors).

In addition to vegetation structure affecting seed removal patterns, the reverse can also be true. Granivores can affect plant community composition particularly if they preferentially removal seeds from microsites that are
suitable for plant establishment (Hulme 1997). However, significantly different seed removal among microsites (10-cm-scale) was related only to one vegetation factor. At the 10-cm-scale in A. cristatum stands, seed removal was negatively related to Selaginella densa cover. The lack of seed removal from Selaginella densa should not benefit A. cristatum because Selaginella densa limits A. cristatum seed emergence (Romo 2005). It seems unlikely that Selaginella densa could obscure seeds since it exists in the form of a dense mat with very little vertical growth. Lower seed removal on A. cristatum is possibly due to an avoidance of Selaginella densa by grassland birds (Dieni and Jones 2003).

The most important determinants of granivory levels are likely the species composition and abundance of granivore (Pearson and Callaway 2008). Changes in granivore species composition and increases in abundance following A. cristatum invasion seemed plausible due to increased standing crop (Williams et al. 1992, Pearson et al. 2000, Gosper et al. 2006) or decreased predation risk (Orrock et al. 2008, Mattos and Orrock 2010). Granivory rates in A. cristatum stands, however, were similar to those in native stands, indicating that if a change in food or vegetation structure by A. cristatum occurred, it did not result in
higher granivory rates. Vegetative cover and litter depth are often key determinants of small mammal species composition (Birney et al. 1976, Grant et al. 1982, Morris 1984), and A. cristatum stands had similar cover and litter depth to native stands (Table 2.4). However, along an invasion front, A. cristatum often produces larger tussocks than those produced in a planted A. cristatum stand. These larger tussocks may provide refuge for small consumers, resulting in greater granivory and herbivory on establishing plants near the tussocks, but not in the more open interspaces between the tussocks. This has not been tested though.

2.6.1 Summary

Granivory rates were similar between native grasslands and A. cristatum stands, indicating no evidence of apparent competition through granivory. Forb cover and season had the greatest influence on granivory rates, with granivory rates increasing with cover of forbs and date during the growing season. Effects of forb cover and season on granivory rates appear to result from their effects on granivore abundance. Despite the relationships between granivory rates and forb cover and season in 2009, no variables affected forb cover in 2010, which indicates
uncertainty regarding the importance of forb cover and season on granivory rates. A Bromus inermis stand had greater granivory rates than a native grassland, which may result from greater vegetative cover and deeper litter layers.
3. GRANIVORE SEED PREFERENCES FOR COMMON PLANT SPECIES IN
NATIVE GRASSLANDS AND AGROPYRON CRISTATUM STANDS IN THE
NORTHERN GREAT PLAINS

3.1 ABSTRACT

Granivores could contribute to invasive plant dominance if they preferentially select seeds of native plants over those of invasive plants, thereby limiting native plant establishment. Knowledge of what factors affect granivory in the northern Great Plains is lacking. I used exclosures in native grasslands and stands of the invasive grass *A. cristatum* to determine granivore seed preferences among seven common native and exotic plant species, and to determine if small consumers affected plant species abundances. Seed mimics, which consisted of small pieces of plastic or toothpicks and were similar to seeds in size and weight, were used to investigate seed removal by abiotic factors. Granivores generally did not prefer native seeds to exotic seeds and showed little seed preference among the seven species of seeds, although a slight preference was shown for *Petalostemon purpurea*, a native legume. Seed removal was not related to seed mass for vertebrate granivores, but invertebrates showed a preference for smaller seeds. The exclusion of small
consumers had no effect on either type of plant community after two growing seasons, except in *A. cristatum* stands at one site where invertebrate-accessible plots had significantly greater cover of litter than mammal-accessible plots. The rate of experimental seed mimic removal from seed dishes, presumably due to abiotic factors, was similar to the rate of seed loss during spring. Although rates of mimic loss were significantly lower than rates of seed loss during early and late summer, mimic loss rates were still > 50% of seed loss rates, suggesting that results from seed dishes can overestimate removal rates if abiotic factors are not taken into account. Small consumers did not appear to contribute to *A. cristatum* dominance.

### 3.2 INTRODUCTION

Small consumers can contribute to plant invasions by preferentially consuming seeds and tissues of native plants over those of invasive plants (Cappuccino and Carpenter 2005). For example, in California, the invasive *Brassica nigra* forms stands that are taller and denser than native plant communities. The greater vegetative cover that *Brassica nigra* provides to herbivores reduces predation risk (Bowers 1990) and results in increased small mammal
abundance (Grant and Birney 1979). These small mammals negatively impact native plants but not the invasive Brassica nigra (Orrock et al. 2008, Orrock et al. 2010). The fly Urophora affinis, a biocontrol agent of the invasive forb Centaurea maculosa, elevates Peromyscus maniculatus (deer mouse) populations by providing additional food (Pearson et al. 2000). Peromyscus maniculatus prefer native seeds to Centaurea maculosa seeds, contributing to Centaurea maculosa dominance (Pearson and Callaway 2008).

Alternatively, there may be differences in palatability that favour invaders. For example, cafeteria trials suggest that invasion success by Bromus inermis may be enhanced by the low palatability of its seed compared to that of other grassland species (Everett et al. 1978).

Small consumers have dramatic effects on many plant communities. Birds and ants affect plant communities primarily though granivory (Howe and Brown 1999, MacMahon et al. 2000) while small mammals affect plant communities through both granivory (Howe and Brown 2000, Anderson and MacMahon 2001) and herbivory (Hulme 1994a, Howe and Brown 1999, MacDougall and Wilson 2007). However, small mammals generally remove more seed than birds and ants in North
American herbaceous plant communities (Mares and Rosenzweig 1978, Kelrick et al. 1986, Reed et al. 2004).


The difficulty of accurately predicting granivore impact on plant communities is complicated by seed removal data that may not be representative of seed removal in nature. The seed dish method is the most commonly employed technique, where investigators place seeds in dishes to determine removal rates. However, as Reader (1997) pointed out, the artificial dishes may make the seeds more detectable than they would be under natural conditions. Although some have voiced concern about the suitability of
seed dishes, only Parmenter et al. (1984) and Pérez et al. (2006) have attempted to evaluate the seed dish technique. Permenter et al. (1984) determined that seed dishes violated many of the assumptions necessary to draw biologically useful conclusions, including the assumption that seed removal by each granivore is proportional to that granivores’ true seed removal in the field, and the assumption that seed removal is due exclusively to granivores. Pérez et al. (2006) concluded that the seed dish method overestimates granivory intensity.

Authors of some seed removal studies have cited wind and rain as potentially responsible for seed displacement, which would affect calculated granivory rates (Hulme 1994b, Manson and Stiles 1998). Wind has been eliminated as a factor in some experiments by conducting trials when winds were light (Mittlebach and Gross 1984). However, in the prairies of my study site, winds were rarely light. Also, vegetation and litter were often sparse, providing the seeds little protection from wind. These two factors made conducting trials only during light winds impractical. Methods that do not attract or repel granivores and do not allow seeds to be displaced by wind or rain are likely to yield the least biased results.
I conducted all research in paired sites of native grasslands and *A. cristatum* stands. To determine if granivores were contributing to *A. cristatum* success, I used exclosures to measure relative granivory rates and seed preferences for seven common seeds of native and exotic plants by small mammals, birds and invertebrates. I used seed mimics in conjunction with seeds in seed dishes to determine removal by abiotic factors and their effects on interpretations of seed removal data. I also determined the effect of exclusion of small consumers on plant communities.

3.3 STUDY AREA

I worked at Grasslands National Park (49°22’ N, 107°53’ W), 7 km south of Val Marie, Saskatchewan, and Medicine Lake National Wildlife Refuge (48°28’ N, 104°22’ W), 5 km southeast of Medicine Lake, Montana. Average annual precipitation is 35 cm at Grasslands National Park (Environment Canada, National Climate Data and Information Archive) and 33 cm at Medicine Lake (Western Regional Climate Center) with roughly half of precipitation falling from May–July. Average July temperatures are 18.3 °C at Grasslands National Park and 19.9 °C at Medicine Lake. Average January temperatures are -12.4 °C at Grasslands
National Park and -13.1 °C at Medicine Lake.

Each site contained a pair of grasslands, one dominated by native grasses and one dominated by crested wheatgrass. Paired grasslands had similar topography, soils, and weather. Native grassland vegetation was dominated by *Hesperostipa comata*, *Koeleria macrantha*, and *Bouteloua gracilis*. Common small mammals were *Microtus pennsylvanicus*, *Peromyscus maniculatus*, *Spermophilus tridecemlineatus*, and *Spermophilus richardsonii*. Common granivorous birds included *Sturnella neglecta*, *Eremophila alpestris*, *Calcarius ornatus*, *Anthus spragueii*, *Pooecetes gramineus*, *Passerculus sandwichensis*, *Ammodramus bairdii*, and *Spizella pallida*.

Grasslands National Park sites had not been grazed for > 10 years before the study and were not grazed during the study. At Medicine Lake National Wildlife Refuge, the site was burned in 2005, moderate grazing occurred in the native stand in 2006 and heavy grazing occurred in the *A. cristatum* stand in 2007, but no grazing or burning occurred during the study.

3.4 METHODS

I constructed exclosures to determine seed preferences of small mammals, birds and invertebrates.
These were installed at Grasslands National Park and Medicine Lake National Wildlife Refuge during May 2009 and maintained until August 2010. There were 50 exclosures in each native grassland and *A. cristatum* stand at each site, for a total of 200 exclosures. Within each stand, the 50 exclosures were distributed among 10 stations with each station having five exclosures. The five exclosure treatments at each station were: 1) access by small mammals only; 2) access by invertebrates only; 3) access by birds only; 4) a control treatment with no exclosure; and 5) access by all vertebrates through a pseudo-exclosure that allowed access by mammals and birds, but not invertebrates. The pseudo-exclosure was similar to other exclosures and controlled for exclosures either repelling or attracting granivores.

Exclosures (1.09 m diameter, 0.44 m high) were made with 1.25 cm mesh hardware cloth fencing. To exclude small mammals, I used 15 cm-long ground staples every 1.5 cm around the base of each exclosure to prevent small mammals from burrowing beneath. Ants were removed with ant poison applied on all colonies within the exclosures. Tanglefoot® (The Tanglefoot Co., Grand Rapids, Michigan, USA) was also applied to the ground around the perimeter to exclude crawling invertebrates. I applied ant poison and Tanglefoot
four times each growing season (Blaney and Kotanen 2001, Pearson and Callaway 2008). Birds were excluded with polypropylene netting (1.9 cm) placed over the exclosures. The small mammal-accessible exclosure had three openings (7.5 x 7.5 cm) cut into the fencing at ground level to permit access. I cannot be certain that birds did not enter the mammal-accessible plots through the ground-level opening in the fencing. Pseudo-exclosures had openings at ground level to permit small mammal access, no netting, and only enough ground staples to hold the exclosure in place. Although invertebrates were not excluded from the controls, no invertebrate granivory occurred because seeds were placed on tape and invertebrates were unable to remove them.

3.4.1 Seed removal

I used seeds of eight species common to grasslands in the study area to determine seed preference: two exotic grasses (A. cristatum and Bromus inermis), four common native grasses (Bouteloua gracilis, Hesperostipa comata, Koeleria macrantha and Pascopyron smithii), an exotic legume (Melilotus officinalis), and a native legume (Petalostemon purpurea). Seeds of Bouteloua gracilis, Hesperostipa comata, Koeleria macrantha, Pascopyron smithii
and Petalostemon purpurea were hand-collected from Medicine Lake National Wildlife Refuge. Seeds of A. cristatum, Bromus inermis and Melilotus officianlis were purchased from Big Sky Seeds (Shelby, MT). Eight seed depots, each comprising four seeds of one of the eight species, were placed in each exclosure. Each seed depot consisted of a roofing nail pushed through a small piece of masking tape (2.5 X 2.5 cm) with four seeds stuck to the masking tape. The nail and tape were pushed into the ground with the seeds laying on the tape at ground level. Masking tape is strong enough that seeds were not easily pulled from the tape by wind and water, but could easily be pulled up by rodents and birds.

For the exclosures that allowed access only by invertebrates, four seeds were placed in 3.08-cm diameter petri dishes. A piece of masking tape formed a ramp from the edge of each dish to the bottom of the dish to allow invertebrates to enter and leave. Each dish was buried flush with the ground and a piece of hardware cloth (1.25 X 1.25 cm) was placed over each dish to lower the probability of seed displacement by rain and wind. The eight seed depots within each exclosure were equally spaced with each depot randomly assigned to a location.

I recorded each depot as depredated if less than three
seeds remained. Vertebrate granivores usually eat all seeds upon discovery of a seed depot (Brown et al. 1975, Hay and Fuller 1981, Mittlebach and Gross 1984) and depots in this study exposed to vertebrate granivores typically contained zero or four seeds. Therefore, in instances when three seeds remained, I assumed a seed was removed by abiotic factors and did not record the station as depredated. Invertebrates are less likely to remove all seeds (Brown et al. 1975), but I applied the same rule for determining predation by invertebrates.

In 2010, I used seed mimics to determine seed removal by wind and rain. Seed mimics were similar in size and weight to the eight study species (Table 3.1). I used five different masses of seed mimics made from plastic glitter, confetti or the tips of wooden toothpicks. The seed mimics were placed in petri dishes along with seeds.

In 2009, I conducted seed removal trials at Medicine Lake, during May 24 – June 16, and June 16 – August 6. At Grasslands National Park, I conducted trials during May 27 – June 23 and June 23 – August 12. In 2010, I conducted three trials at Medicine Lake, during May 17 – June 14, June 15 – July 12, and July 13 – August 09. At Grasslands National Park, the three trials were May 19 – June 15, June 16 – July 14, and July 14 – August 15. Melilotus
Table 3.1 Mean mass of seeds (N = 100) and seed mimics (bold font) placed in seed dishes for seed removal trials in 2010.

<table>
<thead>
<tr>
<th>Seed or mimic</th>
<th>Mass (mg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glitter</td>
<td>0.178</td>
</tr>
<tr>
<td>Koeleria macrantha</td>
<td>0.178</td>
</tr>
<tr>
<td>Bouteloua gracilis</td>
<td>0.271</td>
</tr>
<tr>
<td>Confetti</td>
<td>0.623</td>
</tr>
<tr>
<td>Petalostemon purpurea</td>
<td>1.625</td>
</tr>
<tr>
<td>Confetti</td>
<td>1.680</td>
</tr>
<tr>
<td>Melilotus officianalis</td>
<td>2.425</td>
</tr>
<tr>
<td>Bromus inermis</td>
<td>3.000</td>
</tr>
<tr>
<td>Agropyron cristatum</td>
<td>3.049</td>
</tr>
<tr>
<td>Toothpick tip</td>
<td>3.496</td>
</tr>
<tr>
<td>Pascopyron smithii</td>
<td>4.225</td>
</tr>
<tr>
<td>Toothpick tip</td>
<td>5.270</td>
</tr>
<tr>
<td>Hesperostipa comata</td>
<td>5.398</td>
</tr>
</tbody>
</table>
 officinalis data were not used because imbibition in this species occurred frequently even with little precipitation, leading to seed disintegration and problems with identification.

3.4.2 Granivore effects on vegetation

To determine if small consumers had any effect on plant species abundance, I collected vegetation data from plots within all exclosures (Daubenmire 1959). Using 50 X 50 cm plots, I recorded percent cover of total vegetation, live vegetation, litter, graminoids, forbs, woody vegetation, bare ground and all plant species.

Because of differing flowering times between plants, I collected vegetation data in mid-June and mid-August to record the cover data of each species near its highest level of cover for the growing season. I used the highest percent cover value for each species for analysis. Each vegetation plot was marked with stakes to ensure that the same plot was sampled both times.

3.4.3 Data analysis

I used factorial ANOVA (analysis of variance) with site as a random effect and tested for interactions and effects of grassland type, season, granivore taxa and seed
species on granivory rates. Log transformed granivory rates of each granivore taxon were also regressed on seed mass (mg). The dependent variable consisted of an average of granivory rates from the ten stations in each grassland for each unique combination of site, season, granivore taxon and seed species. Vertebrate and invertebrate granivory were analyzed separately. Vertebrate granivory rates were arcsine-square root transformed to improve normality. Seed mimic losses and seed losses were compared using one-way ANOVAs for each season in 2010. I used Student’s t-tests and Tukey’s HSD tests for post hoc analysis of significant main effects. Analyses for granivory data were conducted with JMP 8.0.2 (SAS Institute 2009).

Differences in plant species composition among exclosures were analysed with ANOSIM (analysis of similarity) using station as strata and Bray-Curtis distance matrices with 999 permutations. ANOSIM uses ranked similarities to compare differences within exclosure types to differences between them. ANOSIM produces a p-value and an R-statistic, which indicates the similarity of vegetation among exclosure types. An $R = 1$ indicates that vegetation samples within exclosure types are more similar to each other than they are to samples from other exclosure types. An $R > 0$ indicates that the differences within each
exclosure type are the same as differences among them. Negative R statistics indicate greater differences within exclosure types than among them. I conducted pairwise ANOSIM tests among exclosure types following a significant global ANOSIM result, and conducted ANOVAs for all vegetation categories following a significant pairwise ANOSIM result. All ANOSIM analyses were conducted with R 2.12.0 software (R Development Core Team 2010).

3.5 RESULTS

3.5.1 Seed removal by vertebrates

Granivory rates did not differ significantly between native grasslands and A. cristatum stands in either 2009 ($F_{1,111} = 0.02$, $P = 0.8906$) or 2010 ($F_{1,167} = 0.15$, $P = 0.6948$, Table 3.2, Fig. 3.1). Granivory rates varied significantly among season (trial periods) and granivore taxa. Season had the greatest effect on granivory rates in both years (2009, $F_{1,111} = 152.57$, $P < 0.0001$; 2010, $F_{2,167} = 270.22$, $P < 0.0001$). In 2009, granivory rates were much greater later in the growing season (early summer = 0.74% removal/day, late spring = 0.09%/day, Fig. 3.2). In 2010 granivory rates from late summer (2.34%/day) greatly exceeded rates from early summer (0.25%/day) and late spring (0.30%/day). High granivory rates later in the growing season were
particularly true for Petalostemon purpurea in 2009 (season X seed species interaction, $F_{6,111} = 3.11$, $P = 0.0074$) and 2010 (season X seed species interaction, $F_{12/167} = 5.61$, $P < 0.0001$).

Exclusion treatment affected granivory rates in both years. Granivory rates in control plots (no exclosure; 0.58%/day) were significantly different only from rates in bird-accessible plots (0.33%/day) in 2009 ($F_{3,111} = 3.67$, $P = 0.0144$). In 2010 control plots showed greater seed removal (1.15%/day) than bird-accessible (0.88%/day) or mammal-accessible plots (0.88%/day) ($F_{3,167} = 5.39$, $P = 0.0014$). Granivory in pseudo-exclosure plots was intermediate (0.93%/day) and not significantly different from bird-accessible, mammal-accessible or control plots.

Granivores showed seed preferences among plant species in both years (Fig. 3.3). Petalostemon purpurea and Hesperostipa comata had the highest granivory rates and Koeleria macrantha had the lowest rate in both years. However, in 2009 the rate of Petalostemon purpurea removal was significantly higher than all other species and Hesperostipa comata removal was significantly greater than Koeleria macrantha removal. In 2010, the only significant difference was greater Petalostemon purpurea removal than A. cristatum, Pascopyron smithii, and Koeleria macrantha.
Table 3.2 ANOVA results for effects on vertebrate granivory rates in the northern Great Plains with site included as a random effect.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>2009</td>
<td></td>
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</tr>
<tr>
<td>Grassland type</td>
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<td>0.8906</td>
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<tr>
<td>Granivore taxa</td>
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<td>0.0144</td>
</tr>
<tr>
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<td>Species</td>
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<table>
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<td>Granivore taxa×season×species</td>
<td>36</td>
<td>0.84</td>
<td>0.7271</td>
</tr>
<tr>
<td>Grassland type×granivore taxa×season×species</td>
<td>36</td>
<td>0.92</td>
<td>0.5985</td>
</tr>
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</table>
Figure 3.1 Percent seed removed (mean ± SE) by vertebrate granivores (averaged for bird and mammal accessible plots) by seed species and grassland type (native grassland and *Agropyron cristatum* stands) in 2009 and 2010.
Figure 3.2 Percent seed removed (mean ± SE) by granivore taxa and season in 2009 and 2010 averaged for all seed species. Control plots and pseudo-exclosure plots allowed access by both mammals and birds.
Figure 3.3 Percent seed removed (mean ± SE) by vertebrate granivores (averaged for bird and mammal accessible plots) by seed species and season in 2009 and 2010.
removal. Low Koeleria macrantha removal was due primarily to low removal in native grasslands while low Pascopyron smithii removal was due mostly to low removal in A. cristatum stands (grassland type X seed species interaction, $F_{6,167} = 3.38, P = 0.0036$). There was also a weak grassland type X season X species interaction ($F_{12,167} = 2.05, P = 0.0227$) but it had no effect on interpretations of main effects. Seed mass had no effect on granivory rates in bird ($P = 0.30$), mammal ($P = 0.83$), control ($P = 0.62$) or pseudo-exclosure plots ($P = 0.77$).

### 3.5.2 Seed removal by invertebrates

Seed mimic loss was similar to seed loss in spring 2010 ($F_{1,46} = 0.98, P = 0.328$, Fig. 3.4), but seed loss was greater than mimic loss in early summer ($F_{1,46} = 5.54, P = 0.0229$) and late summer ($F_{1,46} = 7.45, P = 0.0091$). Because seed loss was not greater than mimic loss in spring 2010, I assumed that granivory was responsible for only a negligible amount of seed loss and did not include spring data in the 2010 ANOVA analysis.

Granivory rates were not affected by any factors or interactions in 2009 or 2010 (Table 3.3) except seed mass ($R^2 = 0.493, P = 0.0051$, Fig. 3.5). Smaller seeds were more likely to be removed than larger seeds. Mimic mass was not
Figure 3.4 Mimic and invertebrate seed loss (mean ± SE) of five mimics and seven seed species in 2010. Mimics consisted of small pieces of plastic or toothpicks and were similar to seeds in size and weight. Mimics were used to represent seed removal by abiotic factors.
Table 3.3 ANOVA results for effects on invertebrate granivory rates at two sites in the northern Great Plains with site included as a random effect.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
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<td></td>
</tr>
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<td>0.1523</td>
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</tr>
<tr>
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<td></td>
</tr>
<tr>
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</tr>
<tr>
<td>Grassland type<em>seed species</em>season</td>
<td>6</td>
<td>0.20</td>
<td>0.9728</td>
</tr>
</tbody>
</table>
Figure 3.5 Relationship between seed mass and seed removal by invertebrates ($R^2 = 0.660$, $P = 0.026$). Each point represents the mean seed removal/day of a species.
related to mimic loss ($R^2 = 0.08, P = 0.3090$).

3.5.3 Vegetation composition

Granivore exclusion had no effect on vegetation in *A. cristatum* stands at Grasslands National Park (ANOSIM, $R = -0.2047, P = 0.0342$; Fig. 3.6). The significant p-value arose because there were greater vegetation differences within exclosure types than among them, as shown by the negative R-statistic. Granivore exclusion also had no effect on vegetation in native grasslands at both sites (ANOSIM, Medicine Lake, $R = -0.0247, P = 0.145$; Grasslands National Park, $R = -0.0367, P = 0.239$; Fig. 3.7). ANOSIM indicated a difference in vegetation between exclosure types in *A. cristatum* stands at Medicine Lake but the R-statistic suggested that this difference was weak (ANOSIM, Medicine Lake, $R = 0.0166, P = 0.019$). Pairwise tests revealed differences between invertebrate-accessible and mammal-accessible plots ($R = 0.141, P = 0.002$). Cover of litter was higher in invertebrate-accessible plots than in mammal-accessible plots ($F_{1,18} = 11.14, P = 0.0037$).

3.6 DISCUSSION

3.6.1 Vertebrate seed removal

I found no evidence that small consumers contribute to
Figure 3.6 Non-metric multidimensional scaling ordinations based on Bray-Curtis similarities of vegetation characteristics and species across five treatments in native grasslands and *A. cristatum* stands at Grasslands National Park. Symbols: triangle = control, diamond = invertebrate-accessible, square = bird-accessible, X = mammal-accessible, asterisk = pseudo-exclosure.
Figure 3.7 Non-metric multidimensional scaling ordinations based on Bray-Curtis similarities of vegetation characteristics and species across five treatments in native grasslands and *A. cristatum* stands at Medicine Lake. Symbols: triangle = control, diamond = invertebrate-accessible, square = bird-accessible, X = mammal-accessible, asterisk = pseudo-exclosure.
A. cristatum expansion or persistence through granivory: granivory rates were similar in native grasslands and A. cristatum stands, and granivores showed no preference for native seeds over exotic seeds. In some other situations, the presence of invasive plants has resulted in greater granivory pressure on native species (e.g. Pearson et al. 2000).

Granivores removed more seeds later in the growing season, which was similar to concurrent research done in the area (see Chapter 2) and is likely attributable to increasing consumer abundance during the growing season. Granivores also showed a seed preference, but only for one species, Petalostemon purpurea.

Seed preferences are determined by many factors. Seed size is often an important determinant of seed removal (Mittlebach and Gross 1984, Samson et al. 1992, et Pérez al. 2006). In herbaceous communities, vertebrate granivores commonly prefer the largest seeds among those presented to them (Radtke 2011) because the largest seeds yield the most reward for effort (Azcarate et al. 2005, Howe and Brown 2000, Mittelbach and Gross 1984, Pérez et al. 2006, Reader 1993), yet vertebrate granivores in our study showed no seed size preferences.
Granivore seed preferences are also frequently related to the nutritional and chemical content of seeds (Kelrick et al. 1986), but preferences are variable and often no consistent preference for chemical or physical characters is found (Hay and Fuller 1981). Vertebrate granivores often exhibit a seed preference hierarchy (Hay and Fuller 1981), but this study did not show clear preference or avoidance for most seeds. The only preferred seed was Petalostemon purpurea, a legume with relatively high protein content (McGraw et al. 2004). Protein content is sometimes a determinant of seed preference (Henderson 1990). Because of the general lack of seed preferences in this study, it is difficult to ascribe any seed attributes that would lead to preferential granivory.

Optimal foraging theory suggests that given a choice of multiple seed species, granivores should rank the species by the ratio of seed energy content to seed handling time (Pyke et al. 1977) and some experiments have supported this idea (Pulliam 1980, Kerley and Erasmus 1991). Nonetheless, in nature, granivores will usually eat all the profitable seeds that they find, despite preference hierarchies (Pyke et al. 1977, Pulliam 1980). The similar removal rates of the species in this study may indicate that most of the tested seeds are profitable to granivores.
Those seeds that exhibited greater granivory may have also exhibited greater apparency, or likelihood of being discovered (Henderson 1990).

Granivory rates were higher in control plots (with no exclosures) than in bird-accessible plots in 2009 and bird-accessible and mammal-accessible plots in 2010, indicating that exclosures were successful at excluding birds and mammals and that both birds and mammals acted as granivores. Although pseudo-exclosure plots had fencing and control plots did not, neither plot type excluded birds or mammals. Therefore, granivory rates in pseudo-exclosures were expected to be similar to those in control plots, which they were in both years. However, granivory rates in pseudo-exclosure plots were also not significantly different from bird-accessible and mammal-accessible plots, indicating that the fencing of the pseudo-exclosures may have deterred some vertebrate granivores.

3.6.2 Invertebrate seed removal and mimic loss

Results from the seed mimic experiment showed that the seed dish technique might not be reliable in certain situations. Mimics disappeared at a similar rate to seeds in the first sampling period (spring), indicating that seed loss due to granivory was possibly minimal.
Mimic loss during the second and third sampling periods (both periods were in summer) was greater than mimic loss in the first sampling period. The cause of this difference is unknown. I had expected wind to be a major cause of mimic loss, but the data do not support this hypothesis. At both sites, wind averaged $> 20$ km/h at approximately $1.5$ m above ground for the greatest number of days in the early sampling period, followed by fewer days during the middle sampling period, and the fewest days during the late sampling period (Grasslands National Park, Weather Underground 2011; Medicine Lake National Wildlife Refuge, Western Regional Climate Center 2011). Furthermore, I had expected smaller mimics to be more easily blown from the dishes (Munoz and Cavieres 2006), but mimic loss was also not related to mimic mass. Soil detachment is greater during higher rainfall rates (Rose 1960) and intense rainfall may also displace seeds. I suspect that intense rainfall may be partly responsible for displacing seeds from dishes in the present study, but I cannot evaluate this hypothesis due to insufficient rainfall intensity data.

These results suggest that seed dishes may not be suitable for granivory studies in the Northern Great Plains unless loss due to abiotic factors is quantified. Low
vegetation cover results in seeds being exposed to rain and wind, which may contribute to removal. While few seed dish experiments have attempted to evaluate the abiotic loss of seeds, abiotic loss has been mainly attributed to wind (Munoz and Cavieres 2006) and sometimes rain (Blaney and Kotanen 2001).

Work in shrub-steppe habitat in Wyoming suggested that seed loss due to wind is negligible (Anderson and MacMahon 2001), but research in the Chilean Andes found > 50% seed removal by wind for some species (Munoz and Cavieres 2006). Rates of abiotic seed loss likely will vary depending on the vegetation characteristics of the site, weather, the species of seeds studied, and granivores present. The present study indicates that researchers cannot assume that only granivores are removing seeds from dishes; abiotic seed loss must be quantified in order to accurately estimate seed predation rates.

The only factor that affected seed removal by invertebrates was seed mass, with invertebrates showing a weak preference for smaller seeds. In the northern Great Plains, little research has focused on seed removal by invertebrates except for studies of seed harvester ants (*Pogonomyrmex* spp.) (Kelrick et al. 1986). These large ants sometimes prefer larger seeds (Davidson 1977), but no
Pogonomyrmex spp. were observed or captured in the study area. Ants in this study were smaller than Pogonomyrmex spp., which may explain their preference for relatively small seeds (Kaspari 1996).

3.6.3 Granivore effect on vegetation

After two growing seasons, vegetation was not significantly affected by small-consumer exclosures. The only exception was greater litter cover in plots accessed by invertebrates than in plots accessed by mammals in A. cristatum stands at Medicine Lake. Exclosure studies commonly show that granivores affect seedling densities after experimental seed addition (Howe and Brown 1999, Maron and Simms 2001, MacDougall and Wilson 2007, Fraser and Madson 2008, Bricker et al. 2010), but effects on vegetation are less common in natural communities (Brown and Human 1997, Baez et al. 2006). If an effect is due primarily to granivory rather that herbivory, it will not be evident immediately and may take many years for effects to be apparent (Guo et al. 1995), particularly in communities dominated by perennials. This research was conducted in grasslands dominated by long-lived perennials, making detection of a granivory-effect on vegetation composition difficult after two growing seasons.
In some herbaceous communities, granivory does not appear to alter plant species abundance or composition (Baez et al. 2006). Consumer effects on plant communities often decrease with increasing net primary production (Chase et al. 2000) as precipitation becomes the primary driver of changes in mesic plant communities (Wilson 2007). The present experiment may have been too short to detect any granivore effect in the relatively low precipitation environment of the northern Great Plains, but effects might have become apparent with more time. In the Chihuahuan desert, similar exclosures resulted in few vegetation changes after two years, but differences became apparent after year three and continued to occur after 11 years (Guo et al. 1995).

The importance of granivory is partly determined by the degree of establishment limitation and seed limitation of the various plant species at a site (Maron and Crone 2006, Clark et al. 2007). Most species are both seed- and establishment-limited (Eriksson and Ehrlen 1992, Clark et al. 2007). If establishment limitation is much greater than seed limitation, granivory should have little effect on the plant community (Edwards and Crawley 1999).
3.6.4 Summary

Although native consumers contribute to the success of some exotic plants, consumers in the northern Great Plains appear to affect both native grasslands and *A. cristatum* stands similarly. Seed removal rates did not differ between native grasslands and *A. cristatum* stands, granivores did not prefer native seeds over exotic ones, and consumers did not affect plant species cover or composition in either vegetation type after two growing seasons. Loss of seed mimics from seed dishes indicates that seed removal can occur due to abiotic factors, which must be accounted for to make valid inferences.
4. GRANIVORE SEED SIZE PREFERENCES

4.1 ABSTRACT

Although seed size preference by granivores is relative to the sizes of seeds offered by researchers, preferences are often inappropriately discussed and interpreted as if they are for absolute seed sizes. A review of 18 studies shows that vertebrate granivores prefer relatively small seeds in forests and relatively large seeds in herbaceous communities, although the absolute size of preferred seeds in each is often similar. These results are consistent with predictions of optimal foraging theory. Seed size selection is not only affected by seed size preferences, but also by profitability of seed consumption and by seed apparency. Researchers are encouraged to take heed of optimal foraging theory and both relative and absolute seed size when interpreting seed size preferences.

4.2 REVIEW

Nearly all studies of seed size selection discuss trends as if they are in absolute terms, even though granivores’ seed size preferences are relative to the sizes of seeds presented to them. Many authors also interpret size selection from other studies in absolute terms. For
example, Blate et al. (1998) discussed several studies in which granivores preferred large seeds relative to those offered. Blate et al.’s (1998) research found a granivore preference for small seeds relative to those offered. This was interpreted as a contradiction. However, most seeds in Blate et al.’s (1998) study were fairly large and the relatively small seeds (20–70 mg) that were preferred were still larger than the relatively large seeds that were preferred from the aforementioned studies (Mittelbach and Gross 1984; 2.4–6.9 mg, Podolsky and Price 1990; 5.2 mg).

It is not surprising that different granivores in different plant communities showed similar trends in seed size selection. Optimal foraging theory predicts granivores will choose seeds according to their ratio of food value to handling time (Pyke et al. 1977) and granivore seed selection has been shown to follow this pattern (Vickery 1984). Often, seeds of a certain size are optimal (Davidson 1977, Kerley and Erasmus 1991, Phelan and Baker 1992, Pulliam 1985) and granivore species of similar size commonly show similar seed size preferences (Ivan and Swihart 2000). In herbaceous plant communities, for mammals, birds and sometimes ants, it is relatively large seeds that are closest to optimal size and are therefore preferred (Azcarate et al. 2005, Howe and Brown 2000,
Mittelbach and Gross 1984, Pérez et al. 2006, Reader 1993). The preference for relatively large seeds often breaks down in woody communities where average seed size is much larger than in herbaceous communities (Baker 1972, Moles et al. 2007) and the larger seeds may be too big for optimal foraging by vertebrates (Pulliam 1985). This is particularly true where granivores are of similar size to those commonly present in herbaceous communities (Mendoza and Dirzo 2007). In forest communities, relatively small or intermediate-sized seeds are often preferred over larger seeds (Blate et al. 1998, Mendoza and Dirzo 2007, Moles et al. 2003, Osunkoya 1994) with preferences commonly dependent on granivore body size (Ivan and Swihart 2000, Mendoza and Dirzo 2007). To assess relative and absolute seed size preferences of vertebrates, I compiled data from published granivory studies in herbaceous and woody communities. I used studies that statistically evaluated seed size preference for a minimum of 5 species of seeds. Of the 18 studies used, 14 evaluated preference by vertebrates and 4 did not distinguish vertebrate from invertebrate predation, but used total predation. In the four studies that used total predation, vertebrates were thought to be the dominant granivores.
The compiled data show that the difference in size selection between herbaceous and woody communities is not contradictory since the smaller seeds of forest communities and larger seeds of herbaceous communities are often of similar size (Fig. 1). While there is no single preferred seed size for all vertebrate granivores, preferred sizes from many plant communities tend to converge over a relatively small range of seed sizes. This is likely the result of vertebrate granivores that also tend to converge over a relatively small range of sizes. The range of preferred seed masses is also similar to the global mean seed mass (Moles et al. 2007), which may have implications for the evolution of seed and vertebrate granivore sizes (Hulme 1998b).

Other factors also influence seed selection. The concentration of toxins and chemicals which impact palatability (Henderson 1990, Kollmann et al. 1998, Smith 1987) often increases with increasing seed size (Moles et al. 2003, Osunkoya 1994), as does seed coat thickness and seed coat hardness (Fenner 1983, Osunkoya 1994, Pulliam 1985). These characteristics increase handling time and are inversely related to seed predation rates (Blate et al. 1998, Hau 1997, Howe et al. 2006, Rodgerson 1998) making
Figure 4.1 Seed mass ranges and vertebrate graminivore seed mass preferences of seeds presented in graminivory studies of nine forest and nine herbaceous communities. Each line represents the range of seed masses offered for each seed predation study. ♦ indicates when a seed mass preference occurred at the high, low or intermediate part of the seed mass range. Forest data from left to right from Kollman et al. 1998, Nepstad et al. 1996, Hau 1997, Holl and Lulow 1997, Osunkoya 1994, Blate et al. 1998, Mendoza and Dirzo 2007, Boman and Casper 1995 and Moles and Drake 1999. Herbaceous data from left to right from Marone et al. 1998, Guo et al. 1995, Mittelbach and Gross 1984, Reader 1993, Perez et al. 2006, Hulme 1998a, Kelrick et al. 1986, Munoz and Cavieres 2006 and Booman et al. 2009.
some larger seeds in woody communities unavailable to granivores.

Optimal foraging theory has been underutilized in many seed preference studies. Granivores do not simply choose large or small seeds but rather, choose seeds that maximize their net rate of energy intake (Kerley and Erasmus 1991, Phelan and Baker 1992). Applying this well-supported theory to interpretation of seed preference studies will aid in understanding the underlying reasons for preferences and advance our knowledge of granivory.

Contrary to the observed pattern, the vertebrate granivores studied in Chapter 3 showed no seed size selection. The lack of seed size selection does not necessarily mean that granivores had no seed size preferences. Upon discovering a seed, granivores will typically consume the seed if it is profitable to do so (Pyke et al. 1977, Pulliam 1980). Among seeds that are profitable to consume, the probability of a seed being consumed should equal the probability of that seed being discovered by a granivore. Therefore, it is possible that all seeds offered to granivores in Chapter 3 were profitable to granivores and exhibited relatively equal detectability or seed apparency (Henderson 1990). Seed preferences can be explained by optimal foraging theory,
while the probability of a seed being consumed can be explained by optimal foraging theory and seed apparency.
5. SPECIES COMPOSITION AND ABUNDANCE OF ANTS AND OTHER INVERTEBRATES IN NATIVE GRASSLANDS AND AGROPYRON CRISTATUM STANDS IN THE NORTHERN GREAT PLAINS

5.1. ABSTRACT

The invasion of native grasslands by introduced plants has negative effects on the abundance and diversity of native plants and birds of the Northern Great Plains, but the effects of invasion on important invertebrate communities, such as ants, is unknown. I used pitfall traps to compare ant species richness and abundance and insect species composition of native grasslands and *Agropyron cristatum* stands at two sites. Ant species composition differed between native grasslands and *A. cristatum* stands. However, there were no differences in total ant abundance, abundance of functional groups, or species richness between native grasslands and *Agropyron cristatum* stands. Cover of bare ground and litter were positively correlated with ant abundance, perhaps reflecting effects on temperature. The abundances of other invertebrates were greater in native grasslands than in *A. cristatum* stands, although not significantly so. These results indicate that plant species identity and vegetation structure influence ant communities in the northern Great Plains.
5.2 INTRODUCTION

Ants (Hymenoptera: Formicidae) influence many semi-arid plant communities. In North American desert grasslands, seed harvester ants reduce small-seeded annual plant abundance (Davidson et al. 1984). Ants are the most important post-dispersal seed predators in woodland sites in Australia, where they can reduce seedling recruitment, particularly when seed densities are low (Andersen 1987). Ant nests also affect soil properties, which influence plant abundance, density and composition (Carlson and Whitford 1991, Folgarait et al. 2002). For example, ant nests can decrease soil pH, and increase nutrient concentrations, structural stability and water repellency (Cammeraat et al. 2002).

Despite their importance in many semi-arid plant communities, ants have received little attention in the grasslands of the northern Great Plains. For example, there is no literature on ants in Saskatchewan grasslands other than anecdotal reports. Ants are the major prey item of short-horned lizards, *Phrynosoma* spp. (Powell and Russell 1984), which are found in northern Great Plains grasslands and are listed as a sensitive species by the United States Forest Service and Bureau of Land Management. Knowledge of ant species composition and distribution in potential
Phrynosoma spp. habitats is vital to conservation efforts of these lizards. Additionally, ants are commonly used as bioindicators because they are highly diverse and important in ecosystem function (Rosenberg et al. 1986), and changes in ant species richness and composition often reflect changes in other invertebrate groups (Majer 1983). Therefore, ants have been used as bioindicators of the state of ecosystems associated with land restoration (Majer et al. 1984, Ottonetti et al. 2006), land use (Andersen et al. 2002) and disturbances (King et al. 1998), all of which greatly impact the northern Great Plains. However, to date, ants have not been used as bioindicators in the northern Great Plains.

A. cristatum is an introduced grass from Eurasia that is widespread in the Great Plains (Rogler and Lorenz 1983). A. cristatum stands are associated with lower biodiversity of plants (Christian and Wilson 1999, Krzic et al. 2000) and generally lower diversity of vertebrates (Reynolds and Trost 1980), although vegetation structure also plays on important role in vertebrate diversity in these communities (Reynolds 1980, Sutter and Brigham 1998). I am aware of no research that has assessed the impact of A. cristatum on ant communities.
Vegetation attributes are often predictors of the species composition and richness of ant communities (Majer et al. 1984, Maeto and Sato 2004). Conversely, ant abundance in grasslands is rarely related to abundance of individual plant species. Rather it is related to general characteristics of the plant community, particularly those that affect temperature. Vegetation cover has been shown to affect ant species composition and abundances because of its ameliorating effect on temperature (Retana and Cerdá 2000). Fire alters ant species composition by removing litter and increasing insolation (Andersen 1991), which results in increases of dominant Iridomyrmex spp.

I conducted pitfall trapping to determine if differences exist between native grasslands and A. cristatum stands in the species richness and composition of ants. As well, I examined relationships between vegetation characteristics and abundance of ant species and functional groups. Composition of non-ant invertebrates was also examined.

5.3 STUDY AREA

The study sites were Grasslands National Park (49°22’ N, 107°53’ W), 7 km south of Val Marie, Saskatchewan, and Medicine Lake National Wildlife Refuge (48°28’ N, 104°22’ W;
hereafter referred to as Medicine Lake), 5 km southeast of Medicine Lake, Montana. Average annual precipitation is 35 cm at Grasslands National Park (Environment Canada, National Climate Data and Information Archive) and 33 cm at Medicine Lake (NOAA-Western Regional Climate Center) with roughly half of precipitation falling from May-July. Average July temperatures are 18.3 °C at Grasslands National Park and 19.9 °C at Medicine Lake, while average January temperatures are -12.4 °C at Grasslands National Park and -13.1 °C at Medicine Lake.

Each site contained a pair of grasslands: one dominated by native grasses and one dominated by crested wheatgrass. Paired grasslands had similar topography, soils, and weather. Soils were Mollisols at both sites but Medicine Lake had loam sand to fine sand (USDA-NRCS 2011) while Grasslands National Park had clay loam to loam soil (Saskatchewan Soil Survey 1992). Native grassland vegetation was dominated by *Hesperostipa comata*, *Koeleria macrantha*, and *Bouteloua gracilis*.

Grasslands National Park sites had not been grazed for > 10 years before the study (R. Sissons, personal communication) and were not grazed during the study. At Medicine Lake, the site was burned in 2005, heavy grazing occurred in the *A. cristatum* stand in 2007 and moderate
grazing occurred in the native stand in 2006 (J. Rodriguez, personal communication), but no grazing or burning occurred during the study.

5.4 METHODS

Ants were sampled using five arrays of five pitfall traps each in both native and crested wheatgrass grasslands at each site for a total of 100 pitfall traps (Fig. 5.1). I located each array > 30 m from other arrays. The arrays were arranged like the 5 on a die with 10 cm high sheet metal strips between the pitfall traps to act as drift fences. The corner pitfall traps were 3.2 m apart. Pitfall traps consisted of 100-ml plastic containers with open tops (5.1 cm diameter) that were placed in the soil so that the top of the container was flush with the ground. I filled traps half-full with equal parts 95% ethanol and propylene glycol.

The pitfall traps were installed May 17-19, 2010 and covers were placed over the traps for four weeks prior to operation them to avoid digging-in effects (Greenslade 1973). Traps were operated for 24 hours on June 16-17 and July 13-14, 2010 at Medicine Lake and June 19-20 and July 15-16, 2010 at Grasslands National Park. Invertebrates were identified to order or family and to other functional and
Figure 5.1 Invertebrate pitfall trapping arrays were spaced > 30 m apart and consisted of five pitfall traps and four pieces of sheet metal for drift fences
morphological groups as needed. All ants were pinned and identified to species by James Glasier, University of Alberta, and functional groups were assigned to ant species based on Andersen (1997), who used distribution and behaviour for classification. Ants of the opportunists functional group were considered to be unspecialized species of disturbed sites or other habitats supporting low ant diversity. Cold climate specialists were species with a distribution centered on the cool-temperate zone. Cryptic species were those which foraged predominantly within the soil and litter and had little interaction with ants on the surface.

I collected vegetation data using 50 X 50 cm plots and recorded the percent cover (Daubenmire 1959) of total vegetation, graminoids, forbs, woody plants, litter, bare ground and *Selaginella densa*, a spikemoss. One plot was centered over each pitfall trap and vegetation data were recorded in mid-July.

5.4.1 Data analysis

I summed abundances of invertebrates (excluding ants) over the two sampling periods for analysis. Total invertebrates and all groups of invertebrates were then log-transformed and compared between native grasslands and
A. cristatum stands using sequential Bonferroni-corrected (Holm 1979) analysis of variance (ANOVA).

For ants, I computed rarefaction curves using number of samples instead of abundance (Ellison et al. 2011). I used R statistical software (version 2.12.2, R Development Core Team 2010) for richness analysis. Package “rich” was used to determine differences in ant species richness between sites and between native grasslands and A. cristatum stands within each site. Ant abundance data from both sampling periods were combined and presence/absence was used to determine if ant species assemblages differed between native grasslands and A. cristatum stands. Because sampling did not capture all species of ants present at each site, I estimated total richness using the Chao estimator (Chao et al. 2005) in both grassland types at each site using package “vegan”. I performed analysis of similarity (ANOSIM) using Sørensen distance matrices with 999 permutations to detect differences in ant species composition between native grasslands and A. cristatum stands at each site. ANOSIM produces a p-value and an R-statistic, which indicates the similarity of ant species assemblage among vegetation types. $R = 1$ indicates that all of the most similar ant assemblages from pitfall traps are from the same vegetation. In contrast, $R = 0$ indicates that
the differences in ant assemblages of each pitfall trap within each vegetation type are the same as differences among vegetation types. I performed sequential Bonferroni-corrected (Holm 1979) Fisher exact tests on 2 X 2 contingency tables to determine what species of ants were responsible for significant ANOSIM results.

I used stepwise logistic regression to examine relationships between abundance of ant species and vegetation characteristics. Highly correlated variables ($r > 0.6$) were excluded from logistic regression analyses. Independent variables for all analyses were: site, grassland type, site X grassland type interaction, percent cover of forbs, graminoids, woody plants, litter and bare ground. I used $\alpha = 0.05$ as the significance criterion for removal from the model. I examined the relationships between vegetation characteristics and log-transformed abundance of total ants and each functional group in linear regression. For the nine most abundant species of ants, I summed ant abundance data over trapping dates and used presence/absence of ants in logistic regression. Fisher exact tests and regression analyses were conducted with JMP 8.0.2 (SAS Institute 2009).
5.5 RESULTS

5.5.1 Ants

Between the two field sites I trapped a total of 3,586 ants comprising seven genera and 25 species (Table 5.1). Thirteen species belonged to the opportunists functional group, 11 were cold climate specialists and one was a cryptic species. Twenty-three species were trapped at Medicine Lake and 16 species were trapped at Grasslands National Park. At Grasslands National Park, I trapped 13 species of ants in native grasslands and 13 species in *A. cristatum* stands. At Medicine Lake, I trapped 15 species in native grasslands and 20 species in *A. cristatum* stands. Ant species richness was greater at Medicine Lake than at Grassland National Park (*P* = 0.010). Ant richness was not significantly different between native grasslands and *A. cristatum* stands at Medicine Lake (*P* = 0.110). Total estimated ant richness, estimated using the Chao estimator, at Grasslands National Park was 14.13 (SE = 1.77) in the native grassland and 13.25 (SE = 0.73) in the *A. cristatum* stand. Total estimated richness at Medicine Lake was 26.5 (SE = 17.14) in the native grassland and 44.5 (SE = 31.11) in the *A. cristatum* stand. Sample-based species accumulation curves indicated that continued sampling from the same traps was likely to result in only minor increases in species richness (Figs. 5.2 and 5.3).
Table 5.1 Ant subfamily and species abundances at two sites in native grasslands and *A. cristatum* stands. Functional groups assigned using Andersen (1997). Data in brackets are percent occurrence.

<table>
<thead>
<tr>
<th>Subfamily</th>
<th>Species</th>
<th>Medicine Lake</th>
<th>Grasslands</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Functional group</td>
<td>Agropyron</td>
<td>Agropyron</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>cristatum</em></td>
<td><em>cristatum</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Native</td>
<td>Native</td>
</tr>
<tr>
<td>Dolichoderinae</td>
<td>Tapinoma sessile</td>
<td>115 (76)</td>
<td>216 (76)</td>
</tr>
<tr>
<td></td>
<td>Opportunists</td>
<td>87 (80)</td>
<td>101 (84)</td>
</tr>
<tr>
<td>Formicinae</td>
<td><em>Formica canadensis</em></td>
<td>1 (4)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td>Opportunists</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td><em>Formica comata</em></td>
<td>154 (36)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td>Cold climate specialists</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td><em>Formica laeviceps</em></td>
<td>2 (4)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td>Cold climate specialists</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td><em>Formica lasiodes</em></td>
<td>36 (40)</td>
<td>66 (48)</td>
</tr>
<tr>
<td></td>
<td>Opportunists</td>
<td>4 (4)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td><em>Formica limata</em></td>
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<tr>
<td></td>
<td>Opportunists</td>
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<td>1 (4)</td>
</tr>
<tr>
<td></td>
<td><em>Formica microgyna</em></td>
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<td>0 (0)</td>
</tr>
<tr>
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<td>Cold climate specialists</td>
<td>306 (20)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td><em>Formica montana</em></td>
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<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td>Cold climate specialists</td>
<td>0 (0)</td>
<td>1 (4)</td>
</tr>
<tr>
<td></td>
<td><em>Formica neoclera</em></td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td>Opportunists</td>
<td>2 (8)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td><em>Formica neogagates</em></td>
<td>68 (76)</td>
<td>48 (60)</td>
</tr>
<tr>
<td></td>
<td>Opportunists</td>
<td>54 (56)</td>
<td>22 (44)</td>
</tr>
<tr>
<td></td>
<td><em>Formica obscuripes</em></td>
<td>2 (8)</td>
<td>454 (44)</td>
</tr>
<tr>
<td></td>
<td>Cold climate specialists</td>
<td>7 (24)</td>
<td>2 (8)</td>
</tr>
<tr>
<td></td>
<td><em>Formica obscuriventris</em></td>
<td>8 (4)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td>Cold climate specialists</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td><em>Formica obtusipilosa</em></td>
<td>1 (4)</td>
<td>54 (32)</td>
</tr>
<tr>
<td></td>
<td>Opportunists</td>
<td>7 (12)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td><em>Formica perpilosa</em></td>
<td>17 (28)</td>
<td>39 (28)</td>
</tr>
<tr>
<td></td>
<td>Opportunists</td>
<td>420 (80)</td>
<td>54 (52)</td>
</tr>
<tr>
<td></td>
<td><em>Lasius crypticus</em></td>
<td>54 (64)</td>
<td>30 (36)</td>
</tr>
<tr>
<td></td>
<td>Cold climate specialists</td>
<td>124 (88)</td>
<td>142 (92)</td>
</tr>
<tr>
<td></td>
<td><em>Lasius neoniger</em></td>
<td>29 (28)</td>
<td>163 (60)</td>
</tr>
<tr>
<td></td>
<td>Cold climate specialists</td>
<td>5 (8)</td>
<td>2 (4)</td>
</tr>
<tr>
<td></td>
<td><em>Lasius subumbratus</em></td>
<td>0 (0)</td>
<td>9 (4)</td>
</tr>
<tr>
<td></td>
<td>Cold climate specialists</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td>Myrmicinae</td>
<td><em>Aphaenogaster occidentalis</em></td>
<td>36 (44)</td>
<td>1 (4)</td>
</tr>
<tr>
<td></td>
<td>Opportunists</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td><em>Myrmica crassirugis</em></td>
<td>1 (4)</td>
<td>30 (20)</td>
</tr>
<tr>
<td></td>
<td>Opportunists</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td><em>Myrmica americana</em></td>
<td>42 (44)</td>
<td>425 (68)</td>
</tr>
<tr>
<td></td>
<td>Opportunists</td>
<td>28 (24)</td>
<td>4 (8)</td>
</tr>
<tr>
<td></td>
<td><em>Myrmica fracticornis</em></td>
<td>24 (28)</td>
<td>3 (4)</td>
</tr>
<tr>
<td></td>
<td>Opportunists</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td><em>Myrmica nearctica</em></td>
<td>0 (0)</td>
<td>2 (4)</td>
</tr>
<tr>
<td></td>
<td>Opportunists</td>
<td>0 (0)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td><em>Solenopsis molest</em></td>
<td>25 (44)</td>
<td>8 (20)</td>
</tr>
<tr>
<td></td>
<td>Cryptic species</td>
<td>0 (0)</td>
<td>2 (8)</td>
</tr>
<tr>
<td></td>
<td><em>Temnothorax ambiguus</em></td>
<td>7 (12)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td>Cold climate specialists</td>
<td>6 (20)</td>
<td>4 (8)</td>
</tr>
<tr>
<td></td>
<td><em>Temnothorax rugatulus</em></td>
<td>2 (4)</td>
<td>0 (0)</td>
</tr>
<tr>
<td></td>
<td>Cold climate specialists</td>
<td>13 (32)</td>
<td>17 (40)</td>
</tr>
</tbody>
</table>
Figure 5.2 Estimates of species richness using rarefaction curves for number of pitfall traps versus number of species at Medicine Lake, for one 24 h sampling (open circles) and two combined 24 h samplings (closed circles) in two grassland types: (a) native grassland and (b) Agropyron cristatum. Curves generated using bootstrap estimates.
Figure 5.3 Estimates of species richness using rarefaction curves for number of pitfall traps versus number of species at Grasslands National Park, for one 24 h sampling (open circles) and two combined 24 h samplings (closed circles) in two grassland types: (a) native grassland and (b) *Agropyron cristatum*. Curves generated using bootstrap estimates.
5.5.2 Relationships between ants and vegetation

ANOSIM comparisons showed differences between ant assemblages of native grasslands and A. cristatum stands at Grasslands National Park ($R = 0.0444, P = 0.005$) and Medicine Lake ($R = 0.1353, P = 0.001$). Vegetation data for native grassland and A. cristatum stands at each site is summarized in Table 5.2. Fisher exact tests indicated that abundance of each ant species was similar between native grasslands and A. cristatum stands at Grasslands National Park. At Medicine Lake, Formica obscuripes ($P = 0.0083$) was significantly more abundant in native grasslands than in A. cristatum stands. Aphaenogaster occidentalis ($P = 0.0019$) and Formica comata ($P = 0.0016$) were significantly more abundant in A. cristatum stands than in native grasslands.

The total ant abundance model ($R^2 = 0.27$) included the grassland type X site interaction ($P = 0.0001$), site ($P = 0.0207$) and cover of bare ground ($P = 0.0083$) as significant factors. Total ants were more abundant at Medicine Lake than at Grasslands National Park. However, more ants were captured in native grasslands than in Agropyron cristatum stands at Medicine Lake while the reverse was true at Grasslands National Park. For the opportunists functional group, stepwise regression (model $R^2 = 0.20$) revealed that the grassland type X site interaction
<table>
<thead>
<tr>
<th>Ants</th>
<th>Selaginella</th>
<th>Vegetation</th>
<th>Graminoids</th>
<th>Forbs</th>
<th>Woody</th>
<th>Litter</th>
<th>Bare</th>
<th>dense</th>
<th>Soil texture</th>
</tr>
</thead>
<tbody>
<tr>
<td>Medicine Lake NWR</td>
<td></td>
<td>Native</td>
<td>1106</td>
<td>87</td>
<td>74</td>
<td>79</td>
<td>15</td>
<td>0</td>
<td>Loamy sand</td>
</tr>
<tr>
<td>Grasslands National Park</td>
<td>Native</td>
<td>Agropyron cristatum</td>
<td>399</td>
<td>93</td>
<td>72</td>
<td>46</td>
<td>10</td>
<td>7</td>
<td>Loamy sand to fine sand</td>
</tr>
<tr>
<td>Grasslands National Park</td>
<td>Native</td>
<td>Agropyron cristatum</td>
<td>675</td>
<td>90</td>
<td>78</td>
<td>9</td>
<td>78</td>
<td>20</td>
<td>Loamy sand to fine sand</td>
</tr>
<tr>
<td>Grasslands National Park</td>
<td>Native</td>
<td>Agropyron cristatum</td>
<td>1496</td>
<td>93</td>
<td>76</td>
<td>17</td>
<td>15</td>
<td>79</td>
<td>Clay loam to loam</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Ants</th>
<th>Selaginella</th>
<th>Vegetation</th>
<th>Graminoids</th>
<th>Forbs</th>
<th>Woody</th>
<th>Litter</th>
<th>Bare</th>
<th>dense</th>
<th>Soil texture</th>
</tr>
</thead>
<tbody>
<tr>
<td>Medicine Lake NWR</td>
<td></td>
<td>Native</td>
<td>1106</td>
<td>87</td>
<td>74</td>
<td>79</td>
<td>15</td>
<td>0</td>
<td>Loamy sand</td>
</tr>
<tr>
<td>Grasslands National Park</td>
<td>Native</td>
<td>Agropyron cristatum</td>
<td>399</td>
<td>93</td>
<td>72</td>
<td>46</td>
<td>10</td>
<td>7</td>
<td>Loamy sand to fine sand</td>
</tr>
<tr>
<td>Grasslands National Park</td>
<td>Native</td>
<td>Agropyron cristatum</td>
<td>675</td>
<td>90</td>
<td>78</td>
<td>9</td>
<td>78</td>
<td>20</td>
<td>Loamy sand to fine sand</td>
</tr>
<tr>
<td>Grasslands National Park</td>
<td>Native</td>
<td>Agropyron cristatum</td>
<td>1496</td>
<td>93</td>
<td>76</td>
<td>17</td>
<td>15</td>
<td>79</td>
<td>Clay loam to loam</td>
</tr>
</tbody>
</table>

Table 5.2 Summary of total ants trapped, vegetation and soil characteristics at two sites. All values for vegetation parameters are mean percent cover.
(\(P = 0.0019\)) and cover of bare ground (\(P = 0.0281\)) significantly explained variance, with presence of opportunists being positively related to bare ground. The cold climate specialists model (\(R^2 = 0.09\)) only included the grassland type X site interaction (\(P = 0.0191\)). Logistic regression indicated that site was the only significant predictor of the presence of *Formica lasiodes* (\(R^2 = 0.26, \chi^2 = 27.55, P < 0.0001\)), *Lasius neoniger* (\(R^2 = 0.23, \chi^2 = 24.83, P < 0.0001\)), *Formica perpilosa* (\(R^2 = 0.18, \chi^2 = 6.78, P = 0.0092\)), *Formica neogagates* (\(R^2 = 0.07, \chi^2 = 4.45, P = 0.0349\)) and *Temnothorax rugatulus* (\(R^2 = 0.25, \chi^2 = 22.10, P < 0.0022\)). *Formica lasiodes*, *Lasius neoniger*, *Formica perpilosa*, and *Formica neogagates* were more likely to be found at Medicine Lake while *Temnothorax rugatulus* was more likely to be present at Grasslands National Park. *Myrmica americana* presence (model \(R^2 = 0.23\)) was predicted by site (\(\chi^2 = 11.52, P = 0.0007\)) and woody cover, \(\chi^2 = 4.44, P < 0.0351\)). *Myrmica americana* was more likely to be found at Medicine Lake than at Grasslands National Park and its presence increased with increasing woody cover. No variables significantly predicted presence of *Formica obscuripes* or *Tapinoma sessile*. 
Table 5.3 Arthropods collected in pitfall traps at two sites in native grasslands and *Agropyron cristatum* stands.

<table>
<thead>
<tr>
<th>Order, suborder, family or group</th>
<th>Common name</th>
<th>Medicine Lake</th>
<th>Grasslands Park</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td><em>Agropyron</em> native cristatum</td>
<td><em>Agropyron</em> native cristatum</td>
</tr>
<tr>
<td><strong>Araneae</strong>&lt;sup&gt;1&lt;/sup&gt;</td>
<td>Spiders</td>
<td>228</td>
<td>117</td>
</tr>
<tr>
<td><strong>Coleoptera</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Adephaga</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caribidae</td>
<td>Ground beetles</td>
<td>23</td>
<td>20</td>
</tr>
<tr>
<td>Polyphaga</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Curculionidae</td>
<td>Snout beetles</td>
<td>22</td>
<td>14</td>
</tr>
<tr>
<td>Elateridae</td>
<td>Click beetles</td>
<td>17</td>
<td>0</td>
</tr>
<tr>
<td>Scarabaeidae</td>
<td>Scarab beetles</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Staphylinidae</td>
<td>Rove beetles</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Tenebrionidae</td>
<td>Darkling beetles</td>
<td>14</td>
<td>14</td>
</tr>
<tr>
<td>Unknown Polyphaga</td>
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<td>80</td>
</tr>
<tr>
<td><strong>Diptera</strong></td>
<td>Flies</td>
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<td>111</td>
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<td><strong>Hemiptera</strong></td>
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</tr>
<tr>
<td>Auchenorrhyyncha</td>
<td>Leaf hoppers and spittlebugs</td>
<td>30</td>
<td>14</td>
</tr>
<tr>
<td><strong>Heteroptera</strong></td>
<td>True bugs</td>
<td>162</td>
<td>27</td>
</tr>
<tr>
<td><strong>Hymenoptera</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Formicidae</td>
<td>Ants</td>
<td>1496</td>
<td>625</td>
</tr>
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<td>Velvet ants</td>
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<td>6</td>
</tr>
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<td>Parasitica</td>
<td>Parasitic wasps</td>
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<td><strong>Lepidoptera</strong></td>
<td>Butterflies and moths</td>
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<td>5</td>
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<td><strong>Orthoptera</strong></td>
<td>Grasshoppers</td>
<td>43</td>
<td>206</td>
</tr>
<tr>
<td><strong>Psocoptera</strong></td>
<td>Psocids</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>

<sup>1</sup> Araneae abundances are from the first sampling only. All other abundances are combined from two samplings.
5.5.3 Other invertebrates

I trapped a total of 2,477 invertebrates other than ants (Table 5.3). More invertebrates were trapped at Medicine Lake than at Grasslands National Park ($F_{1,98} = 32.151, P < 0.001$). The abundance of total invertebrates was greater in native grasslands than in *A. cristatum* stands at each site, although not significantly so ($0.10 > P > 0.05$).

At Medicine Lake, grasshoppers (Orthoptera, $F_{1,48} = 56.805, P < 0.0001$) were more abundant in the *A. cristatum* stand than in the native grassland. In contrast, spiders (Araneae, $F_{1,48} = 10.463, P = 0.0022$), click beetles (Elateridae, $F_{1,48} = 8.745, P = 0.0048$) and true bugs (Heteroptera, $F_{1,48} = 22.941, P < 0.0001$) were more abundant in native grasslands than in *A. cristatum* stands. At Grasslands National Park, leaf hoppers and spittlebugs ($F_{1,48} = 32.038, P < 0.0001$) and true bugs ($F_{1,48} = 31.328, P < 0.0001$) were more abundant in native grasslands than in *A. cristatum* stands.

5.6 DISCUSSION

5.6.1 Ant species composition and richness

Ant species composition differed between native grasslands and *A. cristatum* stands, while ant species
richness did not. These findings echo those of many other studies in which habitat alteration or disturbances affected ant composition but not richness. For example, a review of Australian ant communities found that disturbances result in species composition changes, but not necessarily changes in species richness or abundance (Hoffman and Andersen 2003). Studies examining factors such as grazing intensity (Kerley and Whitford 2000, Hoffman 2010), rangeland condition (Nash et al. 2001), plant species invasion (French and Major 2001), restoration, successional stages (Heithaus and Humes 2003, Dauber and Wolters 2005), management regimes (Dahms et al. 2005) or a combination of these alterations (Whitford et al. 1999) typically find changes in species composition but no effect on ant species richness. Although disturbance levels differed within these studies, soil attributes often did not, which may explain why ant species richness did not vary. Soil attributes are typically more important than grazing and vegetation (Bestelmeyer and Wiens 2001, Boulton et al. 2005) in determining ant species richness.

Australian ant species richness is negatively associated with soil moisture (Lassau and Hochuli 2004), perhaps because increasing soil moisture results in a decreased ability of ants to dig (Mikheyev and Tschinkel 2004). Ant
species richness in northern California grasslands decreases with percent clay content and increases with percent sand content (Bestelmeyer and Wiens 2001), probably because of the difficulty in nesting in high-clay soil. Similarly, ant species richness at Medicine Lake, which has sandy soil (USDA-NRCS 2011), was significantly higher than at Grasslands National Park, which has high clay content (Saskatchewan Soil Survey 1992).

5.6.2 Relationships between ants and vegetation

The most important vegetation characteristic associated with ant abundance was the cover of bare ground, and it was always a positive association. This association appeared to have been driven by the opportunists functional group because the cold climate specialists showed no association with bare ground. The relationship may exist because of soil type, as ant abundance increases as soils get dryer (Wang et al. 2001) and sandier (Boulton et al. 2005), and dry and sandy soils also tend to have more bare ground (Lassau and Hochuli 2004, Graham et al. 2009). Insolation levels also increase with bare ground and are important determinants of species composition (Andersen 1991, Retana and Cerdá 2000). Because most ant foraging activity occurs at surface temperatures of 20 to 50 °C
(MacMahon et al. 2000), many ant species in temperate grasslands may select areas with greater cover of bare ground because of its higher temperature, although ants of the cold climate specialists functional group would not be expected to do so. Ants of the opportunists functional group are associated with sites experiencing environmental stress or disturbance (Andresen 1997), which may tend to have more cover of bare ground.

Unlike other species of ants, *Tapinoma sessile* and *Formica obscuripes* were the only abundant species to show no association to site or any vegetation characteristics. This is not surprising because these species are ubiquitous in the Great Plains and inhabit a variety of habitats (Fisher and Cover 2007). Because this research is largely exploratory, future research is necessary to determine the significance and cause of the potential ant-vegetation relationships described here.

Despite the associations I found between ant abundance and vegetation characteristics, both ants and vegetation respond strongly to soil characteristics and the relationships between ants and vegetation may exist only because of their simultaneous response to soil (Boulton et al. 2005). Site was more important to many ant species than were vegetation characteristics, possibly due the
difference in soils between the two sites. Although the literature contains many studies showing associations between ants and vegetation, when soil and vegetation are studied in concert, soil effects on ant abundance and diversity override those of vegetation (Way et al. 1997, Johnson 1992, Bestelmeyer and Wiens 2001, Boulton et al. 2005).

5.6.3 Non-ant invertebrates

Although native grasslands supported greater abundance of non-ant invertebrates than did A. cristatum stands, the differences were only marginally significant. At Medicine Lake, many insect groups were more abundant in native grasslands, but grasshopper abundance was much greater in A. cristatum stands. Grasshopper abundance is frequently higher in A. cristatum stands than in native grasslands (Onsager 2000) and grasshoppers negatively affect native forbs in A. cristatum stands (Branson and Sword 2009). Further research using appropriate methods for all invertebrate taxa (Standen 2000) is needed to determine differences in non-ant invertebrate communities between native grasslands and A. cristatum stands.
5.6.4 Conclusions and future research

Ant richness was similar between native grassland and *A. cristatum* stands, but species assemblages differed. Abundance of ant functional groups was related to vegetation characteristics, but these relationships may be caused by thermal and soil characteristics, which are also related to vegetation and can result in different microclimates for ants. Because ants are often highly and quickly responsive to environmental change, and ant communities of the northern Great Plains appear to be sufficiently rich and diverse, ants may be used as indicator species. Use as indicator species deserves further attention given the current and projected future levels of oil, natural gas, potash and coal extraction in the northern Great Plains. These activities result in removal of topsoil and require reclamation when mining has been completed.

To understand ant communities of the northern Great Plains, more extensive sampling of ants, as well as determination of how soil moisture and texture and other vegetation characteristics affect ants, is necessary. Because spatial distributions of ant species are strongly dependent on interactions with other ants, knowledge of behavioral dominance is also important (Andersen 1992).
6. GENERAL CONCLUSIONS

Plant invasions commonly accompany changes in ecosystem structure and function. Whether these ecosystem changes are the cause or result of plant invasions varies by invader (MacDougall and Turkington 2005). Additionally, interactions can develop after invasion has occurred, which result in stability of the invaded species. These ecosystem alterations can result in feedback loops that are beneficial to the invasive species and detrimental to native ones, and consumers often play a role in these feedback loops. Alterations caused by plant invasions include changes in abundances and species composition of consumers (Braithwaite et al. 1989). Even in the absence of altered consumer dynamics, consumers can still benefit invasive plants if they prefer to consume native plants. To determine plant-consumer relationships, I studied granivory and ant species composition and abundance in native grasslands and A. cristatum stands.

Granivory rates were similar between native grasslands and A. cristatum stands. This was true when using seven locally abundant seed species as well as when using millet seeds over a larger geographic area. Other invasive plants result in greater granivory after invasion of native
communities (Maron and Vilà 2001, Meiners 2007, Dangremond et al. 2010). The increased consumer pressure with invasion in these plant communities is attributed to greater food (Noonburg and Byers 2005, Pearson and Callaway 2008) in the invasive plant stand. However, A. cristatum does not appear to provide consumers with greater food or refuge from predators. Grasshoppers, an important food item for some consumers (Flake 1973, Wiens and Rotenberry 1979), are more abundant in A. cristatum stands than in native grasslands, but I found that many other invertebrates were more abundant in native grasslands than in A. cristatum, suggesting that food for small consumers may not be more abundant in A. cristatum. Invasive species that result in increased consumer pressure on native plants by providing consumers a refuge from predators (Orrock et al. 2008, Mattos and Orrock 2010) is a more common form of apparent competition than is the provision of greater food by invasive plants. This is termed refuge-mediated apparent competition (Orrock et al. 2010) and has been demonstrated for several invasive species (Orrock et al. 2008, Dangremond et al. 2010, Mattos and Orrock 2010). Refuge-mediated apparent competition typically occurs when the invasive species provides greater vegetative cover than the native species (Orrock and Witter 2008, Mattos and Orrock
However, both vegetative cover and litter depth in *A. cristatum* stands are similar to those in native grasslands. Therefore, the two main forms of consumer-mediated apparent competition with invasive species, increased food and refuge for consumers, do not appear to occur in *A. cristatum*.

Although consumer pressure is not higher in *A. cristatum* stands than in native grasslands, granivores can still contribute to exotic plant stability and invasions if granivores prefer native seeds to exotics ones. This has also been demonstrated for some invasive plants. In western Montana, seeds of the strongly invasive *Centaurea stoebe* receive less seed predation than seeds of naturalized or weakly invasive *Centaurea* spp. (Pearson et al. 2011). Greater seed predation of native species than exotic species also occurs for shrubs in eastern North American forests (Shahid et al. 2009). However, the granivores studied here showed little consistent preference among the seeds offered, showing a preference in both years for only one species, a native legume.

Consumer pressure in the northern Great Plains appears to be affected by factors other than vegetation type. Vegetation characteristics (Brown et al. 1975, Thompson and Brown 1991, Sassi et al. 2006) and granivore species
composition (Asquith et al. 1997, Sassi et al. 2006) and abundance (Brown et al. 1975, Murillo et al. 2007) are the factors most often directly responsible for variation in granivory rates. In the present study, granivory rates in paired native grasslands and A. cristatum stands were affected only by forb cover and season and only for one year. A Bromus inermis stand had higher plant cover and greater litter depth than an adjacent native grassland, which resulted in a change in granivore species composition (Birney et al. 1976, French et al. 1976). The Bromus inermis stand also received greater granivory than the adjacent native grassland. The hypothesis that Bromus inermis invasion results in refuge-mediated apparent competition with native plants (Orrock et al. 2010) deserves further attention.

Vertebrate granivores typically prefer relatively large seeds in herbaceous plant communities and relatively small seeds in forests. However, in the present study, vertebrate granivores showed no seed size preferences, even though granivores have demonstrated seed preferences elsewhere in the northern Great Plains. Although seed preferences do exist, granivores often will not ignore seeds that are discovered in order to search for more preferred seeds (Kaufman and Collier 1981, Pulliam 1985).
Although planting of A. cristatum stands does not appear to result in different plant-consumer interactions than those in native grasslands, it does result in different species composition and abundance of ants. Additionally, abundance of ant functional groups was also related to vegetation characteristics. These relationships may be caused by thermal and soil characteristics, which are also related to vegetation. Ants are not important granivores in the northern Great Plains, but they may affect northern Great Plains plant communities in other ways. Ants are important seed dispersers for many plants (Handel et al. 1981), including some invasive plants (Pemberton and Irving 1990, Jensen and Six 2006), but typically will only disperse seeds that have elaiosomes (Mittlebach and Gross 1984) and few plant species in the northern Great Plains have elaiosomes (Lengyel et al. 2010). Ants can also affect the composition and spatial distribution of plant communities (Beattie and Culver 1977, Folgarait et al. 2002). The interactions between ants and plant communities of the northern Great Plains deserve further attention.

In summary, granivores appeared to interact similarly with native grasslands and A. cristatum stands. However, granivory rates in a Bromus inermis stand were higher than
those in an adjacent native grassland. Although seed removal rates were similar between native grasslands and A. cristatum stands, ant species composition and abundance were not. Future research is needed to determine if ants affect native grasslands and A. cristatum similarly. Future research is also needed to determine the interactions between granivores and Bromus inermis invasion and stability.
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APPENDIX A  Animal care clearance certificate.

UNIVERSITY OF
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OFFICE OF RESEARCH SERVICES
MEMORANDUM

DATE: April 21, 2008

TO: Scott Wilson
    Troy Radtke
    Department of Biology

FROM: M. Schmidt
      Research and Ethics Officer

RE: Animal Utilization Protocol – Protocol No. 08-06

The President’s Committee on Animal Care has reviewed your protocol entitled, Small mammal trapping using Sherman live traps (Protocol No. 08-06). This protocol has been granted interim approval. Full approval will be granted at the next meeting of the PCAC. However, you may begin your project with the interim approval in place.

Good luck with your research project. Thank you.

M. Schmidt
Senior Research Officer