

AN ABSTRACT OF THE DISSERTATION OF

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Title: Complexity of Food Web Interactions in a Large Mammal System

Abstract approved:

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Food webs consist of a combination of bottom-up (resource-driven) and top-down (predator-driven) effects. The strength of these effects depends on the context in which they occur. I investigated food web (trophic) relationships between wolf (*Canis lupus*) predation, elk (*Cervus elaphus*) herbivory, aspen (*Populus tremuloides* Michaux) recruitment, and fire. The study setting, in the central portion of the Crown of the Continent Ecosystem, spans the US/Canada border and encompasses Glacier National Park (GNP), Montana and Waterton Lakes National Park (WLNP), Alberta. I stratified my observations across three spatially distinct areas, the North Fork Valley, in the western portion of GNP; the Waterton Valley, in the eastern portion of WLNP; and the Saint Mary Valley, in the eastern portion of GNP. All valleys are elk winter range (low-lying grasslands with patches of aspen). The valleys have three different observed wolf population levels (Saint Mary: low; Waterton: moderate; North Fork: high), which represent three levels of long-term predation risk (the probability of an elk encountering a wolf). Ecological characteristics (e.g., climate, soils, elevation,

plant associations) are comparable among valleys. Fire has occurred in 90% of the North Fork.

My objective was to examine the relative influence of bottom-up (fire) and top-down (predation risk) factors and the context-dependence of these relationships via data gathered during a three-year time span. I found complex elk responses to bottom-up and top-down factors that could influence habitat use by elk. Pellet transect data demonstrated that elk exhibited the same risk reduction behavior at all wolf population levels, even at very low levels. Predation risk variables that provided impediments to detecting or escaping wolves had a similar and negative influence on occurrence of elk (pellet piles), regardless of wolf population density. Fire had a negative effect on elk density and a positive effect on wolf density (per scat piles) in aspen communities where a high wolf population existed. Aspen cover, which may be riskier than open grassland, also had a negative effect on elk density, except at very high wolf levels without fire. The risk of wolf predation alone did not drive elk behavior.

Conversely, focal animal (elk vigilance behavior) data suggested a positive relationship between wolf population and elk vigilance. However, when I deconstructed vigilance, elk demonstrated complex, context-dependent adaptive behavior in response to the long-term risk of predation by wolves. Commonly identified drivers of elk vigilance (group size, impediments to wolf detection and escape) appeared to be important drivers at an intermediate level of long-term predation risk (e.g., Waterton). These drivers ceased to function in this manner when

the long-term predation risk level increased (The North Fork). At high levels of long-term predation risk, vigilance was high, but not driven by these common factors. In some cases, the relationship between vigilance and risk factors was reversed (e.g., group size). And at a low level of long-term predation risk (Saint Mary), elk did not respond to these drivers of vigilance.

When I measured aspen demography (browse, recruitment), browse was lower in the North Fork, where there was a high wolf population, suggesting a top-down effect. However, I found low aspen recruitment in the absence of fire in all valleys, which indicates a bottom-up effect in that aspen is highly fire-dependent. Top-down predictors of aspen recruitment (e.g., plot position and stand size, which are related to predation risk) had no effect on browse levels regardless of wolf population level.

In sum, the risk of wolf predation alone did not drive the food web relationships I observed. Bottom-up and top-down forces worked together in valleys that contained well-established wolf populations, and to a lesser degree in a valley with a low wolf population. Commonly used measures of predation risk responses (e.g., vigilance) reversed their relationship as the wolf population increased. Low aspen recruitment in the absence of fire demonstrates the importance of bottom-up effects. Bottom-up and top-down effects may be important joint engineers of aspen communities. My findings invite deeper inquiry into the interaction between bottom-up and top-down effects in large mammal systems.

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Complexity of Food Web Interactions in a Large Mammal System

By Cristina Eisenberg

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorized release of my dissertation to any reader upon request.

Cristina Eisenberg, Author

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Complexity of Food Web Interactions in a Large Mammal System

CHAPTER 1: GENERAL INTRODUCTION

Cristina Eisenberg

All ecological communities consist of a network through which energy flows. The resulting trophic interactions are typically referred to in ecology as food webs (Paine 1966). The food web in an ecological community is a scientific construct that provides a description of trophic linkages among species. A food web consists of a hierarchy of trophic levels, or groupings, of species of similar trophic status that make up the dynamic core of the community (Elton 2001; Hutchinson 1959). This conceptual simplification enables ecologists to study how communities function (Paine 1969). However, the interactions that make up a food web affect a vast number of species, from microbes to plants to large mammals (Winemiller 1990; Lavigne 1995).

Food webs are structured around three fundamental components. These components are: primary producers, (plants); consumers (herbivores); and predators (Hairston et al. 1960). Predators can include apex predators, defined as a carnivore species that dominates its trophic class (Terborgh et al. 2010), and which can have a strong effect on other food web components (Navarrete and Menge 1996; Soulé et al. 2005).

Food webs involve highly complex energy flows (Winemiller 1990). Energy primarily flows through food webs from the bottom up, via sunlight and resources available to plants. This is termed a bottom-up effect. Bottom-up effects stimulate or reduce vegetation growth (Borer et al. 2005). For example, the amount of soil moisture influences plant growth (Bassett 1963). Availability of nutrients such as

nitrogen and phosphorus may increase after fire, also stimulating growth, although in some cases (e.g., coniferous systems), fire may induce nutrient loss (Agee 1993).

Bottom-up effects include vegetation effects on herbivores, such as availability of food resources (Murdoch 1966).

Predation also can strongly influence movement of energy through a food web, from the top-down (Navarrete and Menge 1996; Paine 2010; Estes et al. 2011).

Trophic cascades are ecological relationships in which an apex predator produces direct effects on its prey and indirect changes in faunal and floral communities at other trophic levels (Paine 1980; Crooks and Soulé 1999). Hairston et al. (1960) first proposed that, across a broad variety of ecosystems, removing predators causes herbivores to consume plants unsustainably, thereby simplifying ecosystem structure and altering energy flow. Ecologists have widely observed that when apex predators such as wolves (*Canis lupus*) are removed, prey irrupt (Leopold et al. 1947; Paine 1969). This permits excessive and unsustainable consumption of food resources and indirectly affects other species dependent on these plant communities (deCalesta 1994; Berger et al. 2001; Bailey and Witham 2002; Hebblewhite et al. 2005).

Hypothetically, returning an apex predator to an ecosystem re-establishes these trophic linkages by reducing prey numbers and making prey more wary (Schmitz et al. 1997; Laundré et al. 2001), and allows vegetation to grow above browse height (Ripple and Beschta 2007), a top-down effect (Polis and Strong 1996).

An ecologically effective population of an apex predator is necessary to produce top-down trophic cascades (Soulé et al. 2003; Estes et al. 2010). Thus the strength of the top-down effect driven by an apex predator depends on the context in which interactions between it and prey occur (Terborgh et al. 2010).

Food webs consist of a combination of bottom-up and top-down effects (Swanson et al. 2010). Strong bottom-up effects that prevail in all systems can buffer or attenuate top-down effects (Polis 1994). Thus, in most ecological settings, trophic interactions do not cascade, they trickle from the top-down, occurring along with bottom-up energy flows. Studies in a variety of ecosystems have documented weak top-down flows, termed trophic trickles: an apex predator is present, but has limited indirect effects on vegetation (Power 1990; Hunter and Price 1992; Strong 1992; McAnn et al. 1998; Halaj and Wise 2001; Dawes-Gromadski 2002; Menge 2005; Kauffman et al. 2010).

I investigated the trophic relationships between wolf predation, elk (*Cervus elaphus*) herbivory, aspen (*Populus tremuloides* Michaux) recruitment, and fire. The study setting, in the central portion of the Crown of the Continent Ecosystem, spans the US/Canada border and encompasses Glacier National Park (GNP), Montana and Waterton Lakes National Park (WLNP), Alberta. I stratified my observations across three spatially distinct areas, the North Fork Valley, in the western portion of GNP; the Waterton Valley, in the eastern portion of WLNP; and the Saint Mary Valley, in the eastern portion of GNP. All valleys are elk winter range (low-lying grasslands with

patches of aspen). The valleys have three different wolf population levels (Saint Mary: low; Waterton: moderate; North Fork: high), which represent three levels of long-term predation risk (the probability of an elk encountering a wolf) (Creel et al. 2008). Ecological characteristics are comparable in all valleys (e.g., climate, soil, elevation, plant associations), and precipitation is distributed similarly throughout the year (Western Region Climate Center 2010; Parks Canada 2011; Achuff et al. 2005; Hop et al. 2007). These valleys shared similar fire histories until recently. Saint Mary and Waterton had no wildfire since 1890. In the North Fork, 90% of aspen stands have burned between 1988 and 2003.

My objective was to examine, using a variety of approaches, the relative influence of bottom-up (e.g., incident radiation and temperature, fire) and top-down (e.g., wolf predation) factors in an aspen community, and the context-dependence of these relationships. I investigated bottom-up and top-down effects. Indicators of these effects included elk browse; aspen recruitment, defined as growth above the height elk typically eat (2.5 meters); and wolf density, as measured by density of wolf scats. Each chapter of this thesis focuses on a different aspect of these food web relationships. My study took place over a three-year time span. Such short-term studies can only provide part of the story about trophic process and pattern (Peterson 2007). However, this study can help elucidate that, as in aquatic systems, these trophic relationships are not simple, linear, or independent of context (Menge and Sutherland 1986).

Ecologists use models to characterize food webs and to provide a framework for exploration of interaction directions and strengths. Such models allow examination of how bottom-up and top-down effects function (Carpenter et al. 1985) and can help quantify these effects (Grace 2006; Reisner 2010). Accordingly, I created a conceptual model to graphically depict the food web I studied (Figure 1.1). This model represents the fundamental components of the wolf→elk→aspen food web, and includes bottom-up and top-down effects. However, many more food web components would be possible, if one were to build an interaction web model for this system. Such a model could contain, for example, humans, songbirds, and mesopredators (e.g., coyotes) (Crooks and Soulé 1999). My intention was to create a simpler model, to illustrate the trophic patterns I observed within a classic tri-trophic perspective (Hairston et al. 1960).

I used three methods/scales to quantify wolf presence. First, I used assessment at the population scale, to determine wolf population by valley. The geographically separate valleys thus represent three different wolf populations. These populations, and the criteria for defining them, are described in Chapters 2-4. Second, I used an index of species density, to determine actual wolf presence within the valleys on a finer scale (McComb et al. 2010, p. 144). This measure was based on counts of wolf scats in transects. This enabled me to compare, for example, wolf presence within a valley in burned and unburned sites, and to stratify my sample by these and other ecological site characteristics (e.g., grass vs. aspen), as recommended by McComb et

al. (2010, p. 144). Third, I used wolf GPS and radio-collar data to establish presence of a subset of individuals in the North Fork. The collar data were used to inform interpretation of my analysis results in Chapter 3.

In Chapter 2, my objective was to investigate the relationship between predation risk perceived by elk and this species' resource selection in its winter range. To measure elk and wolf density, I conducted fecal pellet and carnivore scat surveys in elk winter range in GNP and WLNP during two spring seasons. I then used an information-theoretic approach to fit a series of predictive models that incorporated bottom-up and top-down effects. I included as a predictor the trophic mechanism whereby elk avoid sites with topography, debris, or deadfalls that make it more difficult to see or escape wolves. I also included the bottom-up effects of food and incident radiation.

In Chapter 3, my objective was to examine the relationship between predation risk perceived by elk, as evidenced by this species' vigilance behavior, and the context for this relationship. Here I report on the focal animal observations I completed during two winter seasons. In my analysis, I deconstructed vigilance by examining the variables that make up predation risk in the three valleys, and fitted a model that incorporated those variables.

In Chapter 4, my objective was to explore a variety of environmental influences on the growth of young aspen into the forest canopy, termed recruitment. Here I report on data gathered during two summer seasons. In my analysis, I assessed

predictors of aspen demography, which include herbivory and bottom-up influences. Top-down predictors of aspen recruitment were site topographical characteristics that made it more difficult for elk to see or escape wolves.

In the Conclusion I present variations on my basic conceptual model, to reflect the trophic relationships found in each valley. Collectively, these models provide a synthesis of what I learned about how food webs function and their complexity in a wolf→elk→aspen system. In four iterations of the basic model, I weight the model components (arrows) to depict the strength (from non-existent to strong) of bottom-up and top-down effects (Figure 1.1). Because ecosystems are highly variable, making broad generalizations about how they function is difficult (Essington 2010). However, my conceptual models show the trophic trends that emerged when I synthesized my results.

Ecological context (e.g., modern human land use) has a strong influence on trophic relationships. While my chapters focus on current food web responses within the time frame of my field observations, I acknowledge that this context was created by events that occurred within the last 10,000 years and earlier. More recent factors that shaped the context of my study setting include fire suppression and predator extirpation. Wildlife management and modern land use reduced the scale of elk migration (Houston 1982). I acknowledge these influences in the chapters that follow.

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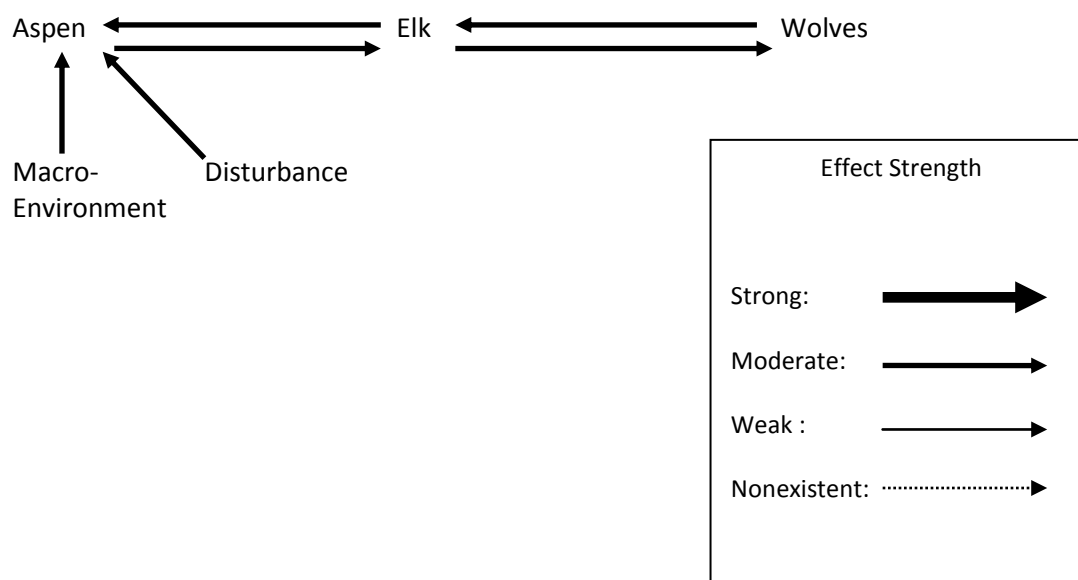
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Figure 1.1. Conceptual model of top-down and bottom-up effects in a wolf→elk→aspen food web. In these conceptual models, Wolves represent predation; Elk represents herbivory; Aspen represents vegetation. The model below portrays a situation where all effects are of moderate strength. These effects can vary (legend), and the model can be adjusted to depict various levels of herbivory (elk impacts on aspen), predation (wolf impacts on elk), aspen recruitment, and disturbance. Arrows pointing up or right represent bottom-up effects. Arrows pointing left represent top-down effects. Effect strength of food web components is quantified as follows: Wolves=wolf density via scat counts; Elk=elk density via pellet counts; Aspen=aspen stem density (relative abundance) in the >2.5 cm ht <5cm DBH size class (e.g. recruiting aspen); Macro-environment=ecosystem resources (e.g., moisture, sunlight); Disturbance=fire. There was no drought during the study, and precipitation was within the normal range for the area. Multiple, large (>5000 ha) fires occurred in portions of the North Fork. No fire occurred in the other valleys.



CHAPTER 2: EFFECTS OF PREDATION RISK ASSESSMENT ON ELK
RESOURCE USE IN A WOLF-DOMINATED SYSTEM

Cristina Eisenberg

Abstract

Food availability and quality, use of habitat, and avoidance of predation are important drivers of herbivore behavior. By altering prey utilization of vegetation, apex predators can cause lethal and non-lethal cascading ecological effects, termed trophic cascades. These predator-prey dynamics shape ecosystems, via top-down (predator-driven) effects. However, in food webs, top-down effects interact with bottom-up (resource-driven) energy. To measure the relationship between predation risk perceived by elk (*Cervus elaphus*) and elk resource selection in its winter range, I conducted fecal pellet and carnivore scat surveys during 2007 and 2008. I stratified my observations across three geographically separate areas: the North Fork Valley, in the western portion of Glacier National Park (GNP), Montana; the Waterton Valley, in the eastern portion of Waterton Lakes National Park, Alberta; and the Saint Mary Valley, in the eastern portion of GNP. The valleys have three different observed wolf (*Canis lupus*) population levels (Saint Mary: low; Waterton: moderate; North Fork: high), which represent three levels of long-term predation risk (the probability of an elk encountering a wolf). In the North Fork, 90% of aspen stands have burned between 1988 and 2003. Based on pellet pile counts, I found a high elk density in all valleys ($\geq 8 \text{ km}^{-2}$). I predicted that elk use of a landscape (e.g., occurrence as measured by elk pellet pile density) would increase with food palatability and solar radiation; would decrease as predation risk increased; and would be influenced by bottom-up and top-down factors. I evaluated these dynamics in burned and unburned sites. I created a set

of predictive models that incorporated bottom-up variables (food nutritional value, Cover Type, in 4 levels: Grass, Aspen, Shrub, Other; Heatload), and top-down variables (impediments to detecting or escaping wolves, View and Debris in three levels: 1=low, 2=moderate, 3=high). I included the interactions of View \times Debris and Cover Type \times Debris. I selected models that best predicted elk pellet pile density ($\Delta AIC < 4$). Elk and wolves were the dominant herbivore and apex carnivore in this system. Measured wolf density (scats 100 m⁻²) was similar in all valleys where there was no fire. In burned areas (North Fork), wolf density was more than one order of magnitude greater than in all other areas, including unburned areas of the same valley. Elk showed a density-mediated response to wolf presence in the North Fork. Elk avoided aspen in all valleys, with the exception of unburned areas of the North Fork. In all valleys, elk density declined as impediments to detecting or escaping wolves increased, independently of wolf density. Cover Type only appeared in the top models in Waterton and the North Fork, where Aspen Type had a negative effect on elk density. While the structure of the food web I studied (apex predator \rightarrow dominant herbivore \rightarrow plants) was simple, the flow of energy and effects along the pathways that linked these food web components was not. The risk of wolf predation alone did not drive elk behavior. Elk avoided aspen, a valuable food source that may be riskier than other food sources, with the exception of aspen stands that had not burned in a valley where wolves spent most of their time in burned areas. Bottom-up and top-down forces worked together in valleys that contained well-established wolf populations,

and to a lesser degree in a valley with a low wolf population. Elk showed complex responses on multiple levels to long-term risk of predation by wolves.

Introduction

Animals select habitat and move within a landscape using complex decision-making strategies. Food (availability and quality) is an important driver of animal behavior and habitat use (Power 1990; Aebischer et al. 1993; Dawes-Gromadski 2002), as is predation (Werner et al. 1983; Navarrete and Menge 1996; Brown, et al. 1999; Schmitz, et al. 2004).

The ability of an animal to assess and behaviorally control its risk of being preyed upon strongly influences feeding decisions (McArthur and Pianka 1966; Werner et al. 1983; Lima and Dill 1990). In a low predator density system, herbivores will eat the most nutritionally profitable foods before browsing foods of lower nutritional value. In a high predator density system, decisions herbivores make about food consumption are also strongly mediated by avoidance of predation (Stephens and Krebs 1986). Landscape features can increase the risk of predation (Hebblewhite, et al. 2005a; Kauffman et al. 2007; Ripple and Beschta 2004), and can cause prey to alter foraging decisions (Trussell et al. 2006; Hebblewhite et al. 2005b; Heithaus et al. 2008). For example, grasshoppers (*Melanoplus femurrubrum*) respond to predation risk by selecting vegetation for foraging (e.g., shrubs) that offers more hiding cover

from predatory spiders (*Pisaurina mira*), despite having a lower nutritional value than grass (Schmitz et al. 1997).

By altering prey utilization of vegetation, predation can cause lethal and non-lethal cascading ecological effects, termed trophic cascades. These food web effects move from predator to prey to vegetation and indirectly affect other taxa (Paine 1969). Apex predators thereby create top-down influences on energy flow in ecosystems (Hairston et al. 1960; Paine 1980; Estes et al. 2011).

Conversely and additionally, energy moves through ecosystems from the bottom-up, from plants. Bottom-up effects include factors that can increase or decrease the abundance of plants (food), such as moisture, disturbance, and solar radiation (Power 1992; Menge et al. 1999). Because plants have primacy in energy production, these dynamics also structure ecosystems by influencing herbivore abundance and resource selection (Murdoch 1966; Schmitz et al. 1997; Borer et al. 2005).

Ecological communities contain both top-down and bottom-up effects that influence animal populations and habitat (i.e., resource) use across multiple trophic levels (Halaj and Wise 2001; Strong 1992; Power 1992; Polis and Strong 1996). In North America, among the most studied wildlife/habitat selection relationships are those that focus on ungulate species. Elk (*Cervus elaphus*) have been the subject of many such studies, due to this species' economic value and its impact on habitat for other taxa via over-consumption of resources (e.g., intense herbivory) (Houston 1982;

Frank and McNaughton 1992; Singer et al. 1994; Wagner 2006). Factors historically linked to elk habitat use include food, climate, topography (Skovlin et al. 2002, pp. 531-533), and human disturbance (Rost and Bailey 1979; Wisdom et al. 2004 a-c; Friar et al. 2005; Shanley and Pyare 2011). In the past decade, scientists have linked predator presence to elk behavior and habitat use. Such studies have concentrated on the potential influence of the gray wolf (*Canis lupus*), identified as an apex predator (Soulé et al. 2003), and considered the leading elk predator (Geist 2002, pp. 394-405; Mech and Peterson 2003).

The mid-1990s northern Rocky Mountain wolf reintroduction created opportunities to test these relationships via a natural experiment (Smith et al. 2003). Emerging research from Yellowstone National Park (YNP) stimulated a scientific debate about whether wolves create behavioral changes in elk, via predation risk, and if so, whether these effects are indirectly influencing other trophic levels, by causing elk to alter feeding choices (Ripple and Beschta 2007; Creel and Christianson 2009; Kauffman et. al 2010).

Optimal foraging theory would predict a shift from elk foraging in high predation risk sites, despite the presence of highly nutritious foods (Stephens and Krebs 1986; Brown et al. 1999). Some authors have documented, via fecal pellet counts, elk avoidance and differential use of aspen (*Populus tremuloides* Michaux) habitat in areas with a wolf population (White et al. 2003; Larsen and Ripple 2005), and avoidance of places with impediments to detecting and escaping wolves (Ripple

and Beschta 2005; 2007; Halofsky and Ripple 2008). Other YNP research alternatively suggests that topography and vegetation characteristics that may enhance wolf predation risk have no influence on elk use of habitat (Creel and Christianson 2009; Kauffman et. al 2010).

I worked from the following primary a priori question: Does risk of predation by wolves influence how elk use a winter range landscape? Several fundamental hypotheses related to elk behavior guided my analysis. First, I asked whether predation risk would be a strong driver of elk habitat use. I then examined the interaction of observed elk responses to bottom-up and top-down factors in their use of habitat on a landscape scale.

I formulated several simple hypotheses in a mathematical model about elk habitat use. I predicted that elk occurrence would increase with food palatability; would increase with solar radiation; and would decrease with an increase in impediments to detecting and escaping wolves. These hypotheses were used to generate models that contained useful predictive variables that best described the data collected, using an information-theoretic approach.

I selected aspen as a focal species for this analysis, because 1) aspen is a species others have found heavily impacted by elk in this ecosystem; 2) aspen is of conservation concern due to its purported decline in the Intermountain West; and 3) to deepen the investigation of wolf-elk-fire-aspen relationships done in previous

scientific studies (Martinka 1978; Singer 1979; White et al. 1998; Barnett and Stohlgren 2001; Beschta and Ripple 2007; Halofsky and Ripple 2008).

Context provides a key factor that influences elk resource selection. Because I studied valleys with three very different wolf population levels (low, moderate, and high), and three correspondingly different levels of predation risk, these case studies enabled me to examine the effects of wolf population (context) on elk population and use of the landscape. However, because I lacked replicates for each valley, I was unable to make statistical inferences based on wolf population. Nevertheless, my research has the potential to indicate broad trends in elk decision-making within the context of long-term predation risk (Creel et al. 2008).

Study Area

The study setting, in the central portion of the Crown of the Continent Ecosystem, spans the US/Canada border and encompasses Glacier National Park (GNP) and Waterton Lakes National Park (WLNP). Located in northwest Montana, GNP contains 4,047 km² of forest, alpine meadows, and lakes. WLNP lies in southwestern Alberta and encompasses 520 km²; biotic communities are similar to those in GNP (Achuff et al. 2005; Hop et al. 2007).

Modern land use (e.g., ranching) and historic and recent wolf management policies in this ecosystem created the context for this research. I studied the following three geographically separate valleys, which are elk winter range (Figure 2.1):

- The North Fork, a Valley located in the northwestern edge of GNP, west of the Continental Divide;
- Waterton, a WLNP Valley east of the Divide; and
- Saint Mary, a Valley in the eastern portion of GNP, also east of the Divide.

Ecological resources are comparable in all valleys (e.g., climate, soil, elevation) and precipitation is distributed similarly throughout the year (Western Region Climate Center 2010; Parks Canada 2011; Achuff et al. 2005; Hop et al. 2007). The measured areas of these study sites (ArcGIS 10.1) are: Saint Mary 1,392 ha; Waterton 2,741 ha; and North Fork 5,705 ha. The valleys are located in the Foothills Parkland Ecoregion, which consists of low-elevation valley bottoms (Achuff et al. 2005; Hop et al. 2007). While ecoregions are broad ecological classifications, within these parks, the Foothills Parkland is limited to the extent of the valleys, and ranges in elevation from 1,024 m to 1,700 m.

As is found throughout the Rocky Mountains, the winter range in this study consists of low-elevation grasslands occurring in sheltered valleys. Winter range offers elk snow depth < 0.7 m, protection from the wind, and additional food sources that consist of patches of aspen, shrubs, and conifers (Singer 1979; 1996; Houston 1982; Skovlin et al. 2002, 531-534; Wagner 2006). Rough fescue (*Festuca scabrella*) is the dominant grass in the valleys. Codominant grasses are the same, and consist of Richardson needlegrass (*Achnatherum richardsonii*), Junegrass (*Koeleria macrantha*),

oatgrass (*Danthonia* spp.), and bluebunch wheatgrass (*Agropyron spicatum*) (Kujit 1982; Lesica 2002; Achuff et al. 2005; Hop et al. 2007).

Geomorphic forces, such as uplift and overthrusting of pre-Cretaceous limestone blocks, shaped the Crown of the Continent Ecosystem landscape (Rockwell 1995). More recently, glaciers deposited long, winding ridges of sand and gravel that resemble embankments, termed eskers (Trenhaile 2007, pp. 188-191). Foundational to the ecology of this region (Achuff et al. 2005; Hop et al. 2007), such geomorphic processes created a heterogeneous topography in elk winter range, which includes grassy uplands and benches, relatively flat valley bottoms, and stream banks.

Wildfire has been present in this ecosystem for many millennia. In the 1890s, European settlers instituted fire suppression (Singer 1979; Levesque 2005), but fire has been allowed to return since 1988. On the east side of GNP, which includes the North Fork Valley, there have been six large (>5,000 ha), mixed-severity wildfires since 1988, the most recent occurring in 2003 (Hop et al. 2007). These fires have cumulatively burned 90% of North Fork aspen stands; the other stands in this valley and the other valleys have not burned since 1890. The 1910 Big Burn, which burned 1.2 million ha in the Intermountain West, did not burn my study sites (Singer 1979; Barrett 1996; Barrett and Arno 1999, pp. 50-64).

Ungulate herbivores in the study area include elk, white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and moose (*Alces alces*) (Achuff et al. 2005), with elk the dominant herbivore (Singer 1979; Martinka 1978; Neff et al.

1965; Hudson and Haigh 2002). Large carnivores include wolf, cougar (*Puma concolor*), grizzly bear (*Ursus arctos*), and black bear (*U. americanus*). Throughout the study area I found via scat analysis (Eisenberg, unpublished data) that wolves preyed primarily on elk, but also on deer and moose. Other studies have found that wolves are the leading elk predator, because bears hibernate when elk are on their winter range, and cougars prey mostly on deer (Kunkel et al. 1999; Logan and Sweanor 2009; Watt 2007-2009; Banfield 2010). I occasionally observed cougars preying on adult elk, although these observations were rare. Cougar density was 9-16 1000 km⁻² in GNP (MFWP 2011) during my study. A cougar density has not been established for WLNP, but their numbers are thought to be robust (Watt 2007-2009).

While all valleys currently offer similar wolf habitat, their wildlife management policies and practices have varied, resulting in low, moderate, and high wolf population levels during the course of this study. Thus the valleys differed in the probability of elk encountering wolves.

Defining a wolf population is problematic and lacks conventions. However, a wolf population that consists of multiple packs, some of which may be producing multiple litters annually, is generally considered high (Fuller et al. 2003). A wolf population that has one breeding pair that produces one litter per year is generally considered moderate (Fuller et al. 2003). A wolf population with no breeding pair is generally considered low to nonexistent (USFWS 1994; Fuller et al. 2003). I defined the wolf populations in the valleys accordingly.

Wolf abundance in the entire Crown of the Continent Ecosystem was very low overall from the 1880s until the mid-1970s, due to European settlement and subsequent wolf extirpation (Flathead Transboundary Network 1999; Weaver 2001; Arjo et al. 2002). Wolves were functionally extirpated from GNP by 1917. In the mid-1970s, wolves from northern Canada began to recolonize this ecosystem naturally, returning to the North Fork Valley in 1979 in low numbers, and were confirmed denning there in 1986 (Singer 1975; Ream et al. 1990; Martinka 1991). In less than 5 years those wolves increased to >20 individuals in multiple (2-3) packs (Pletscher et al. 1997). They have continued to den in the North Fork and other portions of the Crown of the Continent since then, although their population distribution is not uniform. Wolves returned to the Waterton Valley later, and were not confirmed denning there until 1992 (Fox and VanTieghem 1994; USFWS et al. 2010). Parallel data on wolf recolonization were not available for the Saint Mary Valley because wolves had not established a breeding population there.

I characterized Saint Mary as having a low wolf population (Fuller et al. 2003). Although wolves have attempted to recolonize Saint Mary since the 1980s, no stable wolf population has been established in that valley. No breeding pair or pack of wolves occurred there during my study (USFWS et al. 2007; Sime et al. 2009; Sime et al. 2010; USFWS et al. 2010).

I characterized Waterton as having a moderate and variable wolf population (Fuller et al. 2003). Wolves have never been protected outside of WLNP and are

subject to hunting, trapping, and legal take by landowners, although no harvest occurs within the Park. During my study, wolves in that valley numbered between 4-12 individuals within the one pack that denned inside the Park (Watt 2007-2009).

I characterized the North Fork as having a high wolf population (Fuller et al. 2003). During my study, North Fork wolves ranged from 12-29 individuals in 2 packs per agency reports (USFWS et al. 2007; Sime et al. 2009; Sime et al. 2010; USFWS et al. 2010). In 2008, I documented a wolf population of 38 individuals in 2 packs by field observations; both packs produced multiple litters.

Human presence in study sites was minimal during winter. Most of the primary and secondary roads that lead into the areas where I collected data were gated and closed to vehicular traffic from early November through early May. Humans sporadically snowshoed or skied into the valleys. No use of other motorized vehicles (e.g., snowmobiles) was permitted.

Field Methods

I sampled all patches of elk winter range within the valleys. I defined patches of elk winter range as discrete grasslands that contain small to moderately-sized sub-patches (<1 ha) of shrubs and aspen, and have a low elevation (<1800 m) and mean snow depth of <0.7 m (Singer 1979; Martinka 1978; Houston 1982; Skovlin et al. 2002, 537-542). I confirmed my designation of elk habitat in this ecosystem via park Geographic Information System (GIS) maps, which I ground-truthed while doing focal

animal observations in 2007-2009 that involved observing elk in their winter range (Chapter 3, this thesis).

I used ungulate fecal pellet counts and counts of large carnivore scats to derive an index of ungulate and carnivore occurrence, density, and utilization of the landscape in each valley. Pellet counts are the process of estimating, via fecal pellet piles, the relative numbers of mammals in a given area (Neff 1968), and are among the most commonly used indices of ungulate density (Eberhart and Van Etten 1956; Neff 1965; Fuller 1991; Kunkel 1997; White et al. 2003; Radeke et al. 2002, p. 482-484; Forsythe 2005; McComb et al. 2010, p. 144). For elk and deer, such surveys have been used to evaluate these species' responses to roads (Rost and Bailey 1979); habitat preferences (Collins and Urness 1981); population changes (Fuller 1991; Forsythe 2005); and utilization of aspen (White et al. 2003; Ripple et al. 2001). Scat counts are similarly used to survey for carnivores at large spatial scales (Gomper et al. 2006). While similar information can be derived via radio-collar data, the advantage of pellet count surveys is that they can inexpensively estimate the entire observable population using a study site.

Reviews of fecal pellet survey methods have examined the reliability of these methods (Eberhardt and Van Etten 1956; White and Eberhardt 1980; Fuller 1991; Neff 1968; Kunkel 1997; Krebs et al. 2001; White and Feller 2001; Forsythe 2005; St. Laurent and Ferron 2008; Sanchez et al. 2009; McComb et al. 2010 p. 144). If observer and detection bias are addressed, a sample of sufficient size is used, and

counts in rapid decomposition sites (e.g., in areas of high moisture or with a high population of dung-eating insects) are avoided, fecal pellet survey methods provide a reliable manner to evaluate species density and habitat use. These methods are less useful to measure population change over time (Neff 1968; Fuller 1991; McComb et al. 2010, p. 144); or temporal habitat use on a fine scale, due to variability in color change in pellets as they age (Sanchez et al. 2009). Additionally, they can present statistical analysis challenges, such as over-dispersion of data. Pellet count data by nature will be aggregated for ungulates that form herds (Geist 2002, pp. 389-433; Neff 1968; White and Eberhardt 1980).

Finally, scat counts can be biased by detectability and behavior by species. For example, cougars sometimes cover their scat, while other carnivore species do not (Murie et al. 2007). This could cause counts of cougar scats to be lower than in actuality. Wolves deposit scat as territorial markers, so wolf scat presence may be an indicator of wolf territories, beyond wolf density (Harrington and Asa 2003).

My surveys took place between snowmelt and green-up, because snow cover and tall grass can diminish pellet and scat detectability (Neff 1968; Lehmkuhl et al. 1994). I surveyed Waterton and Saint Mary in spring 2007, and the North Fork in spring 2008. To reduce observer bias, a single observer conducted all counts, with assistance in the field. I confirmed identification of carnivore scats via a DNA test of randomly selected carnivore scats ($n=11$ scats), and obtained results of 100% detection accuracy.

Decomposition rates and manipulation or consumption of scats by animals could bias studies that use scat to investigate life-history parameters (Sanchez et al. 2004). To test persistence, I observed wolf scat near known wolf dens in a variety of terrain. Most wolf scats tended to persist for one year. They were not moved by other species during the period of observation. I assumed that carnivore scats would have similar detectability and persistence across cover types, including the burned-unburned contrast, because these scats were very large (e.g., >2 cm in diameter), and because data were collected in spring between snowmelt and greenup, when vegetation did not interfere with detectability.

Pellet transects were 2 m wide and 1 km long. I used this design, versus circular or square plots, to best capture landscape heterogeneity (Neff 1968; Forsythe 2005). A large-scale sampling strategy is indicated for carnivore scat surveys (Gomper et al. 2006). I also selected this transect design to match methods used by Parks Canada in Banff National Park, Alberta (Thomson 2002; White 2007).

Each pellet transect was associated with one or more aspen stands. In the study setting, aspen are well distributed in elk winter range, and tend to appear as discrete patches, generally <1 ha in area, within a grass matrix. (Achuff et al. 2005; Hop et al. 2007). While all pellet transects ran through an aspen stand, transects encompassed a variety of cover types and geographic variation, to capture the range of habitat variation available to elk, as recommended by Neff (1968; Forsythe 2005).

Pellet transects were oriented on a chosen azimuth (measured with a sighting compass, 1°-360°), parallel to the elevational gradient of the landscape (Neff 1968), which trended east-west throughout all valleys (Achuff et al. 2005; Hop et al. 2007). Pellet transects began from a random start <25 m in from the northern or southern edge (randomly determined) of each elk winter range patch. Thereafter, pellet transects were positioned systematically, parallel to one another every 50 m in each patch. All transects were straight and a full 1 km in length. I subdivided pellet transects into 20 contiguous 50 m sub-transects, and defined the sampling unit as the 50 m sub-transect.

With pellet counts, sampling intensity depends on a variety of factors, such as density of wildlife utilization of a landscape. Sampling intensity was determined by my need to accurately capture data from species whose presence in the landscape may have been low (e.g., the carnivores) (Hutchinson 1959; Elton 2001). A post-hoc power analysis conducted on similar pellet transect data in Banff National Park suggested a minimum sample size of 160 2×50 m sub-transects (Whittington and White 2007). A robust sample was further indicated by the potential over-dispersion of data from pellet counts (White and Eberhardt 1980), and the complexity of the models I intended to fit. My sample size thus consisted of: North Fork $n=1820$ sub-transects (91 full transects); Waterton $n=2200$ sub-transects (110 full transects); and Saint Mary $n=740$ sub-transects (37 full transects). I evenly sampled all elk winter range in the valleys, using the same sampling intensity.

A secondary objective was to confirm the identity of the dominant ungulate and carnivore in this system and create an index of their densities. Thus, in each sub-transect, I counted the number of piles of elk, deer, and moose pellets, and scats of all large predators (e.g., wolf, bear, cougar), as well as those of the mesopredator (mid-sized predator), the coyote (*Canis latrans*). While coyotes are not a primary elk predator in this ecosystem (Kunkel et al. 1999), they can contribute significantly to food web dynamics involving ungulates (Soulé et al. 2005; Berger and Gese 2007).

Each count consisted of a pile of pellets, which corresponded to a single defecation incident. I defined a pile as five or more pellets (Neff 1968) located within a transect. While diet can greatly influence elk pellet color when fresh, as pellets age and decompose, they turn gray. In high ungulate density areas, I was able to reliably identify discrete pellet piles by color. I did not count pellets when they were wet (e.g., from rain), as moisture darkens their color, rendering old and new pellets indistinguishable. If it began to rain while we were working, I halted sampling until the pellets dried out, to avoid detection bias. Only intact pellets were counted (Forsythe 2005). I was unable to differentiate deer pellets by species (e.g., *O. hemionus* versus *O. virginianus*).

At the start of each count, a transect tape was positioned to run along the center of the sub-transect, length-wise. From the starting end of the tape, I measured Universal Trans Mercator (UTM) grid coordinates and elevation with a Global Positioning System (GPS) hand-held unit (in meters; error \pm 2-6 m); aspect (arcsine

transformation; ranging from 1°-360°) with a sighting compass; and slope (percent) with a clinometer. The count progressed along the transect line. All counts were cross-checked to verify accuracy.

I identified the dominant cover type (e.g., Grass, Aspen, Shrub, Other) in each sub-transect using visual assessment. These land cover types denoted broad food types utilized by elk in winter in the Rocky Mountains (Constan 1972; Hobbs et al. 1981; Canon et al. 1987; Cook 2002 pp. 288-296), and specifically in Crown of the Continent Ecosystem (Wasem 1963; Martinka 1978; Singer 1979). Shrubs occurred in a mix of serviceberry (*Amelanchier alnifolia*), western snowberry (*Symphoricarpos occidentalis*, *S. albus*), and rose (*Rosa* spp.). Western snowberry and rose provide low nutritional content, while serviceberry provides high nutritional value (Cook 2002, p. 288-296). The Other level was designated for cover types that offer low to negligible nutrition (Constan 1972; Hobbs et al. 1981; Canon et al. 1987; Cook 2002 pp. 288-296) and consisted of lodgepole pine (*Pinus contorta*), spruce (*Picea* spp.), rocks, and bare mineral soil. While bare mineral soil may attract elk as a salt source, elk do not rely on salt for nutrition and thrive without it (Skovlin et al. 2002, p. 544).

The need of an elk to conserve energy in winter influences its landscape use (Ager et al. 2003). In winter range, elk tend to use south-facing slopes, because these retain more heat and are the first to become free of snow, which can increase plant availability (Chen et al. 2002; Skovlin et al. 2002, pp. 536-537). Accordingly, I estimated the effect of landscape heat retention capability on elk utilization. To do this

I calculated Heatload, which incorporated the sub-transect slope and latitude, in radians, per McCune and Keon (2002). To approximate Heatload, I folded aspect (cosine transformed) about the north-south line. To more accurately depict the trajectory of the sun, aspect was shifted from a maximum on south slopes to a maximum on southwest slopes and a minimum on northeast slopes:

$$\text{Folded Aspect} = 225 - \text{Aspect}$$

Heatload provides an index of potential direct incident radiation and temperature. Because it is a unitless index, it can't be converted into a cumulative measure of temperature, such as degree days. It does not account for cloud cover and shading by adjacent vegetation or topography (McCune and Keon 2002).

I identified landscape attributes that could create predation risk (view impediments and debris), and rated these elements on a categorical scale as low, moderate, or high, (Table 2.1). Areas of high view impediments or debris are potentially risky places for elk to be in an ecosystem that contains wolves, because they hamper the ability of an elk to detect or escape wolves (Ripple and Beschta 2004).

My data represented a 3-year deposition of ungulate pellets, as in this ecosystem, ungulate pellets take approximately 3 years to decompose in elk winter range (White 2007). I did not test pellet decomposition rate. Data for carnivore scats, which have a rapid decomposition (Thomson 2003), provide a 1-year window into carnivore activity. The discrepancy between ungulate and carnivore fecal matter

decomposition rates did not create an issue, because I did not use these data to make inferences about carnivore use of habitat beyond the 1-year time frame of the survey.

Analysis

I evaluated summary statistics for all variables to determine trends and plotted densities for elk, deer, wolves, bears, and cougars. I calculated summary statistics (mean, 95% confidence interval) of the number of pellet piles and individual carnivore scats, per sub-transect (100 m^{-2}) by species. I took the mean by species for each valley, and stratified this sample to examine relationships to factors such as predation risk and food. I focused on Aspen and Grass Cover Types because they are important cover types used by elk in the winter range I studied (Marktinka 1978; Singer 1979), and because they represent two extremes (grass=low; aspen=high) in terms of impediments to detecting or escaping wolves. Elk prefer grass over aspen, and use aspen primarily after grass has been depleted in winter (Skovlin 2002, pp. 531-533). I used a modeling approach to explore the influence of other cover types (e.g., shrub, conifer, bare mineral soil) on elk pellet pile density. I tested for fire effects in the North Fork only, when sample size permitted.

For each valley, I calculated elk actual densities km^{-2} in winter range. I cross-checked elk density results against aerial count data, per Neff (1968). I was unable to perform a similar calculation for deer, due to the comingled presence in the study area

of migratory (mule) and non-migratory (white-tailed) deer in unknown quantities, and lack of aerial count data for deer.

To calculate elk actual density I multiplied the mean density of elk pellet piles per sub-transect (100 m^{-2}) in the entire valley by 10,000 (1 km^{-2}). I assumed that elk have a mean defecation rate of 12.52 times per day (Neff 1965), and that elk pellets take 3 years to decompose in this ecosystem (White 2007). Defecation rate can be influenced by food quality and quantity (Neff 1968), and decomposition rate can be influenced by precipitation and insects (Lehmkuhl et al. 1994). I felt comfortable using a defecation rate that represents a mean among defecation rates observed for both captive and free-ranging elk and deer (Neff 1965; 1968). In the study area, standing water and heavy precipitation did not present issues, nor did infestations of dung-eating insects.

I applied the formula:

$$\phi = \frac{[\alpha]/12.52/3}{\beta}$$

where

ϕ = mean elk density km^{-2}

α = mean piles of pellet piles km^{-2}

β = days per year elk spent in their winter range

I quantified the number of days elk spent in their winter range per year via my year-round field observations and park records (Watt 2007-2009). In the Rocky Mountains, the period of ungulate occupancy of winter range for migratory species

can be estimated within reasonable limits by performing diligent field observations (Neff 1968). Elk spent 203 days in Saint Mary winter range (November 20-June 10); 314 days in Waterton winter range (August 15-June 15); and 203 days (October 15-May 6) in the North Fork. These dates remained consistent during my study (Watt 2007-2009). In Waterton, approximately 18% of the herd was non-migratory, per elk GPS-collar data (Eisenberg, unpublished data). I accounted for this by incorporating the proportion of the herd present during summer months into density calculations, per Neff (1968). I tested the accuracy of elk density results by comparing them to concurrent WLNP aerial survey data. My results fell within 10% of Park counts. Elk aerial count data does not exist for GNP, so I was unable to similarly verify results in that park.

I used mean elk pellet piles as the response variable. Explanatory variables included bottom-up effects (Cover Type, Heatload), top-down effects (View, Debris—impediments to detecting and escaping wolves), and location effects (Northing, Easting). I tested for normality and found the data (number of pellet piles) non-normally distributed, with a strongly skewed distribution (e.g., range: 0-276; mean=28, Table 2.2; Appendix A). Because the data were so skewed, and were count data (not continuous data), I had to use a gamma distribution after first trying Poisson and negative binomial distributions in a generalized linear model. A gamma distribution has a mean/variance relationship (σ^2/μ^2) that enables it to incorporate tremendous variance and change (McCullagh and Nelder 1982). I was unable to graph

the effects of Heatload on the number of elk pellet piles because of issues presented by the non-normal distribution of the response variable.

I used model selection based on Akaike's Information Criterion (AIC) (Burnham and Anderson 2002) to identify and investigate the effects of variables that influenced the occurrence of elk pellet piles. As is customary in this approach, I began by generating a set of specific hypotheses (Table 2.4). These hypotheses guided me in developing variables (Table 2.5) and biologically plausible models (Table 2.6), which I then compared using model selection methods (AIC). Models included bottom-up variables (Cover Type, in 4 levels: Grass, Aspen, Shrub, Other; Heatload); top-down variables [View, in 3 levels, low (V1) to high (V3) and Debris, in 3 levels, low (D1) to high (D3)]; and location coordinates (Northing, Easting) (Table 2.6).

I developed a set of 40 models from my specific hypotheses (Table 2.6), and fit the same set of models in each valley. I included models testing specific interactions. For example, I incorporated interactions between impediments to detecting wolves (View) and impediments to escaping wolves (Debris), to determine whether these effects worked together, as both factors can affect the ability of an elk to avoid wolf predation (Ripple and Beschta 2004), and may be collinear. I also tested the interaction between Cover Type (i.e., palatability, food) and impediments to escaping wolves (Debris), as Cover Type may contribute to impediments to escaping wolves (e.g., Grass, Shrub and Aspen provide different terrain). I wanted to know whether these interactions influenced elk pellet pile occurrence when all other variables were

considered. Sources of variation were all non-fixed effects, i.e., Cover Type, Heatload, View, and Debris.

I fitted a generalized linear model to describe $G(\mu)$, elk mean vigilance, for a set of p explanatory variables, structuring this model as follows:

$$G(\mu) = \beta_0 + \beta_1 X_{1i} + \beta_2 X_{2i} + \beta_3 X_{3i} + \beta_4 X_{4i} + \dots + \beta_p X_{pi} + \varepsilon_i$$

where $\varepsilon_i \sim N(0, \sigma^2/\mu^2)$ and all the ε_i and ε_i s are independent, and $\beta_1 \dots \beta_p$ are the linear coefficients associated with the explanatory variables, $X_1 \dots X_p$, respectively. I expressed the expected elk value of elk pellet piles (that is, the mean density of elk pellet piles) with the mixed linear model:

$$G(\mu) = \beta_0 + \beta_1 X_{1ijkl} + \beta_2 X_{2i} + \beta_3 X_{3ijk} + \beta_4 X_{4ijk} + \beta_3 X_{3ijk} \times \beta_4 X_{4ijk} + \beta_1 X_{1ijkl} \times \beta_4 X_{4ijk} + \beta_5 X_{5i} + \beta_6 X_{6i}$$

where

Y	natural log transformed elk pellet piles,
X_{1ijkl}	Cover Type ($ijkl$ = Grass, Shrub, Aspen, Other),
X_2	Heatload, an index,
X_{3ijk}	View (ijk = V1, V2, V3),
X_{4ijk}	Debris ($ijkl$ = D1, D2, D3),
$X_{3ijk} \times X_{4ijk}$	the interaction of View and Debris,
$X_{1ijkl} \times X_{4ijk}$	the interaction of Food and Debris,
X_5	Easting,
X_6	Northing

with the variance of a single observation given by $\text{Var}(Y_i | X_1 \dots X_p) = \sigma^2/\mu^2$.

I did not include carnivore density as an explanatory variable due to the low numbers of carnivores present, which would have created orthogonality issues (e.g., inadequate representation in models when all other levels of all other variables were considered). Instead, I examined carnivore effects via predation risk factors.

The sub-transects were likely subject to spatial auto-correlation issues, due to elk herding behavior (Geist 2002, pp. 389-433; (Neff 1968; White and Eberhardt 1980). I used several tests of independence. In interpreting these and other statistical analyses I used a p -value of 0.05 as the upper threshold for statistical significance. To interpret p -values, I employed criteria recommended by Ramsey and Schafer (2002, p. 46) in which p -values $>0.05 < 0.10$ provide suggestive, but inconclusive evidence; $\leq 0.05 > 0.01$ provide moderate evidence; and ≤ 0.01 provide convincing evidence of statistical significance. A variogram of the deviance residuals indicated spatial dependence of the variables, with gamma leveling off at 200 m in each valley (Appendix B; Appendix E). I obtained Moran's I statistics of $p < 0.00001$ in all valleys. While the above tests showed evidence of spatial autocorrelation, due to a large sample size, my findings can be used to identify trends in the factors influencing elk habitat use of the valleys.

I next explored the results of adjusting the sampling strategy statistically. Neff (1968) suggests that the most efficient sampling strategy statistically is one where the interval between plots along the transect (sub-transects) is equivalent to the interval

between adjacent transects. I tested this by creating new datasets that only included data from alternate sub-transects, and in which I staggered the sub-transects in adjacent transects. In the North Fork, I obtained a higher Moran's I statistic ($p=0.03$). While this provided moderate evidence of spatial autocorrelation, the resulting dataset ($n=220$) was so reduced that I did not consider it adequate for the data to be orthogonal, given the complexity of my model. Finally, to further explore and address spatial autocorrelation issues with these data, I fitted an additional set of models that included the UTM grid coordinates (Northing and Easting) (Table 2.6).

I tested model goodness-of-fit via an information-theoretic approach (AIC). While AIC allows data-based selection of the most parsimonious model that best describes the effects supported by the data, an information-theoretic approach allows inferences to be based on more than one model (Burnham and Anderson 2002, p. *viii*). AIC enables the analyst to identify variables that play a role in explaining the observed variation in the response variable. Models that best approximate the effects described by the data have the lowest AIC score. Models within 4 Δ AIC values of the best model have considerable support (Burnham and Anderson 2002, p. 446). All variables in the models within this range are then evaluated as important or useful predictors of the response variable. This enables exploration of ecological relationships (Johnson 1999; Hobbs and Hilborn 2006).

Sample sizes (sub-transects) in all valleys were sufficient for AIC model-fitting. However, I lacked a sufficient sample size to permit separate AIC model-

fitting for North Fork unburned sub-transects. Given the orthogonality issues presented by a reduced dataset, I combined the data for all North Fork sub-transects. An alternative analysis could involve reducing the number and complexity of the models and variables to allow a comparison of burned and unburned sub-transects in this valley.

I reported the scale parameter, AIC, and Δ values. I used TIBCO Spotfire S+ and SAS v9.1 (SAS Institute, Cary, NC, USA) software for analyses, using a mixed model approach and quasi-likelihood estimation methods (QAIC). A quasi-likelihood approach entailed manually ranking and calculating the differences between the models, using AIC. QAIC is indicated for count data, to account for potential overdispersion (Burnham and Anderson 2002, p. 70).

Results

Elk actual densities were 21 km⁻² in Saint Mary; 24 km⁻² in Waterton; 9 km⁻² in North Fork sites with no fire; and 8 km⁻² in North Fork sites with fire. Relative densities (absolute pile densities) of elk, deer, wolf, cougar, bear, and coyote were evaluated. (Tables 2.2 and 2.3). The mean elk density was 24.24 ± 1.34 (100 m⁻²; 95% CI) in Saint Mary; 28.25 ± 1.48 in Waterton; 11.09 ± 1.47 in North Fork sub-transects with no fire; and 9.94 ± 0.71 in North Fork sub-transects with fire. Deer mean density was 0.16 ± 0.04 in Saint Mary; 1.15 ± 0.09 in Waterton; 2.2 ± 0.35 in North Fork sub-transects with no fire; and 3.49 ± 0.13 in North Fork sub-transects with fire. Because

deer defecate at the same daily rate as elk (~12.52 times per day) and produce a pellet mass considerably smaller than that of elk (Neff 1965; Neff 1968; Murie et al. 2005), elk were the dominant herbivore in the study area (Singer 1979; Martinka 1978). Moose densities were <0.1 per 100 m^{-2} in all valleys (Table 2.2), very low relative to the other ungulate species surveyed, so I omitted this species from further analysis.

Carnivore densities overall were lower than elk and deer densities (Table 2.3), which was expected (Elton 2001). In Saint Mary, all surveyed carnivore species densities were similar. In Waterton, bears had the highest density, followed by wolves and coyotes, which had similar densities. Cougar densities were the lowest of all the carnivore species in this valley. In the North Fork, wolves had the highest density of all the predators, but only in sub-transects with fire. Bear and coyote densities were similar, and cougars had the lowest density. I found wolf densities of 0.02 (100 m^{-2} ; $95\% \text{ CI} \pm 0.01$) in Saint Mary and Waterton; 0.01 ± 0.01 in North Fork sub-transects with no fire; and 0.17 ± 0.08 in North Fork sub-transects with fire (Table 2.3).

Elk response (pellet pile density) to increasing levels of risk (Table 2.1) was the same, regardless of wolf population level or presence of fire: elk use was highest in low predation risk areas, intermediate in moderate predation risk areas, and lowest in high predation risk areas (Figure 2.2-a-f; Appendix C). The effect of debris was stronger than the effect of view. Wolves did not respond to these measures of predation risk (Figure 2.2-a-f; Appendix C).

To examine predator/prey use of habitat, I plotted elk and wolf densities in grass and aspen habitat (Figure 2.3-a-c; Appendix D). Saint Mary and Waterton sub-transects showed similar trends, in which elk use of grass was significantly higher than aspen. (Figure 2.3-a). However, in North Fork sub-transects with no fire, there was no significant difference between elk use of grass and aspen. In North Fork sub-transects with fire, elk use of grass was significantly higher than aspen. Lack of a difference in elk use of grass versus aspen in North Fork sub-transects with no fire represents a deviation from the pattern of elk use of Cover Type in the valleys. (Figure 2.3-a). Wolf use of grass versus aspen did not differ within any of the valleys, nor in sub-transects with fire and with no fire (Figure 2.3-b).

Several themes emerged from the models that fell within the 0-4 Δ AIC range. Cover Type did not occur in any of the top models in Saint Mary, the valley with the least number of wolves. In Waterton and the North Fork, Aspen had a large effect on the number of elk pellet piles, compared to the other levels of this variable (Figure 2.4-a-b). In both valleys, there were fewer piles of elk pellets in Aspen Cover Type than in the Other Cover Type (the reference level of Cover Type) (Table 2.7-b-c; Figure 2.4-a-b). Heatload appeared in half of the top models in all valleys and had a positive effect on the number of elk pellet piles when it appeared in models with no interaction terms (Table 2.7-a-c). In all valleys, in models in which View and Debris appeared without an interaction of the two variables, there was a negative relationship between both predictors of predation risk, View and Debris, and the density of elk pellet piles.

The higher the risk level, the lower the density of pellet piles (Figure 2.5-a-c).

Location coordinates occurred in all the top models in all valleys (Table 2.7-a-c), which is indicative of elk herding behavior.

The interaction between View and Debris appeared in the third and fourth-ranked Saint Mary models, and in all the top-ranked Waterton models. It did not appear in any North Fork models. The relationship between view and debris was not independent in Waterton, but appeared to have a weak effect on the mean piles of elk pellets based on graphical analysis of this interaction (Figure 2.5-b). The relationship between Cover Type and Debris (obstacles to escaping wolves) was not independent in the second Waterton model, but appeared to have a weak effect on the response variable (Figure 2.6).

Most of the models included a combination of bottom-up and top-down effects (Tables 2.7; 2.10). Only the second and fourth-ranked models in Saint Mary contained top-down variables alone (View and Debris and their interaction). None of the models with $\Delta AIC < 4$ consisted of bottom-up variables alone.

Discussion

In assessing and behaviorally controlling their risk of being preyed upon, herbivores use adaptive decision-making processes (McArthur and Pianka 1966; Werner et al. 1983; Lima and Dill 1990). Landscapes with greater impediments to escaping or detecting wolves have been hypothesized by others as increasing the risk

of predation (White 2003; Ripple and Beschta 2004; Kauffman et al. 2007; Halofsky and Ripple 2008). In all ecological settings, top-down (predator-driven) effects operate along with bottom-up (resource-driven) effects, which include factors that increase or decrease plant abundance, thus improving herbivore habitat (Polis and Strong 1996). Therefore, I designed my hypotheses to explore top-down and bottom-up effects (Table 2.6; Table 2.7).

In evaluating whether risk of predation by wolves influenced how elk use a winter range landscape, I began by identifying the dominant herbivore and carnivore in this system, and patterns of habitat use by both. Elk were the dominant herbivore, present in high density in the three valleys, although their density differed among valleys. This matched the findings of Singer (1979), in which he reported the results of the ungulate ecology survey in the North Fork, during a pre-wolf, pre-fire era (the early 1970s). In my study, the wolf was the dominant elk predator, per scat data. Wolves were present in low density in all areas that had not burned. However, the North Fork wolf density in sub-transects with fire was more than one order of magnitude higher than in sub-transects with no fire (Table 2.3). This finding is key in evaluating trophic dynamics in this study. Similar wolf densities in Saint Mary and Waterton reflect my field observations of transient wolves moving through Saint Mary. Burned areas typically contain more down wood and large debris than unburned areas. This may make it more difficult for elk to escape wolves (Halofsky and Ripple 2008), and may give wolves, which can maneuver through forests more easily than

elk, an advantage (Kauffman et al. 2007). However, the high wolf density in sub-transects with fire in the North Fork did not appear to generate a trophic cascade, because I found no corresponding difference in elk density between sub-transects with fire and sub-transects with no fire (Figure 2.2-a).

Trends in elk density do show some correspondence to wolf density (Table 2.2; Figure 2.2-a; 2.3-a). The lower mean density of elk pellet piles in the North Fork (8 km^{-2}) than in the other two valleys (Table 2.2-a), while still high, suggests a density-mediated (mortality) response. However, the fact that elk winter range had greater area in the North Fork than in the other valleys, may have influenced elk density. By comparison, in YNP, post wolf recovery elk densities ranged from $6\text{-}13 \text{ km}^{-2}$ in the year 2000, considered high (White et al. 2012). While density-mediated responses (wolves killing elk) alone do not suggest trophic cascades, they are an essential component of such food web relationships (Paine 1980). Such responses have been observed widely where wolves have returned (Peterson 2007; Houston 1982). Other factors (e.g. climate and habitat) that could be linked to a decline in elk numbers, were comparable in the valleys (Frank and McNaughton 1992; Vucetich et al. 2005; Achuff et al. 2005; Hopp et al. 2006).

Elk resource selection trends were similar in the valleys, with one exception. Elk density was negatively influenced by predation risk factors in all valleys (Table 2.7-a-c; Figure 2.2-a,d; Figure 2.5-a-c). Regardless of wolf population level, elk avoided aspen (Figure 2.3-a; Figure 2.4 a-b; Table 2.7). Survey results from 1973-

1974, a pre-wolf, pre-fire period (e.g., no wolves since 1910; no fire since 1890), indicated a similar pattern: 88 % versus 3 % utilization of grass versus aspen in the North Fork (Singer 1979). The fact that predation risk variables that provided impediments to detecting or escaping wolves had a negative influence on occurrence of elk (pellet piles), regardless of wolf population, may be a contra-indicator to a top-down effect. However, in my survey of North Fork sub-transects with no fire, I found a very different pattern. In sub-transects with no fire, elk use of aspen was similar to their use of grass (Figure 2.3-a).

Why were elk using unburned aspen in a valley with a high wolf population? Perhaps because unburned stands are safer than burned aspen (e.g., less large down wood and debris on the forest floor) and provide valuable food in winter, when grass has been depleted as a food source (Ripple and Beschta 2007; Jones 1985; Cook 2002, pp. 290). Further, it is possible that elk were using unburned aspen as cover, to minimize detection by wolves. Similar elk responses to wolf presence have been identified in other studies (Hebblewhite et al. 2005a; Creel et al. 2005; Creel et al. 2008). However elk were not using unburned aspen in Saint Mary or Waterton. Elk use of forest cover has been widely found to be unrelated to thermal cover, and is primarily related to food and hiding from predators. Elk may consider starvation a greater threat than wolf predation (Cook et al. 1998).

Were the food web relationships I found linking elk resource selection, wolf resource selection, and fire indicative of trophic cascades? To evaluate this, one must

consider the Cover Type component of this food web relationship. In North Fork stands with no fire, aspen stem densities were similar to those in Waterton and Saint Mary. Further, in North Fork stands with and without fire, relative stem density of browsable aspen was similar in the size class of aspen most easily accessible to elk in winter (stems $>1<2.5$ m ht) (Chapter 4, this thesis). This indicates that elk selection of unburned aspen was not necessarily a food effect (e.g., more browsable food in unburned North Fork aspen). However, North Fork unburned stands only represented 10% of aspen available to elk in this valley. Yet wolves were largely in the other 90% (burned aspen), forcing elk to use only 10% of all aspen in this valley. This may explain the higher pellet density in unburned aspen (although elk still preferred grass), but raises a question about why wolves were not selecting the unburned aspen, where there was significant elk activity. In the other valleys, because all the aspen were unburned, and thus perhaps did not have the same predation risk factor as burned aspen, the elk were more generally distributed throughout a larger population of aspen.

Bottom-up factors alone were not driving the trend I found in elk resource selection. While it is possible that the choice of where elk spend their time (e.g., their feeding location), could be influenced by the lower amount of forage available in areas with a high elk density, I do not think this was an important factor in this study. I found the same patterns of elk use of habitat in all valleys, in sub-transects that did not have fire, regardless of elk density (Figure 2.2; Figure 2.3). Heatload appeared in half of the AIC models with in all valleys, with similar effects (Table 2.4-a-c). The variable

Cover Type occurred in both Waterton and North Fork candidate models, also with similar effects (Figure 2.4-a-b). In Waterton and the North Fork, which have well-established wolf populations, elk use of aspen was lower than all other Cover Types overall (Figure 2.4-a-b). Thus, the high elk use of unburned aspen in the North Fork may be a top-down effect moderated by bottom-up effects, although I was unable to prove that.

The fact that wolves were spending far more time in North Fork sub-transects that had burned is not fully indicative of top-down effects. Elk densities were not lower overall in the North Fork where there were more wolves, although their density was lower in aspen that had burned (Figure 2.2-a, c; Figure 2.3-a, c). As predicted by optimal foraging theory, wolves may have been capitalizing on elk vulnerability in such sites (Stephens and Krebs 1985; White et al. 2003). However, beyond this I did not find food web patterns in which wolves spent more time in high risk areas overall in any valley (Figure 2.2 c, f). Thus, wolf decision-making may have been influenced by a combination of elk vulnerability and elk density (Figure 2.3-c) (Creel et al. 2005; Hebblewhite et al. 2005a; Kauffman et al. 2007).

Taken together, my findings create a picture of differential use of resources by elk driven by a complex suite of factors. These factors include staying warm in winter and staying safe from wolves by avoiding high-risk areas. In the case of predation risk avoidance, elk decision-making was influenced by both top-down and bottom-up factors. For example, elk avoided aspen, a valuable food source that may have been

riskier than other food sources, with the exception of unburned aspen stands in a valley where wolves spent most of their time in burned areas.

Had I only studied one valley, I would have possibly concluded that in the North Fork what I observed was a strong top-down effect. However, because I studied three valleys whose differences (e.g., fire, elk density, wolf density) were quantifiable, I was able to observe the complexity of what on the surface seemed like a simple food web relationship (e.g., elk using unburned aspen versus burned aspen) (Figure 2.3-a). Overall, my results suggest that a suite of bottom-up and top-down factors work together in valleys that contain well-established wolf populations, and to a lesser degree in a valley with a low wolf population (Table 2.7-1-c).

Conclusion

One of my objectives was to determine the effect of wolf population on elk resource selection. I am not certain that wolf number had a strong effect on elk resource selection, because of the many similarities I found between elk resource selection and the models that had the best fit in the three valleys. Elk response to predation risk variables such as View and Debris was similar in all models in all valleys (Figure 2.5-a-c). This suggests that 1) a low number of wolves may alter elk resource selection via predation risk; and 2) other factors, such as fire, moderate the effects of wolf population. It also indicates that View and Debris may be related to

factors that help elk hide from predators (e.g., Cover Type), although I only found weak evidence of this in Waterton (Figure 2.6).

Food webs involve highly complex energy flows (Strong 1992). Accordingly, I did not find a simple explanation of elk resource selection. While the structure of the food web I studied (apex predator→dominant herbivore→plants) was simple, the flow of energy and influence along the pathways that link these components was not. As with any faunal species in any setting, the threat of predation alone did not drive elk resource selection decisions (Borer et al. 2005). Further study is indicated to elucidate these complex interactions.

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Table 2.1. Definition of predation risk variables Debris and View.

Variable	1 – No to Low	2 – Moderate	3 – High
Debris	Grass cover type, debris found <100 m consisting of shrub cover type <15 cm ht, and no downed wood or rocks ≥15 cm in diameter. No landscape characteristics that represent escape impediments for an ungulate.	Debris found ≥50 m<100 m consisting of low shrubs, occasional pieces of downed wood, trees, and occasional rocks ≥15 cm<30 cm in height or diameter. Mild slopes (<5%) and drop-offs that represent moderate escape impediments for an ungulate.	Debris found <50 m consisting of shrubs, trees, and rocks ≥30 cm in height or diameter. Sharp slopes (≥5%), sharp drop-offs, or ravines that represent severe escape impediments for an ungulate.
View	No landscape features that represent impediments within 100 m that hinder visually detecting a predator for an ungulate.	Landscape features in <180° of the viewshed of an animal, within ≥50 m<100 m that represent impediments to visually detecting a predator for an ungulate.	Landscape features in ≥180° of the viewshed of an animal, within <50 m that represent impediments to visually detecting a predator for an ungulate.

Table 2.2. Ungulate density in three valleys. These data represent piles of elk and deer pellets counted (100 m^2 plots), expressed as a density.

Valley	Elk			Deer			Moose		
	Mean	$\pm 95\%$ CI	Range	Mean	$\pm 95\%$ CI	Range	Mean	$\pm 95\%$ CI	Range
Saint Mary	24.24	1.34	0-129	0.16	0.04	0-3	0.02	0.01	0-2
Waterton	28.25	1.48	0-276	1.15	0.09	0-16	0.04	0.02	0-6
North Fork (All)	10.11	0.64	0-117	3.31	0.23	0-36	0.06	0.02	0-8
North Fork (No Fire)	11.09	1.47	0-99	2.20	0.35	0-22	0.10	0.06	0-5
North Fork (Fire)	9.94	0.71	0-117	3.49	0.25	0-36	0.05	0.04	0-8

Table 2.3. Large carnivore density in three valleys. Data represent carnivore scats counted in 100 m² plots.

Valley	Wolf			Coyote			Bear			Cougar		
	Mean	±95% CI	Range	Mean	±95% CI	Range	Mean	±95% CI	Range	Mean	±95% CI	Range
Saint Mary	0.02	0.01	0-2	0.01	0.02	0-2	0.02	0.02	0-1	0.01	0.01	0-2
Waterton	0.02	0.01	0-3	0.03	0.02	0-1	0.08	0.02	0-3	0.004	0.003	0-2
North Fork (All)	0.15	0.07	0-53	0.01	0.007	0-1	0.03	0.01	0-3	0.002	0.001	0-1
North Fork (No Fire)	0.01	0.01	0-1	0	0	0	0.004	0.01	0-1	0	0	0
North Fork (Fire)	0.17	0.08	0-53	0.01	0.004	0-1	0.04	0.01	0-3	0.002	0.002	0-1

Table 2.4. Specific hypotheses used to develop models for AIC analysis.

<i>A priority Hypotheses</i>	
<hr/>	
Bottom-up (resources) Factors	
<i>Hypothesis 1</i>	Elk pellet pile occurrence increases with food palatability
<i>Hypothesis 2</i>	Elk pellet pile occurrence increases with solar radiation.
 Top-down (risk) Factors	
<i>Hypothesis 3</i>	Elk pellet pile occurrence decreases with an increase in impediments to detecting wolves (e.g. “view”).
<i>Hypothesis 4</i>	Elk pellet pile occurrence decreases with an increase in impediments to escaping wolves (e.g. “debris”).

Table 2.5. Variables used in statistical analyses. Variable levels for View and Debris are defined in table 2.1.

Variable	Definition	Type	# Levels	Top-down and Bottom-up Factors
Cover Type	dominant vegetation cover type	indicator	A, G, S, O	Bottom-up
Heatload	solar radiation within transect	Index	0-1	Bottom-up
View	impediments to detecting a wolf	indicator	1, 2, 3	Top-down
Debris	impediments to escaping a wolf	indicator	1, 2, 3	Top-down
Easting	easting location coordinate	meters	continuous	n/a
Northing	northing location coordinate	meters	continuous	n/a

Table 2.6. Candidate models for AIC analyses in each of the three valleys.

Model Type	Models without location coordinates	Models with location coordinates
Full model	(1)Cover Type, Heatload, View, Debris, View*Debris, Cover Type*Debris	(21)Cover Type, Heatload, View, Debris, View*Debris, Cover Type*Debris, Easting, Northing
Single factor bottom-up	(2)Cover Type	(22)Cover Type, Easting, Northing
	(3)Heatload	(23) Heatload, Easting, Northing
Single factor top-down models	(4)View	(24) View, Easting, Northing
	(5)Debris	(25) Debris, Easting, Northing
Two-factor bottom-up model	(6)Cover Type, Heatload	(26) Cover Type, Heatload, Easting, Northing
Two-factor top-down model	(7)View, Debris	(27) View, Debris, Easting, Northing
Two-factor bottom-up and top-down models	(8)Cover Type, View	(28) Cover Type, View, Easting, Northing
	(9)Cover Type, Debris	(29) Cover Type, Debris, Easting, Northing
	(10)Heatload, View	(30) Heatload, Easting, Northing
	(11)Heatload, Debris	(31) Cover Type, Easting, Northing
Three-factor bottom-up and top-down models	(12)Cover Type, Heatload, View	(32) Cover Type, Heatload, View, Easting, Northing
	(13)Cover Type, Heatload, Debris	(33) Cover Type, Heatload, Debris, Easting, Northing
	(14)Cover Type, View, Debris	(34) Cover Type, View, Debris, Easting, Northing
	(15)Heatload, View, Debris	(35) Heatload, View, Debris, Easting, Northing
Four-factor bottom-up and top-down model	(16)Cover Type, Heatload, View, Debris	(36) Cover Type, Heatload, View, Debris, Easting, Northing
Multi-factor bottom-up and top-down models with interaction	(17)View, Debris, View*Debris	(37) View, Debris, View*Debris, Easting, Northing
	(18)Cover Type, View, Debris, View* Debris	(38) Cover Type, View, Debris, View*Debris, Easting, Northing
	(19)Heatload, View, Debris, View*Debris	(39) Heatload, View, Debris, View*Debris, Easting, Northing
	(20)Cover Type , Heatload, View, Debris, View*Debris	(20) Cover Type, Heatload, View, Debris, View*Debris, Easting, Northing
Null model	Intercept only	

Table 2.7. Results of the AIC analyses for density of piles of elk pellets in three valleys. Only models with delta < 4 and that are at least 4 delta values better than the null model are shown. Parameters listed under Model indicate the additional covariates added to the null model. Parameter estimates, deltas values (Δ) and the scale parameter are shown for the models. The reference levels for categorical variables are: View (V1=low, V2=medium, with V3=high as the reference level); Debris (D1=low, D2=medium, with D3=high as the reference level); Cover Type (G=grass, A=aspen, S=shrub, with O=other as the reference level).

a) Saint Mary

Models	Partial equation showing parameter estimates of covariates, p-values, and 95%CI's	Scale Param	AIC	Δ
Model 1				
Heatload + View + Debris + Easting + Northing	0.5148*Heatload + 0.3709*V1 + 0.3657*V2 + 1.3258*D1 + 0.7507*D2 + -0.0001*Easting + 0.0002*Northing (0.1052) (0.0027) (0.0017) (<.0001) (<.0001) (<.0001) (<.0001) (-0.11, 1.14) (0.13, 0.61) (0.14, 0.59) (1.10, 1.55) (0.54, 0.96) (-0.0002, -0.0001) (0.0001, 0.0002)	0.87	5641.9	0.00
Model 2				
View + Debris + Easting + Northing	0.3851*V1 + 0.3715*V2 + 1.3219*D1 + 0.7284*D2 + -0.0001*Easting + 0.0002*Northing (0.0019) (0.0015) (<.0001) (<.0001) (<.0001) (<.0001) (0.14, 0.63) (0.14, 0.60) (1.1, 1.55) (0.52, 0.94) (-0.0002, -0.0001) (0.0001, 0.0002)	0.87	5642.7	0.79
Model 3				
Heatload + View + Debris + View*Debris + Easting + Northing	0.4458*Heatload + -1.1776*V1 + -0.1242*V2 + 1.3093*D1 + 0.6916*D2 + 1.5751*V1D1 + (0.1648) (0.0303) (0.8200) (<.0001) (<.0001) (0.0055) (-0.18, 1.07) (-2.24, -0.11) (-1.19, 0.95) (1.05, 1.57) (0.45, 0.93) (0.46, 2.69)	0.87	5643.3	1.33
	1.6258*V1D2 + 0.4629*V2D1 + 0.5855*V2D2 + -0.0001*Easting + 0.0002*Northing (0.0075) (0.4198) (0.3036) (<.0001) (<.0001) (0.43, 2.82) (-0.66, 1.59) (-0.53, 1.70) (-0.0002, -0.0001) (0.0001, 0.0002)			
Model 4				
View + Debris + View*Debris + Easting + Northing	-1.2207*V1 + -0.2225*V2 + 1.3040*D1 + 0.6697*D2 + 1.6324*V1D1 + 1.6809*V1D2 + 0.5674*V2D1 + (0.0246) (0.6811) (<.0001) (<.0001) (0.0039) (0.0056) (0.3188) (-2.29, -0.16) (-1.28, 0.83) (1.04, 1.57) (0.43, 0.91) (0.52, 2.74) (0.49, 2.87) (-0.55, 1.68)	1.04	5643.3	1.36
	0.6937*V2D2 + -0.0001*Easting + 0.0002*Northing (0.2187) (<.0001) (<.0001) (-0.41, 1.8) (-0.0002, -0.0001) (0.0001, 0.0002)			

b) Waterton

Models	Partial equation showing parameter estimates of covariates, p-values, and 95%CIs	Scale Param	AIC	Δ
Model 1				
Cover Type + View + Debris + View*Debris + Easting + Northing	$-0.4080*A + -0.1072*G + -0.1804*S + 1.7067*V1 + 1.2249*V2 + 0.9707*D1 +$ (<.0001) (0.2893) (0.1227) (0.0457) (<.0001) (<.0001) (-0.60, -0.22) (-0.31, 0.09) (-0.41, 0.05) (0.03, 3.38) (0.85, 1.6) (0.83, 1.11) $0.6080*D2 + -0.8797*V1D1 + -0.5995*V1D2 + -0.8762*V2D1 + -0.8167*V2D2 +$ (<.0001) (0.3044) (0.4889) (<.0001) (<.0001) (0.47, 0.74) (-2.56, 0.8) (-2.3, 1.09) (-1.3, -0.49) (-1.24, -0.4) $-0.0001*Easting + 0.0001*Northing$ (<.0001) (0.0001) (-0.0001, -0.00010) (0.0001, 0.0002)	1.38	16874.8	0.00
Model 2				
Cover Type + Heatload + View + Debris + View*Debris + Cover Type*Debris + Easting + Northing (full model)	$-0.3314*A + 0.0716*G + 0.1473*S + 0.3413*Heatload + 1.5890*V1 + 1.1777*V2 +$ (0.0012) (0.5443) (0.2851) (0.1019) (0.0630) (<.0001) (-0.53, -0.13) (-0.16, 0.30) (-0.42, 0.12) (-0.07, 0.75) (-0.09, 3.26) (0.8, 1.55) $1.0271*D1 + 1.1516*D2 + -0.7662*V1D1 + -0.4735*V1D2 + -0.8263*V2D1 + -0.8199*V2D2 +$ (<.0001) (<.0001) (0.3714) (0.5851) (<.0001) (0.0002) (0.57, 1.49) (0.61, 1.69) (-2.45, 0.91) (0.2, 1.23) (-1.22, -0.43) (-1.25, -0.39) $-0.0849*AD1 + -0.4383*AD2 + -0.1584*GD1 + -0.6722GD2 + 0.4064*SD2 +$ (0.7996) (0.1699) (0.5148) (0.0171) (0.2014) (-0.74, 0.57) (-0.06, 0.19) (-0.64, 0.32) (-1.22, -0.12) (-1.03, 0.22) $-0.0001*Easting + 0.0001*Northing$ (<.0001) (<.0001) (-0.0001, -0.0001) (0.0001, 0.0002)	1.38	168756	1.20

c) North Fork

Models	Partial equation showing parameter estimates of covariates, p-values, and 95%CIs							Scale Param	AIC	Δ
Model 1										
Cover Type + View + Debris + Easting + Northing	-0.3139*A ($<.0001$) (-0.45, -0.18)	+ -0.0571*G (0.3537) (-0.18, 0.06)	+ 0.0345*S (0.6163) (-0.1, 0.17)	+ 0.2353*V1 (0.0024) (0.08, 0.38)	+ 0.1179*V2 (0.0267) (0.01, 0.22)	+ 1.1671*D1 ($<.0001$) (1.02, 1.31)	+ 0.6414*D2 ($<.0001$) (0.53, 0.75)	0.72	9984.4	0.00
	-0.0004*Easting + -0.0002*Northing ($<.0001$) ($<.0001$) (-0.0004, -0.0004) (-0.0003, -0.0002)									
Model 2										
Cover Type + Heatload + View + Debris + Easting + Northing	-0.3123*A ($<.0001$) (-0.45, -0.18)	+ -0.0560* G (0.3628) (-0.18, 0.06)	+ 0.0359*S (0.6022) (-0.09, 0.17)	+ 0.8106*Heatload (0.3676) (-0.95, 2.57)	+ 0.2400*V1 (0.0020) (0.09, 0.39)	+ 0.1222*V2 + (0.0221) (0.02, 0.23)		0.72	9985.7	1.21
	1.1676*D1 + 0.6403*D2 + -0.0004*Easting + -0.0002*Northing ($<.0001$) ($<.0001$) ($<.0001$) ($<.0001$) (1.03, 1.31) (0.53, 0.75) (-0.0004, -0.0004) (-0.0003, -0.0002)									

Figure 2.1. Map of study areas in Glacier National Park, Montana and Waterton Lakes National Park, Alberta..

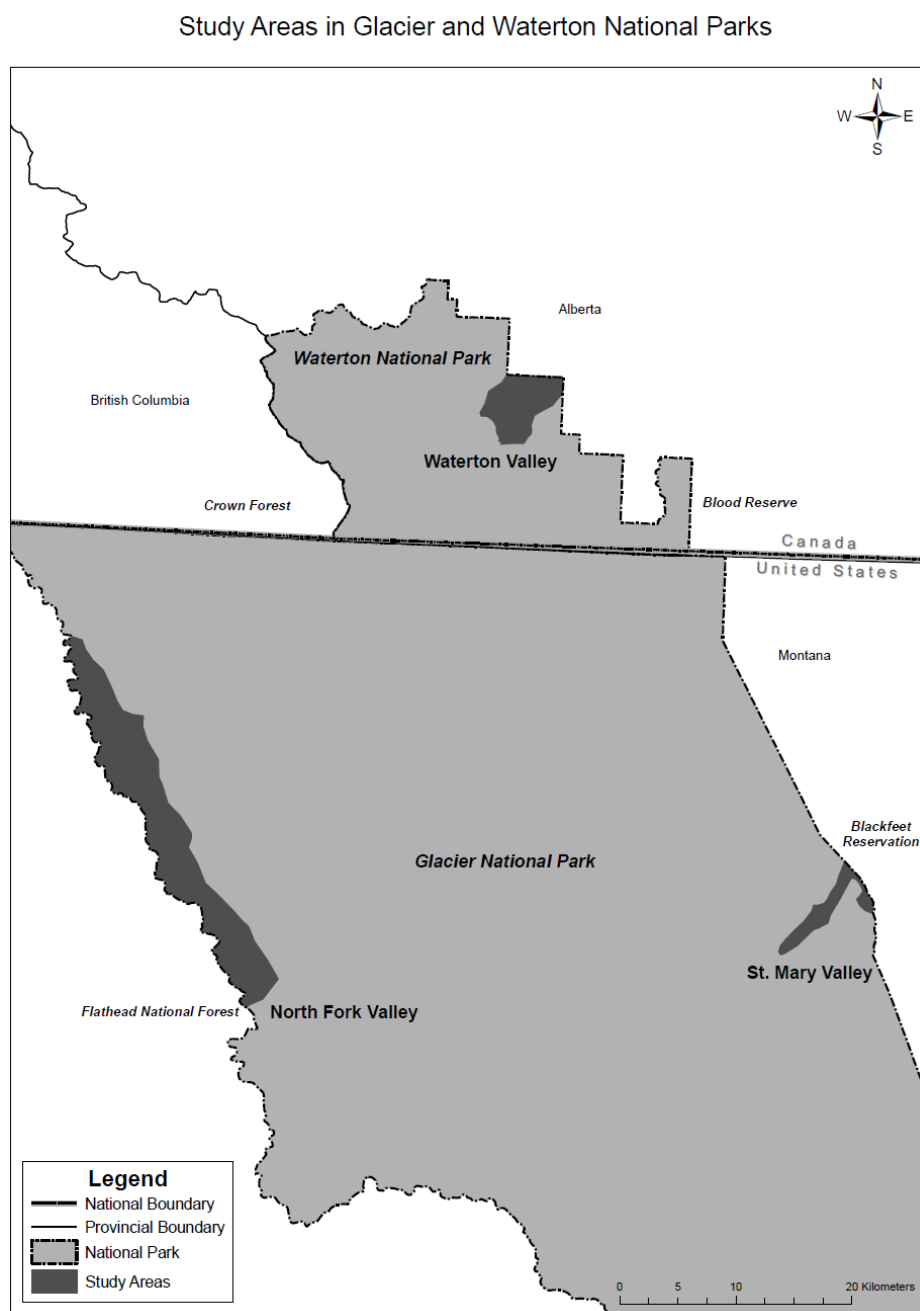
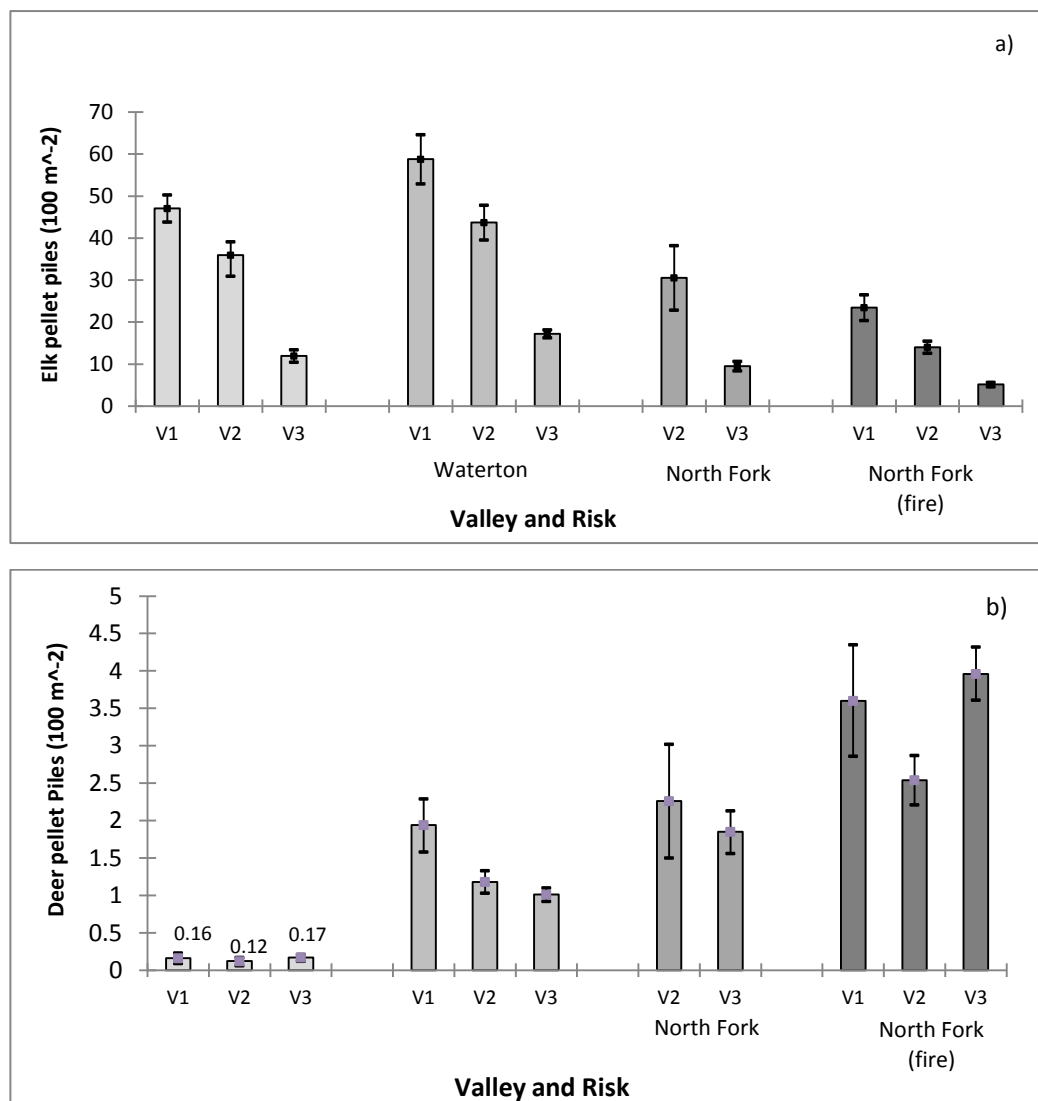
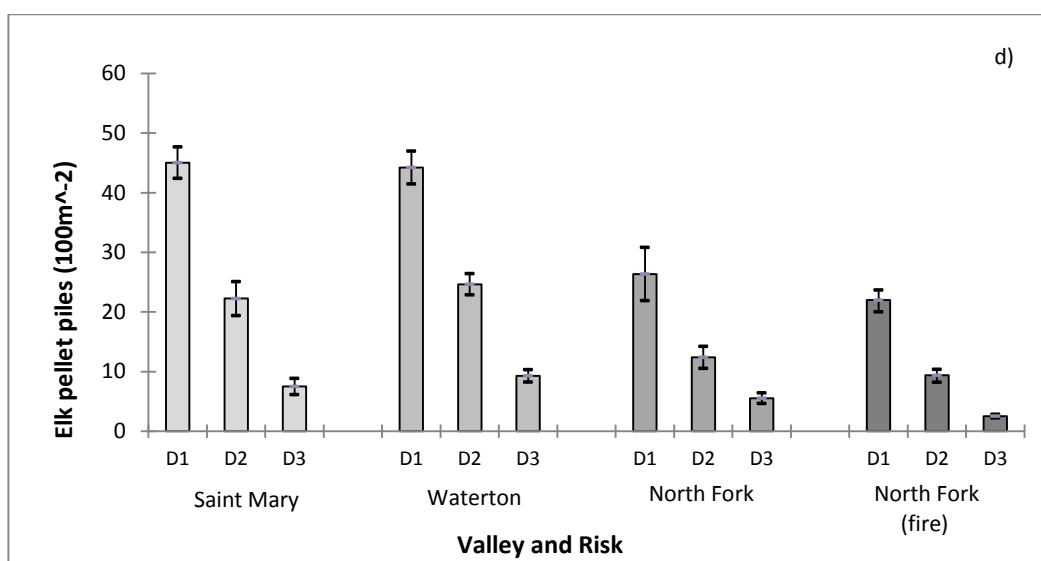
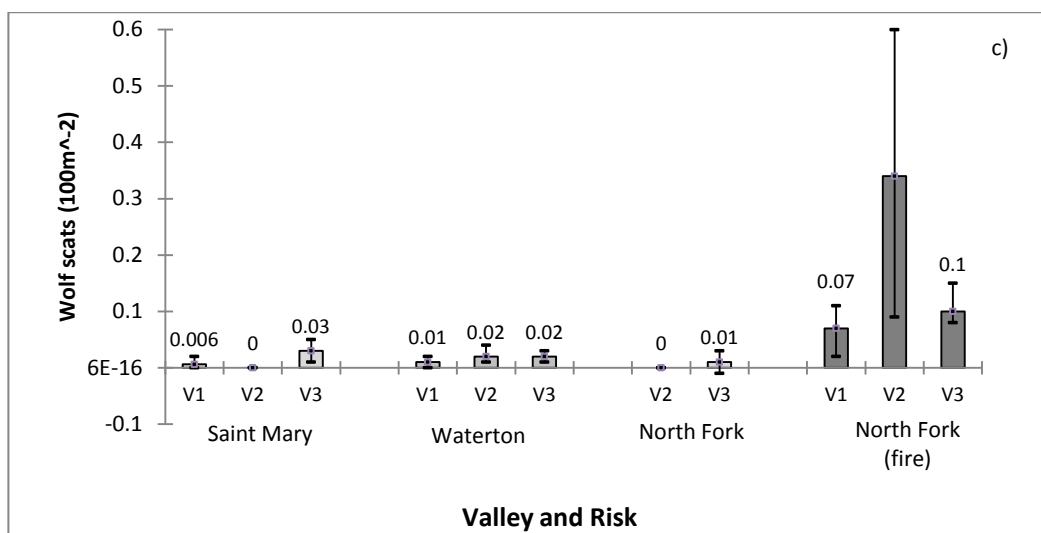


Figure 2.2. Elk, deer, and wolf densities by predation risk. Predation risk categories are as defined in Table 2.1. These data represent piles of elk and deer pellets and single wolf scats counted in plots 100 m², expressed as a density. Error bars represent 95% confidence intervals.





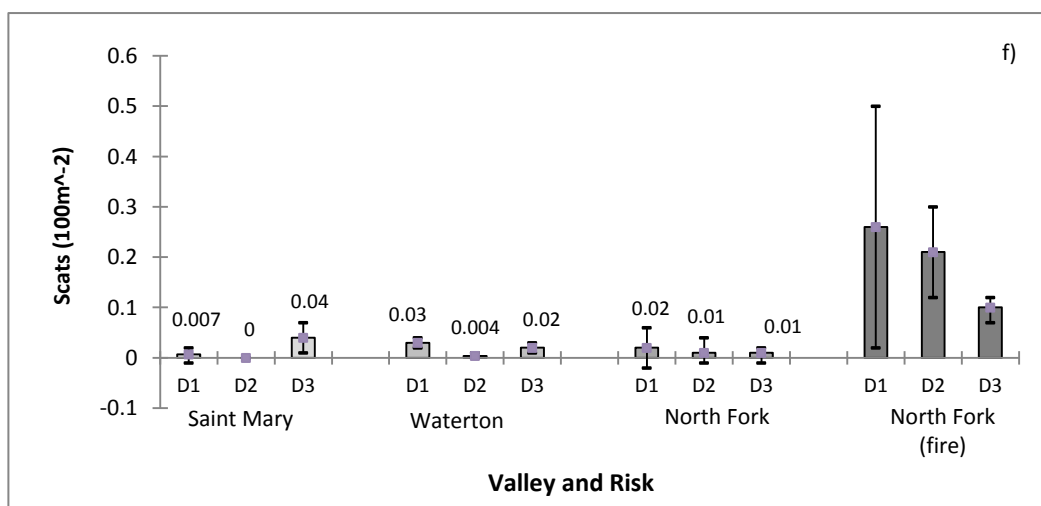
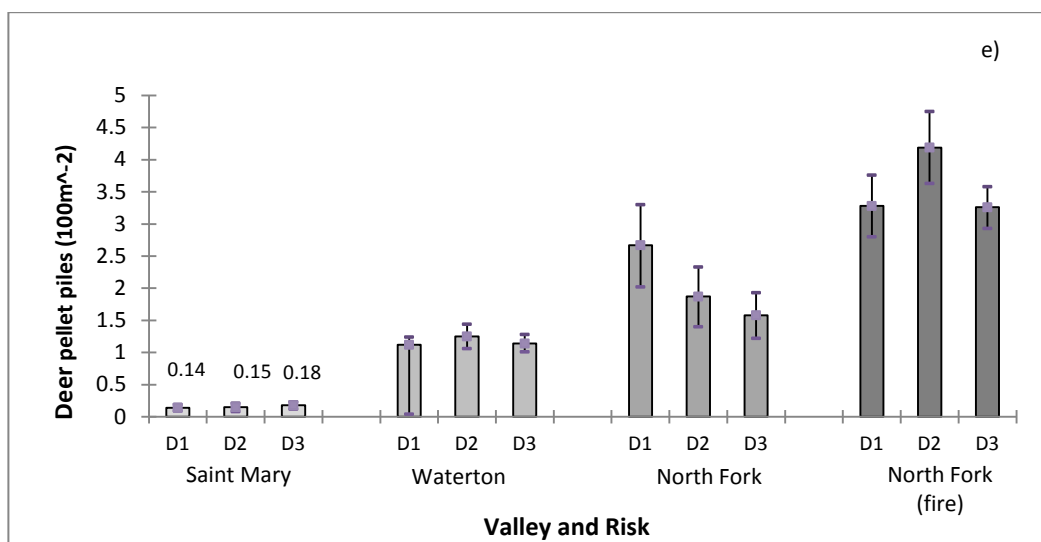
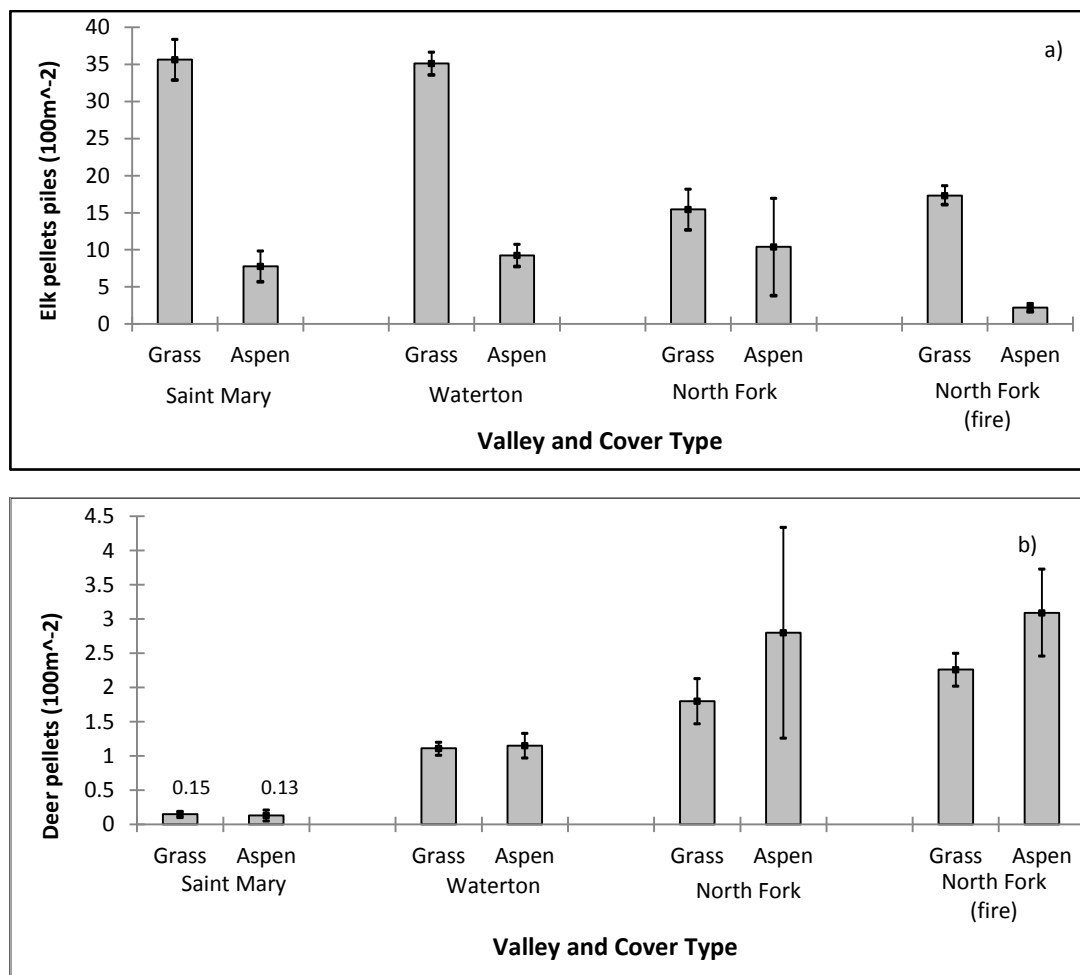


Figure 2.3. Elk, deer and wolf densities in aspen and grass. Data represent piles of elk and deer pellets and individual carnivore scats counted in plots 100 m², expressed as a density. Error bars represent 95% confidence intervals.



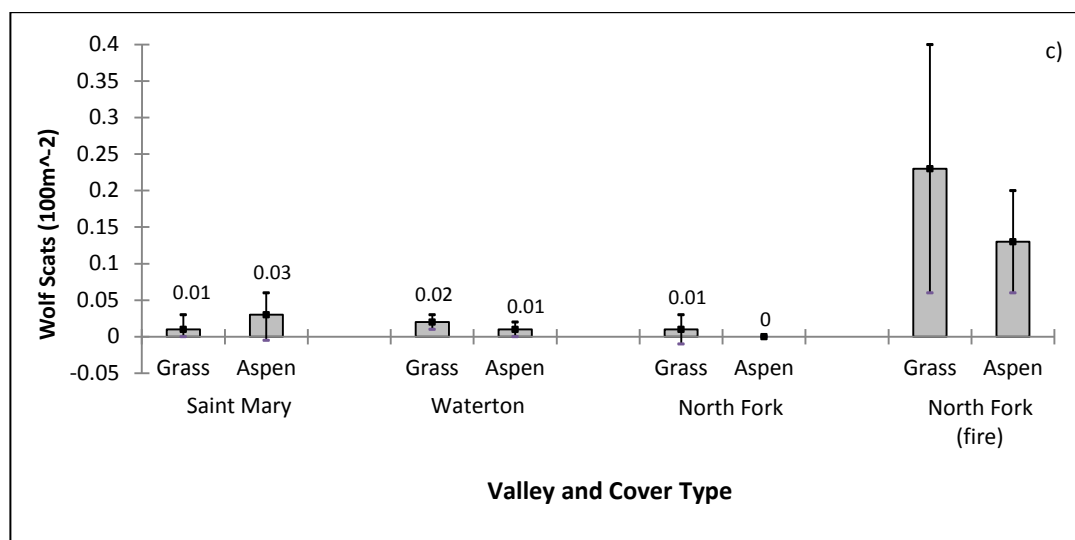
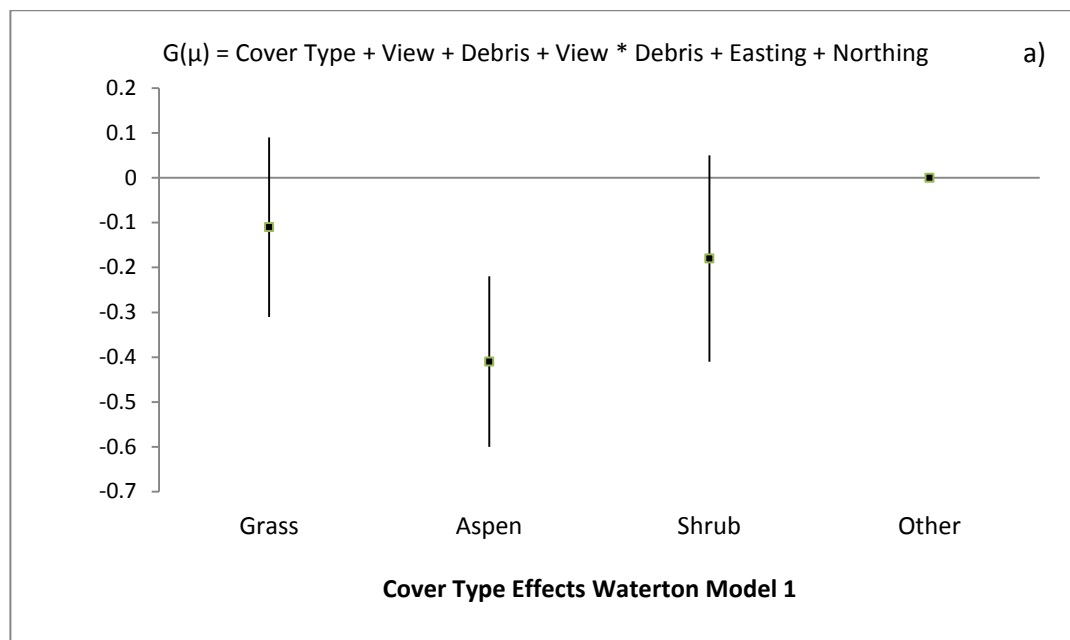


Figure 2.4. Influence of Cover Type in Model 1 in two valleys. Panel a) depicts results in the Waterton Valley; and Panel b) depicts results in the North Fork Valley. Cover Type did not appear in any of the candidate models (Δ AIC 0-4) in the Saint Mary Valley. The Y axis represents the β values for each of the four levels of this variable (influence on log mean elk pellet piles). The Other category represents the reference level. Error bars represent 95% confidence intervals.



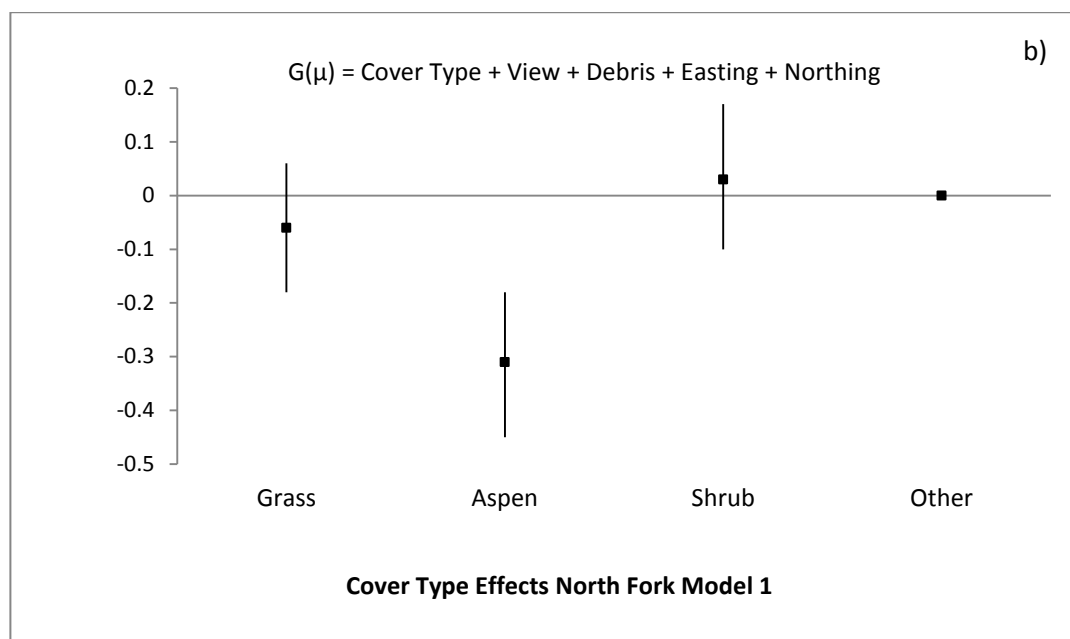
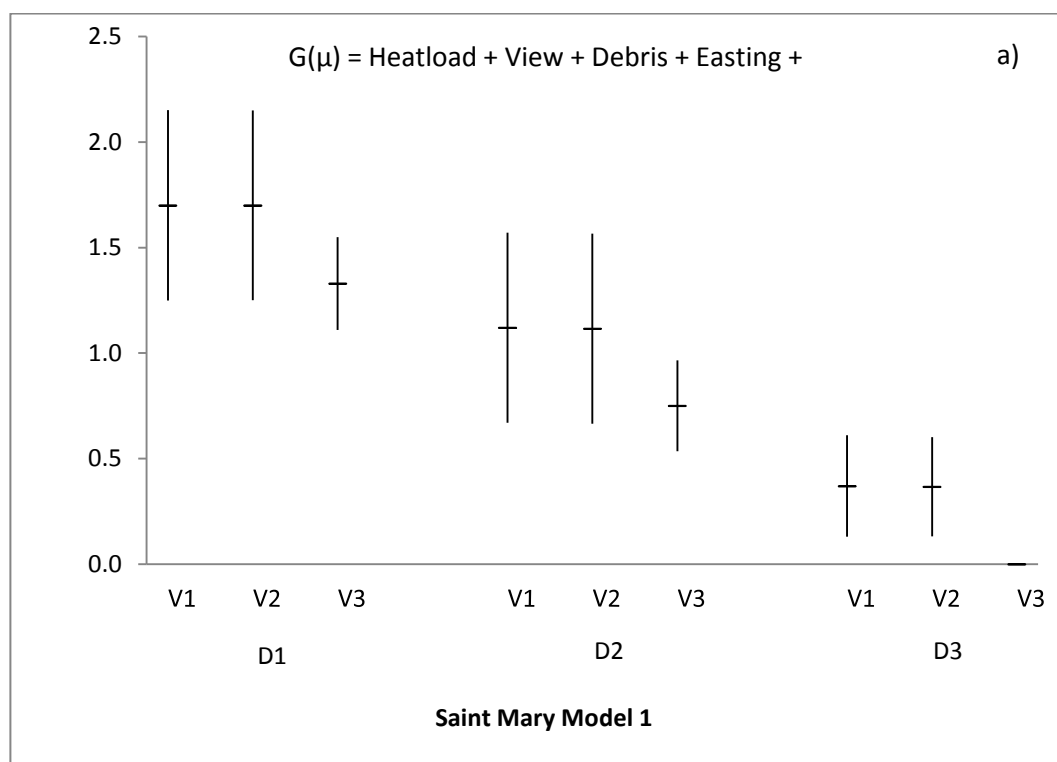
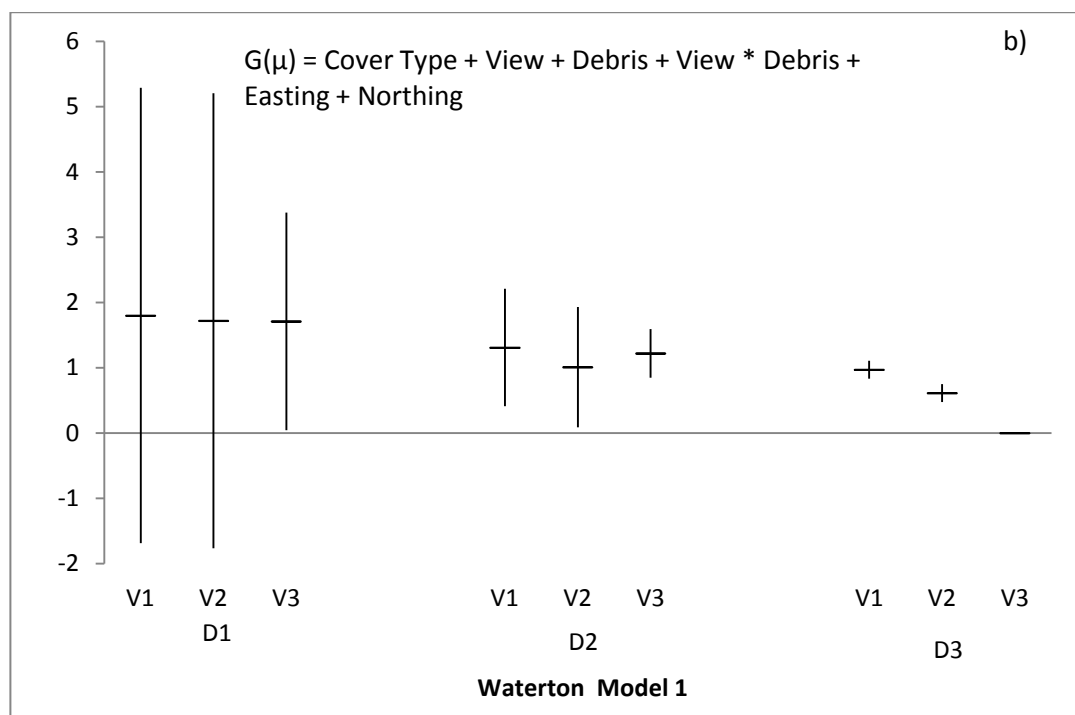


Figure 2.5. View by Debris in Model 1 in three valleys. Predation risk categories are as defined in Table 2.1. Full model variables are defined in Table 2.10. The Y axis represents the β values for each of the three levels of View and Debris (influence on log mean elk pellet piles). Categorical variables are described in Table 2.1. The V3 and D3 represent reference levels. Error bars represent 95% confidence intervals.





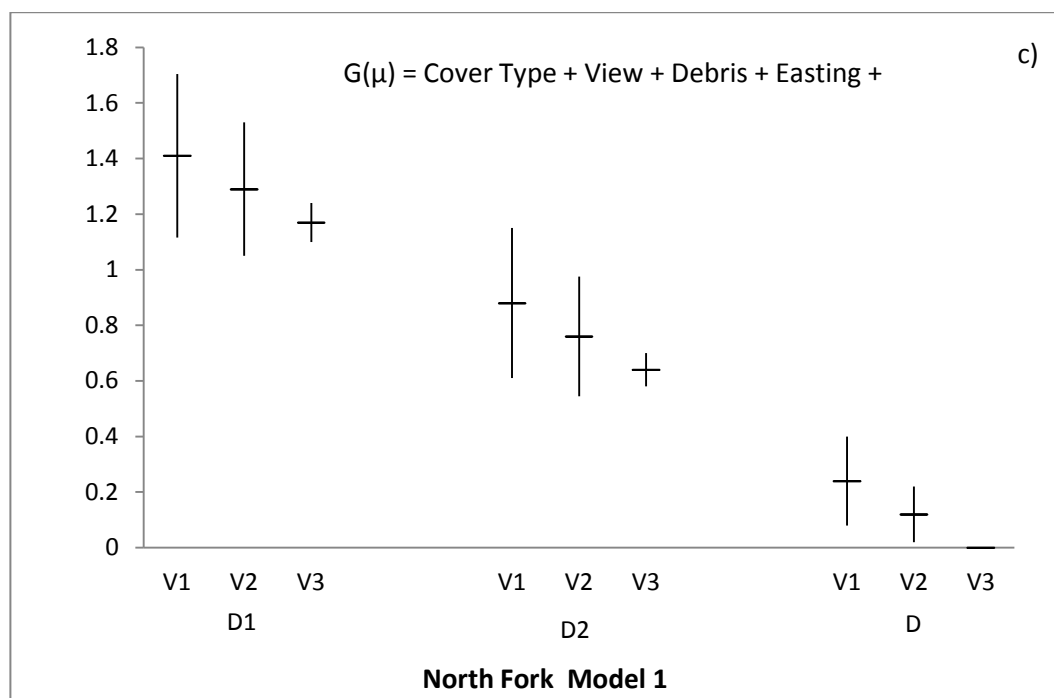
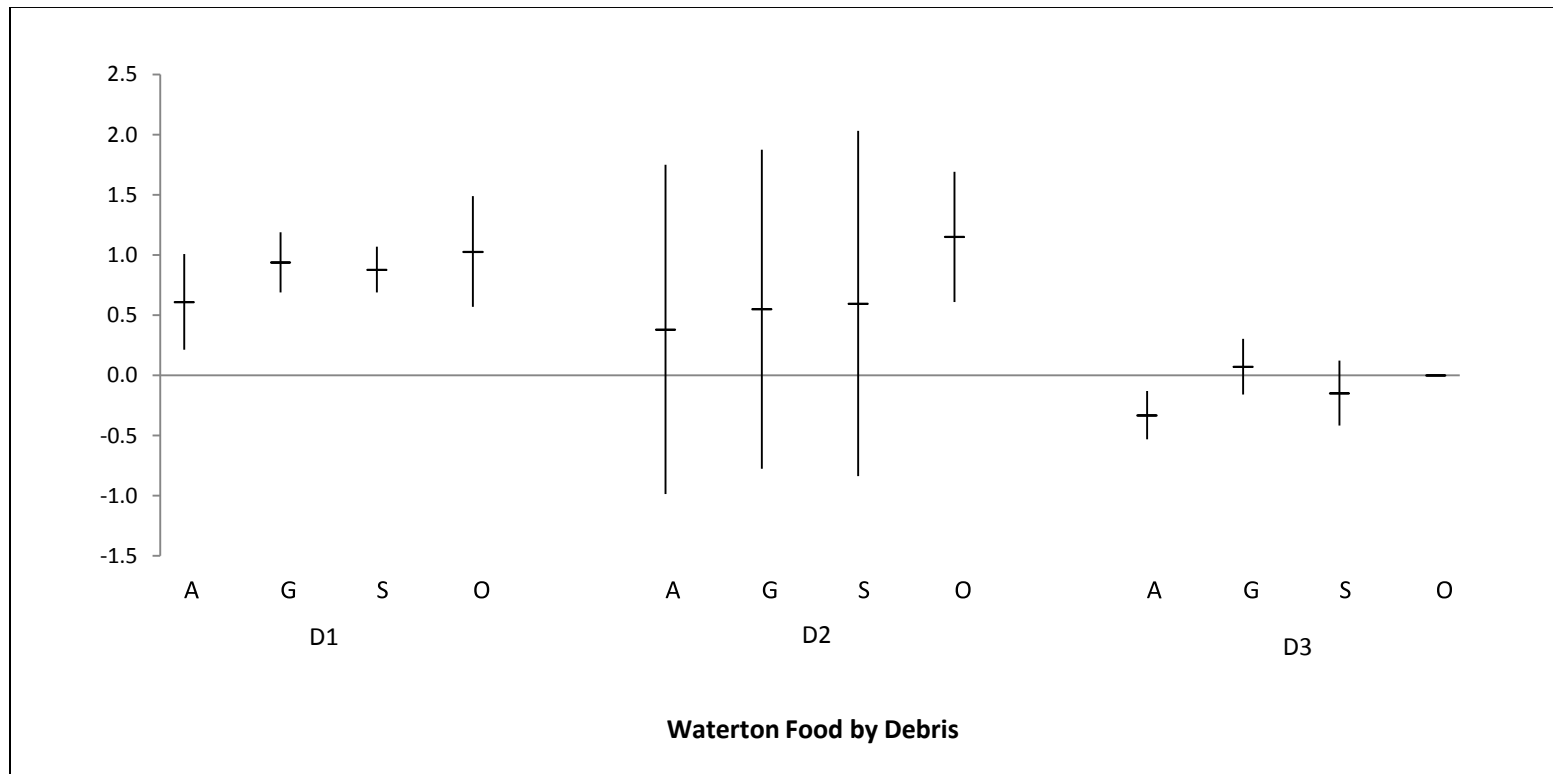


Figure 2.6. Interaction of Cover Type and Debris. The Y axis represents the β values for each of the four levels of the interaction of these variables (influence on log mean elk pellet piles). This interaction only appeared in Model 2 in the Waterton Valley. Categorical variable levels are described in Table 2.1; 2.5. The Other and D3 categories represent the reference level of these variables. Error bars represent 95% confidence intervals.



CHAPTER 3: CONTEXT DEPENDENCE OF ELK VIGILANCE BEHAVIOR AND WOLF PREDATION RISK

Cristina Eisenberg

Abstract

To measure the relationship between predation risk perceived by elk (*Cervus elaphus*) as evidenced by this species' vigilance behavior and the context for this relationship, I conducted focal animal observations in elk winter range as defined below. I stratified my observations across three spatially distinct areas, the North Fork Valley, in the western portion of Glacier National Park (GNP), Montana; the Waterton Valley, in the eastern portion of Waterton Lakes National Park, Alberta; and the Saint Mary Valley, in the eastern portion of GNP. These valleys have three different wolf (*Canis lupus*) population levels (Saint Mary: low; Waterton: moderate; North Fork: high), which represent three levels of long-term predation risk (the probability of an elk encountering a wolf). In Waterton, due to sporadic harvest by humans, wolves have a variable presence. While I found the lowest elk vigilance in Saint Mary and the highest in the North Fork (low to high wolf numbers), a careful analysis of factors that can contribute to vigilance revealed a much more complex picture. I deconstructed vigilance by examining the variables that may contribute to elk perception of predation risk in these valleys, e.g., distance to nearest forest edge; group size (number of individuals); distance to nearest primary road; social class (bull, spike bull, adult cow, adult cow with calf); and impediments (low, moderate, and high) and fitted a general mixed linear model that incorporated these variables. In Saint Mary, none of the variables I tested were significant predictors of vigilance. In Waterton, vigilance

decreased as elk group size increased ($p < 0.00001$) and increased as impediments increased ($p = 0.0005$). In the North Fork, vigilance increased as group size increased ($p = 0.03$), and decreased by social class ($p = 0.02$), with bulls more vigilant than adult cows with calves and the other social classes. The interaction between group size and impediments was significant ($p = 0.03$). Here, vigilance increased initially as group size and impediments increased. However, as impediments increased from moderate to high, and group size continued to increase, elk vigilance declined. In none of the valleys was elk vigilance significantly affected by distance to road or distance to forest. At a low level of long-term predation risk (Saint Mary), elk did not respond to drivers of vigilance. Where a high wolf population existed (North Fork), elk did not exhibit a uniform or expected response to factors that can modify predation risk, such as group size. Where wolves had a more variable presence (Waterton), elk showed a convincing response to predation risk variables such as group size and impediments to detecting and escaping wolves. Thus, the effects of wolf population and the apparent association between vigilance and some predictors of vigilance were non-linear. Wolves appeared to be driving elk vigilance; however other factors may have modified this complex relationship.

Introduction

Herbivore behavior is shaped by avoidance of predation (Schmitz et al. 2004). Prey use vigilance is a key survival mechanism (Lima and Dill 1990). Optimal

foraging by prey involves balancing risk avoidance with energy expenditure and food needs (McArthur and Pianka 1966; Abrams 1991; Illius and Fitzgibbons 1994; Schmitz et al. 2004). This vigilance level represents a response to demographic (number and population characteristics of prey and predators) and environmental conditions (impediments, land cover) (Brown et al. 1999; Laundré et al. 2001).

Prey interactions with predators have two complementary components: predators killing prey, and predators scaring prey (Lima and Dill 1990). While the lethal (density-mediated) effects of predation have been well-documented (Volterra 1926; Lotka 1932; Taylor 1984; Messier 1994), more recent research suggests non-lethal (trait-mediated) effects may have strong influence on prey behavior and ecosystems (Bekerman et al. 1997; Gude et al. 2006; Laundré et al. 2010; Wirsing and Heithaus 2008).

Elk (*Cervus elaphus*) and their primary predator, the wolf (*Canis lupus*) (Geist 2002, pp. 394-405; Mech and Peterson 2003), have been the subjects of several studies of behavioral response to predation risk (Creel et al. 2008; Creel and Christianson 2009; Halofsky and Ripple 2008). A suite of complex factors influences these dynamics, such as predator population size and movements, and forage biomass available to herbivores (Altendorf et al. 2001; Fortin et al. 2005; Hernandez and Laundré 2005; Mao et al. 2005). Vigilance, defined in large terrestrial mammals as the proportion of time an individual spends with its head raised above its shoulders,

scanning for predators, is one of the key elk responses to the threat of predation (Childress and Lung 2003).

Landscape features that create impediments to detecting or escaping wolves may increase the vulnerability of an elk to predation (Bergman et al. 2006; Hebblewhite et al. 2005; Creel et al. 2005; Halofsky and Ripple 2008). Thus, elk 1) may avoid sites with high impediments; 2) demonstrate higher vigilance in these sites; 3) and browse less intensively (Ripple and Beschta 2007; Halofsky and Ripple 2008).

Elk group size also influences vulnerability to predation (Hebblewhite and Pletscher 2002; Hebblewhite et al. 2005; Creel and Winnie 2005; Lung and Childress 2007). The selfish herd adaptive strategy, whereby individuals associate closely to minimize probability of selection by predators (Hamilton 1971), consists of the Dilution Effect, where chance of being taken by a predator diminishes in proportion to group size; the Position Effect, where predators are more likely to take an individual at the periphery of a group; and the Many Eyes Effect, where prey ability to detect predators increases with group size (Geist 2002, p. 399).

Other factors that may increase elk vulnerability to predation include social class, distance to road, and distance to forest edge. Of all social classes (e.g., bull, spike bull, adult cow, adult cow with calf), adult cows with calves tend to be the most vigilant (Wolff and Van Horn 2003; Halofsky and Ripple 2008), because calves are the most vulnerable to predation (Laundré et al. 2001). Elk tend to avoid roads due to the human presence roads represent (Rost and Bailey 1979; Wisdom et al. 2004a;

2004b; St. Clair and Forest 2009). Findings about the effects of proximity to forest cover are more complex. Elk utilization of forest cover is not related to thermal cover (Cook et al. 1998). Elk use forest cover primarily for food and protection from predators (Geist 2002, pp. 397-404; Creel et al. 2005; Fortin et al. 2005). However, some studies have found elk more vulnerable to predation inside and near forests, due to the impediments trees and large dead wood provide to seeing or escaping from predators such as wolves (Halofsky and Ripple 2008).

Context may affect elk response to wolves (Kauffman et al. 2007; Creel et al. 2008; Creel and Christianson 2009). The ecological effectiveness of wolves in influencing elk behavior may be a function of wolf population and distribution (Mao et al. 2005; Soulé et al. 2003; Estes et al. 2010), although this will not be a linear, single cause-effect relationship. Because I studied valleys with three very different wolf population levels (low, moderate, and high), I was able to examine the effects of spatial variation (context) in the long-term risk of predation on elk vigilance across sites.

My objective was to investigate the role of the probability of an elk encountering a wolf, termed long-term predation risk (Creel et al. 2008), and environmental factors in influencing elk vigilance. To that end, I observed elk vigilance in this species' winter range in three separate valleys. My null hypothesis was that elk behavior would be unaffected by impediments to detecting or escaping wolves. Alternatively, I hypothesized that elk would spend more time with their heads

above their shoulders (vigilant) in places with more impediments to detecting or escaping wolves.

Study Area

The study setting, in the central portion of the Crown of the Continent Ecosystem, spans the US/Canada border and encompasses Glacier National Park (GNP) and Waterton Lakes National Park (WLNP). Located in northwest Montana, GNP contains 4,047 km² of forest, alpine meadows, and lakes. WLNP lies in southwestern Alberta and encompasses 520 km²; biotic communities are similar to those in GNP (Achuff et al. 2005; Hop et al. 2007).

Modern land use (e.g., ranching) and wolf management policies in this ecosystem created the context for this research. I studied three geographically separate valleys (Figure 3.1), which are elk winter range:

- The North Fork, a Valley located in the northwestern edge of GNP, west of the Continental Divide;
- Waterton, a WLNP Valley east of the Divide; and
- Saint Mary, a Valley in the eastern portion of GNP, also east of the Divide.

Ecological resources are comparable in all valleys (e.g., climate, soil, elevation) and precipitation is distributed similarly throughout the year (Western Region Climate Center 2010; Parks Canada 2011; Achuff et al. 2005; Hop et al. 2007). The measured

areas of these study sites (ArcGIS 10.1) are: Saint Mary 1,392 ha; Waterton 2,741 ha; and North Fork 5,705 ha. The valleys are located in the Foothills Parkland Ecoregion, which consists of low-elevation valley bottoms (Achuff et al. 2005; Hop et al. 2007). While ecoregions are broad ecological classifications, within these Parks, the Foothills Parkland is limited to the extent of the valleys, and ranges in elevation from 1,024 m to 1,700 m.

As throughout the Rocky Mountains, the winter range in this study consists of low-elevation grasslands occurring in sheltered valleys. Winter range offers elk snow depth < 0.7 m, protection from the wind, and additional food sources that consist of patches of aspen, shrubs, and conifers (Singer 1979; 1996; Houston 1982; Skovlin et al. 2002, 531-534; Wagner 2006). Rough fescue (*Festuca scabrella*) is the dominant grass in the valleys. Codominant grasses are the same, and consist of Richardson needlegrass (*Achnatherum richardsonii*), Junegrass (*Koeleria macrantha*), oatgrass (*Danthonia* spp.), and bluebunch wheatgrass (*Agropyron spicatum*) (Kujit 1982; Lesica 2002; Achuff et al. 2005; Hop et al. 2007).

While all valleys offer similar wolf habitat, their wildlife management policies and practices have varied, resulting in a range of wolf populations among the valleys. Thus, the three valleys differed in long-term predation risk. Similar comparisons have been made in Yellowstone, both spatially and temporally, to determine the effect of wolf presence on elk behavior (Laundré et al. 2001; Childress and Lung 2003; Mao et al. 2005; Creel et al. 2008). However, because I lacked collared wolves in two of the

valleys, I was unable to consider fine-scale temporal variation in risk (e.g., wolf movements).

Defining a wolf population is problematic and lacks conventions. However, a wolf population that consists of multiple packs, some of which may be producing multiple litters annually, is generally considered high (Fuller et al. 2003). A wolf population with one breeding pair producing one litter per year is generally considered moderate (Fuller et al. 2003). And a wolf population with no breeding pair is generally considered low to nonexistent (USFWS 1994; Fuller et al. 2003). I defined the wolf populations in the valleys accordingly.

Wolf abundance in the entire Crown of the Continent Ecosystem was very low overall from the 1880s until the mid-1970s, due to European settlement and subsequent wolf extirpation (Flathead Transboundary Network 1999; Weaver 2001; Arjo et al. 2002). Wolves were functionally extirpated in GNP by 1917. In the mid-1970s wolves from northern Canada began to recolonize this ecosystem naturally, returning to the North Fork Valley in 1979 in low numbers, and were confirmed denning in the North Fork in 1986 (Singer 1975; Ream et al. 1990; Martinka 1991). In less than 5 years those wolves increased to >20 individuals in multiple (2-3) packs (Pletscher et al. 1997). They have continued to den in the North Fork since then, although their population distribution is not uniform. Wolves returned to the Waterton Valley later, and were not confirmed denning there until 1992 (Fox and VanTieghem

1994; USFWS et al. 2010). Parallel data on wolf recolonization were not available for Saint Mary Valley because wolves had not established a breeding population there.

I characterized Saint Mary as having a low wolf population (Fuller et al. 2003). Although wolves have attempted to recolonize Saint Mary since the 1980s, no stable wolf population has been established in that valley. No breeding pair or pack of wolves occurred there during my study (USFWS et al. 2007; Sime et al. 2009; Sime et al. 2010; USFWS et al. 2010).

I characterized Waterton as having a moderate and variable wolf population (Fuller et al. 2003). Wolves have never been protected outside of WLNP and are subject to hunting, trapping, and legal take by landowners, although no harvest occurs within the Park. During my study, wolves in that valley numbered between 4-12 individuals within the one pack that denned inside the Park (Watt 2007-2009).

I characterized the North Fork as having a high wolf population (Fuller et al. 2003). During my study, North Fork wolves ranged from 12-29 individuals in 2 packs per agency reports (USFWS et al. 2007; Sime et al. 2009; Sime et al. 2010; USFWS et al. 2010). In 2008, I documented a wolf population of 38 individuals in 2 packs by field observations; both packs produced multiple litters.

Elk vigilance could be influenced by the presence of other large carnivores. In my study sites, these include cougar (*Puma concolor*), grizzly bear (*Ursus arctos*), and black bear (*U. Americanus*). Wolves are the leading elk predator, because bears hibernate when elk are on their winter range, and cougars prey mostly on deer (Kunkel

and Pletscher 2001; Watt 2007-2009; Banfield 2010). I occasionally observed cougars preying on adult elk, although these observations were rare. Cougar density was ~9-16 1000 km⁻² in GNP (MFWP 2011a) during my study. A cougar density has not been established for WLNP, but their numbers are thought to be robust (Watt 2007-2009).

Field Methods

Focal sampling involves observing a single individual continuously for a specified period of time (Martin and Bateson 1993, p. 84). I conducted a total of 622 focal observations of free-ranging elk actively feeding in WLNP and GNP over a two-year period (April 11, 2007 through March 17, 2009), avoiding observations during the rut (Wolff and Van Horn 2003).

The sampling unit was the individual elk. I stratified observations by valley and by social class (bull, spike bull, adult cow, adult cow with calf) (Wolff and Van Horn 2003; Halofsky and Ripple 2008). I selected individuals haphazardly to sample as evenly as possible across all social classes (Table 3.1). The observation period ranged from October 28 to April 11, when elk were reliably present in their winter range.

I defined a group as ≥ 3 elk not more than 100 m apart (Childress and Lung 2003). Within a group, I observed individual elk, until a group was no longer observable. To reduce the likelihood of observing the same individual more than once, I only observed 1-4 focal individuals in each group per day, and only revisited groups

at a particular location if they contained >10 individuals (Childress and Lung 2003).

However, it is likely that I may have observed the same individual more than once.

Observations took place from park roads and in natural blinds away from roads, using binoculars (10×50 mm) and a spotting scope ($20\text{-}60 \times 65$ mm), when the animals were visible and active between 0415 and 1940 hours. Observation sites were selected to provide best viewing access to elk without disturbing them. For each group observed, I haphazardly selected individuals engaged in feeding. All observations were made at a distance of ≥ 50 m from each focal animal. I waited 5 minutes from arrival at an observation site before beginning the first observation period. To address the bias potentially created by road adaptation, I included distance to road as an explanatory variable.

Each observation was 3-20 min. in length, and ended when the focal animal walked out of sight, ended a feeding bout, or the time limit was reached. During this interval, I used a tape recorder to continuously observe and record behavior. Data were transcribed afterward, using a stopwatch, to determine the amount of time spent in vigilance and other behaviors. Behavior was classified into feeding, raised head, and other behavior (e.g., grooming and interacting with conspecifics). I subdivided raised head into vigilant and locating food/moving to another feeding location. Due to differences in observation length, vigilance was normalized as a proportion (percent of time spent vigilant). I obtained the azimuth from the observation point to the focal animal, Universal Trans Mercator (UTM) grid coordinates of the observation point (in

meters; error \pm 2-6 m), and distance to focal animal (using a Leica laser rangefinder, in meters, error \pm 1m), to collect landscape and habitat data, as defined below.

Data were gathered on variables identified as spatially and ecologically potentially influencing the long-term risk of focal animal being preyed upon (Berger 1978; Bednekoff and Ritter 1994; Laundré et al. 2001; Childress and Lung 2003; Creel et al. 2005; Fortin et al. 2005; St. Clair and Forrest 2009; Halofsky and Ripple 2008). Variables included group size (number of individuals); position within group (peripheral, intermediate, central); topography (valley, upland, gully); distance to forest edge; distance to road (nearest primary); view impediments (low, moderate, high); debris (low, moderate, high); snow depth; and social class (bull, spike bull, adult cow, adult cow with calf). Table 3.1 displays the details of sample sizes for categorical variables.

I determined the position of an animal in a group per methods established by Bednekoff and Ritter (1994). Thus, I defined peripheral animals as those with no neighbors in one direction; central animals as those located in the group center with neighbors on all sides; and intermediate animals as those intermediately located between the group center and its periphery. In cases where there were <5 elk, all animals were designated as peripheral. I used visual observation and topographical maps to identify landscape characteristics defined as follows: valley (an elongated lowland between ranges of mountains, hills, or other uplands, often having a river or stream running along the bottom); upland (high land; ground elevated above valleys);

and gully (a deep ditch or channel cut in the earth by running water). These landscape categories pertain to the types of topography encountered by elk. I used topography, rather than plant community, because it allowed for finer-scale evaluation of landscape features that could affect elk behavior. I used a laser rangefinder to measure distance to forest edge, primary road, and view impediments. I used a leveling rod to measure escape impediment height and snow depth. Impediments to the ability of an elk to detect wolves (view) and to escape wolves (debris) (Table 3.2) were collinear, so I created a new variable, impediments, that combined the effects of view and debris (Table 3.3).

The contribution of predation risk to herbivore vigilance can be difficult to assess without accounting for the potential confounding effect of forage biomass (Fortin et al. 2005). In the valleys, all observations took place in grassland habitat that had similar type and height of vegetation, so I did not include vegetation as a variable.

Hunting of elk by humans also can influence elk vigilance (Proffitt et al. 2008). During my study, hunting took place immediately outside my study areas, on public and private lands. Elk hunting seasons were September 3-November 29 in the North Fork Valley; September 10-December 4 in the Saint Mary Valley (on Blackfoot tribal land); and September 1-February 21 in the Waterton Valley (BNFW 2007; Watt 2007-2009; SRD 2010; MFWP 2011b). The extended season outside of Waterton, in which antlerless elk were targeted, may have increased vigilance proportions in Waterton elk, although late season harvest was low (20 permits/20% successful harvest rate) (SRD

2010). Collectively, these hunting season caused elk to stay inside both Parks, to avoid being hunted by humans, and this may have influenced group size.

To evaluate the potential effects of wolf presence on elk behavior, I radio-collared wolves. I was unable to radio-collar wolves in Saint Mary, due to the low wolf population there. My efforts to radio-collar wolves in Waterton were unsuccessful, due to the high wariness of the wolves there, which are harvested by humans outside the Park. However, in the North Fork, I was able to GPS collar wolves ($n=5$), gather data for pre-existing Very High Frequency (VHF) collared wolves ($n=4$), and utilize historical VHF collared wolf data gathered between 1997 and 2007 ($n=10$). This yielded a total sample size of $n=19$ collared wolves, described below.

I fitted 5 of the members of the 2 packs in the North Fork with Telonics TGW-4500 Global Positioning System (GPS) collars. The collars were programmed to collect location coordinates every 3 hours and drop off after 24 months, after which the collar data were downloaded. Four North Fork wolves had pre-existing VHF radio-collars. I stored all wolf collar data in an Access (Microsoft Corporation, 2010) database. To eliminate potential error, I used only GPS collar data points that had been acquired via ≥ 4 satellite fixes.

All collared animals (VHF and GPS collars) were radio-tracked daily. Wolf locations were established via standard triangulation methods (Millsaugh and Marzluff 2001). Locations had an accuracy of $< \pm 1$ km, and were calibrated via blind trials, to determine their accuracy. Any observations that may have been biased by

signal bounce or other sources of location error were discarded (Millspaugh and Marzluff 2001).

GNP provided access to 10 years (1997-2007) of pre-existing VHF collar location data for North Fork wolf packs. While these data transcended the time frame of my study, they helped document wolf presence and long-term predation risk in the North Fork (Berger 2007).

Analysis

I examined elk mean vigilance, treating each valley as a case study, because I had no replication of wolf population. The response variable, vigilance, represents the proportion of time a focal animal spent with its head above its shoulders, scanning for predators (arcsine transformation). I evaluated normality for the response variable by observing its distribution, and further tested for deviation from model assumptions by observing residual plots.

For the purpose of graphical presentation of data, I transformed group size, distance to forest edge, and distance to road into categorical variables as follows: Group (small ≤ 25 elk; moderate $>25 \leq 75$ elk; large >75 elk); Forest (close ≤ 50 m; moderate $>50 \text{ m} \leq 100 \text{ m}$; far $>100 \text{ m}$); and Road (close $\leq 150 \text{ m}$; moderate $>150 \text{ m} \leq 300 \text{ m}$; far $>300 \text{ m}$) (Figure 3.3). I defined these categories based on my field observations of elk ecology and behavior and on the scientific literature (Childress and Lung 2003). However, for all multivariate analyses I used group size, distance to

forest edge, and distance to road as continuous variables, to best represent the potential variation in the mean proportion of elk vigilance in response to these variables (Table 3.5).

I created a correlation matrix and discarded from further analysis one of each pair of variables that were collinear or had potential for bias. Position in group was problematic because of its correlation to group size, and thus could create overdispersion if both variables occurred in a model. I opted to keep group size, a variable used most often in analyses of elk vigilance (Brown 1999). Snow depth was problematic, because I did not find a sufficient range of values for these data to be orthogonal or to reliably represent the potential effect of snow depth on elk foraging decisions (Hobbs et al. 1981; Houston 1982; Canon et al. 1987) (Table 3.4), so I did not use it. Topography was problematic because of its correlation to impediments. I opted to use impediments, the finer-scale of the two variables, which may better represent variation in spatial risk.

I fitted a general linear model (GLM) to describe Y_i , elk mean vigilance, for a set of p explanatory variables, structuring this model as follows:

$$Y_i = \beta_0 + \beta_1 X_{1i} + \beta_2 X_{2i} + \beta_3 X_{3i} + \beta_4 X_{4i} + \dots + \beta_p X_{pi} + \varepsilon_i$$

where $\varepsilon_i \sim N(0, \sigma^2)$ and all the ε_i and ε_i s are independent, and $\beta_1 \dots \beta_p$ are the linear coefficients associated with the explanatory variables, $X_1 \dots X_p$, respectively. I expressed the expected value of elk mean vigilance (that is, the mean proportion of elk vigilance) with the mixed linear model:

$$E(Y_i) = \beta_0 + \beta_1 X_{1i} + \beta_2 X_{2i} + \beta_3 X_{3i} + \beta_4 X_{4ijkl} + \beta_5 X_{5ijk} + \beta_2 X_{2i} \times \beta_5 X_{5ijk}$$

where

Y	arcsine of elk vigilance,
X ₁	distance to forest edge,
X ₂	group size,
X ₃	distance to road,
X _{4ijkl}	social class (ijkl = adult bull, spike bull, adult cow, adult cow with calf),
X _{5ijk}	impediments (ijk = low, moderate, high),
X ₂ × X _{5ijk}	interaction of group size and impediments,

with the variance of a single observation given by $\text{Var}(Y_i | X_1 \dots X_p) = \sigma^2$.

I included the interaction between impediments and group size to determine whether a relationship existed between increased safety that elk perceive when in larger groups, combined with impediments. I wanted to know whether this interaction influenced elk vigilance when all other variables were considered. I did not include other interactions, due to lack of biological significance (e.g., distance to road × distance to forest).

I ran all analyses using the PROC MIXED function in SAS v9.1 (SAS Institute, Cary, NC, USA). I used a *p*-value of 0.05 as the upper threshold for statistical significance. To interpret *p*-values, I employed criteria recommended by Ramsey and Schafer (2002, p. 46) in which *p*-values >0.05 < 0.10 provide suggestive,

but inconclusive evidence; $\leq 0.05 > 0.01$ provide moderate evidence; and ≤ 0.01 provide convincing evidence of statistical significance. I presented all means with a 95% confidence interval.

Results

The mean elk group size was 91 ± 6.5 in Saint Mary; 342 ± 39 in Waterton; and 76 ± 7.5 in the North Fork (Table 3.4). Overall elk vigilance was $9.41\% \pm 1.45$ in Saint Mary; $13.74\% \pm 2.33$ in Waterton; and $19.72\% \pm 3.33$ in the North Fork (Figure 3.2). Summary statistics indicated that elk vigilance was not different within each valley by group size, position in group, social class, distance to forest edge, impediments, or distance to road (Figure 3.3).

In Saint Mary, the model that I fitted yielded no significant effect of any of the variables (Table 3.5). In Waterton, proportion of vigilance was negatively related to group size ($p < 0.0001$) (the larger the group, the less vigilant the focal animal), and positively related to impediments ($p = 0.0005$) (the greater the impediments, the more vigilant the focal animal). None of the other variables were significant (Table 3.5). In the North Fork, the proportion of vigilance was positively related to group size ($p = 0.03$) (the larger the group, the more vigilant the focal animal), and bull elk were more vigilant than the other social classes ($p = 0.02$). Coefficients indicated that for the interaction of group size and impediments ($p = 0.03$), initially vigilance increased as group size and impediments increased. However, as impediments increased from

moderate to high, and group size continued to increase, vigilance declined (Table 3.5; Figure 3.4). In the North Fork, current and historical wolf collar data showed sustained use by wolves of these sites (Figure 3.5), both historically and during the time of the study.

Discussion

I studied elk winter range vigilance behavior in valleys that had different wolf populations due to wildlife management practices. This study examined three cases of long-term predation risk. Vigilance is a complex phenomenon. Past research has shown that it can increase as group size diminishes (Frid 1997), is greater for cows with calves (Wolff and Van Horn 2003), and is greater where there are impediments to detecting and escaping wolves (Ripple and Beschta 2004; Halofsky and Ripple 2008). Additionally, proximity to road has been linked to heightened vigilance (St. Clair and Forrest 2009).

In Saint Mary, where no well-established wolf population existed, and transient wolves were sporadically present during the time of the study, my finding of the lowest elk vigilance and no significant effects of any explanatory variable (Figure 3.2) suggests that the low Saint Mary wolf population may not be effective in stimulating elk vigilance behavior. In Waterton, a well-established, moderate wolf population had denned within the park since 1994, but its number and distribution were highly variable temporally (Watt 2007-2009). Waterton elk response to factors

such as group size was similar to what has been found by others (Halofsky and Ripple 2008). However, elk in this valley failed to respond to predation risk variables such as distance to road and social class, which have been identified as important (Halofsky and Ripple 2008; Friar et al. 2005). As has been found elsewhere, Waterton elk became less vigilant as group size increased. In the North Fork, wolf location data gathered between 1997-2010 from 19 radio-collared wolves showed sustained, high wolf presence in elk winter range (Figure 3.4). North Fork elk were more vigilant than Waterton elk (Figure 3.2), but responded to predation risk factors in ways that were not fully consistent with the scientific literature. For example, my finding of elk vigilance increasing there as group size increased differed from studies that show that vigilance decreases as group size increases (Lung and Childress 2007).

Some studies have found complex and non-linear relationships between wolf presence and elk behavioral responses. Hebblewhite et al. (2005) found that wolf encounter and attack rates may increase for large groups. Creel and Winnie (2005) found group size formation to be an adaptive behavior. They found that when wolves are present, group sizes remain small, but when wolves are absent, group sizes increase, perhaps as a foraging response. My findings suggest that elk were using similar adaptive strategies to avoid predation by wolves as identified in those studies. However, lack of consensus exists in the literature about elk response to predation risk, possibly due to differences in methods used to measure predation risk (e.g., Ripple and Beschta 2004; Kauffman et al. 2007).

Wolves detect prey via sight and smell (Harrington and Asa 2003, p. 89). The different elk vigilance responses to group size in the North Fork and Waterton may be related to how wolves detect prey. If wolves rely on olfaction to detect elk, they could detect a large group of elk from a greater distance than a small group of elk. Thus, if the density of wolves is high (e.g., the North Fork), individual elk in larger groups could be more vigilant, because of the increased chance there of being detected by wolves in a larger group (Hebblewhite et al. 2005).

In Saint Mary, where there was no established wolf population, and wolves passed through, low vigilance and lack of responsiveness to predation risk factors may have been due to elk perception of the low long-term risk in that valley. Thus, in a low-predator system, behavioral compensation by elk to predator presence may be attenuated.

An ecologically effective population of an apex predator is one capable of creating both behavioral and density-mediated (e.g., mortality) responses in its preferred prey (Soulé et al. 2003; Berger 2007; Estes et al. 2010; Estes et al. 2011). While there were some wolves in Saint Mary, such a low population of this species may have been insufficient to be ecologically effective.

In the North Fork, bulls were more vigilant than all the other social classes. This finding counters studies in which adult cows with calves demonstrate the highest levels of vigilance (Laundré et al. 2001; Childress and Lung 2003). A possible explanation of these bulls' elevated vigilance may be that perhaps in the North Fork,

wolf predation on male elk was higher than for other social classes of healthy individuals (Boyd et al. 1994; Kunkel et al. 2004). This may be because post-rut bulls were in a weakened condition due to the high energy expenditure during the rut, and therefore were easier prey (Geist 2002; pp. 420-421). Studies on wolf predation have not been done in the other valleys, so parallel data does not exist, but these dynamics could be similar in the other valleys.

In the North Fork, elk did not show a response to the predation risk variable impediments alone. This may be because those elk lived in a landscape with such a high population of wolves that while elk remained vigilant, they diminished their responses to impediments as they balanced foraging needs and predator avoidance (Lima and Dill 1990; Creel and Winnie 2005). Apparently, impediments had little to do with risk when wolves were very abundant.

A rich body of work exists on the complexity of prey response to predator presence. In the Greater Yellowstone Ecosystem, elk demonstrated heightened vigilance upon wolf reintroduction, but these effects diminished for some social classes over the next five years, as elk adjusted their vigilance levels and reassessed predator lethality (Laundré et al. 2001). In that same ecosystem, Creel et al. (2008) found elk vigilance levels lower at a site with a higher proportion of time spent at risk (higher number of wolves), and higher vigilance at a site with fewer wolves, whether predators were immediately present or absent. Several empirical studies have attributed reduced vigilance in systems with a high predator population to prey

differential adaptive decision-making in response to complex cues (Barros et al. 2008; Ferraria et al. 2010). The dynamics I observed in the North Fork, where elk response to impediments was not significant (Table 3.5), were similar to the results of the studies cited above.

I had further unexpected findings. Distance to forest edge has been identified as having a significant influence on elk vigilance (Geist 2002, p. 397; Creel and Winnie 2005; Liley and Creel 2008). Some researchers have documented elk shifting to the forest edge in the presence of wolves (Creel et al. 2005; Fortin et al. 2005), while others have observed elk increasing their vigilance near forest edges (Friar et al. 2005; Halofsky and Ripple 2008). Distance to forest edge had no effect in my study. Similarly, distance to road had no effect in my study. However, a study conducted in WLNP, and other research, have shown that elk tend to avoid human-made edges, such as roads (Friar et al. 2005; St. Clair and Forrest 2008). The difference between my findings and St. Clair and Forrest (2008) may be because that earlier study took place during the rut.

In summation, I found that some of the commonly identified drivers of vigilance (group size, impediments) appeared to be important drivers at an intermediate level of long-term predation risk (e.g., Waterton). But these drivers ceased to function in this manner when the long-term predation risk level increased (The North Fork). At high levels of long-term predation risk, vigilance was high, but not driven by these common factors. Even more interestingly, in some cases, the

relationship between vigilance and risk factors was reversed. And at a low level of long-term predation risk (e.g., Saint Mary), elk did not respond to these drivers of vigilance. Thus, it is possible that the Saint Mary wolf population may not have been ecologically effective (Soulé et al. 2003; Berger 2007). I further found that other key drivers of vigilance (e.g., distance to forest, distance to road) had no effect regardless of the wolf population.

Elk reduce predation risk via a variety of strategies. They can make larger or smaller groups, depending on predator presence and proximity. They can seek open ground or forest cover for feeding, to diminish predation risk, also depending on predator presence and proximity (Houston 1982; Laundré et al. 2001; Geist 2002, pp. 394-405). I found differences in responses to predation risk variables, associated with differences in wolf population size and stability. The valleys I studied provide compelling landscape-scale case-studies of the complexity of elk behavioral responses to the threat of predation.

Conclusion

This study documented the potential context dependence of elk vigilance, using a two-year window to examine a complex set of relationships. I found the highest elk vigilance in a valley with a high wolf population and the lowest elk vigilance in a valley with a low wolf population. Vigilance increased with wolf numbers. However, when I deconstructed vigilance by examining the variables that

comprised predation risk in these valleys and fitting a model, I found complex dynamics. Taken together, these findings suggest that the apparent association between vigilance and wolf population may be weak or non-linear. While wolves drive elk vigilance, other factors may be modifying this complex relationship.

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Table 3.1. Categorical explanatory variable stratification and sample sizes in three valleys." See Table 3.3 for definition of the variable Impediments.

Valley	Impediments (number of observations)			Social Class (number of observations)				Total Sample
	Low	Moderate	High	Bull	Spike Bull	Adult Cow	Adult Cow w/Calf	
Saint Mary	17	82	117	28	50	67	69	214
Waterton	194	27	21	57	68	53	64	242
North Fork	62	54	50	46	34	49	37	166

Table 3.2. Definition of predation risk variables Debris and View.

Variable	1 – No to Low	2 – Moderate	3 – High
Debris	Grass cover, debris found <100 m of the focal animal consisting of shrub cover <15 cm ht, and no downed wood or rocks ≥15 cm in diameter. No landscape characteristics that represent escape impediments for an elk.	Debris found ≥50 m<100 m of the focal animal consisting of low shrubs, occasional pieces of downed wood, trees, and occasional rocks ≥15 cm<30 cm in height or diameter. Mild slopes (<5%) and drop-offs that represent moderate escape impediments for an elk.	Debris found <50 m of the focal animal consisting of shrubs, trees, and rocks ≥30cm in height or diameter. Sharp slopes (≥5%), sharp drop-offs, and ravines that represent severe escape impediments for an elk.
View	No landscape features that represent impediments within 100 m of the focal animal that hinder visually detecting a predator for an elk.	Landscape features in <180° of the viewshed of the focal animal, within ≥50 m<100 m of the focal animal, that represent impediments to visually detecting a predator for an elk.	Landscape features in ≥180° of the viewshed of the focal animal, within <50 m of that animal that represent impediments to visually detecting a predator for an elk.

Table 3.3. New variable Impediments. Predation risk variables Debris e.g., impediments to escape for an elk, in three levels (low=1, moderate=2, high=3) and View, e.g., impediments to visually detecting a predator in three levels (low=1, moderate=2, high=3) and all of their possible combinations have been used to create the variable Impediments, which represents their interaction, in three levels (low=1, moderate=2, high=3).

Impediments	Debris	View
Low		
	1	1
1	1	2
	2	1
Moderate		
	1	3
2	2	2
	3	1
High		
	3	2
3	2	3
	3	3

Table 3.4. Summary statistics of continuous explanatory variables.

Valley	Group (# of individuals)			Distance to Forest Edge (m)			Distance to Road (m)			Snow Depth (cm)		
	Mean	±95% CI	Range	Mean	±95% CI	Range	Mean	±95% CI	Range	Mean	±95% CI	Range
Saint Mary	91	6.5	6-193	257	22	1-633	269	22	15-711	3	0.5	0-5
Waterton	341	39	6-700	142	13	2-537	494	55.5	2-1730	7	1	0-35
North Fork	76	7.5	6-149	133	19.5	0-800	302	32.5	1-1114	0.8	0.2	0-3

Table 3.5. Results of fitting a general linear model to describe Y_i , elk mean vigilance, for a set of explanatory variables and the interaction of group and impediments. The Effect column indicates a positive or negative effect, based on the β values obtained by fitting the model. For categorical variables, “0” represents the reference level.

Valley	Variable	Variable Type	Variable Levels	Effect	<i>p</i> -value
Saint Mary	Distance to Forest Edge	Continuous	N/A	-	0.12
	Group	Continuous	N/A	-	0.35
	Distance to Road	Continuous	N/A	-	0.27
	Social Class	Categorical	Bull	-	0.06
			Cow	-	
			Cow w/Calf	-	
			Spike Bull	0	
	Impediments	Categorical	Low	0	0.68
			Medium	+	
			High	+	
	Group × Impediments	Categorical	Low	0	0.38
			Medium	+	
			High	+	
Waterton	Distance to Forest Edge	Continuous	N/A	+	0.85
	Group	Continuous	N/A	-	<<0.01
	Distance to Road	Continuous	N/A	-	0.49
	Social Class	Categorical	Bull	-	0.17
			Cow	-	
			Cow w/Calf	-	
			Spike Bull	0	
	Impediments	Categorical	Low	0	<<0.01
			Medium	+	
			High	+	
	Group × Impediments	Categorical	Low	0	0.07
			Medium	-	
			High	-	
North Fork	Distance to Forest Edge	Continuous	N/A	-	0.59
	Group	Continuous	N/A	+	0.03
	Distance to Road	Continuous	N/A	-	0.15
	Social Class	Categorical	Bull	+	0.02
			Cow	-	
			Cow w/Calf	-	
			Spike Bull	0	
	Impediments	Categorical	Low	0	
			Medium	-	0.46
			High	+	
	Group × Impediments	Categorical	Low	0	0.03
			Medium	+	
			High	-	

Figure 3.1. Map of study areas in Glacier National Park, Montana and Waterton Lakes National Park, Alberta..

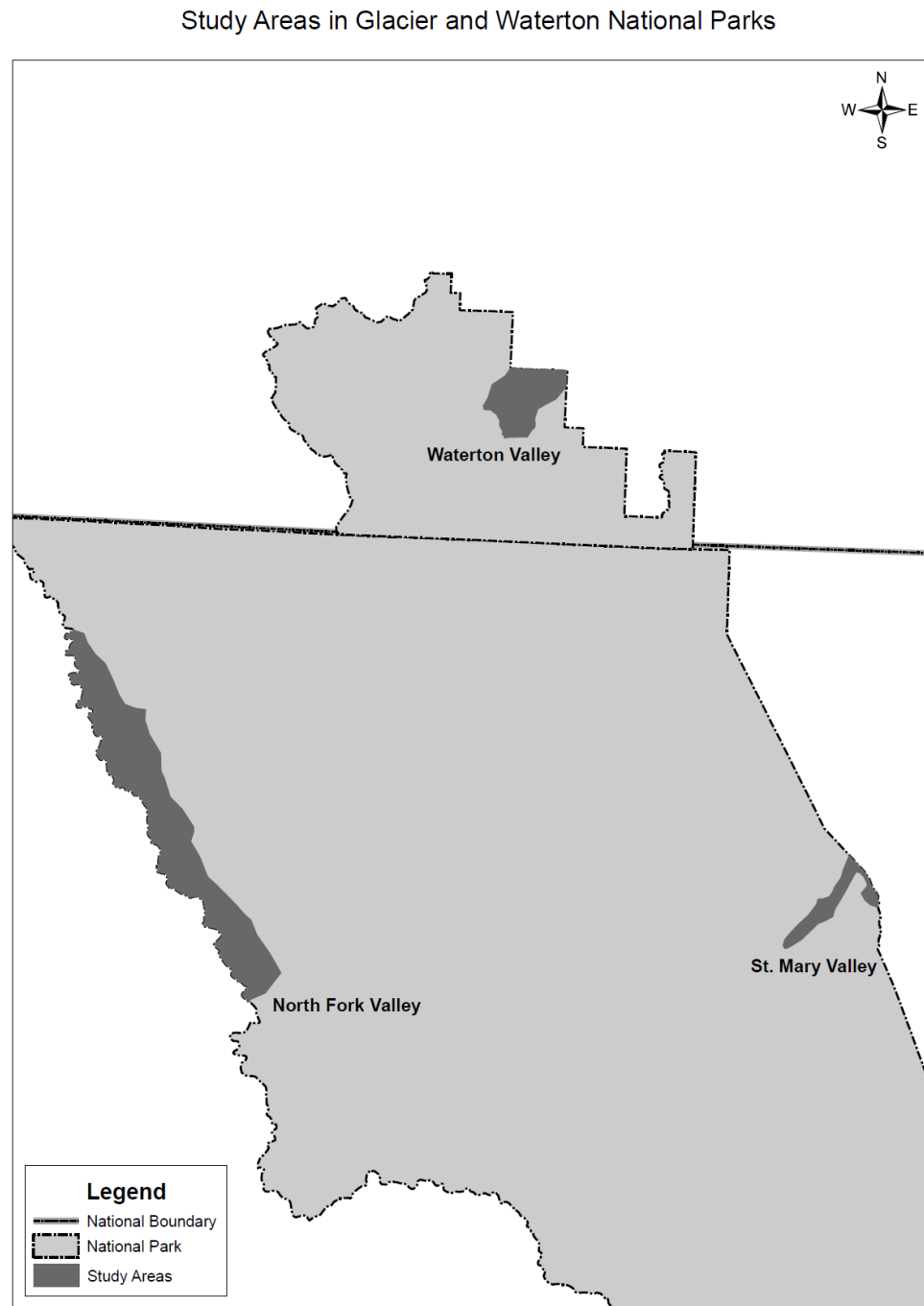


Figure 3.2. Elk mean vigilance in three valleys. The error bars represent 95% confidence intervals.

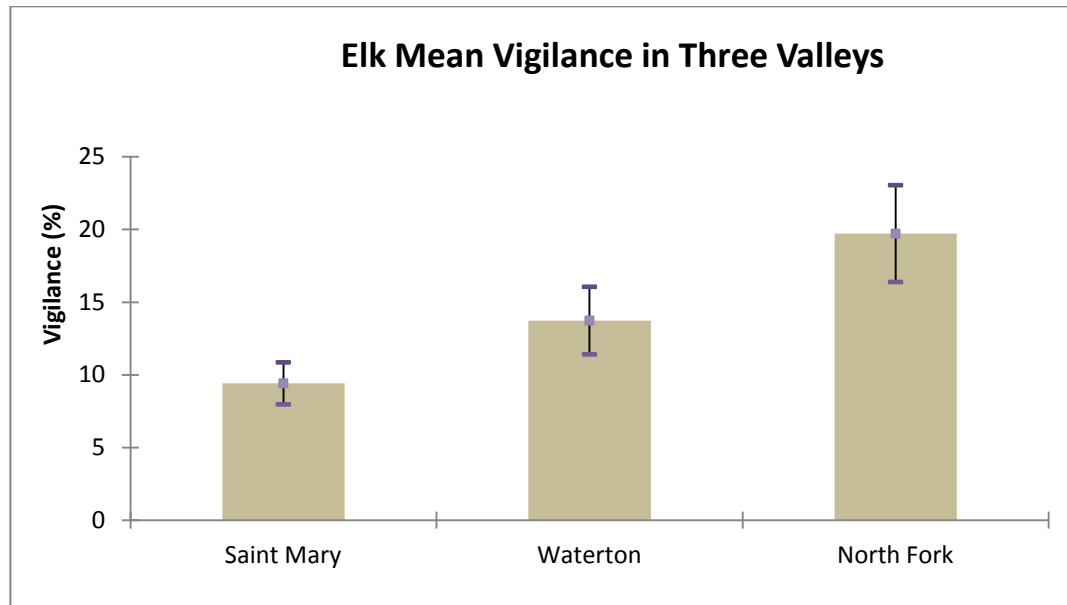
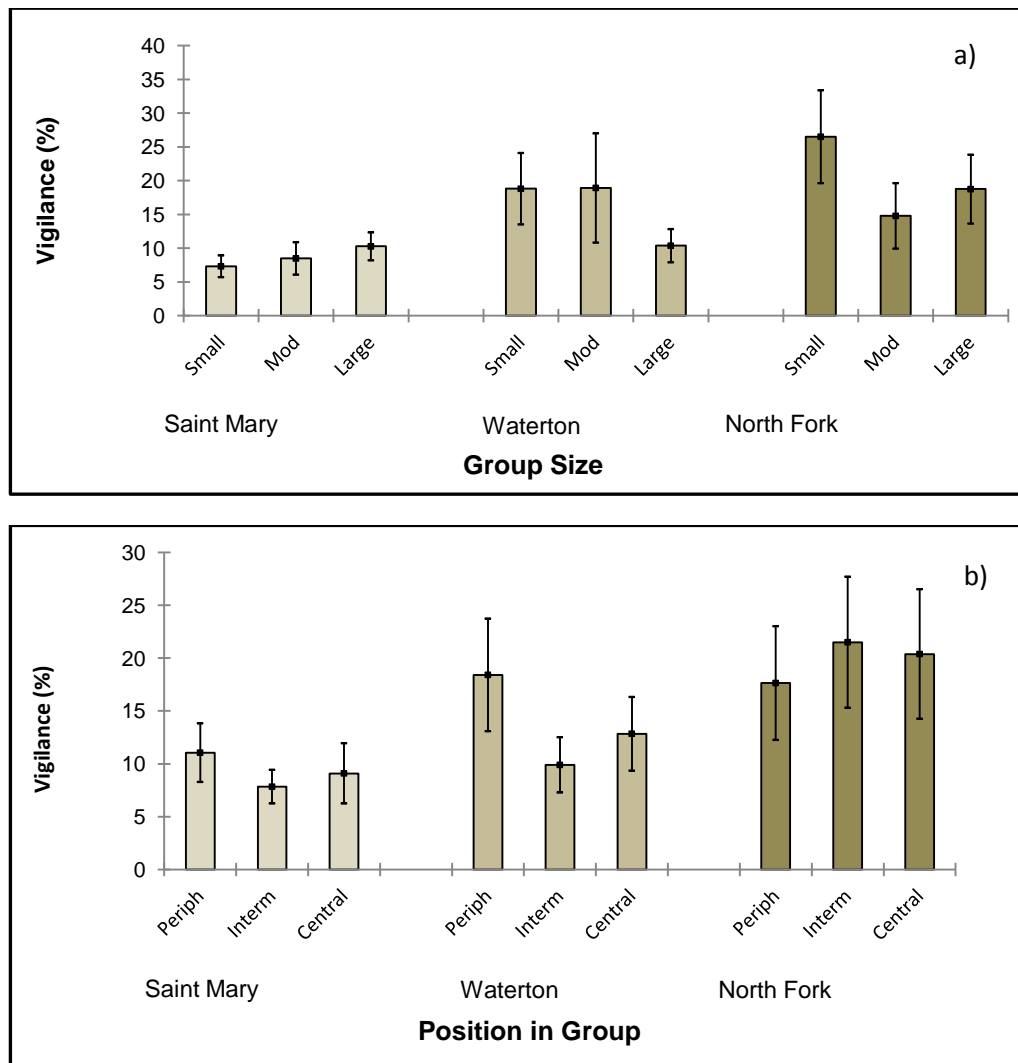
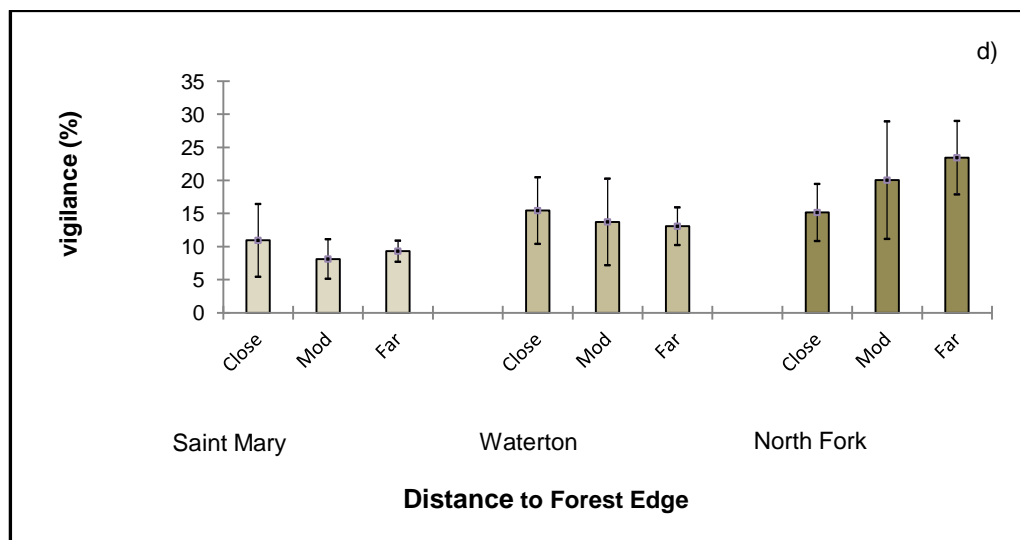
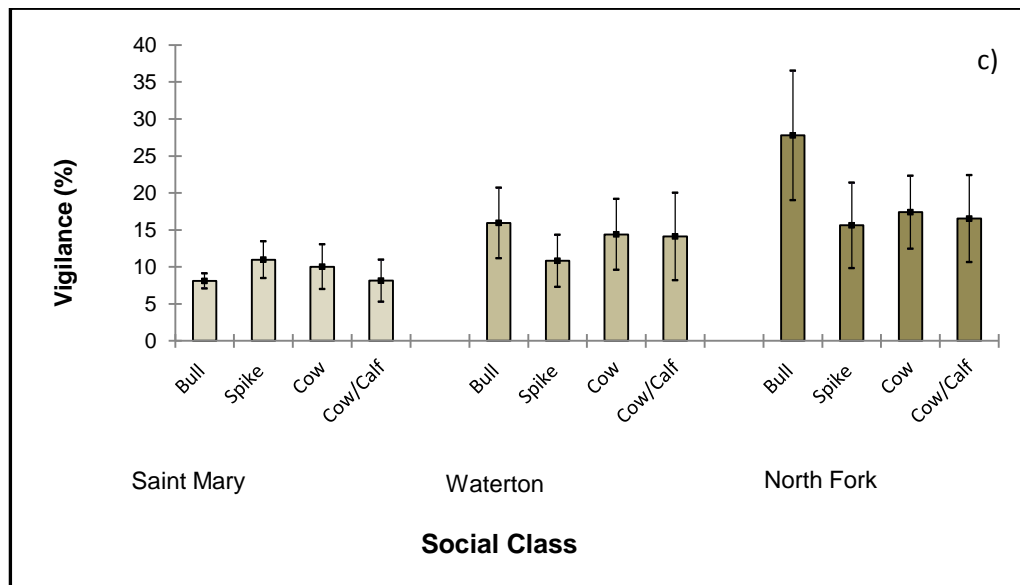


Figure 3.3 a-f. Influence of predation risk variables on elk mean vigilance. The error bars represent 95% confidence intervals. I define group size categories as small ≤ 25 elk; moderate $>25 \leq 75$ elk; and large >75 elk. I define position in group categories as: peripheral=animals in a group as those with no neighbors in one direction; central=animals in a group as those with neighbors on all sides that were located in the center of the group; and intermediate=animals intermediately located between the center of the group and its periphery. I define social class categories per Table 3.2. I treated the distance to forest edge as a categorical variable, defined as close ≤ 50 m; moderate $>50 \text{ m} \leq 100$ m; and far >100 m). I defined impediments per Table 3.2 and 3.3. I treated distance to road as a categorical variable, defined as close ≤ 150 m; moderate $>150 \text{ m} \leq 300$ m; and far >300 m.





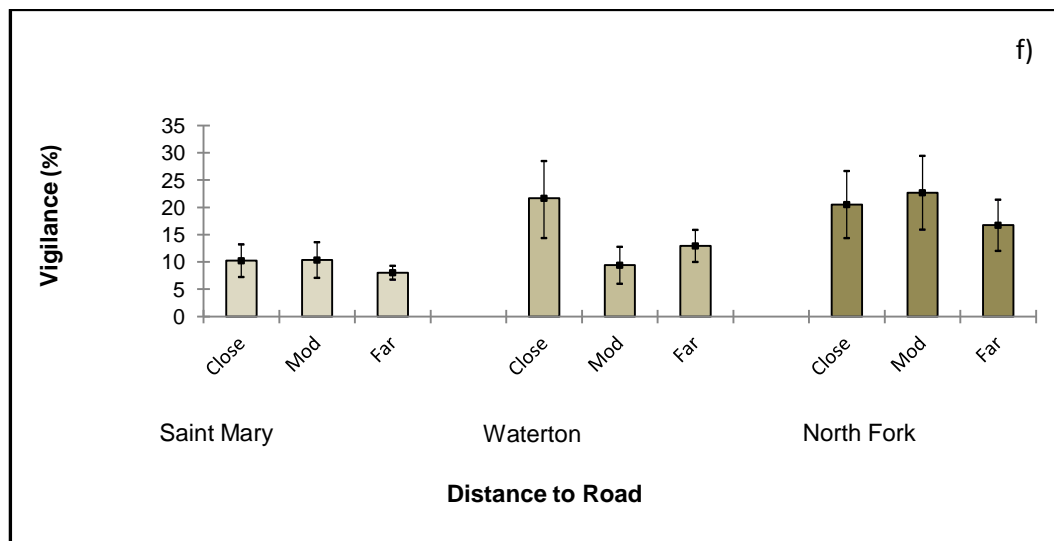
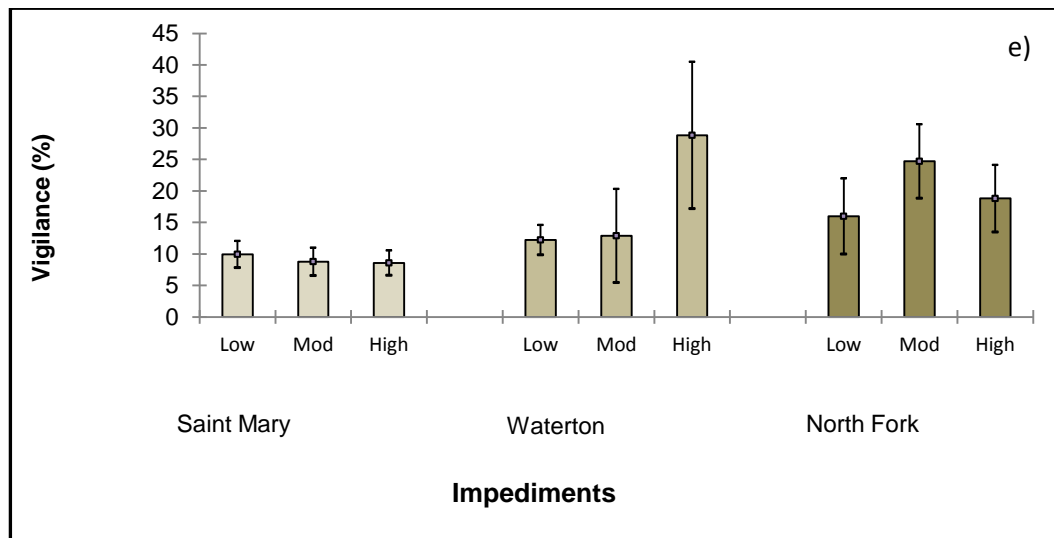


Figure 3.4. Group Size by levels of Impediments. Group is a continuous variable, and Impediments is a variable in 3 categories, Low, Medium, and High, as defined in Table 2.2. I used Low as the reference level of this variable. Group size increases as Impediments levels increase. The Y axis represents the coefficient values of this interaction. The response variable is the proportion of time elk spent vigilant. Error bars represent 95% confidence intervals.

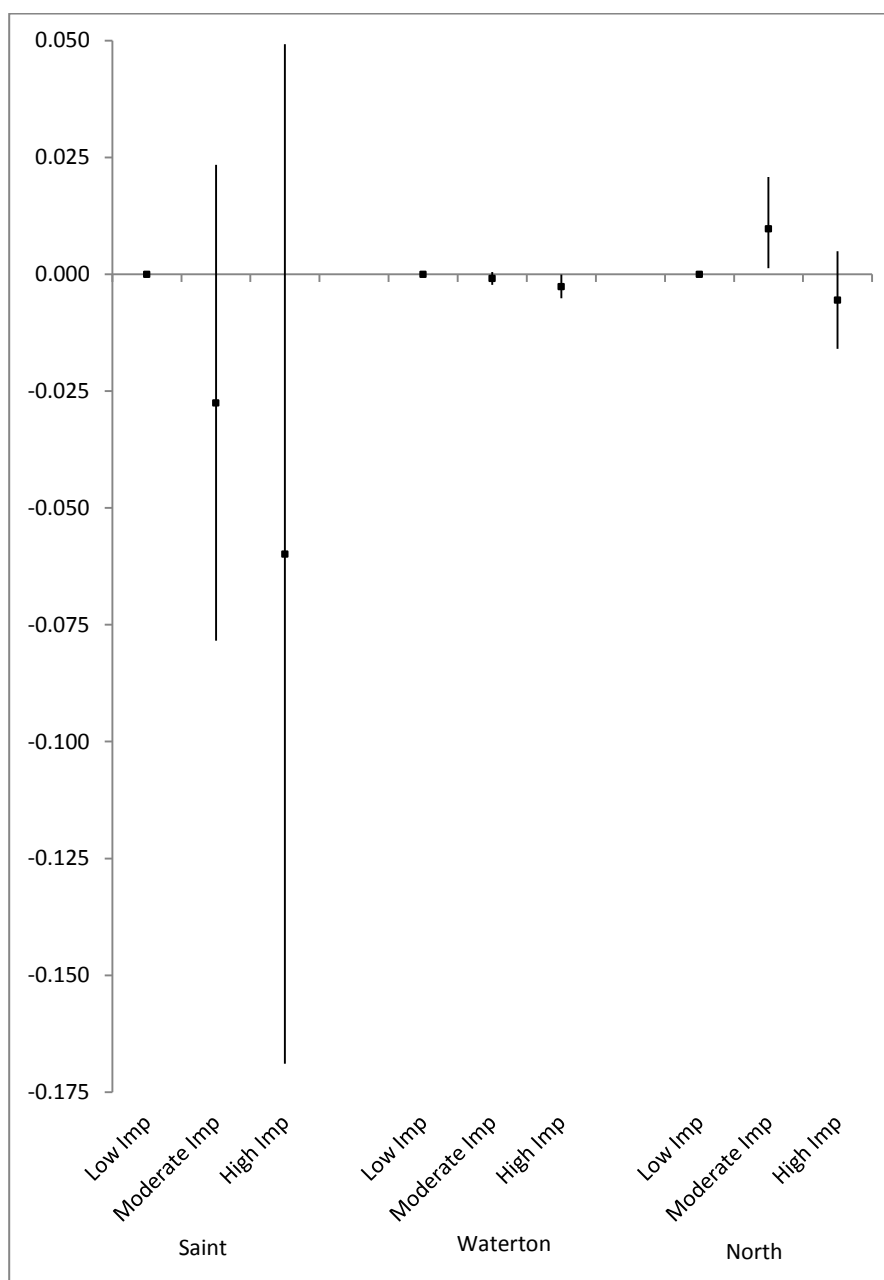
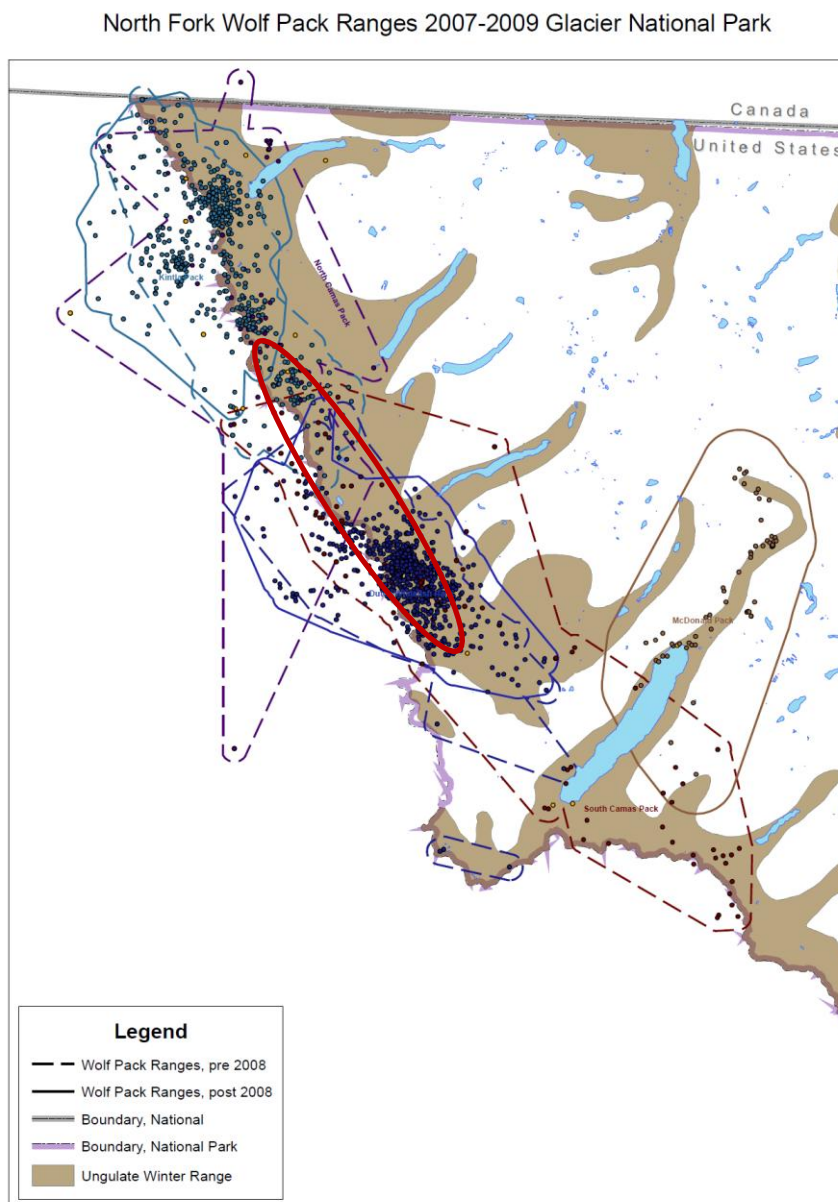


Figure 3.5. Wolf distribution in the North Fork. Data represent wolf locations between 1997 and 2010 for 19 VHF and GPS-collared wolves, derived via triangulation (accuracy $< \pm 1$ km). The red oval represents the area where focal animal observation data were gathered. Field observation sites were limited by road access in winter. Polygons marked with a dotted line represent historic (pre-2008) wolf pack territories. Polygons marked with a solid line represent wolf pack territories from 2008 on.



CHAPTER 4: ASPEN RESPONSE TO TOP-DOWN (WOLF) AND BOTTOM-UP
(FIRE) EFFECTS

Cristina Eisenberg

Abstract

Growth of young trees into the forest canopy is influenced by a variety of environmental conditions. I investigated the relationship between wolf predation, herbivory, aspen (*Populus tremuloides* Michaux) recruitment, and fire, by measuring aspen stands in Glacier National Park, Montana and Waterton Lakes National Park, Alberta. I assessed indices of aspen demography, which include herbivory and bottom-up influences (e.g., incident radiation and temperature, moisture, disturbance). I included as a predictor the trophic mechanism hypothesized in the scientific literature whereby in ecosystems containing wolves, elk (*Cervus elaphus*) avoid sites with topography, debris, or deadfalls that make it more difficult to see or escape wolves (*Canis lupus*). This top-down (predator-driven) effect may indirectly facilitate aspen recruitment (growth above 2.5 m ht, the maximum height an elk can browse). I stratified my observations across three geographically separate areas: the North Fork, Waterton, and Saint Mary Valleys. They share ecological characteristics (soils, climate, elevation, plant associations) and have elk as the dominant ungulate herbivore, but have three different levels of wolf population (number and breeding status) (Saint Mary: low; Waterton: moderate; North Fork: high). These valleys had similar fire histories until recently. Saint Mary and Waterton had no wildfire since 1890. In the North Fork, 90% of aspen stands have burned between 1988 and 2003. I recorded aspen stem densities by size class, annual browse, height growth by aspen stand type (upland, prairie, riparian), and fire history. I compared browse in each

valley by the following factors: stand size, edge versus interior plots, potential direct incident radiation and temperature (heat load), and, in North Fork stands, by fire history. In Saint Mary, prairie stands were growing significantly more than upland stands ($p=0.04$). Aspen in the three valleys exhibited a gradient in browse, with Saint Mary having the highest proportion of browse. Waterton had less browse than Saint Mary, and the North Fork the least. Within each valley, browse was not significantly different in proportion by any of the factors tested. North Fork burned stands had significantly more recruitment than unburned stands ($p=0.007$). While bottom-up processes (e.g., fire) stimulate aspen regeneration, in the North Fork I did not find significantly higher total aspen stem density in burned compared to unburned stands. The differential abundance of recruitment between burned and unburned stands in the North Fork suggests a bottom-up response. Lack of a significant difference in browse between burned and unburned stands in this valley suggests that wolves are not influencing elk avoidance of higher-risk burned stands. In the North Fork, low recruitment in unburned aspen stands compared to burned stands demonstrates the importance of bottom-up effects. Further, in all valleys, fire is necessary for aspen to recruit above elk browse height at all levels of wolf population observed.

Introduction

Growth of young trees into the forest canopy, termed recruitment, is influenced by a variety of environmental conditions. These conditions include nutrient and

moisture availability, disturbance, and browsing by herbivores (Franklin et al. 2002; Horsley et al. 2003; Littell et al. 2008). The ability of a forest to persist over time depends in part on successful recruitment of young trees into the canopy (van der Valk 2009).

From the mid-1920s until recently, in the Intermountain West, researchers have found predominately even-aged, single-storied aspen (*Populus tremuloides* Michaux) stands, which are composed largely of trees >80 years old (Mueggler 1989). Many of these stands arose after stand-replacing wildfires (Kulakowski et al. 2004). This even-aged structure is not an historic condition, being the result of largely unsuccessful recruitment over the last 80 years (Romme et al. 1995). In addition to lack of fire and intense browse by ruminant herbivores (Singer 1996; Baker et al. 1997; Johnston 2001; Vavra et al. 2005), low recruitment has been linked to predator extirpation (Romme et al. 1995; Naiman and Rogers 1997; White et al. 1998).

Aspen forest cover has a variable extent and dynamic in the Intermountain West. Reports range from declines that could lead to aspen disappearance (Kay 1997) to persisting or increasing stands in Waterton Lakes National Park (WLNP) and other areas (Romme et al. 2001; Levesque 2005; Kurzel et al. 2007). Some of the decline may simply be the result of normal forest community succession toward conifer dominance in the absence of fire (Shepperd et al. 2001).

By the mid-1920s, humans had effectively extirpated wolves (*Canis lupus*) from the conterminous United States. In 1925, in Grand Teton and Yellowstone

(YNP) National Parks, Olaus Murie observed intense herbivory, which he attributed to elk (*Cervus elaphus*) irruptions (Leopold 1943) caused by wolf removal (Murie 1925-1954). Fifty years later, McLaren and Peterson (1994) discovered that wolf presence on Isle Royale National Park indirectly stimulated recruitment of previously suppressed balsam fir (*Abies balsamea*), and that these effects were more pronounced in areas with a higher number of wolves. In 1995, the YNP wolf reintroduction inspired research on potential indirect wolf effects on aspen and other woody species (Naiman and Rogers 1997; White et al. 1998).

Ungulate herbivory can significantly modify the composition of plant communities and ecosystems (Houston 1982; Hobbs 1996; Karl and Doescher 1996; Barmore 2003; Vavra et al. 2005; Wisdom et al. 2006). Although primarily grazers, elk subsist on woody browse species when snow depth exceeds 50 cm. Aspen is considered to be high-quality browse and can provide up to 60% of elk diet during winter months (Hobbs et al. 1981; Canon et al. 1987). Deer (*Odocoileus* spp.) and domestic ungulates browse aspen in summer. Elk browse aspen in winter, when aspen are dormant, and typically remove the apical bud. Deer browse aspen side branches and leaves (DeByle 1985; Cook 2002 pp. 281-290; Kaye et al. 2005). Sprouts subjected to repeated browse develop a stunted, shrubby growth form, and ultimately fail to recruit into the canopy (Keigley and Frisina 1998). Both deer and elk can suppress aspen, although in Rocky Mountain elk winter range, elk have the strongest impacts on aspen (Debyle 1985).

Large-scale, stand-replacing wildfire plays a key role in perpetuating aspen stands and enhancing elk habitat (Cook 2002, pp. 344-345). A fire of sufficient intensity and severity to kill the aspen forest overstory stimulates abundant suckering, although some suckers arise after a light fire, or even in its absence (Bartos and Mueggler 1981). Conifer invasion, a by-product of fire suppression, can reduce aspen stand size. While conifers have longer lifespans and can grow taller than aspen, fire eliminates young conifers from the understory (Smith and Smith 2005). In the absence of fire and with ongoing intense elk herbivory, aspen stands fail to successfully recruit new stems, leading to decadent, even-aged stands (White et al. 1998). In Glacier National Park (GNP), Singer (1979) attributed aspen decline to decades of fire suppression combined with elk browse.

Trophic cascades are ecological relationships in which a predator produces direct effects on its prey and indirect changes in faunal and floral communities at other trophic levels (Paine 1980; Crooks and Soulé 1999). Across a wide variety of ecosystems, removing predators causes herbivores to consume plants unsustainably, thereby simplifying ecosystem structure and altering energy flow (Hairston et al. 1960). Ecologists have widely observed that when apex predators (i.e., a predator species that dominate its trophic class), such as wolves, are removed, prey irrupt (Leopold et al. 1947; Paine 1969). This permits excessive and unsustainable consumption of food resources and indirectly affects other species dependent on those plant communities (Berger et al. 2001; Bailey and Witham 2002; Hebblewhite et al.

2005). Hypothetically, returning an apex predator to an ecosystem re-establishes these trophic cascades by reducing prey numbers, and making prey more wary, thereby changing elk feeding behavior (Schmitz et al. 1997; Laundré et al. 2001) and allowing vegetation to grow above browse height (Ripple and Beschta 2007), a top-down effect (Polis and Strong 1996). Where elk are the dominant large herbivore, browse height is generally defined as the height below which elk typically browse aspen, 2.5 m. (White et al. 2003). To produce top-down trophic cascades, an ecologically effective population of an apex predator is necessary (Soulé et al. 2003; Estes et al. 2010).

Bottom-up effects stimulate or reduce vegetation growth (Borer et al. 2005). Examples include moisture and fire. For example, the amount of soil moisture influences plant growth (Bassett 1963). Availability of nutrients such as nitrogen and phosphorus may increase after fire, also stimulating growth, although in some cases (e.g., coniferous systems), fire may induce nutrient loss (Agee 1993). Bottom-up effects include vegetation effects on herbivores, such as availability of food resources (Murdoch 1966).

In food webs, complex energy flows are generated by bottom-up effects, and modified by top-down effects (Polis and Strong 1996; Swanson et al. 2010). The strong bottom-up effects that prevail in all systems may buffer top-down effects (Polis 1994). Studies in a variety of settings have documented weak top-down flows, termed trophic trickles: an apex predator is present, but has limited indirect effects on

vegetation (Power 1990; Hunter and Price 1992; Strong 1992; McAnn et al. 1998; Halaj and Wise 2001; Dawes-Gromadski 2002; Menge 2005; Kauffman et al. 2010).

My objective was to assess aspen demography in GNP and WLNP. This required examining structural stand attributes and using them to determine the effects of past and ongoing herbivory in aspen communities. I worked in three geographically separate valleys that had low, moderate, and high wolf population levels (number of wolves and breeding status). I hypothesized that aspen browse would be lower and recruitment higher where wolf populations are higher. Additionally, I hypothesized that bottom-up (fire) and top-down (wolf population) factors would both influence aspen demography.

Study Area

The study setting, in the central portion of the Crown of the Continent Ecosystem, spans the US/Canada border and encompasses GNP and WLNP. Located in northwest Montana, GNP contains 4,047 km² of forest, alpine meadows, and lakes. WLNP lies in southwest Alberta and encompasses 520 km²; biotic communities are similar to those in GNP (Achuff et al. 2005; Hop et al. 2007). The Continental Divide runs diagonally through GNP and creates the western boundary of WLNP (Figure 4.1).

Modern land use (e.g., ranching) and historic and recent wolf management policies created the context for this research. I studied the following three geographically separate valleys (Figure 4.1), each of which is elk winter range:

- The North Fork, a Valley located in the northwestern edge of GNP, west of the Continental Divide;
- Waterton, a WLNP Valley east of the Divide; and
- Saint Mary, a Valley in the eastern portion of GNP, also east of the Divide.

The measured areas of these study sites (ArcGIS 10.1) are: Saint Mary 1,392 ha; Waterton 2,741 ha; and North Fork 5,705 ha. The valleys are located in the Foothills Parkland Ecoregion, which consists of low-elevation valley bottoms (Achuff et al. 2005; Hop et al. 2007). While ecoregions are broad ecological classifications, within these parks, the Foothills Parkland is limited to the extent of the valleys and ranges in elevation from 1,024 m to 1,700 m.

As throughout the Rocky Mountains, the elk winter range in this study consists of low-elevation grasslands occurring in sheltered valleys. Winter range offers elk snow depth < 0.7 m, protection from the wind, and additional food sources that consist of patches of aspen, shrubs, and conifers (Singer 1979; 1996; Houston 1982; Skovlin et al. 2002, 531-534; Wagner 2006).

Ecological resources are comparable in all valleys. Precipitation is distributed similarly throughout the year (Western Region Climate Center 2010; Parks Canada

2010) (Table 4.1). The valleys have similar soils, made up of calcareous parent materials (Achuff et al. 2005), which provide excellent substrate for aspen growth (Jones and DeByle 1985). These soils include chernozemic, luvisolic, and regosolic orders. Here, chernozems occur on dry upland sites associated with sparse aspen and shrubs. Luvisols occur on moister prairie sites associated with vigorous aspen and shrubs. Regosols occur on riparian and wetland sites associated with dense aspen, cottonwood (*Populus* spp.), wet shrubs, and sedges (Achuff et al. 2005) (Table 4.2).

Grassland species composition is similar throughout the valleys. Rough fescue (*Festuca scabrella*) is the dominant grass in the valleys. Codominant grasses are the same, and consist of Richardson needlegrass (*Achnatherum richardsonii*), Junegrass (*Koeleria macrantha*), oatgrass (*Danthonia* spp.), and bluebunch wheatgrass (*Agropyron spicatum*) (Kujit 1982; Lesica 2002; Achuff et al. 2005; Hop et al. 2007).

Aspen ecological characteristics are similar throughout the valleys. The mean aspect of aspen stands in the valleys is comparable, and has a southeast trend (Table 4.1). The mean stand elevation is similar, ranging from 1137 m in the North Fork to 1404 m in Saint Mary. Aspen grows from sea level to 3,000 m (Jones 1985); my study area constitutes a narrow band (267 m) within that elevational range. The same plant associations occur in the aspen stands in the valleys, suggesting similar ecology. These plant associations are: aspen/Saskatoon/cow parsnip (*Populus tremuloides*/Amelanchier alnifolia/Heracleum lanatum); aspen/western snowberry (*Populus tremuloides*/symphoricarpos occidentalis); aspen/thimbleberry (*Populus*

tremuloides/rubus parviflorus); and aspen/nettle (*Populus tremuloides/urtica dioica*) (Achuff et al. 2005; Hop et al. 2007).

Wildfire has been present in this ecosystem for many millennia. In the 1890s, European settlers instituted fire suppression (Singer 1979; Levesque 2005), but fire has been allowed to return since 1988. On the east side of GNP, which includes the North Fork Valley, there have been six large (>5,000 ha), mixed-severity wildfires since 1988, the most recent occurring in 2003 (Hop et al. 2007). These fires have cumulatively burned 90% of North Fork aspen stands; the other stands in this valley and in the other valleys have not burned since 1890. The 1910 Big Burn, which burned 1.2 million ha in the Intermountain West, did not burn my study sites (Singer 1979; Barrett 1996; Barrett and Arno 1999, pp. 50-64).

Ungulate herbivores include elk and deer (Achuff et al. 2005), with elk the dominant herbivore in the study sites (Martinka 1978; Singer 1979; Neff et al. 1965; Hudson and Haigh 2002). Large carnivores include cougar (*Puma concolor*), grizzly bear (*Ursus arctos*), and black bear (*U. Americanus*). Scat analysis provided evidence that wolves preyed mainly on elk throughout the study sites, but also on deer and moose (Eisenberg unpublished data). Other studies have found that wolves are the leading elk predator, because bears hibernate when elk are on their winter range and cougars prey mostly on deer (Kunkel et al. 1999; Watt 2007-2009; Banfield 2010).

While all valleys provide similar wolf habitat, wildlife management policies vary, producing three contrasting wolf populations. I characterized Saint Mary as

having a low wolf population (Fuller et al. 2003). Although wolves have attempted to recolonize Saint Mary since the 1980s, no stable wolf population has been established in that valley. No breeding pair or pack of wolves occurred there during my study (USFWS et al. 2007; Sime et al. 2009; Sime et al. 2010; USFWS et al. 2010).

I characterized Waterton as having a moderate and variable wolf population (Fuller et al. 2003). Wolves have never been protected outside of WLNP and are subject to hunting, trapping, and legal take by landowners, although no harvest occurs within the Park. During my study, wolves in that valley numbered between 4-12 individuals within the one pack that dened inside the Park (Watt 2007-2009).

I characterized the North Fork as having a high wolf population (Fuller et al. 2003). During my study, North Fork wolves ranged from 12-29 individuals in 2 packs per agency reports (USFWS et al. 2007; Sime et al. 2009; Sime et al. 2010; USFWS et al. 2010). In 2008, I documented a wolf population of 38 individuals in 2 packs by field observations; both packs produced multiple litters.

Aspen Sampling Methods

I defined regeneration as aspen stems that sprout above the ground, and browse height as the height below which elk typically browse aspen, 2.5 m. I defined recruitment as an aspen stem that grows above browse height, ≥ 2.5 m. I referred to sprouts < 1 m in height as suckers, and those ≥ 1 m < 2.5 m as ramets. I classified stems

≥ 2.5 m in height and < 5 cm diameter at breast height (DBH) (1.4 m) as juvenile aspen, and those ≥ 5 cm DBH as mature aspen.

Aspen is a moisture-limited species that does not thrive in arid conditions (Jones 1985; Worrall et al. 2010). As a surrogate for moisture availability, I categorized aspen stands by topographic position, i.e., stand type (upland, prairie, riparian), based on soil type and associated aspen community characteristics (Table 4.2). While topographic position and soil type are not precise measures of soil moisture, they do indicate general moisture availability (Jones and DeByle 1985; Burke and Kasahara 2011).

The sampling unit was the individual aspen stand within a valley, defined by a minimum stand size of three trees. I sampled all stands in the valleys (North Fork $n=104$; Waterton $n=50$; and Saint Mary $n=29$), and assessed stand demography in transects and plots. I determined the area of each aspen stand and categorized it as small, medium, large, or extensive (Table 4.3). To determine sampling intensity, I measured stand size (m^2) with transect tapes and a laser rangefinder, by walking the stand length, width, and circumference (Table 4.3).

I sampled with belt transects 4 m in width, positioned to evenly sample each stand. This involved establishing an axis along the dominant dimension of an aspen stand and then placing the first transect at a perpendicular bearing to that axis at a randomly chosen distance < 25 m from the end of the long axis. The remaining transects occurred at 50 m intervals thereafter. Small stands received 1 transect;

medium stands received 2 transects; large stands received 3 transects; and extensive stands received 4 transects. Thus, small, medium, and large stands were fully sampled (all of the transects that could fit in a stand were sampled), but in extensive stands, sampling stopped before reaching the other end of the stand (Table 4.3, Figure 4.2). To avoid potential bias, I randomly alternated the end from which I began sampling a stand.

All transects ran from where aspen sprouts (suckers) were first visible above the ground outside of the stand of mature trees, through the stand, and ended at the last visible sucker on the other side of the stand. Transects varied in length based on stand dimensions (Figure 4.3). There were 2 stands in each valley that began in grass habitat and trended upslope into a stand of conifers. For these stands, I used a threshold of 50% dominance of mature aspen to define stand boundaries.

I measured the slope and aspect along the belt transect line, taking this measurement once, from the transect start. The transect bearing was measured with a compass (1° - 360°), and slope (%) with a clinometer, by aiming this instrument at a landmark 50 m distant (distance measured with a transect tape) along the belt transect line. I measured the DBH of all aspen ≥ 2.5 m in height. Levesque (2005) confirmed lack of significant conifer encroachment in aspen communities in the Crown of the Continent Ecosystem, so I did not include conifer basal area in my survey.

Within each transect, I established circular plots 2 m in radius every 20 m, with the first and last plots placed at the ends of the transect (Figure 4.2). In these plots I

measured understory aspen height and DBH of all suckers and ramets, and browse on each of them for the 2 years prior to my survey. I assessed browse and height growth (cm) on the 4 aspens ≤ 2.5 m in height closest to the plot center, for every year each stem had been alive (Keigley et al. 2003). I used a subset of unbrowsed stems of the 4 stems sampled to document annual height growth by measuring the distance (cm) between terminal bud scars 2 years prior to my survey.

Other factors that can influence height growth and morphology include environmental effects, such as snow-loading, wind stress, and disease. I did not measure height growth of sprouts in which these factors could create detection bias. I categorized aspen disease as low ($<33\%$ of stems affected); moderate ($\geq 33\%$ to $<66\%$); and high ($\geq 66\%$). The primary diseases in my study area were *Pollaccia radiosa* (Shepherd's Crook) and *Marsonnina populii* (Black Leaf Spot) (Jones and DeByle 1985). No aspen stands exhibited high or unusual level of disease.

Analysis

I examined aspen annual height growth in the three valleys, stratifying my data by stand type (upland, prairie, riparian). I conducted a one-way ANOVA to compare aspen height growth among the three stand types. Normality was evaluated for the response variable (mean annual height growth) in this and other analyses by observing its distribution, and testing for deviation from assumptions of normality by observing residual plots.

I measured aspen absolute density. Aspen relative density (arcsine transformation) was evaluated in four size classes of aspen: suckers (<1 m ht); ramets (≥ 1 m < 2.5 m ht); juvenile aspen (≥ 2.5 m ht and < 5 cm DBH); and mature aspen (≥ 5 cm DBH). In the North Fork I compared the relative stem density in stands with fire to those with no fire by conducting 2-way ANOVA with fire, size class, and their interaction.

I examined browse (arcsine transformation) based on stand size and plot position within large stands. Only browse on four-year-old stems was included, to eliminate the bias potentially created by comparing proportion of browse on stems of various ages. I performed a 2-way ANOVA to look at browse with stand size, plot position, and their interaction. As a relative measure of stand size, I used the total number of plots sampled within a stand (small=1-3 plots; medium=4-7 plots; large= ≥ 8 plots). I compared browse in edge plots, located on the edge of aspen stands, to browse in interior plots, located with a plot center at 62 m from the beginning of the transect. I selected just one plot from each transect as an interior plot, for consistency of measurement, and to enable a one-to-one comparison. By comparing the plots with a center at 62 meters to edge plots (plot center at 2 m), I systematically tested elk utilization of the interior of a stand. This also eliminated the potential bias of gradient effects. I did not use plots that occurred near major openings in the stand canopy, as these could constitute an edge. In the North Fork, I excluded stands with no fire, due

to a small sample of interior plots ($n=6$). In this valley, I conducted a t -test to compare browse in stands with fire to those with no fire.

The ability of an aspen stand to retain heat, via its slope and aspect, can have significant ecological effects. South-facing slopes retain more heat than north-facing slopes. Moreover, steeper south-facing slopes can retain more heat than slopes that are less steep (Skovlin et al. 2002, pp. 535-545). Via these dynamics, slope and aspect can influence aspen growth (Chen et al. 2002). The need of an elk to conserve heat in winter influences its landscape use. Elk favor south-facing slopes with a moderate slope, which potentially have greater plant availability because the snow melts more rapidly on them (Ager et al. 2003; Skovlin et al. 2002, pp. 535-545).

I measured the effect of aspen stand heat retention capability on browse. This involved creating a new variable, heat load, that incorporated the transect slope and latitude, in radians, per McCune and Keon (2002). To approximate heat load, aspect (cosine transformed) was folded about the north-south line. To more accurately depict the trajectory of the sun, I shifted the aspect from a maximum on south slopes to a maximum on southwest slopes and a minimum on northeast slopes:

$$\text{Folded Aspect} = 225 - \text{Aspect}$$

Heat load provides an index of potential direct incident radiation and temperature. Because it is a unitless index, it can't be converted into a cumulative measure of temperature, such as degree days. It does not account for cloud cover and

shading by adjacent vegetation or topography (McCune and Keon 2002). I used linear regression to examine the relationship between browse and heat load.

I used TIBCO Spotfire S+ and SAS v9.1 (SAS Institute, Cary, NC, USA) software for analyses. I used a p -value of 0.05 as the upper threshold for statistical significance (Ramsey and Schafer (2002, p. 46).

Results

Aspen mean height growth of unbrowsed stems did not differ among the valleys (Table 4.1). There was no statistically significant difference in height growth (cm/yr) by stand type in Waterton and in North Fork burned stands (Table 4.4, Figure 4.3). I was unable to include North Fork unburned stands in this analysis due to low sample size (upland $n=1$; prairie $n=1$; riparian $n=9$). Only in Saint Mary did I detect a significant difference in height growth between the three stand types ($p=0.04$) (Table 4.4). A post hoc Tukey test demonstrated that prairie and upland stands had the two means that differed most, with prairie stands growing significantly more than upland stands. While riparian stands were also growing more than prairie stands, the Tukey test did not identify this difference as significant.

The North Fork had a lower absolute density of aspen stems per hectare in burned and unburned stands than the other two valleys (Table 4.5). In all valleys, the lowest proportion of stems occurred in the juvenile aspen size class (>2.5 ht <5 cm DBH) (Table 4.5, Figure 4.4), with the exception of North Fork stands with fire. When

I compared stem density in North Fork burned and unburned stands, I found a significant difference only for juvenile aspen ($t=2.77$, 102 df, $p=0.007$) (Table 4.5, Figure 4.4-c).

Summary statistics indicated that browse was highest in Saint Mary, lower in Waterton than in Saint Mary, and lowest in the North Fork stands that burned. Within the North Fork, there was no difference in browse in burned and unburned stands ($t=-1.36$, 12 df, $p=0.2$) (Figure 4.5-a). There was no difference in browse among stand sizes and plot positions in Saint Mary ($F_{2,26}=0.96$, $p=0.40$; $t=1.43$, 9 df, $p=0.33$), Waterton ($F_{2,81}=0.36$, $p=0.87$; $t=0.49$, 34 df, $p=0.63$), and in North Fork stands with fire ($F_{2,26}=0.96$, 0.40; $t=0$, 42 df, $p=1$) (Figure 4.5-b-c). There was no relationship between browse and heat load in the three valleys (Saint Mary $t=0.85$, 43 df, $p=0.40$; Waterton $t=0.25$, 89 df, $p=0.80$; North Fork $t=1.01$, 103 df, $p=0.31$).

Discussion

Because elk are the dominant ungulate herbivore in the study area (Neff et al. 1965; Martinka 1978; Singer 1979; Hudson and Haigh 2002), aspen demography may be strongly influenced by elk behavior (utilization of stands). A top-down perspective suggests that wolves indirectly influence aspen demography by killing elk and by causing elk to avoid aspen forests, due to the difficulty of detecting and escaping wolves there (Larsen and Ripple 2005). An bottom-up perspective suggests that elk use the forest, but make decisions about habitat use primarily based on energetic

expenses, because the energetic costs of moving through a structurally complex landscape may be greater than in one that is more open (Skovlin et al. 2002).

I tested the hypothesis that aspen browse would be lower and recruitment higher where wolf populations are higher. Additionally, I hypothesized that bottom-up (fire) and top-down (wolf population) factors would both influence aspen demography. I tested for top-down influences of wolves by 1) examining structural aspen stand attributes; and 2) using these attributes to determine the effects of past and ongoing browse on aspen communities. I tested for bottom-up effects by evaluating the influence of fire on aspen growth, stem density, and recruitment, as well as other bottom-up factors (heat load; stand type). I made predictions about aspen recruitment based on elk density and wolf population. I found that top-down and bottom-up processes were important joint engineers of aspen communities. Further, I found that elk browse was lower where there was a high wolf population, but that fire was necessary for aspen to recruit regardless of wolf population.

The mean elk density was 24.24 ± 1.34 (100 m^{-2} ; 95% CI) in Saint Mary; 28.25 ± 1.48 in Waterton; 11.09 ± 1.47 in North Fork sub-transects with no fire; and 9.94 ± 0.71 in North Fork sub-transects with fire. This suggests a density-mediated response, with higher elk density in valleys with a lower wolf population. First, I expected that Saint Mary and Waterton, which had similar elk densities, would show the highest browse and lowest aspen recruitment, and that the North Fork, which had a lower elk density, would show the lowest browse and highest recruitment (White et al.

2003; Hebblewhite et al. 2005). Second, I predicted that while the Saint Mary would show the highest browse and lowest aspen recruitment; Waterton would show an intermediate level of browse and recruitment; and the North Fork the lowest browse and highest recruitment.

Browse levels in each valley matched my second prediction (Figure 4.5-a). However, trends in browse were not paralleled by even a mild concurrent trend in aspen recruitment in unburned stands in the valleys (Figure 4.4). Lack of recruitment in unburned aspen stands in the three valleys was similar to trends found in the North Fork pre-wolf recolonization. In an elk winter range habitat survey conducted in the North Fork in 1973-1974, when there were no wolves in this valley and had been no fire since 1890, Singer (1979) found no aspen recruitment. I found a bottom-up effect in the North Fork, where even with high wolf presence and a lower elk density than in the other valleys, in the absence of fire, aspen failed to significantly recruit into the canopy.

To further explore the relationships between elk density, wolf population, and browse, I examined predation risk factors. Larger stands may be riskier than small stands, as they contain more interior versus edge area. Similarly, elk habitat in interior plots may provide greater predation risk than that in edge plots, due to the greater difficulty of escaping a predator in the interior of stands versus open terrain (Ripple and Beschta 2004). Stands with fire, which typically contain more large dead wood than stands with no fire, may be riskier (Halofsky and Ripple 2008). In fact, neither

stand size or plot location within a stand proved to be significant predictors of browse level. In the North Fork, browse in burned stands was not lower than in unburned stands (Figure 4.5-a).

Aspen browse was lower and recruitment was higher where wolf populations were higher, but this was likely a bottom-up effect (fire), not a top-down wolf effect. This suggests the importance of bottom-up effects in influencing aspen demography. I could not rule out the potential influence of wolves on aspen recruitment, or the presence of a trophic trickle. However, I was unable to test for such relationships, because I lacked a valley with no wolves and with fire. None of the bottom-up environmental factors I examined beyond fire appeared to significantly influence aspen recruitment. I did find some potential top-down relationships for browse, but was unable to make inferences about wolf presence. From the divergence in aspen recruitment in burned versus unburned stands in the North Fork ($p=0.0007$; Figure 4.4 a-c), I can conclude that aspen requires another ecological force—fire—to recruit vigorously.

Halofsky and Ripple (2008) investigated aspen stand dynamics in the presence and absence of wolves and fire. In comparing aspen growth in an area burned by the Greater Yellowstone Ecosystem 1988 fire to an adjacent unburned area, they found greater density of young aspens and less browse in the burned area relative to the unburned area. My findings differed from Halofsky and Ripple (2008) in two principal ways: 1) stem density; and 2) herbivory. In the North Fork, a valley that has a high

wolf population, stem densities of young aspens did not differ significantly in burned versus unburned stands, with the exception of in the $>2.5\text{m ht}<5\text{cm DBH}$ size class. This size class represents recent recruitment into the canopy. I found no difference in browse in this valley between burned and unburned aspen.

My findings are similar to earlier YNP findings of significant differences in browsing intensity among burned and unburned stands in a system that did not have wolves. Romme et al. (1995) found that elk browsed nearly all sprouts that were accessible, leading to a lack of recruitment. They, and others, suggested that this effect may be linked to lack of wolf predation on elk (Romme et al. 1995; White et al. 1998). The lack of significant differences in browse I detected between burned and unburned stands in the North Fork (Figure 4.5-a), and the lack of recruitment in unburned stands in all valleys, regardless of wolf population, suggest lack of top-down (e.g., wolf) effects on elk.

The link between recruitment and fire in a wolf→elk→aspen system is complex. Fire stimulates root sprouting, which I did not observe in North Fork stands with fire. Additionally, fire creates impediments. Decreased browsing in aspen stands with fire could be attributed to predation risk avoidance (Halofsy and Ripple 2008; White et al. 2003) or to elk avoiding such stands to conserve energy (i.e., stands that have burned generally have down logs that require more energy to move through) (Seager 2009). However, studies throughout the Rocky Mountains in elk winter range with no wolves have found that elk do not avoid stands that have burned (Martinka

1976). Indeed, such stands draw elk, resulting in little to no post-fire aspen recruitment (Romme et al. 1995; Baker et al. 1997; Barnett and Stohlgren 2001; Kay 2001; Hessl and Graumlich 2002; Bailey and Witham 2002).

My work illustrates the complexity of ecological communities and trophic relationships, and the importance of disturbance. The interaction of disturbance and other bottom-up forces with apex predator effects has been studied extensively in aquatic communities, using an experimental approach (Power 1990; Menge et al. 1997). Such an approach is generally not feasible when working with large-bodied terrestrial mammals that travel widely. Yet, while food web research in terrestrial ecosystems lags behind that in aquatic ecosystems (Power 1992), some important experimental work has been done with invertebrates. Working in an arthropod terrestrial system, Halaj and Wise (2001) reported trophic trickles in which apex predation became attenuated by bottom-up effects and failed to create a strong release in vegetation due to food web complexity. Low aspen recruitment in the absence of fire in three valleys demonstrates the importance of fire. In the case of the North Fork, low aspen recruitment in the absence of fire may indicate a trophic trickle; however I was ultimately unable to test for this. My findings invite deeper inquiry into the interaction between top-down and bottom-up effects in large mammal systems and forest communities.

Conclusion

In the Crown of the Continent Ecosystem, top-down and bottom-up processes are important joint engineers of aspen communities. I found that elk browse was lower where there was a high wolf population, but that fire was necessary for aspen to recruit regardless of wolf population. An integrated ecological perspective that accounts for the role of top-down and bottom-up processes has the potential to inform natural resources management as we strive to create more vigorous and resilient aspen ecosystems.

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Table 4.1. Aspen stand landscape summary statistics in three valleys.

Valley	Aspect (degrees)			Elevation (m)			Height Growth stems <2.5 m ht (cm yr)		
	Mean	± 95% CI	Range	Mean	± 95% CI	Range	Mean	± 95% CI	Range
Saint Mary	134	11	30-350	1404	8.5	1292-1480	19	5	4-38
Waterton	136	7	30- 360	1334	4.0	1137-1397	22	9	7-40
North Fork (no fire)	133	43	4-355	1163	25.0	1112-1303	35	8.5	20-56
North Fork (fire)	136	6.5	3-360	1137	6.5	1082-1250	30	7	5-59

Table 4.2. Aspen stand types. Soil types and aspen stand and vegetation characteristics per Achuff et al. (2005).

Stand Type	Soil Type	Aspen Community Characteristics	Soil Characteristics
Upland	Chernozem	Dry, scrubby aspen and sparse scrubby shrubs	non-wet, thin
Prairie	Luvisol	moister prairie sites associated with vigorous aspen and shrubs	non-wet, deep
Riparian	Regosol	wetland sites with dense aspen, cottonwood, wet shrubs, and sedges	wet, deep

Table 4.3. Aspen sampling strategy based on stand size.

	Aspen Stand Size			
	Small	Medium	Large	Extensive
Rectangular stand dimensions	<50 m × 50 m	≥50 m × 50 m to <100 m × 100 m	≥100 m × 100 m to <250 m × 250 m	≥250 m × 250 m
Area	<0.25 ha	≥0.25<1 ha	≥1<6.25 ha	≥6.25 ha
Transect length and spacing	Variable length, every 50 m along dominant axis	Variable length, every 50 m along long dominant axis	Variable length, every 50 m along dominant axis	200 m-long transects, every 200 m along downslope edge
Plot spacing	20 m intervals	20 m intervals	20 m intervals	20 m intervals
# transects	1	2	3	4

Table 4.4. Aspen height growth of unbrowsed stems by stand type for stems <2.5 m ht. Stand type was characterized per Table 4.2. Lack of data is indicated by “n/a.”

Valley	Stand Type	Height Growth by Stand Type (cm yr ⁻¹)			ANOVA results	
		Mean	± 95% CI	Range	F-statistic	P-value
Saint Mary	Upland	11	5	5-17	F _{2,19} =3.78	0.04
	Prairie	29	28	8-50		
	Riparian	20	6	4-38		
Waterton	Upland	22	9	8-32	F _{2,30} =0.08	0.92
	Prairie	21	4	7-40		
	Riparian	23	9	13-34		
North Fork Fire	Upland	29	4	11-52	F _{2,74} =2.3	0.10
	Prairie	33	5	18-59		
	Riparian	28	7	11-38		
North Fork No Fire	Upland	n/a	n/a	n/a	n/a	n/a
	Prairie	n/a	n/a	n/a		
	Riparian	36	9	20-56		

Table 4.5. Summary statistics for aspen absolute and relative density in three valleys.

Valley	Absolute Density (stems/ha-1)			Relative Density Stems ≤ 1 m ht (%)			Relative Density Stems >1≤2.5 m ht (%)			Relative Density Stems >2.5 m ht < 5cm DBH (%)			Relative Density Stems > 5 cm DBH (%)		
	Mean	± 95% CI	Range	Mean	± 95% CI	Range	Mean	± 95% CI	Range	Mean	± 95% CI	Range	Mean	± 95% CI	Range
Saint Mary	12052	2250	3629- 23163	64.50	8.97	16.45- 98.80	26.70	6.90	0-60.89	2.20	1.22	0 - 11.21	6.60	2.40	0- 25.19
Waterton	11787	1684	8285- 13047	72.35	7.09	18.68- 100	14.71	4.83	0-65.5	2.59	1.17	0-20.38	10.35	3.23	0- 44.74
North Fork (no fire)	6430	4519.5	1086- 24153	57.14	20.95	0- 97.59	26.29	12.96	0- 64.13	7.15	8.50	0-43.98	9.42	7.43	0-35.34
North Fork (fire)	7808	1126.5	682- 33778	39.37	5	0-100	26.04	3.96	0- 67.05	23.60	4.35	0-91.44	10.99	3.48	0 -100

Table 4.6. Ungulate browse on aspen in three valleys. Total browse represents all stands sampled, with the exception of unburned stands, which were not included in this analysis due to a very small sample size ($n=6$). Browse in stands used for browse by plot position includes only stands that had in them at least one transect with ≥ 7 plots, to allow comparison of edge (plot center 2 m from edge of stand) and interior (plot center 62 m from edge of stand) plots.

Valley	Total Browse (%)			Browse in Stands Used for Browse by Plot Position Analysis (%)		
	Mean	\pm 95% CI	Range	Mean	\pm 95% CI	Range
Saint Mary	64.50	7.35	32.86-85.71	45.40	22.12	14.29-57.69
Waterton	38.36	5.75	0-100	19.10	6.07	7.14-35.00
North Fork (no fire)	26.36	15.05	0-75	n/a	n/a	n/a
North Fork (fire)	16.71	4.40	0-77.78	10.72	6	1.32-25

Figure 4.1. Map of study areas in Glacier National Park, Montana and Waterton Lakes National Park, Alberta.

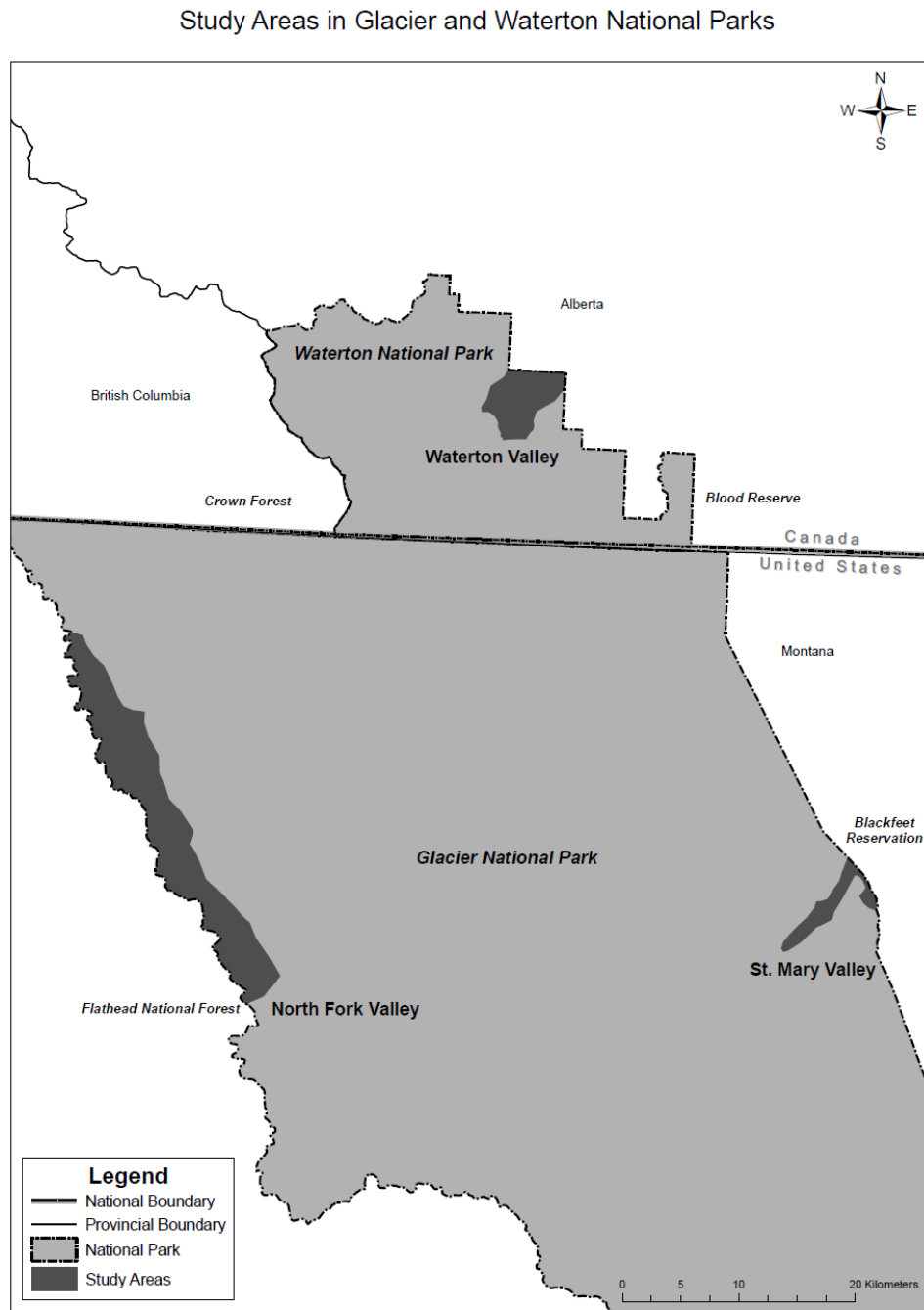


Figure 4.2. Aspen stand belt transect and circular plot layout.

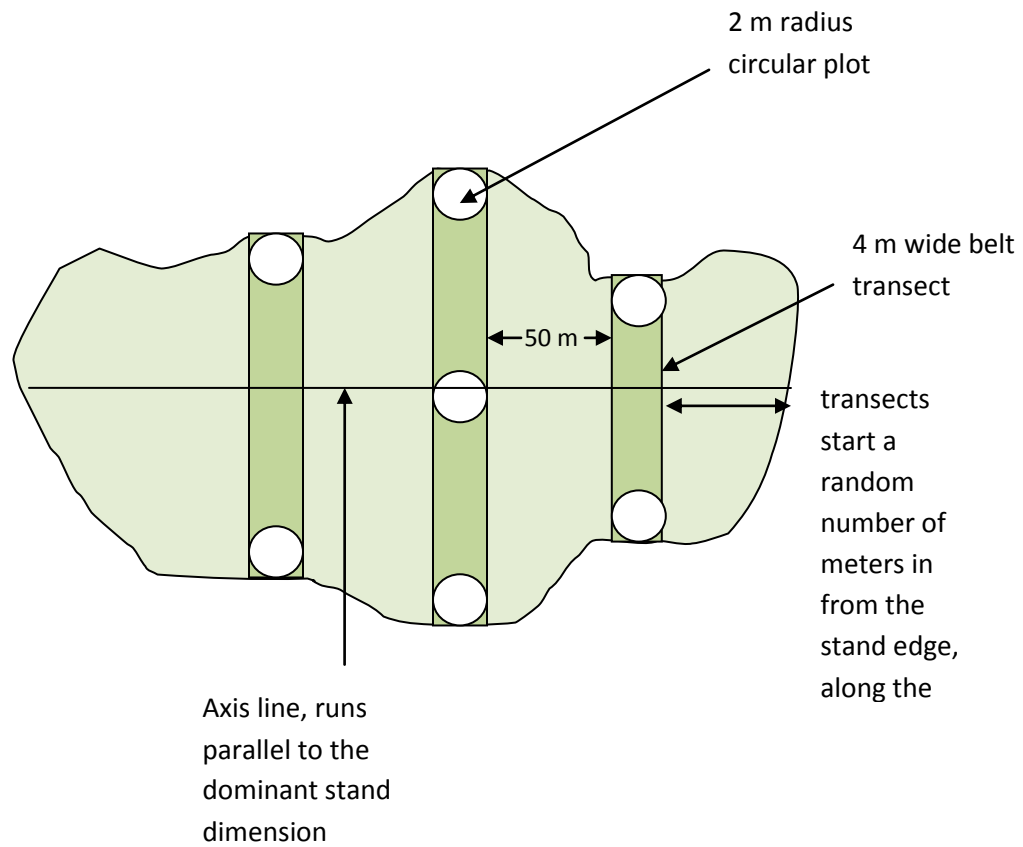


Figure 4.3. Aspen height growth by stand type in three valleys. Error bars represent 95% confidence intervals. Means followed by the same letter within a valley are not significantly different (Tukey test).

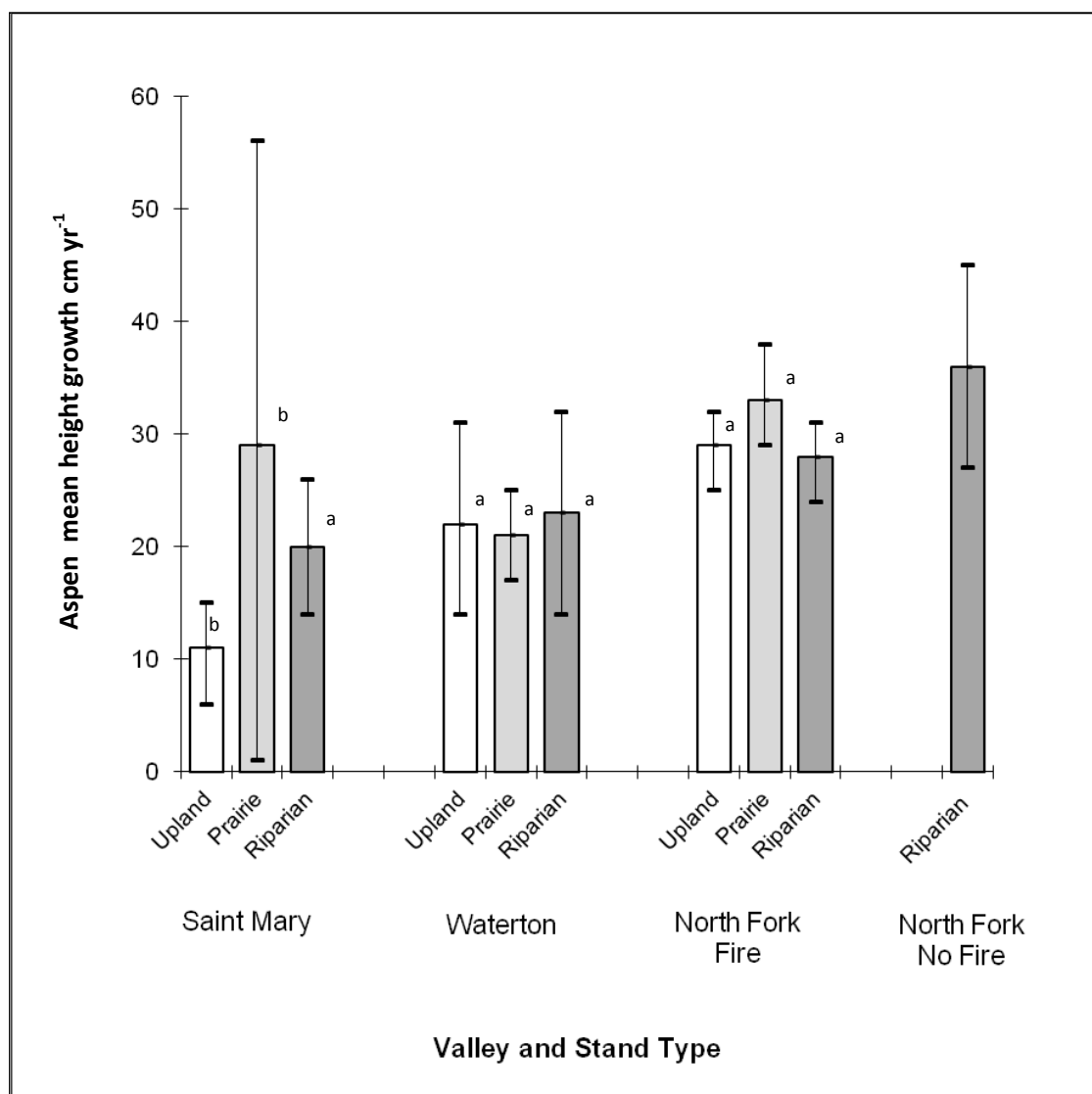


Figure 4.4. Aspen density by size class in three valleys. Light gray histogram bars represent aspen stands with no fire. Error bars represent 95% confidence intervals.

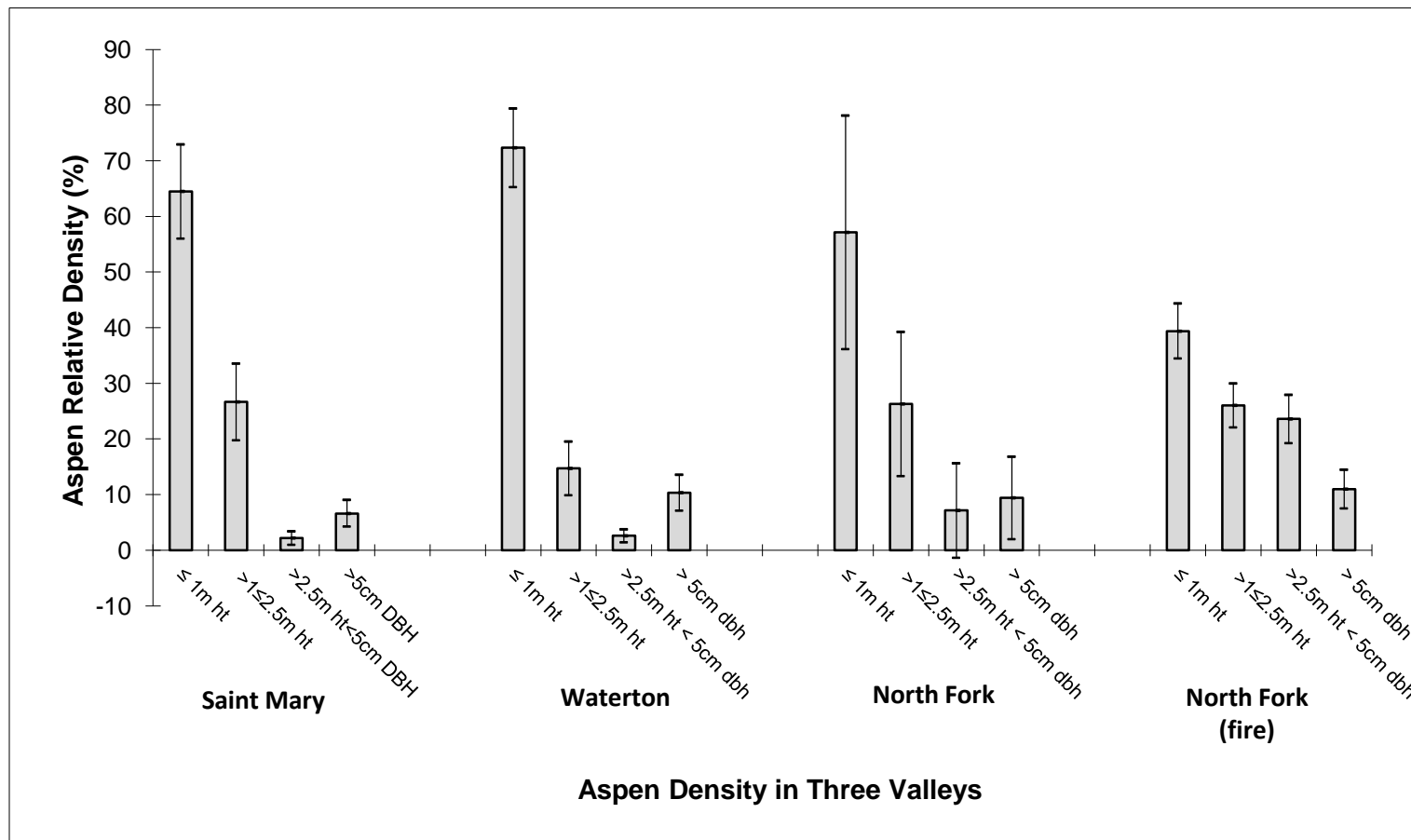
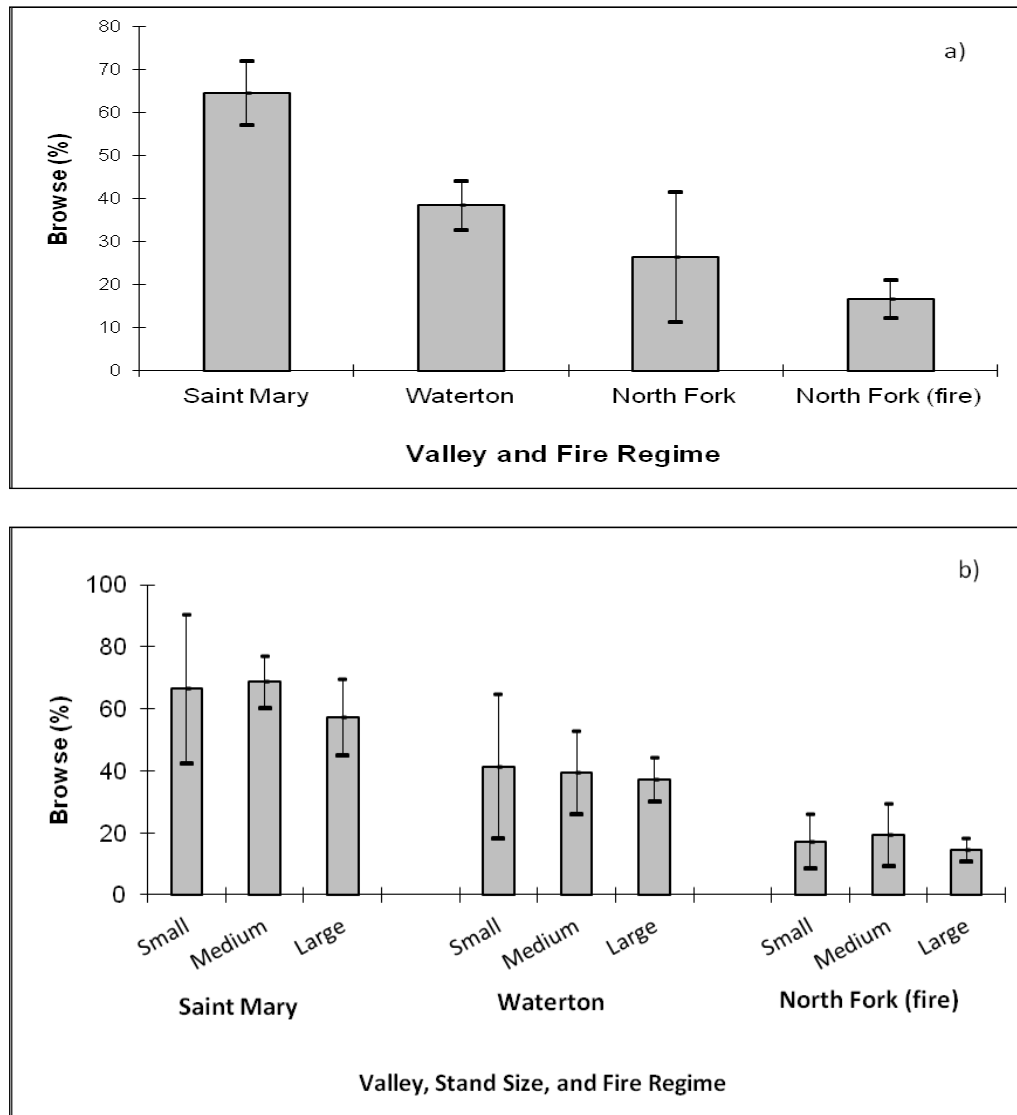
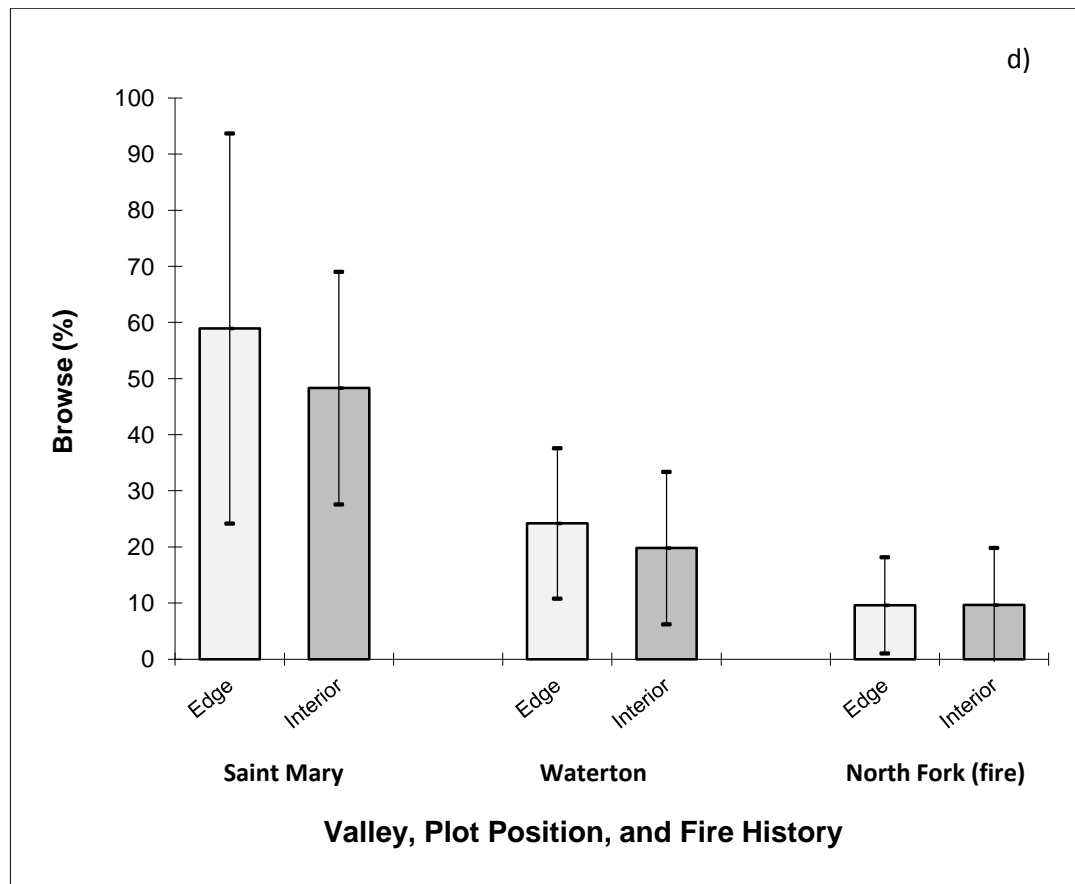
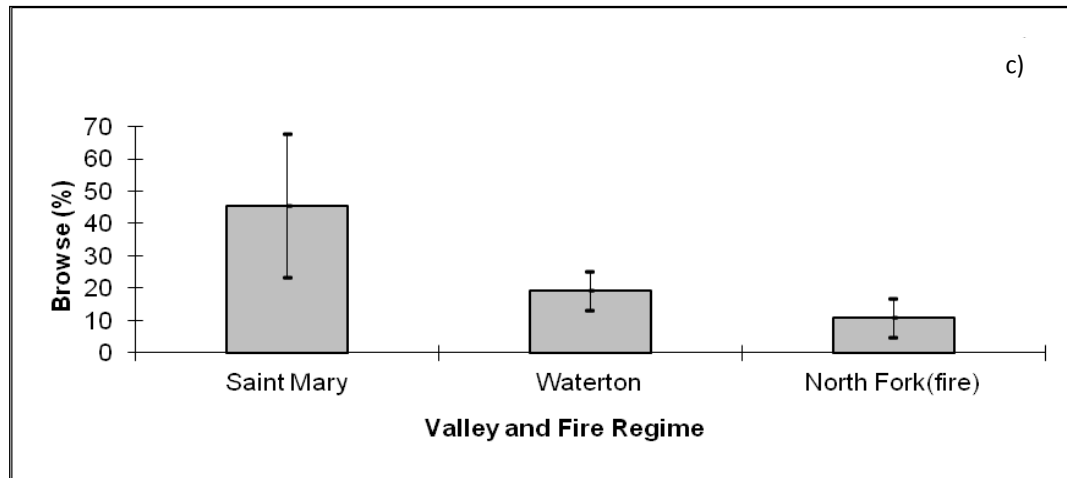


Figure 4.5. Browse in aspen stands in three valleys. All panels depict browse in four-year-old stems only. Panel A depicts total browse (all stands sampled in all valleys); Panel B depicts browse by stand size (small contain <4 plots; medium contain $\geq 4 < 8$ plots; and large contain ≥ 8 plots); my low sample size did not allow me to include in this analysis stands with no fire in this analysis. Panel C depicts browse in the three valleys for stands that contained at least one transect with ≥ 7 plots, the basis for Panel D; Panel D depicts the comparison of browse in edge (plot center 2 m from stand edge) and interior (plot center 62 m from stand edge) plots. Error bars represent 95% confidence intervals.





CHAPTER 5: CONCLUSION

Cristina Eisenberg

Food webs consist of a combination of top-down (predator-driven) and bottom-up (resources-driven) effects (Borer et al. 2005; Swanson et al. 2010). The strong bottom-up effects that prevail in all systems can buffer or attenuate top-down effects, which are termed trophic cascades (Polis 1994; Menge et al. 2005). Thus, in most ecological settings, trophic interactions do not always cascade, they can trickle from the top-down, occurring along with bottom-up energy flows (Hunter and Price 1992). In the case of a trophic trickle, an apex predator may be present, but has limited indirect effects on vegetation (Power 1990; Hunter and Price 1992; Strong 1992; McAnn et al. 1998; Halaj and Wise 2001; Dawes-Gromadski 2002; Menge 2005; Kauffman et al. 2010).

I investigated the relationship between wolf (*Canis lupus*) predation, elk (*Cervus elaphus*) herbivory, and aspen (*Populus tremuloides* Michaux) recruitment. The study setting, in the central portion of the Crown of the Continent Ecosystem, spans the US/Canada border and encompasses Glacier National Park (GNP), Montana and Waterton Lakes National Park (WLNP), Alberta. I stratified my observations across three spatially distinct areas, the North Fork Valley, in the western portion of GNP; the Waterton Valley, in the eastern portion of WLNP; and the Saint Mary Valley, in the eastern portion of GNP. These valleys have three different wolf population levels (Saint Mary: low; Waterton: moderate; North Fork: high), which represent three levels of long-term predation risk (the probability of an elk

encountering a wolf) (Creel et al. 2008). Ecological characteristics are comparable in all valleys (e.g., climate, soil, elevation) (Western Region Climate Center 2010; Parks Canada 2011; Achuff et al. 2005; Hop et al. 2007).

My objective was to examine, using a variety of approaches, the relative influence of top-down and bottom-up factors in an aspen community, and the context-dependence of these relationships. Each chapter of this thesis focused on a different aspect of these food web dynamics.

To aid in synthesizing my results, I created a series of conceptual models (Figure 5.1 a-d). My guiding goal in creating these models was to identify trends in the tri-trophic system I studied. Thus, the models individually depict food web relationships and relative interaction strengths in each valley, and in burned and unburned sites. Conceptual models are typically used to examine how bottom-up and top-down effects function. Mathematical models are used to quantify these interactions empirically, via experimental testing of interaction strength (Carpenter et al. 2005; Grace 2006; Reisner 2010). While not mathematical in nature, my models could be used as a foundation to create more complex models within an experimental framework to explore trophic relationships in greater depth.

I quantified the models with field data, gathered as described in Chapters 2-4 (this thesis). Specifically, elk effects equal the proportion of herbivory observed in aspen stands. I chose herbivory rather than pellet density, in order to best document elk ecological impacts, which may be different than their density. Wolf effects equal

the mean number of wolf scats observed. Aspen effects equal the mean proportion (relative density) of stems recruiting above browse height (e.g, stems >2.5 m ht <5cm DBH) (Table 5.1). Stems of this size escaped herbivory 3 to 10 years prior to the study, so they represent wolf/elk interactions then. However, wolf and elk populations have been reasonably stable in the valleys in the past decade, within the populations and ranges of variation described in Chapters 2-4 (this thesis).

The food web components that represent the key drivers of trophic relationships in the system I studied are: wolf density, elk herbivory, and density of recruiting aspen. I quantified disturbance and macro-ecology (e.g., environmental resources) with Park data. Saint Mary, Waterton, and a portion of the North Fork had no fire since 1890 (Singer 1979; Levesque 2005); the majority of the west side of GNP, which includes the North Fork, had experienced a high amount of fire (e.g., 6 fires >5000 ha) between 1988 and 2003 (Achuff et al. 2005; Hop et al. 2007). Ninety percent of aspen stands in this valley have been burned by these recent fires. No significant drought occurred during my observations, and there was no unusually high level of precipitation (Western Region Climate Center 2010; Parks Canada 2011), so I quantified macro-ecology as moderate. The resulting models depict the relative strength of each effect via arrow thickness.

Using these conceptual models, I present a synthesis here of my findings, identify trends in top-down and bottom-up effects in the aspen communities I examined, and suggest areas for further investigation. While the structure of the food

web I studied (apex predator→dominant herbivore→plants) was simple, the flow of energy and influence along the pathways that linked these food web components was not. Complexity was the principal theme that emerged from my analyses collectively, regardless of the measures I used to examine trophic mechanisms.

In Chapter 2, I reported on my investigation of the relationship between predation risk perceived by elk and this species' resource selection in its winter range. I conducted fecal pellet and carnivore scat surveys in GNP and WLNP elk winter range during two spring seasons. I then fit a series of multivariate generalized linear models that incorporated bottom-up and top-down effects and evaluated them using an information-theoretic approach.

I found complex elk responses to bottom-up (fire) and top-down (predation risk) factors. In the North Fork transects with fire, a top-down effect could be suggested but not proven. Predation risk variables that provided impediments to detecting or escaping wolves had a negative influence on occurrence of elk (pellet piles), regardless of wolf population, a contra-indicator to a top-down effect. Additionally, fire had a negative effect on elk density and a positive effect on wolf density (per scat piles) in aspen communities where a high wolf population existed. Aspen cover, which may present higher predation risk than grass (Ripple and Beschata 2004; 2007), also had a negative effect on elk density. Taken together, all of this may indicate a situation where the risk of wolf predation alone is not driving elk behavior, and top-down effects can become attenuated by bottom-up forces.

In Chapter 3, I examined the relationship between predation risk perceived by elk, as evidenced by this species' vigilance behavior (time spent with their heads up, scanning for predators, versus eating) (Childress and Lung 2003), and the context for this relationship. In my analysis, I deconstructed vigilance by examining the variables that make up predation risk in the three valleys, and fitted a general linear model that incorporated those variables.

Some of the commonly identified drivers of vigilance (group size, impediments) appeared to be important at an intermediate level of long-term predation risk (e.g., Waterton). But these drivers ceased to function in this manner when the long-term predation risk level increased (The North Fork). At high levels of long-term predation risk, vigilance was high, but not driven by these common factors. In some cases, the relationship between vigilance and risk factors was reversed (e.g., group size). And at a low level of long-term predation risk (e.g., Saint Mary), elk did not respond to these drivers of vigilance. Accordingly, it is possible that the Saint Mary wolf population may not be ecologically effective as measured by vigilance (Soulé et al. 2003; Berger 2007). I further found that other key drivers of vigilance (e.g., distance to forest, distance to road) (Friar et al. 2005; St. Clair and Forest 2009) had no effect regardless of the wolf population.

In Chapter 4, I explored a variety of environmental influences on the recruitment of young aspen into the forest canopy. In my analysis, I assessed predictors of aspen demography, which included herbivory and bottom-up influences

(e.g., incident radiation and temperature, moisture, disturbance). The landscape-scale top-down predictor was wolf population (long-term predation risk). Fine-scale, top-down predictors of aspen recruitment were site topographical characteristics that made it more difficult to see or escape wolves.

I found low aspen recruitment in the absence of fire in all valleys, including a valley with a high wolf population. Lack of recruitment indicated lack of a top-down effect. Fine-scale, top-down predictors of aspen recruitment (e.g., plot position and stand size, which are related to predation risk) had no effect. I only detected a potential top-down (wolf) effect in North Fork stands with fire.

Taken as a whole, the following patterns emerged from the trophic processes I studied. In Chapter 2, I found elk avoiding risky places (aspen) equally in all valleys, regardless of wolf population differences. In Chapter 4 I found significant aspen recruitment only in North Fork stands that had burned. In Chapter 3 I found a positive relationship between wolf population and elk vigilance. However, when I deconstructed vigilance, I found elk demonstrated complex, context-dependent adaptive behavior in response to the long-term risk of predation by wolves. Further, I found that elk showed low vigilance across all measures of such behavior, in a valley with a low wolf population.

The conceptual models I created further elucidated broad trophic trends. Saint Mary, Waterton, and portions of the North Fork that did not burn all show the same level of bottom-up forces (moderate Macro-Environment; nonexistent Disturbance)

(Figure 5.1 a-c). The valleys show similar food web patterns beyond that. All three of these case studies have a low observed wolf density (per scat counts). While only Saint Mary has strong ungulate herbivory impacts on aspen as measured by browse, in all of these cases, the aspen are showing weak recruitment, and elk are providing abundant food resources for wolves. This suggests that at any density, wolves do not exert sufficient pressure on elk to release aspen from herbivory. Such a release has been widely identified as a trophic cascades signature (White et al. 2003; Ripple and Beschta 2007).

The North Fork, in areas with fire, presents a very different pattern (Figure 5.1-d). Disturbance and wolf density are high (per scat counts), but herbivory is low. Aspen are showing strong recruitment into the canopy. Elk are providing abundant food resources for wolves.

Beyond these patterns, when one looks at all of the models collectively, perhaps the most striking effect of disturbance is that where there has been fire, aspen are recruiting. In the case of the North Fork, low aspen recruitment in the absence of fire may indicate a trophic trickle. However I was ultimately unable to test for this, because I lacked a valley with fire and no wolves. My findings suggest that top-down and bottom-up processes are important joint engineers of aspen communities. The combination of fire and a high wolf density resulted in aspen recruitment. However, I was unable to quantify how much of the aspen recruitment was attributable to bottom-up and top-down effects respectively.

My conceptual models represent a simple rendering of the tri-trophic food web I studied. Community interactions are far more complex than these models. The processes I measured respond variably to factors acting at different scales, which may confound interpretation of interactions. Structural Equation Modeling could provide a means to evaluate complex, multivariate hypothesis of the causal network of factors and processes predicted to influence trophic relationships (Reisner 2010; Grace 2008). Such factors could incorporate disturbance (e.g., fire severity) and predation (population, density, collar data, kill rates) effects on various spatial and temporal scales. For example, fire severity could create complex responses in plant communities (Halofsky et al. 2011), which could interact with predator and herbivore density, to influence food web dynamics.

In sum, I found that bottom-up and top-down forces worked together in valleys that contained well-established wolf populations, and to a lesser degree in a valley with a low wolf population. I conclude that elk show complex responses on multiple levels to long-term risk of predation by wolves.

My findings suggest that in the Crown of the Continent Ecosystem, wolves alone do not stimulate recruitment of aspen without fire. Thus, top-down and bottom-up processes may be important joint engineers of aspen communities. These findings are not surprising, as similar food web relationships have been found in a variety of aquatic and terrestrial systems (Borer et al. 2005; Power et al. 1992). However, these

dynamics have not been fully studied in terrestrial large mammal systems, primarily because such systems can be intractable for experimental purposes.

Future horizons for terrestrial large mammal trophic research could entail work that incorporates disturbance in quantitatively evaluating a food web as a complex of inter-level interactions (Grace and Keeley 2006; Reisner 2010). Longer-term research on this topic (i.e., on a decadal scale) is indicated, given the long life spans of the focal species I studied, and the enormous stochastic change over time that can influence context (Peterson 2007).

A more integrated approach that acknowledges ecological complexity is necessary to deepen our understanding of ecosystem structure and function in terrestrial systems. Such an approach may ultimately help managers to create more resilient ecosystems by incorporating predation and disturbance effects into policy and management.

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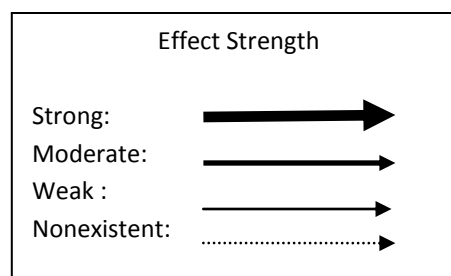
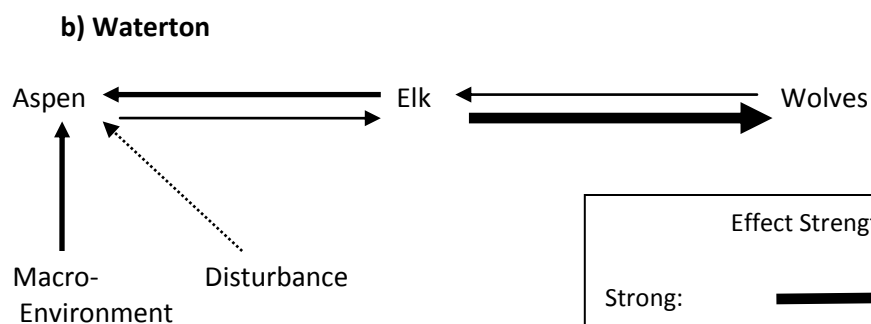
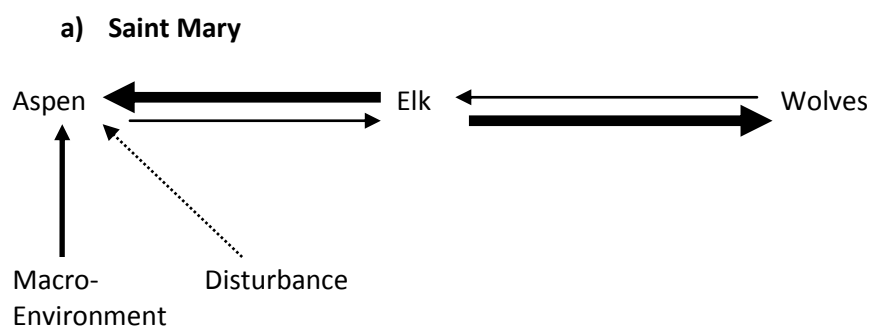
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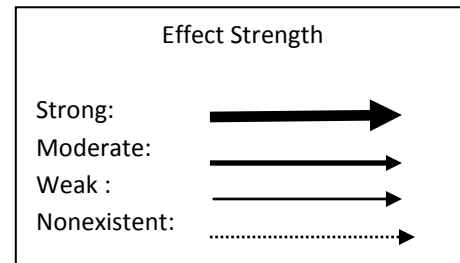
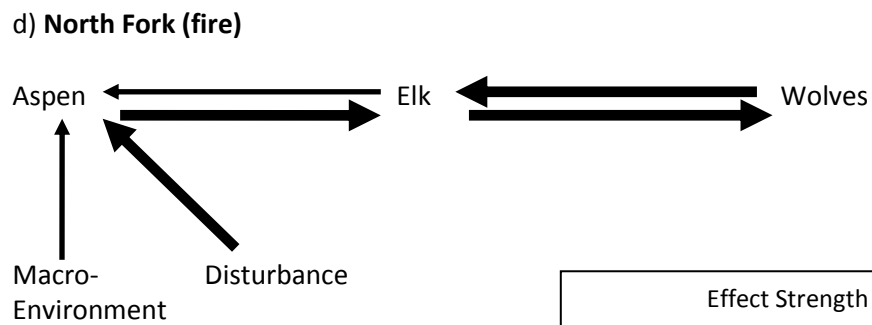
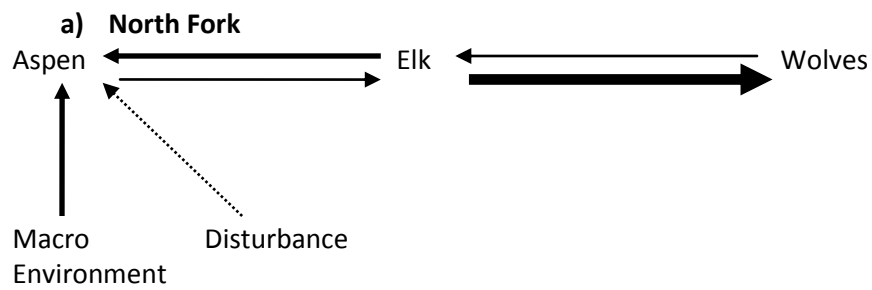
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Table 5.1. Aspen recruitment, herbivory, and wolf density in three valleys. Aspen recruitment data (Chapter 4, this thesis) was gathered via stem density surveys, and represents stems in the >2.5 m ht<5cm DBH size class. Herbivory data (Chapter 4, this thesis) was gathered via herbivory surveys in aspen stands, in the same plots where stem density surveys were conducted, and represents the proportion of browsed stems <2.5 m ht in aspen stands. Wolf density data (Chapter 2, this thesis), was gathered via pellet and scat transects that ran through the same aspen stands surveyed (Chapter 2, this thesis), and represents the mean density of wolf scats per 100 m⁻².

Valley	Aspen Recruitment		Herbivory		Wolf Density	
	Mean	±95% CI	Mean	±95% CI	Mean	±95% CI
Saint Mary	2.20	1.22	64.50	7.35	0.02	0.01
Waterton	2.59	1.17	38.36	5.75	0.02	0.01
North Fork	7.15	8.50	26.36	15.05	0.01	0.01
North Fork (fire)	23.60	4.35	16.71	4.40	0.17	0.08

Figure 5.1. Food web relationships in three valleys. In these conceptual models, Wolves represent predation; Elk represents herbivory; Aspen represents vegetation. Arrows pointing up or right represent bottom-up effects. Arrows pointing left represent top-down effects. Effect strength of trophic cascades food web components is quantified as follows: Wolves=wolf density via scat counts; Elk=elk density via pellet counts; Aspen=aspen stem density (relative abundance) in the >2.5 cm ht <5cm DBH size class (e.g. recruiting aspen) (Table 5.1); Macro-environment=ecosystem resources (e.g., moisture, sunlight); Disturbance=fire. There was no drought during my study, and precipitation was within the normal range for the area. Multiple, large (>5000 ha) fires occurred in portions of the North Fork. No fire occurred in the other valleys.





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APPENDICES

Appendix A. Frequencies of elk pellet piles in 50 m × 2 m sub-transects in three valleys.

<i>X</i>	<i>SM</i>	<i>WLNP</i>	<i>NF</i>	<i>X</i>	<i>SM</i>	<i>WLNP</i>	<i>NF</i>	<i>X</i>	<i>SM</i>	<i>WLNP</i>	<i>NF</i>	<i>X</i>	<i>WLNP</i>	<i>X</i>	<i>SM</i>
0	93	171	432	56	4	15	2	112	1	0	0	171	1	227	0
1	40	55	194	57	5	7	0	113	0	2	0	172	0	228	0
2	27	51	117	58	5	9	2	114	0	0	0	173	0	229	0
3	30	33	110	59	2	13	3	115	0	0	0	174	0	230	0
4	22	52	70	60	0	10	2	116	0	1	1	175	0	231	0
5	28	32	69	61	4	10	0	117	0	0	1	176	0	232	0
6	13	37	61	62	4	8	1	118	0	3		177	0	233	0
7	19	47	45	63	7	11	1	119	0	1		178	0	234	0
8	11	47	45	64	6	5	0	120	0	1		179	0	235	0
9	7	45	35	65	5	7	0	121	0	1		180	0	236	0
10	20	44	45	66	3	5	2	122	0	1		181	0	237	0
11	14	37	34	67	2	9	1	123	0	0		182	0	238	1
12	11	39	33	68	3	7	0	124	0	0		183	0	239	0
13	11	49	29	69	2	8	1	125	0	0		184	1	240	0
14	10	29	27	70	1	9	0	126	0	0		185	0	241	0
15	15	40	34	71	4	4	0	127	0	12		186	0	242	0
16	10	36	38	72	2	2	2	128	0	1		187	0	243	0
17	3	35	28	73	1	2	1	129	0	1		188	0	244	0
18	7	45	14	74	4	4	0	130	0	1		189	0	245	0
19	6	19	23	75	5	8	1	131	1	1		190	0	246	0
20	8	36	18	76	0	1	1	132		0		191	0	247	0
21	10	34	18	77	3	5	1	133		0		192	0	248	1
22	5	18	18	78	1	5	0	134		3		193	0	249	0
23	6	29	13	79	1	2	1	135		0		194	0	250	0
24	4	24	20	80	0	2	0	136		0		195	0	251	0
25	7	34	15	81	2	2	1	137		0		196	0	252	0
26	5	33	17	82	3	4	0	138		0		197	0	253	0
27	7	30	11	83	1	4	0	139		0		198	0	254	0
28	6	32	17	84	3	3	0	140		0		199	0	255	0
29	7	33	18	85	0	2	1	141		1		200	0	256	0
30	6	28	15	85	2	2	1	142		0		201	0	257	0
31	9	36	10	87	0	2	0	143		0		202	0	258	0
32	11	33	8	88	1	2	0	144		0		203	1	259	0
33	7	33	7	89	0	3	0	145		1		204	0	260	0
34	14	21	12	90	1	4	0	146		0		205	0	261	0
35	9	27	4	91	0	0	0	147		0		206	0	262	0
36	9	25	5	92	1	3	0	148		1		207	0	263	0
37	9	22	10	93	0	1	0	149		1		208	0	264	0
38	5	22	5	94	0	2	0	150		0		209	0	265	0
39	6	17	5	95	0	4	0	151		0		210	0	266	0
40	7	20	9	96	0	4	0	152		0		211	0	267	0
41	5	26	1	97	3	1	0	153		0		212	0	268	0
42	7	20	4	98	0	4	0	154		0		213	0	269	0
43	3	22	3	99	0	2	1	155		1		214	0	270	0
44	8	17	5	100	1	2	0	156		1		215	1	271	1
45	7	19	4	101	0	1	0	157		0		216	0	272	0
46	6	20	3	102	1	0	0	158		0		217	1	273	0
47	5	20	2	103	1	1	0	159		1		218	0	274	0
48	5	16	4	104	0	1	0	160		0		219	0	275	0
49	8	18	3	105	0	0	0	161		0		220	1	276	1
50	7	22	2	106	0	2	0	162		0		221	0		
51	2	13	2	107	0	0	0	163		0		222	0		
52	8	12	3	108	0	2	0	163		0		223	0		
53	5	14	1	109	0	1	0	165		0		224	0		
54	5	15	3	110	0	1	0	166		0		225	0		
55	5	12	1	111	0	1	0	170		1		226	0		

Appendix B. Empirical variogram output for three valleys. Gamma values >0 indicate spatial autocorrelation. Distance refers to lag between pairs compared, Gamma represents lack of independence of data, with gamma values >0 indication spatial autocorrelation. NP represents number of pairs that were tested in each lag category.

Saint Mary			Waterton			North Fork		
Distance	Gamma	NP	Distance	Gamma	NP	Distance	Gamma	NP
41.72	0.42	680	43.22	0.32	1553	41.60	0.41	1592
104.71	0.60	6035	105.26	0.39	14197	105.16	0.48	15322
200.99	0.73	8905	201.78	0.46	21203	200.93	0.55	23030
299.37	0.82	9849	300.64	0.48	24262	300.02	0.60	26393
398.16	0.88	9342	400.21	0.49	26216	400.06	0.59	26890
498.53	0.90	8223	499.79	0.49	25392	500.02	0.57	26409
598.33	0.93	6888	599.61	0.47	24055	599.56	0.58	24646
697.81	0.97	5570	699.63	0.49	22641	700.05	0.59	23117
798.16	0.95	4320	799.49	0.51	21159	799.94	0.59	21655
898.20	0.90	3260	899.68	0.49	20079	899.57	0.57	19932
997.85	0.81	2464	1000.42	0.51	19935	999.36	0.56	17456
1098.34	0.73	2047	1101.02	0.54	20170	1099.77	0.56	15698
1199.11	0.62	1861	1201.16	0.56	22335	1199.76	0.57	14768
1299.71	0.57	1786	1300.63	0.56	25697	1300.32	0.59	13980
1400.61	0.59	1844	1401.17	0.54	29169	1400.73	0.63	13596
1500.33	0.77	1965	1501.27	0.54	32339	1500.65	0.63	13966
1600.48	0.86	1979	1600.90	0.54	34573	1601.15	0.61	14908
1700.24	0.85	2041	1700.07	0.52	36109	1700.94	0.59	16104
1800.51	0.80	2094	1800.29	0.50	37438	1800.50	0.59	16825
1900.36	0.73	2215	1900.51	0.51	37917	1900.28	0.59	17343
2000.49	0.71	2347	1999.94	0.50	38277	2000.32	0.61	17641

Appendix C. Ungulate and large carnivore density by predation risk in three valleys. Predation risk categories for view and debris are: Low (1); Moderate (2); High (3) (Table 2.3).

Valley and Predation Risk	Elk density Pellet piles (100m ²)			Deer density Pellet piles (100m ²)			Wolf density Scats (100m ²)		
	Mean	95% CI ±	Range	Mean	95% CI ±	Range	Mean	95% CI ±	Range
Saint Mary									
Debris 1	45.04	2.64	0-129	0.14	0.06	0-3	0.007	0.01	0-2
View 1	47.07	3.23	0-110	0.16	0.07	0-3	0.005	0.01	0-1
Debris 2	22.25	2.85	0-95	0.15	0.07	0-3	0	0	0
View 2	35.05	4.09	0-129	0.12	0.06	0-1	0	0	0
Debris 3	7.51	1.36	0-86	0.18	0.06	0-3	0.04	0.03	0-2
View 3	11.96	1.48	0-95	0.17	0.05	0-3	0.03	0.02	0-2
Waterton									
Debris 1	43.06	2.75	0-276	1.12	0.12	0-15	0.03	0.01	0-3
View 1	57.53	5.86	0-276	1.94	0.36	0-15	0.008	0.01	0-1
Debris 2	23.66	1.78	0-127	1.25	0.19	0-14	0.004	0.01	0-1
View 2	42.13	4.13	0-184	1.18	0.66	0-11	0.02	0.01	0-2
Debris 3	9.30	1.04	0-220	1.14	0.14	0-16	0.02	0.01	0-3
View 3	17.24	0.94	0-220	1.00	0.09	0-16	0.02	0.01	0-3
North Fork (all)									
Debris 1	22.45	1.59	0-117	3.22	0.44	0-36	0.23	0.22	0-53
View 1	23.47	3.06	0-117	3.60	0.25	0-31	0.07	0.05	0-3
Debris 2	9.72	0.98	0-86	3.88	0.5	0-34	0.19	0.08	0-13
View 2	15.01	0.15	0-99	2.52	0.31	0-30	0.32	0.24	0-53
Debris 3	2.99	0.3	0-36	3.01	0.29	0-29	0.08	0.02	0-4
View 3	5.96	0.49	0-67	3.57	0.3	0-36	0.10	0.03	0-6

Appendix D. Elk, deer, and wolf density in aspen and grass in three valleys. These data represents piles of elk and deer pellets and wolf scats counted in 100 m² plots, expressed as a density. In the North Fork, I further stratified species densities by fire regime.

Valley	Elk Density in Aspen (piles of pellets km ⁻²)			Deer Density in Aspen (piles of pellet km ⁻²)			Elk Density in Grass (piles of pellets km ⁻²)			Deer Density in Grass (piles of pellets km ⁻²)			Wolf Density in Aspen (scats km ⁻²)			Wolf Density in Grass (scats km ⁻²)		
	Mean	95% CI±	Range	Mean	95% CI±	Range	Mean	95% CI±	Range	Mean	95% CI±	Range	Mean	95% CI±	Range	Mean	95% CI±	Range
SM	7.78	2.07	0-86	0.13	0.08	0-3	35.64	2.74	0-110	0.15	0.05	0-3	0.03	0.03	0-2	0.01	0.02	0-2
WLNP	9.26	1.50	0-220	1.15	0.18	0-14	35.13	1.54	0-276	1.11	0.10	0-15	0.01	0.01	0-1	0.02	0.01	0-3
NF	10.40	6.56	2-19	2.80	1.54	1-5	15.45	2.75	0-99	1.80	0.33	0-10	0	0	0	0.01	0.02	0-1
NF (fire)	2.23	0.56	0-29	3.09	0.64	0-29	17.31	1.28	0-81	2.26	0.24	0-19	0.13	0.7	0-4	0.23	0.17	0-53

Appendix E. Empirical variogram results obtained after fitting a full model using a gamma distribution, and running the deviance residuals through a correlogram analysis. Panel a) depicts Saint Mary; Panel b) depicts Waterton; and Panel c) depicts the North Fork.

