BEHAVIORAL RESPONSES OF ELK TO WINTER WOLF PREDATION RISK IN THE MADISON HEADWATERS AREA, YELLOWSTONE NATIONAL PARK.

by

Claire Natasha Gower

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APPROVAL

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Claire Natasha Gower

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Dr. Robert A. Garrott, Committee Chair.

Approved for the Department of Ecology

Dr. David Roberts, Department Head.

Approved for the Division of Graduate Education

Dr. Carl A. Fox, Vice Provost.

STATEMENT OF PERMISSION TO USE

Claire Natasha Gower

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DEDICATION

I dedicate this dissertation to my grandmother and friend, Josie Dixon. Her continual encouragement and positive can-do attitude provided me with motivation throughout this program. She has always advised me to never take the easy path in life, and, she has always been an inspiration because of her energy for life and her ingrained wisdom.

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ABSTRACT

Over the past few decades a large body of literature has provided evidence that predators can influence the ways in which prey behave. This in turn may influence prey demography and predator-prey dynamics and therefore predators may influence the structure and function of populations and communities, independent of direct killing. Using data collected from 1991 to 2007, I evaluated the behavior of elk (*Cervus elaphus*) in the Madison headwaters area of Yellowstone National Park in response to the colonization and establishment of wolves (*Canis lupus*). Changes in home range size, fidelity, group size, foraging behavior, and large-scale spatial responses were evaluated. After wolf colonization, elk movements were more dynamic as elk moved more over the landscape as they were increasingly encountered, attacked, and displaced by wolves. Home range sizes were larger, with slight decreases in fidelity. These results show that elk made modest adjustments in space use presumably to reduce their vulnerability from predators at a fine-scale within their range. More dramatic larger scale spatial shifts were also documented as radio-collared elk adopted long-distance dispersal and migratory movements away from high-density wolf areas. These apparent predator-avoidance movements were never observed prior to wolf colonization or from areas where the risk of predation was lower. Prior to wolf colonization, the grouping behavior of elk was relatively stable and predictable as elk attempted to conserve energy and decrease starvation risk in the absence of wolves. Following wolf reintroduction group size and group size variation increased. This more dynamic behavior likely reflects a strategy to minimize predation risk and maximize food acquisition. The decision to forage was heavily influenced by local snow, habitat type, and time of day but remained relatively stable with and without the presence of wolves. The lack of any substantial change in the foraging behavior of elk in the presence of wolves illustrates that elk can maintain the same level of foraging time and retain a relatively constant level of nutrition. Together these results suggest that in a harsh winter environment such as the Madison headwaters, elk can adaptively manage their behavior to cope with environmental constraints both in the presence and absence of wolves. Landscape variation such as snow pack severity and habitat types, complexity, and patch size also influences predation risk and may dictate the way in which prey behave.

CHAPTER 1

INTRODUCTION TO DISSERTATION

Introduction

The ways in which prey change their behavior in response to the threat of predation has become the topic of interest in a growing body of ecological literature over the past few decades (Ives and Dobson 1987, Lima and Dill 1990, Lima 1998). This work has expanded our knowledge base from the classical work on predator-prey interactions where the direct lethal effects of predation were the major focus and prey behavior was typically ignored (Taylor 1984, Murdoch and Oaten 1975). Currently attention is being paid to the indirect consequences of predation that may stem from behavioral modifications. Such advancement in our understanding of predator-prey interactions offers important ecological insights regarding the influence of predators on individuals and communities. This is particularly relevant as we begin to recognize the importance these non-lethal effects may have on prey population dynamics (Ives and Dobson 1987, Lima and Dill 1990, Lima 1998, Werner and Peacor 2003, Nelson et al. 2004, Bolnick and Preisser 2005, Preisser et al. 2005, Schmitz 2005a, Creel and Christianson 2008).

Plasticity in prey behavior associated with the perception of risk is pervasive throughout many different taxonomic groups and anti-predator behavior such as grouping, alterations in foraging behavior, shifts in habitat use, and changes in movement patterns are exhibited by prey species in terrestrial, arboreal, and aquatic environments. Due to the relative ease of manipulating systems with small taxa, with the ability to retain

strict experimental control, much of the seminal work on the behavioral responses of prey to predation risk has been carried out on invertebrates or small vertebrate systems (Sih 1982, Werner et al. 1983, Schmitz 1998, Denno et al. 2003). But, while experiments provide the ability to relate cause and effect, it is sometimes difficult to use laboratory based experiments to test broad scale ecological hypotheses. It is often very hard to generalize the results of experiments to any other natural systems (Schmitz 2005b) and often there is limited breadth as to the applicability of the results from manipulation experiments.

Understanding how systems operate in controlled settings has clearly advanced our knowledge of behavioral ecology of predator-prey systems, but because ecological complexity is hard to capture under controlled experimental design, there is some element of uncertainty as to whether inferences to the behavioral responses of prey from small taxonomic groups can be applied to large mammal predator-prey systems. Therefore, similar work is needed in a field setting before we can generalize these behavioral trends. However, such studies come with their own set of limitations due to the complexity of heterogeneous environments and the inability to completely control for confounding factors. The ability to conclude causal mechanisms is poor and inferences can often be viewed as vague due to the number of confounding variables that cannot be controlled. Despite these limitations, however, observational studies are extremely useful for identifying trends and patterns in large mammal systems and much insight into the behavioral responses of prey to predation threat can be attained in systems when both predator and prey are tractable, predator and prey use the environment in close proximity to one another, and reside within a system where they can easily be observed. The ability

to make inference is also enhanced if information about the system is known over a long enough period of time that encompass periods of ecological change and/or bouts of predation risk vary spatially and temporally.

Gray wolves (*Canis lupus*) were reintroduced to Yellowstone in 1995-96, and since that time a considerable amount of research has contributed to our understanding of prey behavior in response to this newly established top carnivore (alterations in landscape and habitat use; Creel et al. 2005, Fortin et al. 2005, Hernández and Laundré 2005 Mao et al. 2005, Gude et al. 2006, Winnie and Creel 2007; changes in aggregation patterns; Creel and Winnie 2005, Gude et al. 2006; shifts in foraging; Christianson 2008; alterations in vigilance levels; Lung and Childress 2006, Halofsky and Ripple 2008, Liley and Creel 2008; and trade-off's between vigilance and foraging; Laundré et al. 2001, Childress and Lung 2003, Wolff and Van Horn 2003, Winnie and Creel 2007). But, long-term monitoring of the Madison headwaters elk population (*Cervus elaphus*) since 1991, and monitoring of wolves since 1996-97, has resulted in an extensive predator-prey database with which I have been able to effectively expand on the previously mentioned prey behavioral work by gaining an understanding of how prey behaved when predators were absent. By adding a pre-wolf component, I evaluated if, and how, these behaviors have changed with wolf reintroduction. Collectively, this study and other studies throughout Yellowstone National Park and the Greater Yellowstone Ecosystem provide a comprehensive synthesis of the anti-predator behavioral responses exhibited by elk to wolves over a wide ecological range. While this dissertation is only a small part of this larger compilation of work, I have compared our findings with other behavioral studies,

identified disparities in behavioral responses between sites, and explored the mechanisms responsible for the way elk behave.

The major objective of this dissertation was to investigate the behavioral responses exhibited by elk in the Madison headwaters and determine if elk behavior changed when wolves were reintroduced to the landscape. If a behavioral modification was identified over the period of this investigation, then I wanted to determine the relationship between predation, landscape, and climatic factors that contributed to any apparent change. Because most of the above mentioned predator-prey behavioral studies occurred in established predator-prey systems, the dynamics that occurred prior to, and during the transition from a colonized to an established predator population were not described. By dividing the 16-year study period into different phases of wolf reintroduction (pre, colonizing, and establishment), I was presented with the rare opportunity to evaluate if elk behavior was sensitive to the presence of wolves and/or the frequency and magnitude of wolf use. With the magnitude of wolf use varying over the 11-year, post-reintroduction period and being dynamic between drainages, it was also possible to determine whether elk responded spatially and temporally to wolves. More specifically, in Chapter 2, the winter movement patterns of a non-migratory elk herd in the Madison headwaters were quantified prior to the reintroduction of wolves when animals were constrained only by nutritional restrictions. Complimentary data made it possible to compare the same behavior following wolf colonization and establishment, when elk experienced significant wolf predation. Changes in home range size and fidelity were evaluated and broader scale elk movement patterns such as dispersal and migration were described. In Chapter 3, a long-term dataset was analyzed on elk grouping behavior prior

to wolf re-introduction, during the colonization stage, and after wolves became fully established in the system. This allowed for elk grouping tendencies (mean group size and typical group size) to be evaluated in the absence of predators and, following wolf reestablishment, when faced with trade-offs between avoiding predation and acquiring adequate resources. Wolf presence varied spatially and temporally within and among years, so the dynamic nature of the grouping tendencies was also evaluated to determine if variability in group size increased following wolf-reintroduction as elk responded to fine-scale temporal variation in predation risk. In Chapter 4, the foraging behavior of elk was evaluated to assess whether or not elk sacrificed foraging bouts and altered the intensity with which they scanned their surroundings when wolves were present on the landscape. This research provided valuable insights into the indirect costs of predation. Knowledge of how elk responded when faced with predation risk was then synthesized in the summary chapter of this dissertation (Chapter 5). The demographic consequences that occurred following reintroduction of a keystone predator are discussed, and I highlight gaps in our knowledge base and propose the direction of future research. Finally, I discuss the management and conservation implications of changing prey behavior on ecosystem structure and function.

Study Area

The Madison headwaters is a 28,000-ha study area located in the upper Madison River drainage in the west-central portion of Yellowstone National Park, Wyoming, USA, (44° 37'N, 110° 52', W) (Figure 1.1). The area is centered on the Madison, Gibbon, and Firehole rivers with elevations ranging from 2050-2560m and is defined by

the wintering areas of the non-migratory elk population and the migratory central Yellowstone bison herd (*Bison bison*; Bjornile and Garrott 2001, Garrott and White 2009). The topography is complex and varied, but predominately characterized by extensive forested plateaus, steep canyons and flat low elevation meadows running linear to the three major river corridors.

The study area supports a diversity of plant communities, the most dominant being the lodgepole pine (*Pinus contorta*) and spruce-fir (*Picea engalmanni – Abies lasiocarpa*) forest. In addition both wet meadows and dry meadows are present. The wet meadows are characterized by sedges (*Carex* spp.), common horsetail (*Equisetum arvense*), rushes (*Eleocharis flavenscens*), and several grass species (*Agropyron* spp., *Deschampsia* spp.), while sagebrush (*Artemisia* spp) and Idaho fescue (*Festuca idahoensis*) dominate the dry meadows (Despain 1990). Extensive forest fires during the summer of 1988 burned approximately 50% of the study area, resulting in a complex mosaic of burned and unburned forest patches (Christensen et al. 1989, Newman and Watson 2009) which are now at various stages of regeneration. Geothermal areas are widespread throughout the study area (Watson et al. 2009) and are particularly abundant in the Firehole and the Gibbon drainages. The thermal influence is pervasive among many of the major meadow complexes which remain snow free, or have dramatically reduced snow cover, all winter. This allows unique aquatic and terrestrial plant associations to thrive and continue to photosynthesize throughout the year (Despain 1990). Consequently, large herbivores use these snow free areas and use plants that remain available all winter long.

The climate of the study area is typical of northern mountainous regions which is characterized by cool, dry summers and long, cold winters. Snow typically accumulates

at the end of October and starts to melt on the lower elevation sites around mid-March and on the plateaus several weeks later. Peak snow depths range from 115-150cm (Craighead et al. 1973), and average winter temperatures range from 2.5°C in October to minus 11.0°C in December and January, minus 4°C in March, and rising to 6.5°C in May (Newman and Watson 2009).

The Madison headwaters elk herd is a non-hunted, non-migratory herd remaining within the boundaries of the park all year (Craighead et al. 1973; see Figure 1.1). Ground and aerial surveys dating back to 1967 estimated the population to be between 600-700 elk (Craighead et al. 1972), and annual population estimates of the herd that were initiated in 1991 revealed that the population had remained remarkably stable for approximately 3 decades up until the mid to late 1990's (Eberhardt et al. 1998, Garrott et al. 2008a,b). After this time, the population steadily decreased to approximately 150-300 elk (Garrott et al. 2009b), with the decrease predominantly occurring in the Firehole and Gibbon drainages while remaining relatively stable in the Madison drainage (White et al. 2009). Unlike many other populations of large herbivores, this population exists in a protected landscape that is relatively uninfluenced by human factors. Although three major park roads run parallel to the major rivers, the study area is predominantly road-less and there is little human use away from these main roads during winter.

After an almost 60-year absence of wolves in the Yellowstone area, gray wolves were reintroduced into Yellowstone National Park in 1995-96 (Fritts et al. 1997). Using acclimation pens constructed in the Firehole drainage, several soft release efforts resulted in successful establishment of wolves into the Madison headwaters area since 1996-97 (Smith et al. 2008). Since 1996-97, the number of wolves and wolf packs in this system

has varied spatially and temporally, but overall the system has transitioned from no wolves to one with an established wolf population (Smith et al. 2009). Coyotes *(Canis latrans*) are common within the study area year-round and grizzly bears (*Ursus arctos*) and black bears (*Ursus americanus*) are commonly observed in the study area from early spring (late March) to late fall (October-November). Other large predators such as mountain lions (*Puma concolor*) are known to be occasionally present in the study area, but at very low densities.

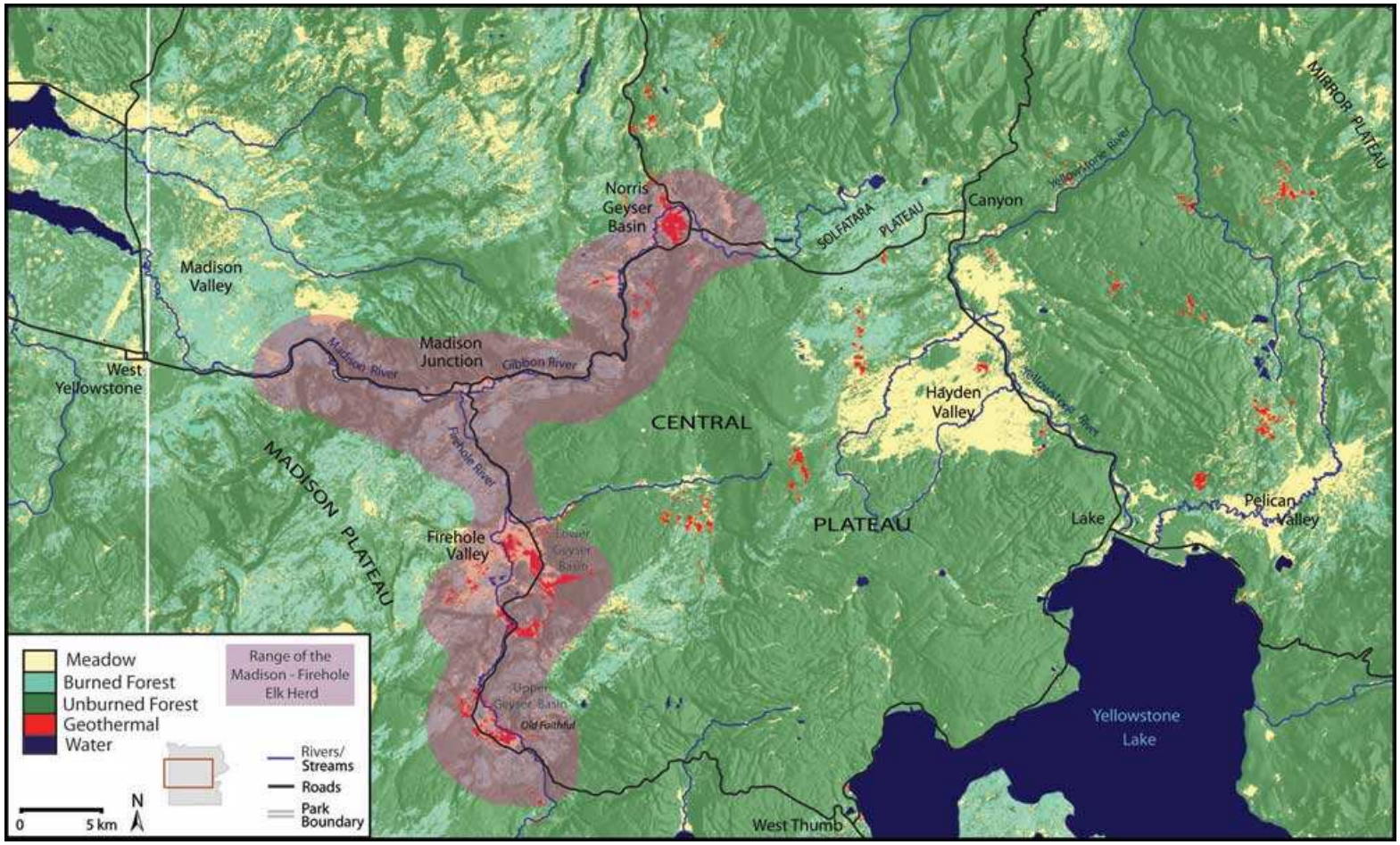

Figure 1.1 The Madison headwaters study area in the West-central portion of Yellowstone National Park (insert). Vegetation types (n = 5) were mapped using Landsat remote sensing acquired on September 23, 2002 (Newman and Watson 2008). The shaded area represents the winter range of the Madison headwaters elk herd (Madison-Firehole elk herd) as defined by Messer et al. 2008.

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CHAPTER 2

SPATIAL RESPONSES OF ELK TO WOLF PREDATION RISK: USING THE LANDSCAPE TO BALANCE MULTIPLE DEMANDS

Abstract

In the absence of an effective predator, spatial patterns of large herbivores in northern temperate regions are largely influenced by food acquisition and energy conservation during winter when resources are limited and the energetic cost of movement is high. In these circumstances animals would be expected to minimize movement to avoid unnecessary energy expenditures. With the addition of a top predator such a strategy may not be compatible with avoiding predation risk, therefore animals may increase their movement to avoid detection or escape capture. During consecutive winters 1991-2007 11,908 locations were collected, and movement patterns of 115 non-migratory adult, female elk (*Cervus elaphus*) in the Madison headwaters area of Yellowstone National Park were quantified. ANOVA and mixed effects regression models were used to evaluate home range size and site fidelity prior to the reintroduction of wolves (*Canis lupus*), and following wolf colonization and establishment. Broader scale elk movement patterns such as dispersal and migration were also described. Prior to wolf colonization, winter movements of elk were constrained and predictable as elk attempted to conserve energy and decrease starvation risk. Home ranges were small and elk displayed strong spatial fidelity. After wolf colonization, elk moved more over the landscape as they were increasingly encountered, attacked, and displaced by wolves. Home range sizes were larger, with modest decreases in philopatry. Elk also adopted long-distance dispersal

movements away from high-density wolf areas which were not observed prior to wolf establishment. This study provides evidence that wolves can induce spatial modification by elk on relatively fine scales within an animal's range, or may be manifested in broader scale responses such as dispersal or migration.

Introduction

Animal movement is a consequence of evolutionary pressures which contribute significantly to the long-term survival and reproductive success of the individual (Gadgil 1971, MacArthur 1972). Ecological requirements dictate spatial and temporal changes in location for most taxonomic groups, with movements often driven by seasonal and changing environmental conditions (Sinclair 1983), resource distribution and habitat quality, forage and prey availability (Pyke 1983), distribution of mates (Greenwood 1983, Ostfeld 1986, Ims 1988), territory maintenance (Ostfeld 1985, 1986), and thermal regulation. Interactions within communities such as intra- and inter-specific competition (Denno and Roderick 1992), and predation (Fryxell et al.1988, Lima and Dill 1990, Mitchell and Lima 2002) also influence how and why animals move.

Hence animal movement is influenced by a combination of top-down and bottom-up forces, with the spatial dynamics of large herbivores often driven by quantity and quality of food in the absence of any other constraints (McNaughton 1985, Senft et al. 1987, Fryxell et al. 2004). This is especially true when forage is patchily distributed across the landscape and predictably governed by fixed features such as soil, slope, aspect, and elevation (Bailey et al. 1996, Frair et al. 2005). While landscape attributes affect the occurrence and distribution of resources, seasonal interactions with temperature and

precipitation, and thus changes in the phenology of plant communities, can also produce substantial spatial and temporal variation in the availability and quality of forage (Thein et al. 2009). This heterogeneity strongly influences how large herbivores move (McNaughton and Banyikwa 1995, Pastor et al. 1997, Anderson et al. 2005, Fortin et al. 2005, Frair et al. 2005, Saïd and Servanty 2005), and the spatial distribution of limiting resources can define the location and size of an animal's home range (Ford 1983, Mitchell and Powell 2004).

Deep snow considerably reduces the availability of food resources for large herbivores in northern temperate regions during many months of the year (Jenkins and Wright 1987), making forage less accessible, and at a lower quality and higher energetic cost. Thus, large herbivores rapidly lose fat reserves and become chronically undernourished for a large portion of the year (Hobbs et al. 1981, Cook 2002, Parker et al. 2005). Also, energy required for thermoregulation during periods of intense cold contributes to their negative energetic state (Gates and Hudson 1979, Cook 2002, Parker et al. 2005). Variation in reproduction has been correlated with poor body condition and nutrition of large herbivores (Clutton-Brock et al. 1983, Testa and Adams 1998, Cook et al. 2004), and snow exacerbates these conditions due to the high energetic costs of locomotion and cratering for unexposed vegetation (Parker et al. 1984, Sweeney and Sweeney 1984, Hudson and White 1985, Fancy and White 1987). Thus, chronic nutritional deprivation and high energetic costs during winter strongly influence the demography of large herbivore populations in mid- to high-latitude environments due to starvation mortality (Clutton-Brock et al. 1985, Gaillard et al. 1998, Garrott et al. 2009a). Whilst migration is considered a strategy to lesson or avoid these costs (Garrott et al.

1987, Nelson 1995), many large herbivores do not migrate entirely out of their winter range but attempt to limit the loss of body reserves and potential for starvation during winter by adopting an energy conservation strategy of minimizing movement, including white-tailed deer (*Odocoileus virginianus*; Ozoga and Gysel 1972, Verme 1973, Moen 1976), moose (*Alces alces*; Miguelle et al. 1992, Renecker and Schwartz 1998, Dussault et al. 2005), woodland caribou (*Rangifer tarandus caribou*; Johnson et al. 2001), and red deer and elk (*Cervus elaphus*; Craighead et al. 1973, Georgii and Schröder 1983, McCorquodale 1993).

While energy conservation strategies are effective at reducing starvation risk, minimal movement can also make animals predictable in their locations, and thus easily encountered and potentially attacked by predators (Mitchell and Lima 2002). Relying on minimal movement to avoid detection in the presence of predators would appear to be an effective strategy in an environment where predator and prey are in close proximity to one another, or where predators require visual cues to detect their prey (Sih 1982, 1992, 1994; Lima and Dill 1990, Azevedo-Ramos et al. 1992, Lima 1998, Sih and McCarthy 2002). Under these circumstances movement by prey would greatly enhance the probability of being detected by predators, and thus pose a dangerous response (Lima 1998). But, in large scale predator-prey systems where predator and prey are both mobile and predators use multiple senses to detect prey and have a well-developed spatial memory, it may be advantageous for prey to increase movement in an attempt to remain unpredictable, avoid encounters, and/or move away from areas of high predation risk (Mitchell and Lima 2002, Sih 1984, Sonerud 1985, Formanowicz and Bobka 1989, Hammond et al. 2007). Additionally, prey could predictably move across the landscape

by utilizing refuges or escape terrain (Brown 1988), or spatially segregate from predators by dispersing or migrating (Fryxell et al. 1988).

Large herbivores often adopt strategies of moving away from predators at a coarse spatial scale via migration (Bergerud et al. 1984, Fryxell et al. 1988, Seip 1992, Bergerud et al. 2008), but non-migratory animals that do not spatially separate themselves from predation must employ an effective movement strategy that addresses predation risk (Rettie and Messier 2001). Elk in particular have reacted to wolves by exhibiting dynamic local movements within their range (Creel et al. 2005, Fortin et al. 2005, Frair et al. 2005, Gude et al. 2006, Winnie and Creel 2007). In addition elk utilize refuges, or adopt long-distance movements away from high-density wolf areas (Hebblewhite and Merrill 2007). Only recently has the effectiveness of these different movement strategies been evaluated (Hebblewhite and Merrill 2007), but how large herbivores modify their movements to address predation risk while still meeting nutritional needs remains unclear. To evaluate the spatial responses of non-migratory elk it is necessary to know how much area is used to meet biological needs; estimation of this requirement is typically employed using the concept of home range, while the stability of this range can be addressed using the metric of site fidelity.

I evaluated the drivers of elk spatial dynamics on multiple spatial and temporal scales to determine whether spatial changes occurred as elk balanced resource acquisition and energy conservation with avoiding wolf predation. Using data collected throughout an intensive long-term investigation on a non-migratory elk herd in the Madison headwaters of Yellowstone National Park, I documented elk spatial patterns prior to the recolonization of wolves in the system, during the recolonizing period, and following the

establishment of an abundant top predator population. I estimated home range size and fidelity for individual radio-collared elk and described broader scale movements such as dispersal and migration for elk that did not remain in the system following wolf recolonization. Prior to wolf colonization, it was predicted that elk constrained their winter movements to minimize energy costs and reduce the rate of depletion of body reserves that was their primary cause of mortality (Garrott et al. 2009a). Thus, it would be expected that home range sizes would be small and site fidelity would be high as elk predictably used the same foraging sites within and among years. After wolf colonization, it was predicted that elk movements would be more dynamic and fluid as they moved to areas of lower immediate risk due to continual encounters with wolves. Thus, home range sizes would be expected to be larger and site fidelity would be lower as elk used more spatially diverse landscape attributes to reduce predation risk and cope with nutritional constraints (Kie 1999).

Methods

The spatial use of elk in the Madison headwaters area were examined during November 15 through April 30 of 16 consecutive winters (1991-92 through 2006-07) but long distance movements detected during the 17th year of study while this manuscript was in preparation were also included. Each winter, 20-35 adult, female elk fitted with VHF radio-collars (i.e., approximately 4-10% of the population) were repeatedly sampled. Collared elk were typically monitored for multiple winters (median = 4, range = 1-16 years) until death, collar failure or detachment, or dispersal from the study area. Each animal was located approximately two to three times per week following a stratified

random sampling regime that ensured sampling times were distributed throughout daylight hours to capture variation in space use. For this sampling regime the study area was divided into geographically defined drainages (i.e., the Madison, Firehole, and Gibbon drainages), which were further stratified into areas within each of the three drainages. Radio-collared elk that inhabited the selected strata were located by randomly determining the order with which they were to be sampled and all groups within the study area were sampled once before re-sampling occurred. Hand-held telemetry equipment and homing procedures were employed to visually locate radio-collared animals. Home range area and home range (site) fidelity were calculated for use as response variables in the analyses and to describe the dispersal behavior of elk in the Madison headwaters.

Elk Winter Home Ranges

Home range has been defined as the extent of the area an animal occupies during a specified time frame and is an important indicator of the area used by an animal to meet its biological needs (Burt 1943, White and Garrott 1990). Kernel density estimation was used to estimate the utilization distribution (UD) (Silverman 1986, Worton 1989), and home range was defined as the area encompassing 95 % of the cumulative UD. Fixed rather than adaptive kernel was selected based on goodness-of-fit simulations (Horne and Garton 2006a) on a sample of the elk location data. Fixed and adaptive kernel techniques were ranked as the two top competing estimators, with fixed kernel chosen for the majority of the sampled datasets. The Likelihood Cross Validation method (Silverman 1986:53, Horne and Garton 2006b) was used to objectively estimate the kernel bandwidth smoothing parameter. Likelihood Cross Validation method was selected due to its ability

to perform well with small sample sizes (Horne and Garton 2006b) compared to the commonly used Least Squares Cross Validation and reference bandwidth (Sain et al. 1994, Seaman et al. 1999, Blundell et al. 2001, Hemson et al. 2005). Home ranges were estimated for each radio-collared elk that we had obtained ≥ 20 locations over the period November 15 through April 30, but the inclusion of animal years was restricted to those spanning a minimum time interval of January 1 to March 25 each year. Home range estimators are generally sensitive to the number of locations used in the calculation (Swihart and Slade 1985, Seaman and Powell 1996, Seaman et al. 1999) and because there was a disparity in the number of locations obtained for each animal during each winter of monitoring (N varied from 20 to 59, mean = 32.2, sd = 8.37) I predicted that biological comparisons between animal years would clearly be confounded given this sample size effect. It was confirmed experimentally that the resulting kernel home range area was biased by sample size, and similarly confirmed that the Likelihood Cross Validation optimal bandwidth would also be influenced by samples size, particularly when sample size is small (F.G.Watson and S. Cornish unpublished data). Thus a sample size correction procedure was developed to remove these confounding effects. Specifically, from a sample of N locations from a given animal year (when N was ≥ 20) a standard sub-sample size of n = 20 was selected. I then randomly selected (without replacement) 200 replicate sub-samples of size n. Likelihood Cross Validation was used to estimate the maximum likelihood UD and corresponding home range area for each replicate as recommended by Kernohan et al. (2001: 147). The mean of the replicates was then used as the estimate of home range area for that particular animal year; this

estimate likely incorporated all locations for a given animal year. The comparison between animal years was made in terms of the standardized areas.

Home range areas can be inflated by one or a few outlying points that are a result of occasional sallies (Burt 1943). In the latter half of the study, elk were observed making such movements for one to three days in a winter, representing one to two locations. These locations disproportionately inflated the home range and therefore, a total of ten locations were censored from six independent animal years prior to generating the home range replicates to obtain estimates that more accurately represented the typical area used. Censoring these locations was a conservative approach so that increased movement did not just reflect these outlying points. In addition, three complete sampling years were censored when an insufficient amount of data were collected. This included the first winter (1991-92) when the study was being established and many animals were not collared until after January 1. Also, an insufficient number of locations were collected during winters 1998-99 and 1999-00 to generate home range estimates for a large enough sample of animals.

Site Fidelity

Site fidelity is the "tendency of an animal to either return to an area previously occupied, or to remain within the same area for an extended period of time" (White and Garrott 1990:133). Thus, I evaluated if radio-collared elk remained in the same approximate area each winter by calculating the centroid of each elk's winter distribution as the arithmetic mean of all the X coordinates and the arithmetic mean of all the Y coordinates. The Euclidean distance (km) between centroids from consecutive winter

seasons was used as a metric of fidelity (White and Garrott 1990: 134). A large Euclidean distance represented animals that shifted the area of use between years, whereas a small Euclidean distance reflected high fidelity and little shift in the center of the distribution of locations from year to year. Animals were only included in the analysis if there were ≥ 20 locations spanning a minimum time interval of January 1 to March 25 each year. Estimates of centroids did not appear to vary with sample size, so all the locations for each animal year were included when calculating the centroid, provided an animal was located at least 20 times during the specified period. However, single locations that were >10 km from the next nearest point (n = 9) were censored to avoid distortion of the centroid due to a single non-typical movement. Also, the insufficient number of locations collected in the middle of the study precluded us from comparing estimates of site fidelity between 1998 and 1999.

Long-Distance Movements

Long-distance movements by an animal outside of its normal area were considered by Burt (1943: 351) as occasional sallies that were "perhaps exploratory in nature and should not be considered as part of the home range." Dispersal has been defined as the "one way movement of individuals from their natal site, or an area that has been occupied for a period of time" (White and Garrott 1990:121), while migration is "a round trip movement of individuals between two or more areas or seasonal ranges" (White and Garrott 1990:121). Sallies, dispersal, and migration were collectively termed as long-distance movements by elk away from their original winter ranges. Occasional sallies were defined as movements lasting one to four days and outside of the individuals'

normal range to a location where the home range had not previously encompassed. Dispersal was defined as a long-distance movement (>15 km) away from the area where the animal had remained sedentary for one or more prior winters, or if the radio signal was not located anywhere within the boundaries of the study area. Monitoring radio-collared animals over consecutive winter seasons allowed dispersal behavior to be categorized into one of two states: 1) permanently leaving the drainage where the elk had remained sedentary for one or more prior winters; and 2) temporarily leaving the drainage where the elk had remained sedentary for one or more prior winters, but returning after >1 year and residing in that drainage during subsequent winters. Lastly, a migratory animal was defined as an individual that vacated the drainage during winter where it had remained sedentary for one or more prior years, moving >15 km away from its former range, or if the radio signal was not located anywhere within the boundaries of the study area. These individuals returned and were re-located within the study area during the snow-free period. Although the location where a few of the temporary dispersers moved to was unknown, they all returned to the study area with effectively working collars. Thus, I was confident that animals which were not detected within the boundaries of the study area had left, and dispersal events were not mistaken with premature collar malfunctions. The locations of all permanent dispersers were aerially detected, all individuals were visually observed from the ground, and the collars were retrieved from dead animals. An annual metric of elk dispersal (i.e., dispersal plus migration) was defined as the percentage of the animals that chose to reside in a new location for at least one winter. This metric did not include animals that conducted exploratory fine temporal movements (sallies) within a winter. It was determined that

animals had dispersed after failing to detect them at the start of each winter field season. The percentage "dispersed" was based on the total number of collared animals that were being monitoring at the start of the winter season. The telemetry signals of dispersing and migratory animals were monitored during subsequent summers and winters, using ground-based telemetry and occasional aerial flights to determine locations and fates.

Non-Wolf Covariates of Elk Movement

A validated snow pack simulation model for the central Yellowstone region (Watson et al. 2009a) was used to estimate the mean daily snow water equivalent (SWE, water content of snow in meters) on the elk winter range (landscape SWE). Daily values were averaged over the entire winter season to provide the annual snow pack covariate of mean daily SWE (SWE_{mean}). I felt this metric would most appropriately capture the physical constraints that impede movements and foraging by large herbivores during winter because the sinking depth of an animal is a function of snow depth, snow density, and hardness (Parker et al. 1984) which, in turn, influences energetic costs (Parker et al. 1984, Sweeney and Sweeney 1984).

The spatial arrangement of habitat and terrain features are important for determining the distribution of resources, patterns of ungulate movement (Anderson et al. 2005, Frair et al. 2005), and home range sizes and shapes (Kie et al. 2002, Mitchell and Powell 2004, Kie et al. 2005, Saïd and Servanty 2005, Forester et al. 2007). It was suspected that landscape differences between the three drainages in the Madison headwaters area would influence spatial responses. Thus, a categorical covariate DRAINAGE was defined which classified elk into the Madison, Gibbon, or Firehole drainages. Drainages were

assigned based on the telemetry locations for a given animal year and, on the rare occasion where animals used multiple drainages, assignment was based on where the majority of the locations occurred. For the site fidelity analysis, we assigned DRAINAGE for the drainage used during the first of the pair of consecutive years.

It was suspected that elk density may influence home range size (Tufto et al. 1996, Kilpatrick et al. 2001, Kjellander et al. 2004), but I excluded this potential covariate from analyses because the annual estimate of population size by drainage was highly correlated with the wolf covariates described in subsequent paragraphs (Pearson's Correlation Coefficient = -0.53 and -0.56 with $WOLF_{days}$ and KILLS, respectively). I recognized that age of an animal could affect movements, particularly the tendency to remain faithful to a site. Exploratory movements of large herbivores tend to be made by males (Cederlund and Sand 1994), which had no specific relevance on these analyses, or by first time female breeders (i.e., 2-year-olds) (Garrott et al. 1987). Treating age as a categorical covariate (< 2 and ≥ 2) would have allowed me to incorporate the age effect into the models, but the data had a limited number of the young age class animals in which to effectively incorporate this covariate.

Covariates of Predation Risk

The presence of wolves was detected and quantified in the Madison headwaters from November 15 to April 30 during the winters of 1996-97 through 2006-07. National Park Service biologists captured wolves and fitted radio-collars on animals in each pack (Smith 2005, Smith et al. 2009) and wolf presence and their locations were monitored using ground-based telemetry, snow tracking, and visual observations of collared and un-

collared individuals. Each drainage was intensively monitored for wolf presence daily with crews of three to four people using snowmobiles, vehicles, snowshoes, and high points in the landscape to facilitate telemetry and observations. When packs containing radio-collared wolves were detected, multiple locations of all detected animals through the day were estimated using triangulation (White and Garrott 1990). Snow tracking, visual observations, and counts during aerial monitoring by National Park Service biologists were used to estimate the number of animals per pack and aid in the daily assessments of wolf presence or absence (Becker et al. 2009, Smith et al. 2009). These methods also allowed for a variety of data on wolf landscape use patterns, and the frequency and distribution of kills to be obtained (Bergman et al. 2006, Becker et al. 2009). Detection of un-collared wolves was facilitated by opportunistic observations of tracks and wolves by field personnel working on concurrent elk and bison investigations (Bruggeman et al. 2009, Garrott et al. 2009a, White et al. 2009). The total numbers of individual wolves known to be present in each drainage each day were estimated based on the information obtained from these various wolf monitoring techniques and quantified as wolf-days.

Three wolf covariates were developed to assess the hypotheses about the influence of predation risk on space use of elk in the Madison headwaters. The covariate $WOLF_{period}$ categorized the 16-year data set into three periods of wolf presence: before, during, and after wolf colonization. This covariate was drainage-specific because wolves became established in different drainages during different winters (Firehole: 1997-98; Gibbon: 2000-01; Madison: 2001-02; Smith et al. 2009). No wolves were present in the study area during 1991-92 through 1995-96. To account for the potential transitory behavioral

dynamics due to the initial naïveté of the prey (Berger et al. 2001), the colonizing period was defined as the time immediately following wolf reintroduction, when elk were initially exposed to wolf predation risk, but no wolf pack (≥2 animals) was routinely detected in the drainage. Wolves were considered to be established in a drainage during the first winter that a pack was consistently detected in that drainage. The level of wolf predation risk for elk occupying each drainage was highly variable among winters, and it was suspected that the magnitude or frequency of any behavioral responses of elk to predation risk may also have been scaled to the number of wolves in the immediate area. Thus, a continuous covariate, $WOLF_{days}$, was constructed which described the estimate of the number of wolves in each drainage each day. For the home range analysis, this covariate was the estimated number of wolves in a drainage for a given year. A third wolf metric, KILLS, was also developed that represented the number of wolf-killed ungulates discovered in each drainage in a given year (for methodology see Becker et al. 2009, Smith et al. 2009). For the site fidelity analysis, I used $WOLF_{period}$, $WOLF_{days}$, and KILLS made in that drainage during the first of the two consecutive years because the Euclidean distance was a metric based on two consecutive years.

Statistical Analyses

Analysis of Variance (ANOVA) and Tukey multiple comparisons with unequal sample size (Kutner et al. 2005: 750) were used to evaluate if elk winter home range size and fidelity changed with varying intensities of wolf predation risk. Therefore, differences in the mean home range sizes and mean Euclidean distances were compared between consecutive annual home range centroids among the pre-wolf, colonizing, and

established wolf periods ($WOLF_{period}$). Both home range size and Euclidean distance were *ln*-transformed and diagnostic residual plots were used to evaluate the assumption of constant variance and normality of residuals. I used 95% confidence intervals to quantify uncertainty in parameter estimates.

Mixed-effects linear models (Pinheiro and Bates 2000) were also used to evaluate competing *a priori* models for assessing change in home range size and the Euclidean distance between years. These multiple regression models treated SWE_{mean}, DRAINAGE, and WOLF covariates as fixed effects in the home range and fidelity analyses. Because these datasets included observations of the same individuals through time individual animal identity was treated as a random effect (i.e., intercept-only) to account for individual variability in space use among animals within and between years. For both response variables, this covariate allowed for the variation between individuals (intercept) and within an individual (residual) to be partitioned and I could determine how much of the variation in home range size and site fidelity was accounted for by the fixed and random effects. Combinations of the covariates were included in the additive form for all analyses. I predicted a fixed rate of change in the response variable per unit change in the predictor variable (i.e., linear form). Diagnostic plots were used to assess the assumptions of normality and constant variance of residuals, and both response variables were transformed using the natural log to conform to linear models assumptions. All continuous covariates were centered and scaled to facilitate comparisons and interpretations of covariate coefficients. Variance inflation factors (VIF), which measure multi-colinearity among variables, were calculated for all combinations of predictors. Those models that included predictor combinations with VIF

<6 were retained in the model list. This was a conservative approach because VIF in excess of 10 implies multi-colinearity (Kutner et al. 2005: 409). Correlation coefficients were also calculated to further check for multi-colinearity between the predictor variables. Akaike Information Criteria corrected for small sample size (AIC_c) was used to rank models given the data and compare the relative ability of each model to explain variation in the data (Burnham and Anderson 2002, 2004). Akaike model weights (wi_c) were used to address model selection uncertainty (Burnham and Anderson 2002) and evidence ratios (ratio of wi_c/wj_c) were used to measure the relative likelihood of model pairs (Burnham and Anderson 2002). Covariate coefficients and variance of the random effects were estimated using restricted maximum likelihood. Comparable AIC_c values were calculated using maximum likelihood estimation (Pinheiro and Bates 2000). All statistical analyses were performed using the R statistical package (R Development Core Team 2006).

A Priori Model Suites and Predictions

Hypotheses on elk spatial behavior were expressed as two suites of candidate *a priori* models constructed for home range size (15 models) and site fidelity (7 models; Appendices 2.1 and 2.2). These models were constructed based on literature and field knowledge of the study system and included one or more of the climate or landscape covariates independently or with the inclusion of a single wolf covariate. Every model in both suites also included the individual random effect. A null model was also constructed for each suite which hypothesized constant home range area and site fidelity.

Snow reduces forage availability and creates a wider dispersion of forage over the landscape. Thus, large herbivores may range over greater areas when critical resources are scarce (Geist 2002), resulting in a positive correlation between home range size and snow (Kjellander et al. 2004, Anderson et al. 2005). However, snow conditions in the Madison headwaters routinely reach a depth and density that would impose major constraints to the locomotion of most large herbivores (Craighead et al. 1973, Parker et al. 1984, Fancy and White 1985, Messer et al. 2009). Under these conditions, I predicted that elk would constrain their movements and home range size would be inversely related to SWE_{mean} (Georgii and Schröder 1983, Schmidt 1993, Krasińska et al. 2000, Grignolio et al. 2004, Dussault et al. 2005).

I also hypothesized that the distribution of habitat types, patch size, and topography would influence the way large herbivores moved. Specifically, I predicted that elk residing in drainages that contained a high density of geothermally-heated foraging sites (i.e., the Firehole, and to a lesser degree the Gibbon) would have smaller home ranges and higher site fidelity as they made localized movements within and between patches (Craighead et al. 1973, Kie et al. 2002, Messer et al. 2009). Conversely, mountainous terrain could facilitate movements around landscape features (Kie et al. 2005). Therefore, it was predicted that elk residing in drainages that were more constrained by local topography (i.e., the Madison and to a lesser degree the Gibbon) would move linearly around topographic features and, as a result, have a larger area of use.

In addition, it was predicted that elk movement patterns within and between winters would change as elk responded to variations in predation risk. There is strong evidence among wolf-elk systems that elk move between habitats in response to predation threat or

vacate areas of high wolf use (Creel et al. 2005, Fortin et al. 2005, Frair et al. 2005, Gude et al. 2006, Hebblewhite and Merrill 2007, Winnie and Creel 2007). Consequently, I predicted home range sizes of elk would become larger with less site fidelity within and among years as elk were increasingly encountered, attacked, and displaced by wolves, resulting in elk utilizing multiple habitat components as they attempted to balance predation risk and nutritional demands. I was uncertain which wolf covariate would be the best predictor of these responses. Therefore, I considered *a priori* models with identical non-wolf covariate structures and each of the three wolf covariates ($WOLF_{period}$, $WOLF_{days}$, KILLS).

Based on the outcome of the *a priori* model-selection results, *post hoc* exploratory analyses were conducted to generate hypotheses for future work. I included a WOLF*DRAINGE and WOLF*SWE_{mean} interaction in the top model from the home range model suite because it was predicted that the strength of the wolf effect would differ by drainage and/or with increasing snow pack. I also evaluated different non-linear forms of the continuous covariates (β*(quadratic $(x + x^2)$)), exponential (β*(exp(x))), and negative exponential (β*(exp(-x))). For the site fidelity analysis, I included a WOLF*DRAINGE interaction and evaluated different non-linear forms of the continuous covariates. Changes in AIC_c scores were used to evaluate if models were improved with the covariate additions and substitutions.

Results

A total of 11,908 eight randomly collected elk locations were obtained from repeated sampling of 115 radio-collared, adult, female elk during the winters 1991-92 through

2006-07. From this total, 3927 locations were collected before wolf colonization, 2501 locations were collected during wolf colonization, and 5480 locations were collected after wolf packs became established in the study area. These data were used to generate 277 home range estimates for 91 radio-collared elk (95 Pre, 50 Col., 132 Est.), and 221 Euclidean distances between consecutive winter centriods for 66 radio collared elk (100 Pre, 39 Col., 82 Est.). Wolves were absent from the Madison headwaters area prior to reintroduction in 1995-96. Thereafter, the total number of wolf days increased from 55 in 1996-97 to a peak of 3657 in 2004-05. The Firehole drainage experienced high wolf use immediately following reintroduction, while the Madison and Gibbon drainages did not experience wolf use until several years later and never reached the magnitude of use observed in the Firehole (Figure 2.1). Pack size and number of packs varied both spatially and temporally (Smith et al. 2009).

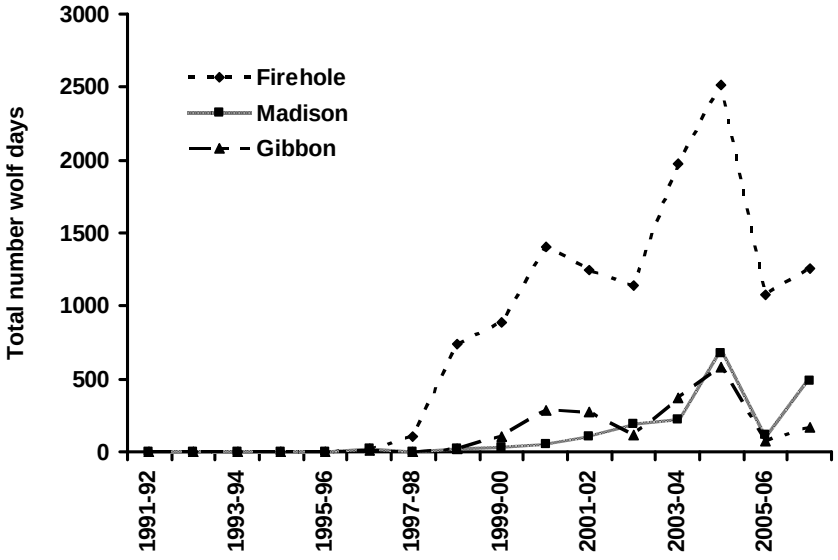

Figure 2.1 Variations in the use of the Madison headwaters area of Yellowstone National Park by wolves during the winters of 1996-97 through 2006-07. Wolf use was estimated in wolf days, defined as one wolf in the study area for one day, respectively. The number of wolves, packs, and the frequency with which they used the Madison headwaters continued to increase until 2004-05, after which it decreased substantially. Wolf use varied substantially between the Firehole, and the Madison and Gibbon drainages.

Home range sizes of radio-collared elk ranged from 2.8 km^2 to 86.0 km^2 (n = 277, mean = 21.2 km^2, sd = 14.3), with an increase of 53 % (P = 0.001) in mean home range size as the system transitioned from no wolves (n = 95, mean = 16.8 km^2, sd = 10.8), through wolf colonization (n = 50, mean = 17.4 km^2, sd = 9.5), to established wolf packs (n = 132, mean = 25.7 km^2, sd = 16.8; Figure 2.2*a*). *Ln*-transformed home ranges were significantly larger after wolf packs became established in the system compared to the pre-wolf ($\hat{D}_{\text{ln(established)-ln(pre-wolf)}}$ = 0.372; 95% CI: 0.162, 0.583; P < 0.001) and colonizing periods ($\hat{D}_{\text{ln(established)-ln(colonizing)}}$ = 0.279; 95% CI: 0.019, 0.538; P = 0.032). No significant differences in home range size were detected between the pre-wolf and colonization periods ($\hat{D}_{\text{ln(colonizing)-ln(pre-wolf)}}$ = 0.094; 95% CI: -0.180, 0.367; P = 0.699). $\hat{D}$ defines the difference in transformed mean home range size between two wolf periods. An advantage of log transformations is that the results can be interpreted on the original scale of the variable (Ramsey and Schafer 2002). So by taking the exponent of the difference in the mean log (Y) between two time periods a multiplicative value for the change in the median (Y) between the time periods was obtained. Consequently the median home range size for the established period was exp (0.372) =1.451 times bigger than the median home range size for the pre-wolf period (95% CI: 1.176, 1.791), and 1.322 times bigger than the median home range size for the colonizing period (95% CI: 1.019, 1.712). Median home range size for the colonizing period was only 1.099 times bigger (95% CI: 0.835, 1.443) than that of the pre-wolf period.

Elk were generally faithful to their winter range within a specific drainage from year to year, with the Euclidean distance between consecutive centroids ranging from 0.02 km to 10.15 km (n = 221, mean = 1.3 km, sd = 1.5). However, a 69 % increase (P = 0.001)

in mean Euclidean distance was observed as the system transitioned from no wolves (n = 100, mean = 1.0 km, sd = 1.1), through wolf colonization (n = 39, mean = 1.0 km, sd = 0.9), to established wolf packs (n = 82, mean = 1.7 km, sd = 2.0; Figure 2.2*b*). $\hat{D}$ defines the difference in transformed mean Euclidean distance between two wolf periods and *ln*-transformed Euclidean distances were significantly larger after wolf packs became established in the system compared to the pre-wolf period ($\hat{D}_{\text{ln(established)-ln(pre-wolf)}}$ = 0.438; 95% CI: 0.081, 0.795; P = 0.012). No significant differences in Euclidean distances were detected on the log scale between pre-reintroduction and colonization ($\hat{D}_{\text{ln(colonizing)-ln(pre-wolf)}}$ = 0.180; 95% CI: -0.273, 0.632; P = 0.617) or between colonization and establishment ($\hat{D}_{\text{ln(established)-ln(colonizing)}}$ = 0.258; 95% CI: -0.208, 0.724; P = 0.394). The lack of a significant difference in Euclidean distance on a natural log scale between the colonizing and established periods likely reflects higher variance in Euclidean distance during the established wolf period compared to the pre-wolf and colonization periods. Median Euclidean distance for the established period was 1.550 times bigger than the median Euclidean distance for the pre-wolf period (95% CI: 1.084, 2.214), and 1.294 times bigger than the median Euclidean distance for the colonizing period (95% CI: 0.812, 2.063). Median Euclidean distance for the colonizing period was 1.197 times bigger (95% CI: 0.761, 1.881) than that of the pre-wolf period.

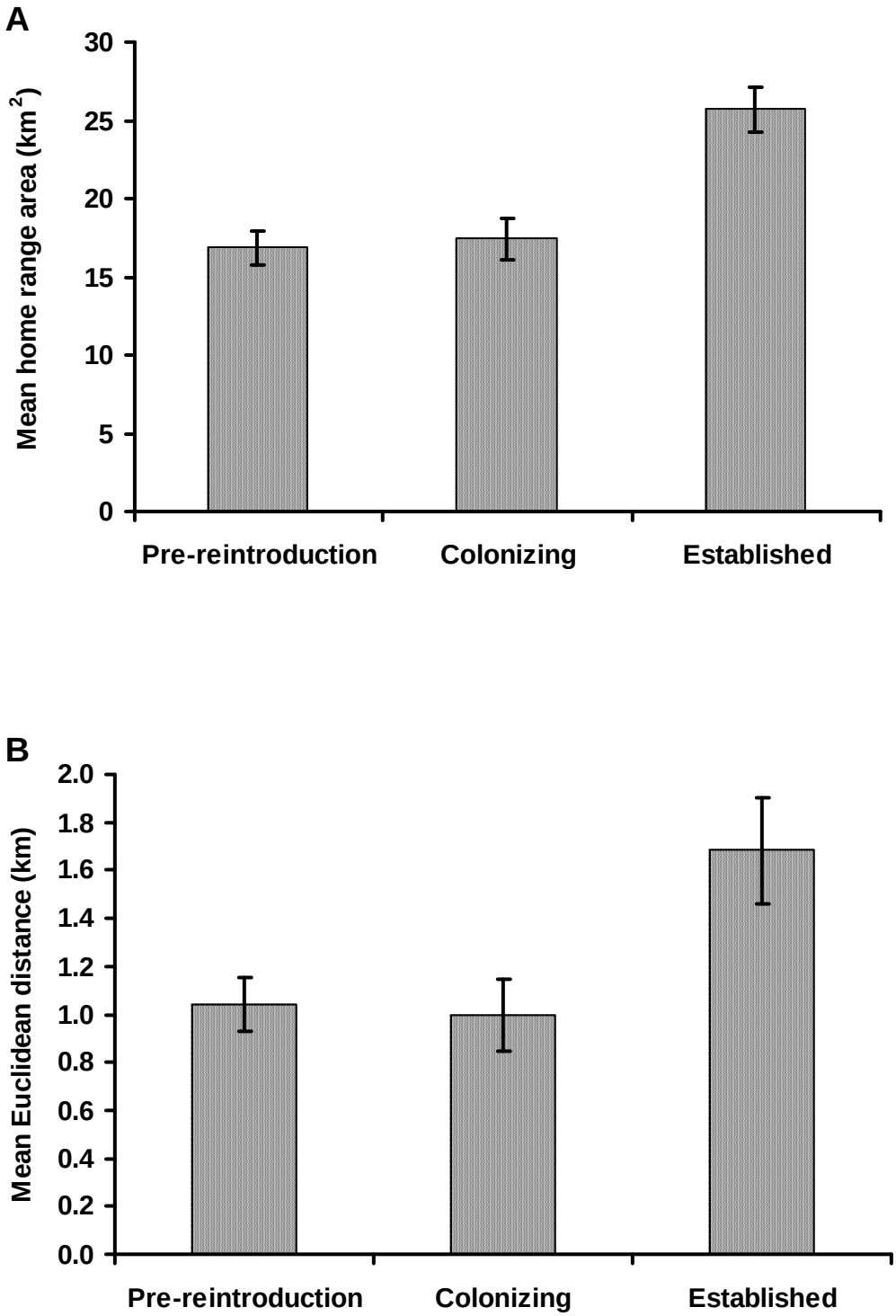

Figure 2.2 Mean 95% fixed kernel home range areas (**A**) and Euclidean distances (**B**) by wolf period. Plotted values are based on the untransformed data, with the error bars representing standard errors.

Mixed Effects Linear Regression Results

Model selection results for the home range size analysis supported two top models that received all of the model weight and contained the covariates SWE_{mean}, DRAINAGE, and $WOLF_{days}$ (Table 2.1). Snow had a negative effect on *ln* home range size ($\hat{\beta}_{SWEmean}$ = -0.065; 95% CI = -0.138, 0.008), but SWE_{mean} only appeared in one of the top ranked models and confidence limits spanned zero. Thus, I did not find substantial support for the prediction that there was a linear relationship between SWE_{mean} and elk home range size. DRAINAGE and $WOLF_{days}$ received all of the predictor weight and appeared in both of the top ranked models. As predicted, the specific drainage where the animals resided played an influential role in the size of the area used by elk during winter. In the absence of wolves, elk in the Madison ($\hat{\beta}_{DRAINAGE(Madison)}$ = 3.092; 95% CI = 2.936, 3.248) and Gibbon ($\hat{\beta}_{DRAINAGE(Gibbon)}$ = 3.017; 95% CI = 2.802, 3.231) drainages used larger areas than elk in the Firehole drainage ($\hat{\beta}_{DRAINAGE(Firehole)}$ = 2.581; 95% CI = 2.429, 2.732; coefficient estimates and 95% CI are provided in the natural-log scale). As predicted, there was a positive correlation between *ln* home range size and the presence of wolves in all three drainages ($\hat{\beta}_{WOLFdays}$ = 0.265; 95% CI = 0.168, 0.362; Figures 2.3 *a*, *b*). Compared to the other wolf covariates $WOLF_{days}$, received all the predictor weight, while $WOLF_{period}$ and KILLS received no predictor weight. Results of the random effect from the mixed modeling indicated that within-animal variability ($\hat{\sigma}^2_W$ = 0.29) was substantially higher than between-animal variability ($\hat{\sigma}^2_B$ = 0.09). The interactions included in *post hoc* exploratory analyses did not provide any improvement over the most supported *a priori* models. However,

including SWE_{mean} into the model as a quadratic or negative exponential improved the model (6.22 and 4.45 ΔAICc units, respectively) over the linear form. The estimated coefficient for SWE_{mean} + SWE_{mean}^2 was -0.189 (95% CI: = -0.299, -0.078) + 0.082 (95% CI: = 0.027, 0.139), while exp (-SWE_{mean}) was 0.112 (95% CI = 0.032, 0.194). Because the confidence intervals did not span zero, SWE_{mean} appeared to be a strong predictor of elk home range size when included in the model in a non-linear form. Changing the functional form changed the coefficients for the best *a priori* model only slightly. Re-fitting the model with the wolf covariates as different functional forms did not make any additional improvements.

Table 2.1. Model selection results for the most supported models examining the natural logarithms of home range size and site fidelity (i.e., Euclidean distance) of elk in the Madison headwaters area of Yellowstone National Park during 1991-92 through 2006-07. All models are ranked according to AIC_c values, and presented along with the number of parameters (*k*), ΔAIC_c value (i.e., change in AIC_c value relative to the best model), and the Akaike weight (w_i). AIC_c values for the top home range and site fidelity models were 514.4 and 594.6, respectively. Abbreviations are: SWE_{mean} (mean daily snow water equivalent), DRAINAGE (Madison, Firehole, Gibbon), $WOLF_{period}$ (pre-reintroduction, colonizing, established), $WOLF_{days}$ (total number of wolf days per drainage per year), and KILLS (total number of wolf-killed ungulates per drainage per year). For the site fidelity analysis the wolf covariates describe wolf use in the particular drainage during the first of the two consecutive years.

Model structure	***k****	**ΔAIC_c**	**w_{ic}**
***ln* (home range area)**			
SWE_{mean} + DRAINAGE + $WOLF_{days}$	7	0.00	0.62
DRAINAGE + $WOLF_{days}$	6	1.03	0.38
SWE_{mean} + DRAINAGE + KILLS	7	12.25	0.00
DRAINAGE + KILLS	6	14.76	0.00
SWE_{mean} + $WOLF_{days}$	5	15.15	0.00
***ln* (Euclidean distance)**			
DRAINAGE + KILLS	6	0.00	0.59
DRAINAGE + $WOLF_{days}$	6	2.62	0.16
DRAINAGE + $WOLF_{period}$	7	2.79	0.15
DRAINAGE	5	4.62	0.06
$WOLF_{period}$	5	7.08	0.02

*Residual error from the mixed modeling accounts for one parameter value.

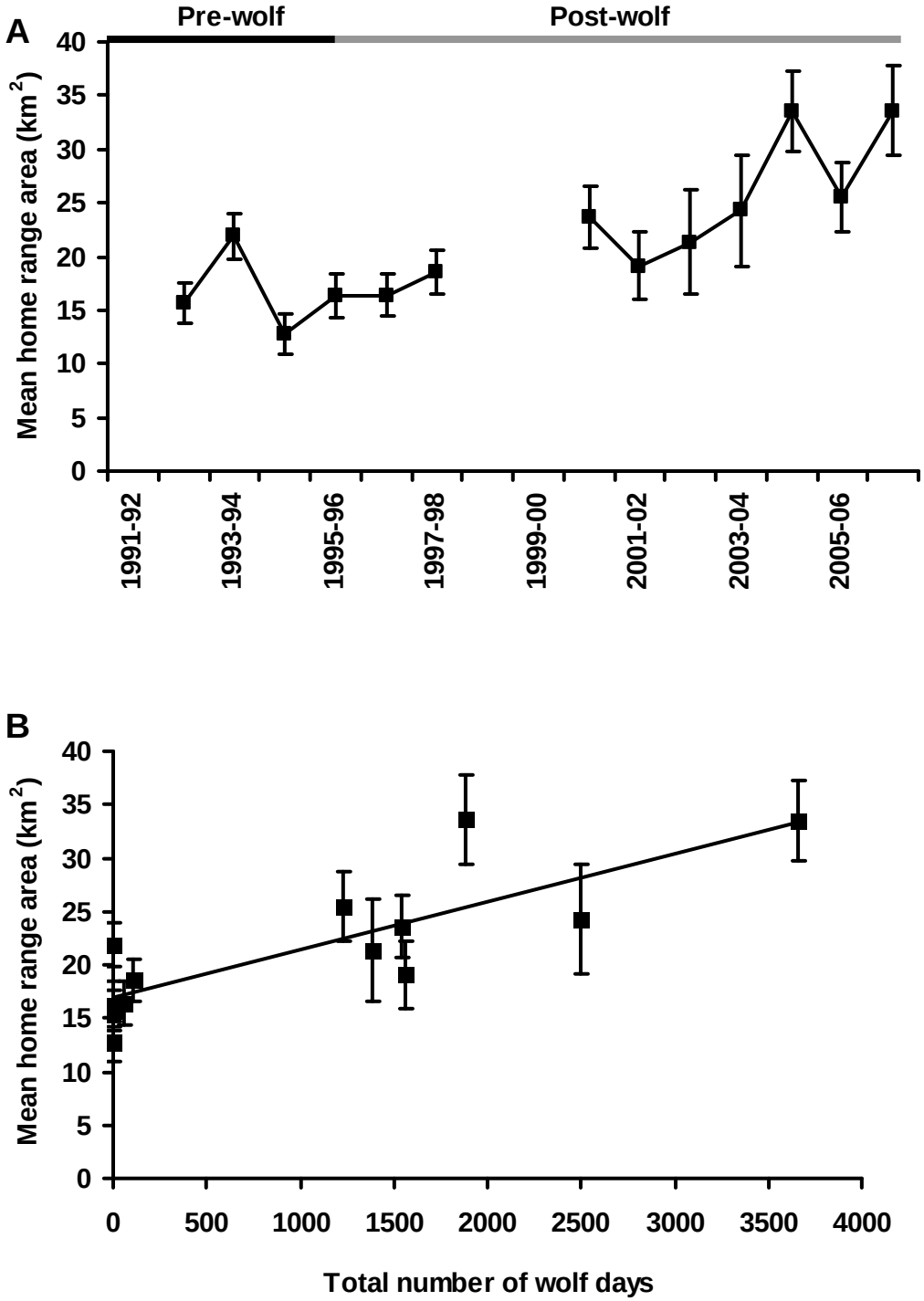

Figure 2.3 Mean annual 95% kernel home range areas for the study area with error bars representing standard error (gaps represent insufficient data collected for 1991, 1998, and 1999) (**A**), and the relationship ($R^2_{adj} = 0.67$, $F_{1,11} = 22.3$, $P < 0.001$) between mean annual 95% fixed kernel home range areas and the total number of wolf days for the study area, with error bars representing standard errors (**B**).

Model selection results for the site fidelity analysis supported one top model that received a model weight of 0.59 and contained the covariates DRAINAGE and KILLS (Table 2.1). DRAINAGE was a highly influential predictor of Euclidean distance, receiving a predictor weight of 0.96. In the absence of wolves, the distance between the centers of consecutive winter distributions was greater in the Madison ($\hat{\beta}_{DRAINAGE(Madison)}$ = 0.016; 95% CI = -0.259, 0.292) and the Gibbon ($\hat{\beta}_{DRAINAGE(Gibbon)}$ = 0.132; 95% CI = -0.266, 0.530) compared to the Firehole drainage ($\hat{\beta}_{DRAINAGE(Firehole)}$ = -0.692; 95% CI = -0.988, -0.395; coefficient estimates and 95% CI are shown in the natural-log scale). As predicted, the distance between consecutive winter centroids was positively correlated with the wolf covariate (Figures 2.4 *a*, *b*). The most influential of the wolf covariates on the *ln* Euclidean distance was the number of kills in a given drainage the prior year ($\hat{\beta}_{KILLS}$ = 0.229; 95% CI =0.064, 0.394). KILLS received a predictor weight of 0.60 compared to predictor weights of 0.17 for both the $WOLF_{period}$ and $WOLF_{days}$ covariates. On the log scale, variance of Euclidean distance between years was relatively high within ($\hat{\sigma}^2_W$ = 0.62) and among ($\hat{\sigma}^2_B$ = 0.31) elk. This finding suggested some animals remained very faithful to a site from year to year, while others demonstrated less philopatric behavior. *Post hoc* exploratory analyses provided no improvement over the *a priori* models.

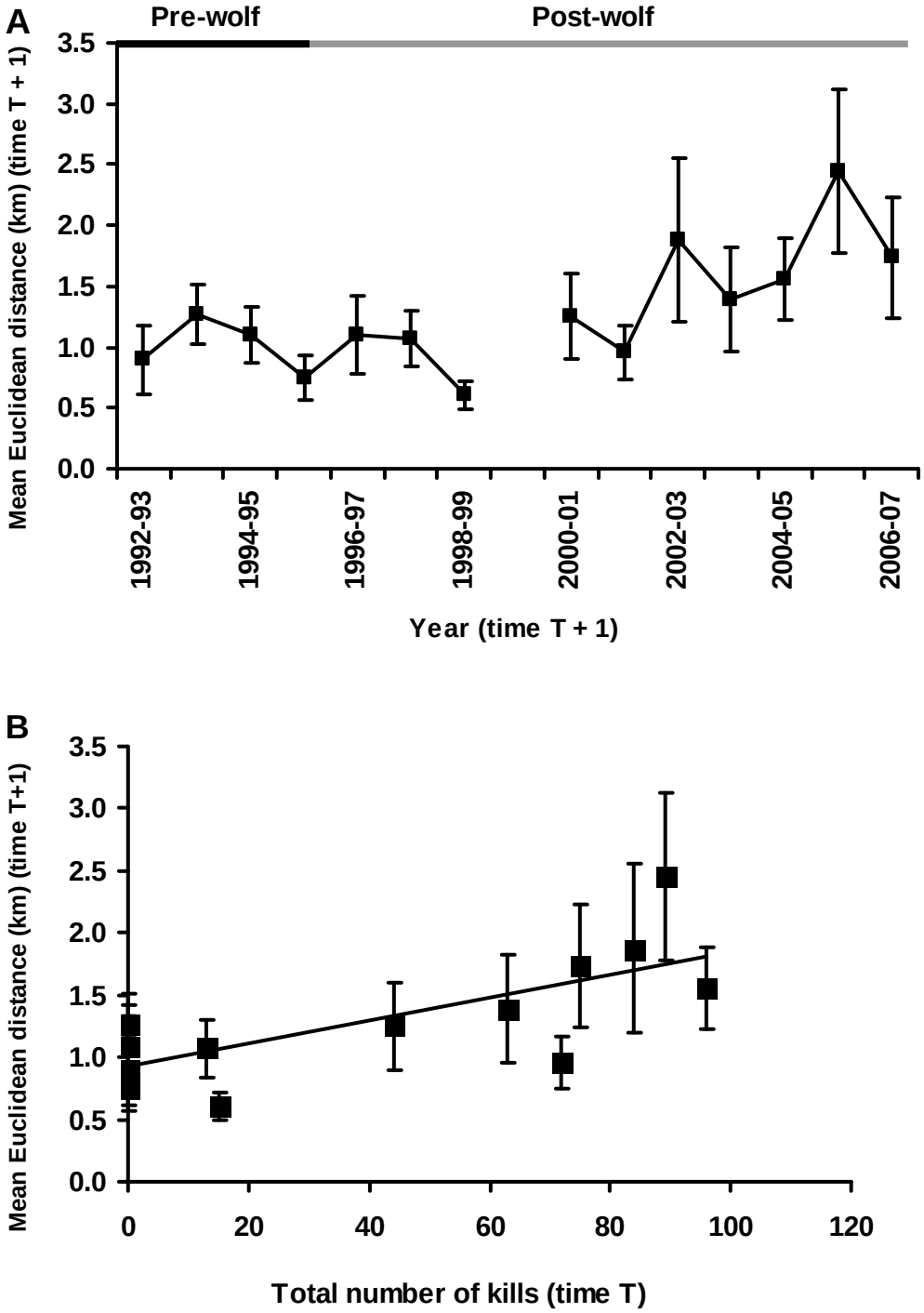

Figure 2.4 Mean annual Euclidean distance for the study area at time T+1 with error bars representing standard error (gaps represent insufficient data collected to compare estimates of site fidelity between 1998 and 1999) (**A**), and the relationship ($R^2_{adj} = 0.54$, $F_{1,12} = 13.87$, $P = 0.002$) between mean annual Euclidean distance at time T+1 and the total number of wolf-killed ungulates for the study area at time T, with error bars representing standard errors (**B**).

Dispersal and Migratory Movements

A total of 115 adult, female elk were radio-collared and monitored during the 17-year study period (mean elk per year = 27, range = 22 to 35), constituting 426 animal years of movement monitoring from 1991-92 through 2007-08. During the first half of the study (1991-92 through 1998-99), when wolves were absent or initially colonizing the study area, 215 animal years of monitoring were accrued and all radio-collared elk remained within the Madison headwaters area during each winter. After wolf packs became established in the system (1999-00 through 2007-08), 211 animal years of monitoring were accrued during which 19 individuals displayed some form of long-distance movement away from the study area and were absent from the Madison headwaters during one or more winters (Figure 2.5). All of these individuals were monitored for 1-6 years prior to their long-distance movement, with data indicating they had been sedentary and part of the non-migratory Madison headwaters population. Of the 19 long-distance movements that were recorded, four collared females that had a history of association left the Gibbon drainage and relocated approximately 21 km away. Three permanently left the drainage, while one became migratory, residing at this new location (Canyon) during the winters and migrating back to the Gibbon drainage during the summer. Nine other collared females (five independently and four jointly) dispersed from the Firehole drainage and were discovered between 18 and 63 km (mean = 43 km, sd = 16.7) from their traditional ranges within the Madison headwaters. Four other instrumented females dispersed from the study area to unknown locations for one winter and returned to their former home ranges in the Madison headwaters the following year. These animals subsequently remained in the study area for 2-4 years until death, collar detachment, or

the end of this study. Two additional individuals became migratory, leaving the study area in autumn and returning to the study area for the summer. These individuals were relocated aerially approximately 55 km to the north in the Gardiner basin area of the northern range. The three migratory animals were sedentary for two, four, and five years prior to changing their behavior, and remained migratory for six, six, and two subsequent winters, respectively. All animals that conducted long-distance movements resided in the Gibbon (n = 5) and Firehole (n = 14) drainages, where their home ranges the previous year had overlapped wolf use areas (Figure 2.6). No collared animals in the Madison drainage performed any long-distance movements during the study. Of these 19 animals that moved long distances from the study area six were killed by wolves in their new locations or upon returning the Madison headwaters. In total 15 of the 79 collared elk which experienced at least one winter with wolf predation risk permanently dispersed or became migratory and wintered outside of the Madison headwaters. Thus, approximately 19% of the collared population altered their traditional patterns of range occupancy in such a way that they were no longer classified as part of the Madison headwaters sedentary herd following wolf reintroduction.

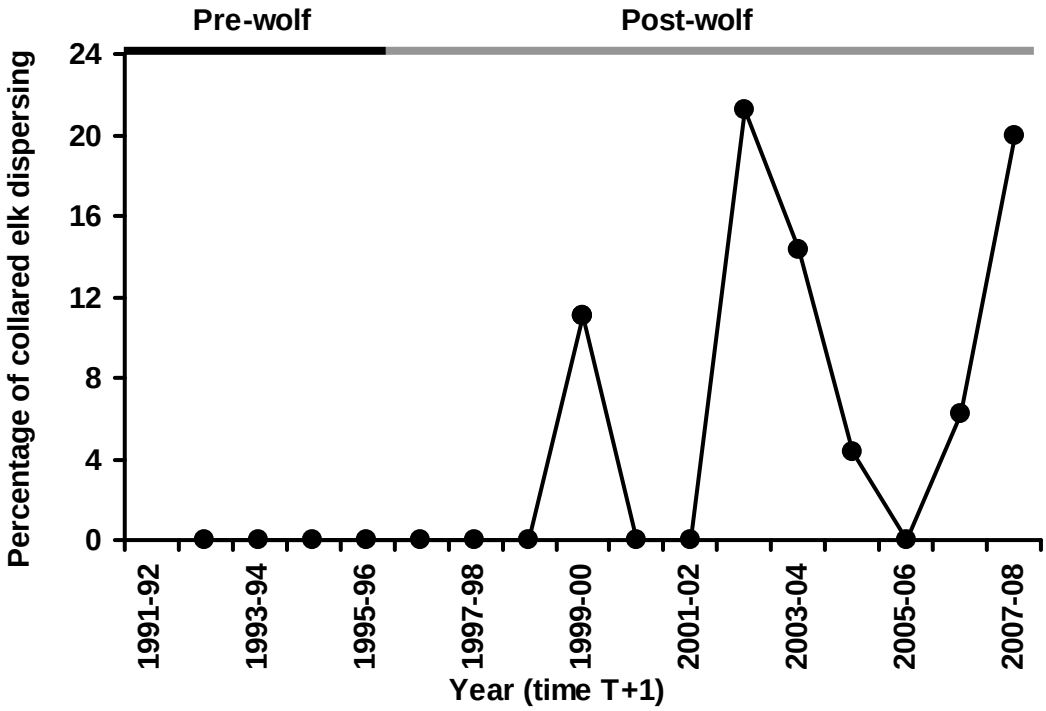

Figure 2.5 The percentages of radio-collared elk dispersing from the Madison headwaters area of Yellowstone National Park during 1992-93 through 2007-08. The percentage "dispersed" each year was estimated as the number of collared animals missing from the Madison headwaters in November divided by the number of collared animals that were being monitored at the start of the winter season. All movements were conducted away from home range areas that overlapped wolf use areas the prior year (Figure 2.6).

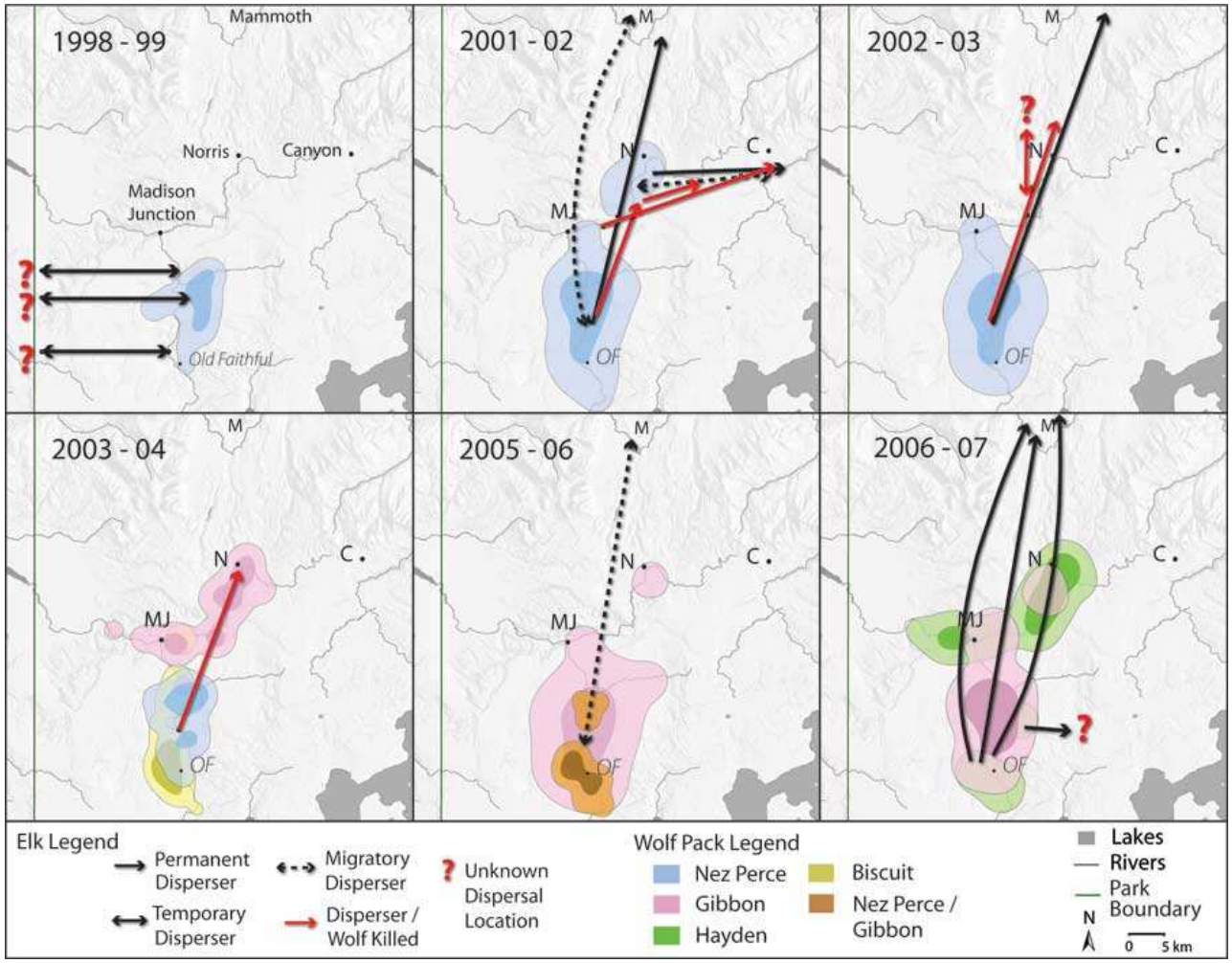

Figure 2.6 Radio-collared elk that dispersed from the Madison headwaters of Yellowstone National Park after wolf colonization appeared to be vacating core wolf use areas (50% and 95% kernel isopleths – darker shading represents 50% isopleth) during the previous winter. One-way arrows depict permanent dispersers, two-way arrows depict animals that returned to the study area after a temporary dispersal event (solid line), or became seasonally migratory (broken line). Red arrows represent animals that dispersed and were subsequently killed by wolves at their new location. Question marks indicate that the dispersal destination was unknown. Arrows start at the centroid of the distribution of locations for a given year.

Discussion

How predators influence space use by large herbivores has become of increasing interest to ecologists over the past decade due to the implications these spatial changes may have on ecosystem structure and functions (Fortin et al. 2005). For example, wolves in Yellowstone have been credited with inducing a trophic cascade of alterations in vegetation structure and composition by a combination of changing elk space use and decreasing elk numbers (Ripple et al. 2001, Beschta 2003, Ripple and Beschta 2003, Smith et al. 2003, Ripple and Beschta 2004, Creel et al. 2005, Fortin et al. 2005). I detected changes in elk movement patterns that supported findings from other wolf-elk systems that showed elk spatially responded to wolves at a localized scale (Creel et al. 2005, Fortin et al. 2005, Frair et al. 2005, Gude et al. 2006, Winnie and Creel 2007) and over larger spatial scales as well (Hebblewhite and Merrill 2007). These results demonstrated modest increases in home range and reduced fidelity, and I documented animals dispersing from the study area or becoming migratory following wolf reintroduction. Unlike other studies, however, I also obtained direct information on elk spatial behavior in the absence of wolves because data collection spanned a period prior to and following wolf reintroduction. Thus, these analyses provided a direct empirical evaluation of the mechanisms driving ungulate movement behavior in the presence and absence of wolves when elk where exposed to various ecological constraints.

Elk occupied smaller ranges before wolf reintroduction or when winter wolf abundance in the system was low. Smaller home ranges in the absence of wolves appear typical of large herbivores that were minimizing movement and using small areas for

food acquisition through winter. White-tailed deer congregate for thermal shelter and relief from deep snow (Ozoga and Gysel 1972, Verme 1973, Moen 1976), and likewise moose (Miquelle et al. 1992, Renecker and Schwarz 1998, Dussault et al. 2005), woodland caribou (Johnson et al. 2001), red deer (Georgii and Schröder 1983), and elk (McCorquodale 1993) restricted foraging activities to small isolated patches, or where snow conditions are locally reduced during winter. These findings also corroborate the work of Craighead et al. (1973) who observed similar-sized home ranges of elk in the Madison headwaters more than two decades before wolves were introduced into the system. Movements in the absence of predators should simply reflect nutritional constraints, and home range sizes should strongly reflect the spatial distribution of forage resources (Ford 1983, Geist 2002, Mitchell and Powell 2004, Anderson et al. 2005).

These results suggest that elk in the Madison headwaters ranged over a wider area, thus, occupying larger home ranges as wolf presence and activity within a given drainage increased. Mitchell and Lima (2002) suggested a predator-prey “shell game” would be established in the presence of a highly mobile predator that has a good spatial memory and the ability to seek out prey locations. Consequently, prey movement would be favored in an attempt to remain unpredictable and elusive in space. However, elk in the Madison headwaters appeared to become more concentrated in their use of preferred habitats following reintroduction (White et al. 2009) so it is unlikely that movement to elude detection was being adopted within this system. More likely, elk were moving within their range following a predation event to avoid any further imminent threat. Groups of elk with a collared animal were frequently observed using foraging areas when wolves were absent, but shifting from one end of the collared animal’s home range to the

other immediately after wolves were active in the vicinity. These observations were similar to those of Gude et al. (2006) who observed elk leaving wolf encounter sites before wolves returned to hunt again, and would corroborate the suggestions of Bergman et al. (2006) that elk would dynamically move among patches over short periods and at a fine spatial scale. Therefore, these ideas support the game-theoretical notion proposed by Mitchell and Lima (2002) that increased prey movement and larger home ranges in the presence of wolves are consistent with patterns of fine-scale predator avoidance within an animal's range. Sih (1986) distinguished between avoidance and escape, defining avoidance as behavior occurring prior to an attack, and the escape as behavior occurring following an attack. Behavioral responses of elk in the Madison headwaters that resulted in increased movement with wolf presence reflected more of an escape strategy than a pre-meditated attempt to avoid wolf encounters. It is doubtful that elk had the capacity to remain elusive in a landscape with a predator that has such well-developed spatial memory as wolves (Mech 1970). However, in this study the terminology "avoidance" was adopted because it was suspect that elk moved to areas of lower immediate predation risk to avoid further attack and/or re-located to less vulnerable locations before further encounters could occur. Because elk are working within the confines of a winter environment, and predation risk is spatially and temporally dynamic (Creel and Winnie 2005, Smith et al. 2009, Chapter 3), a pre-emptive increase in movement to avoid being detected by wolves would not be an efficient or advantageous approach.

Changes in the fidelity of animals to a winter home range were also observed with the addition of wolves to the system. Non-migratory elk in the Madison headwaters were extremely philopatric to their range year after year, particularly prior to the establishment

of wolves. This is similar to other investigations of spatial fidelity on sedentary large herbivores (Franklin and Lieb 1979, Irwin and Peek 1983, Edge et al. 1986, Cederlund and Sands 1992, Krasińska et al. 2000, Millspaugh et al. 2004) with a high degree of philopatry associated with a strong social structure with conspecifics (Edge et al. 1986), and familiarity with resource availability and distribution (Franklin and Lieb 1979, Irwin and Peek 1983, Linnell and Anderson 1995). Geothermal areas and meadow complexes in the Madison headwaters provide access to reduced or snow-free foraging year-round (Craighead et al. 1972, 1973, Watson et al. 2009a, b). Therefore, forage availability remains relatively constant within these habitats from year to year (Messer et al. 2009). Location centroids for elk before wolf reintroduction appear to reflect the spatial arrangement of these foraging sites and the use of the same areas over consecutive years, suggesting high site fidelity during this period, reflects an energetically efficient foraging strategy.

After wolf packs were established in the Madison headwaters, an increasing trend in the Euclidean distance between centroids of consecutive winter ranges was observed, implying that elk became less faithful to a site between successive years. Elk shifted their location of activity when a greater number of wolf kills were detected in the drainage the previous winter. Bergman et al. (2006) reported that elk in the Madison headwaters were more vulnerable in geothermal sites and wolves selected these areas non-randomly as they coursed the landscape. Because wolves have well-developed learning abilities (Mech 1970) and periodically return to the same area within their range (Jędrzejewski et al. 2001; R. A. Garrott, unpublished data) to presumably re-encounter unsuspecting prey (Lima and Steury 2005, Roth and Lima 2007), it was expected that elk

would modify their space use from the pre-wolf strategy of predictably foraging in geothermal areas where the majority of kills were made (Bergman et al. 2006). Surprisingly elk did not re-locate permanently from these areas, as evidenced by the continued use of vulnerable geothermal sites (White et al. 2009). Landscape-level variability in risk has been discussed in ungulate-wolf systems (Kunkel and Pletscher 2000, Hebblewhite et al. 2005, Kauffman et al. 2007), with different habitat and physical attributes of the landscape found to offer different levels of security or vulnerability (Kauffman et al. 2007). Habitats that facilitate hiding or escape may not necessarily provide the best foraging opportunities. Conversely, areas that are attractive for foraging may be accompanied with increased levels of threat (Fortin et al. 2005, Bergman et al. 2006). The continued selection of geothermal sites and other habitats with high snow heterogeneity by elk even after wolf reintroduction (White et al. 2009) was probably because these sites offered the highest availability of forage at the lowest energetic costs during nutritionally critical months. It is likely that this continued use of preferred habitats was possible because many of these sites were adjacent to other habitat components such as meadows (Hebblewhite et al. 2005, White et al. 2008), forests (Wolff and Van Horn 2003, Creel and Winnie 2005, Creel et al. 2005, Fortin et al. 2005), deep rivers (White et al. 2009), and areas with high human activity (Hebblewhite et al 2005, Hebblewhite and Merrill 2007, White et al. 2008) which collectively provided an area that could facilitate escape or provide protection when predation threat was high. The increase in mean Euclidean distance does not imply that elk made long-distance shifts in their use areas or switched drainages between years. Rather, this decrease in site fidelity can be interpreted as a more variable distribution of locations within the elk's

winter range, and selecting a home range that encompassed a wider diversity of landscape components would allow elk to mediate the risk and starvation by moving between areas of relative risk and safety as the level of perceived risk changed (Kie 1999). This suggests that predictable behavior may not be detrimental if landscape attributes serve as refuges, but would appear hazardous if landscape features contribute to the vulnerability of prey, as observed in our system (White et al. 2009). This broader use of landscape characteristics explains the reduced site fidelity and increased home range sizes for elk following wolf colonization.

Large-scale movements such as dispersal and migration have been widely discussed as mechanisms to avoid predation risk by spatially segregating from predators at a much coarser scale (Bergerud et al. 1984, Fryxell et al. 1988, Seip 1992, Fryxell 1995, Hebblewhite and Merrill 2007, Bergerud et al. 2008). Long-distance movements by elk were observed after wolf packs became established in the system. These movements were never observed when wolves were absent from the system. At the finest temporal scale, long-distance sallies by elk from their traditional home ranges were observed following sequences of successful predation attacks by wolves. During the established wolf phase, it was not uncommon to observe elk temporarily leaving their range and moving an average of 10-15 km, but returning several days later. On one occasion, most of the elk in the Old Faithful sub-herd were observed moving north from their typical range after multiple kills were made by wolves. These elk were subsequently located approximately 20 km away. This movement event only lasted for three to four days, after which the elk returned to their traditional range and were again attacked by wolves.

Elk were also observed temporarily (>1 year) or permanently dispersing from the study area the year following intensive wolf use of their traditional range. These movements ranged from between 18-63 km away from their former range in the Madison headwaters. Dispersal would only appear to be a profitable strategy if environmental conditions varied spatially and temporally (Stenseth 1983) and the probability of survival had the potential to be higher in the new location. In this system, this assumes predation risk is not evenly distributed across the landscape and there are relatively safe places for elk to occupy. This assumption was likely correct immediately following wolf reintroduction when packs were unevenly distributed through the park. However, wolf packs continued to expand their range and few areas of the park were devoid of wolves during the latter years of these studies (Smith et al. 2009). Five of the nineteen collared elk that were defined as dispersers were subsequently killed by wolves away from the Madison headwaters, suggesting limited effectiveness of long-distance movements for increasing survival. Dispersing could be considered more perilous than staying within the former home range if unfavorable conditions occur from place to place (Gadgil 1971). Conversely, a 74% chance of survival for the animals that vacated the study area may have been a better outcome than staying in their former ranges where high predation rates by wolves have essentially depleted elk from the Gibbon and Firehole drainages (Garrott et al. 2009b, White et al. 2009).

A switch from sedentary to migratory behavior was also detected in three of the radio-collared, female elk. These animals were monitored as part of the non-migratory herd during the early colonization period, but changed their behavior after wolf packs became established in the system, suggesting that wolf activity was the probable cause

for the abandonment of their tradition winter ranges. While these observations involved only a small number of animals, they allowed us to speculate that while an environment without predation may favor year-round sedentary behavior, migratory movements may be evolving as the environment changes with the addition of wolves. In African systems migration has been suggested as a way to enhance survivorship (Fryxell 1995). Theoretical modeling of migration in the Serengeti ecosystem suggests that population regulation by predators may affect non-migratory animals, while migratory species are more commonly regulated by food (Fryxell et al. 1988). This implies that the top-down effect of predation would dominate in a non-migratory herd such as the Madison headwaters. Thus, it is not surprising that high wolf numbers have contributed to low rates of over-winter adult survival, low calf recruitment, and a significant population decrease (Garrott et al. 2009b, White et al. 2009). In the Madison headwaters, winter is a time when deep snow exacerbates the vulnerability of large herbivores to wolves due to reduced mobility and potential for escape (Mech and Petersen 2003, Becker et al. 2009). It is also the time when wolves have an almost continual presence within the Madison headwaters (Smith et al. 2009). Under these conditions, seasonally escaping predators during winter when vulnerability reaches a peak, and returning in summer when vulnerability is reduced may be more profitable. Interestingly, all long-distance movements that were documented following reintroduction occurred from areas of intensive wolf activity (Firehole, Gibbon). No collared animals vacated the Madison drainage, which is the area wolves frequented the least (Smith et al. 2009). These data thus allow us to speculate that animals that have displayed strong fidelity to a range can actually ‘make a decision’ that their traditional range has changed in a such a

fundamental way that is no longer conducive to remain in this area. Thus, while it has been documented that density dependent factors such as crowding and resource limitation would promote animals to relocate in search of more profitable surroundings (Lambin et al. 2001, Clobert et al. 2004, Ims and Andreassen 2005), these data suggest that the risk of predation can promote a similar response. These results also indicate that while the majority of the decline of the Madison headwaters elk population was attributed to direct predator mortality (Garrott et al. 2009b), permanent dispersal and animals switching from non-migratory to migratory seasonal movement strategies also contributed to the population decline.

These results show that elk in the Madison headwaters made modest adjustments in their use of space during winter, presumably to reduce their vulnerability from predators at a fine-scale within their range (Fortin et al. 2005). It is suspected that these changes were modest because elk were constrained by other attributes of the system and the fundamental energetic limitations of surviving in a severe snow-pack environment. This limited flexibility could explain why elk have been reduced to low densities in most areas of the Madison headwaters (Garrott et al. 2009b, White et al. 2009) and, also, why a relatively large proportion of elk left two of the drainages where wolf predation pressure was exceptionally high. It was expected that one optimal movement strategy would be manifested throughout the Madison headwaters study area, but these results illustrate the contrary. Different animals appeared to adopt different strategies within a given system, which I propose is characteristic of a heterogeneous landscape with considerable variation in predation risk.

In the absence of predation the spatial patterns of elk in the Madison headwaters were heavily influenced by the characteristics of the landscape, as evidenced by the importance of the DRAINAGE covariate in both the home range and site fidelity analyses. Independent of wolves, smaller home ranges and higher site fidelity were observed in the Firehole drainage compared to the other two drainages. This finding is likely a consequence of the evenly distributed thermal areas through much of the Firehole drainage, providing an essentially contiguous snow-free foraging area where elk did not need to travel far between forage sites (Craighead et al. 1973). The Gibbon drainage also contains a high proportion of geothermal areas, but their configuration is quite different (Watson et al. 2009b). The Gibbon drainage has a few large geothermal complexes (e.g., Norris, Primrose) and numerous smaller geothermal sites arranged linearly along river corridors. Therefore, the larger home ranges for elk in the Gibbon likely reflected animals feeding within and between these geothermal areas, with more movements due to the spatial arrangement of these snow-free sites. These finding support the work of Kie et al. (2002) who suggested that when patches were clumped rather than evenly distributed, home range size of mule deer (*Odocoileus hemionus*) were larger because animals had to travel longer distances from one feeding patch to another. The Madison drainage differs from the Gibbon and the Firehole drainages in that it does not contain any geothermal areas. However, movement patterns within this drainage could still be explained by the spatial arrangement of snow-free sites because the nearly continuous, steep, south-facing slope along this drainage provides another topographic feature with reduced snow pack. This slope provided a contiguous area elk used extensively for locomotion and foraging. Movements in the Madison drainage also reflected the

topographic relief (Georgii and Schröder 1983, Kie et al. 2005) and linear arrangement of large meadow complexes. The spatial arrangement of snow-free geothermal areas had a pronounced effect on the way elk moved within the system and I strongly suspect that the assemblage and distribution of these geothermal sites also contributed to the vulnerability of elk in the Madison headwaters (Bergman et al. 2006, White et al. 2009).

Elk in the Madison headwaters appeared to adopt several risk avoidance behaviors over multiple temporal and spatial scales, including: 1) increased use of the landscape at the local scale; 2) long-distance sallies that lasted several days; 3) temporary (>1 year) and permanent long-distance movements away from a former home range; and 4) transitions from sedentary to migratory behavior. While these findings suggest elk were using the landscape in an attempt to mitigate predation risk, there was limited ability from this study to discern if and how effective these spatial responses were at reducing risk (Hebblewhite and Merrill 2007). However, the spatial responses observed in the Madison headwaters elk population suggest animals were making movement decisions under the competing environmental constraints of managing predation risk in addition to starvation risk. Familiarity with foraging resources and knowledge of habitat attributes that help facilitate avoidance and escape will favor spatial responses that occur within the home range (Linnell and Anderson 1995). Spatially avoiding predators is costly, so nutritionally vulnerable prey should have a high tolerance of disturbance by wolves before they completely abandon their range. Also, adopting an integrative approach that couples spatial responses within the range with other anti-predator behaviors such as grouping (Chapter 3), alterations in foraging behavior (Chapter 4), and effective use of landscape features that facilitate escape (White et al. 2009) may be more effective at

mitigating predation risk than trying to completely remain elusive in a high predation risk environment.

These results suggest that elk will manifest a more dynamic movement behavior as wolves course the landscape looking for prey. These results are consistent with the predictions of Fortin et al. (2005) and Gude et al. (2006) that predation may facilitate the dilution of foraging pressure on plant communities if elk are constantly moving to reduce further encounters with wolves. This response could combine with predation-induced changes in the abundance and distribution of large herbivores to cause changes in ecosystem dynamics (Ripple et al. 2001, Beschta 2003, Smith et al. 2003, Fortin et al. 2005). However, these results also suggest that landscape characteristics substantially moderate the magnitude of the spatial response by elk to wolves, which could potentially affect the intensity of the trophic cascade. The spatial distribution of foraging areas in relation to the spatial distribution of safe or vulnerable attributes of the landscape may also determine the degree to which predators inflict direct and indirect costs on their prey.

Summary

1. How elk changed their spatial use of the landscape in the presence of wolves was evaluated by collecting 11,908 locations from 115 radio-collared, adult, female elk in the Madison headwaters area of Yellowstone National Park during winters 1991-92 through 2006-07.
2. Prior to wolf colonization, winter movements of elk were constrained and predictable as elk attempted to conserve energy and decrease starvation risk. Home ranges were small and elk displayed strong spatial fidelity. After wolf colonization, elk

movements were more dynamic as elk moved more over the landscape as they were increasingly encountered, attacked, and displaced by wolves. Home range sizes were larger, with modest decreases in philopatry.

3. 19 long-distance (>15 km, range = 18-63 km) dispersal movements by radio-collared elk away from high-density wolf areas were documented in the Gibbon and Firehole drainages. These apparent predator-avoidance movements were not observed prior to wolf colonization or from areas where the risk of predation was lower.
4. Elk in the Madison headwaters are constrained by deep snow and vulnerable environmental conditions. This provides limited flexibility to mitigate predation risk by modifications in movement within the traditional range. This limited flexibility could explain why elk have been reduced to low densities in most areas of the Madison headwaters and, also, why a relatively large proportion of elk left two of the drainages where wolf predation pressure was exceptionally high.
5. Dynamic movements by prey to mitigate predation risk have important implications for encounter rates, search time, and the functional responses of predators. Likewise, predation-induced changes in the abundance and distribution of large herbivores may have substantial effects through the plant-herbivore-carnivore trophic chain, as well as important implications for managing elk at the landscape level.

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Appendices

Appendix 2.1 Complete model list used in the mixed effects linear regression analysis to evaluate factors influencing home range size of elk in the Madison headwaters area of Yellowstone National Park during 1991-92 through 2006-07. Abbreviations are: SWE_{mean} (mean daily snow water equivalent), DRAINAGE (Madison, Firehole, Gibbon), $WOLF_{period}$ (pre-reintroduction, colonizing, established), $WOLF_{days}$ (total number of wolf days per drainage per year), and KILLS (total number of wolf-killed ungulates per drainage per year).

Model number	**Model structure**
0	NULL
1	SWE_{mean}
2	DRAINAGE
3	$WOLF_{period}$
4	SWE_{mean} + DRAINAGE
5	SWE_{mean} + $WOLF_{period}$
6	DRAINAGE + $WOLF_{period}$
7	SWE_{mean} + DRAINAGE + $WOLF_{period}$
8	$WOLF_{days}$
9	SWE_{mean} + $WOLF_{days}$
10	DRAINAGE + $WOLF_{days}$
11	SWE_{mean} + DRAINAGE + $WOLF_{days}$
12	KILLS
13	SWE_{mean} + KILLS
14	DRAINAGE + KILLS
15	SWE_{mean} + DRAINAGE + KILLS

Appendix 2.2 Complete model list used in the mixed effects linear regression analysis to evaluate factors influencing site fidelity of elk in the Madison headwaters area of Yellowstone National Park during 1991-92 through 2006-07. Abbreviations are as in Appendix 2.1. Wolf covariates describe wolf use in the particular drainage during the first of the two consecutive years.

Model number	**Model structure**
0	NULL
1	$WOLF_{period}$
2	DRAINAGE
3	DRAINAGE + $WOLF_{period}$
4	$WOLF_{days}$
5	DRAINAGE + $WOLF_{days}$
6	KILLS
7	DRAINAGE + KILLS

CHAPTER 3

ELK GROUP SIZE AND WOLF PREDATION: A FLEXIBLE STRATEGY WHEN FACED WITH VARIABLE RISK

Abstract

When predators and prey are in close proximity, prey may change how they aggregate to reduce their probability of being attacked and killed. However, the best strategy to reduce the risk of predation may not be the best strategy to acquire the resources needed to meet physiological demands for body maintenance and reproduction. By collecting 8,373 randomly-selected elk groups during consecutive winters between 1991-92 and 2006-07 the grouping tendencies of non-migratory elk (*Cervus elaphus*) in the Madison headwaters area of Yellowstone National Park were examined. Using mixed effects regression models it was determined that group size and group size variation were negatively correlated with snow pack severity and positively correlated to the presence of wolves (*Canis lupus*) under certain habitat conditions. Elk altered their grouping behavior at multiple temporal scales, including among years, within winters, and daily depending on wolf presence and if a kill had occurred in a given drainage. Group size was relatively stable prior to wolf restoration which was likely due to elk adopting a single feeding strategy based solely on energetic considerations. This behavior became more dynamic following wolf establishment and I suggest this was due to animals trying to balance the conflicting demands of minimizing predation risk and maximizing food acquisition. While this study documented elk aggregating into larger groups in response to wolf predation risk, other studies in close geographic proximity documented different

aggregation patterns in the presence of wolf predation risk. It seems plausible that this disparity in a single response can be attributed to substantial differences in landscapes characteristics such as snow pack severity and habitat types, complexity, and patch size that influence predation risk and dictate different prey behavioral responses.

Introduction

It is widespread in the animal kingdom that animals aggregate (i.e., flocks, schools, groups, and herds) and has long been considered an evolutionary adaptation whereby members derive benefits of communal foraging, mating, thermal regulation, reduced costs of movement, and protection against predators (Allee 1927). Animal grouping is a complex behavioral process driven by a combination of environmental, population, and community processes that change with ecological conditions over relatively short temporal and spatial scales (Chapman and Chapman 2000, Krause and Ruxton 2002). Thus, decisions by individuals to remain solitary or aggregate, and how large an aggregation to tolerate, are clearly influenced by abiotic and biotic factors that individuals confront.

Many drivers of aggregation patterns have been suggested, including that predation risk is reduced when individuals join with conspecifics. Aggregating into larger groups has the benefit of enhancing predator detection and reducing individual vigilance (Pulliam 1973, Elgar 1989, Roberts 1996), individual protection and numerical dilution (Hamilton 1971, Bertram 1978, Dehn 1990), confusion effects, and group cooperative defense (Caro 2005). However, predation may be facilitated by larger aggregations of animals because they are more conspicuous to predators and easier to detect at a distance

(Treisman 1975, Creel and Creel 2002), and larger groups may be more likely to be attacked once detected (Creel and Creel. 2002). Other potential countervailing consequences of aggregating into larger groups include increased intra-specific competition for resources (Chapman and Chapman 2000), increased foraging costs due to local food depletion (Buckel and Strona 2004), higher levels of aggression (Clutton-Brock et al. 1982, Molvar and Bowyer 1994), and higher exposures to diseases and parasites. Eventually, the costs of grouping may exceed the benefits, and often these physiological and competitive constraints limit group size (Pulliam and Caraco 1984, Giraldeau and Caraco 2000, Krause and Ruxton 2002).

Forming smaller groups or remaining solitary may lessen detection by predators and is an advantageous strategy if predators preferentially target larger groups of prey (Hebblewhite and Pletscher 2002, Krause and Ruxton 2002). Under these circumstances, individuals may form small groups, or adopt a solitary existence as an alternative response to predation. If animals succeed in remaining elusive, then they may escape the attention of a predator and, thus, the probability of encounter with a predator may be lower (Jarman 1974, Semeniuk and Dill 2004, Creel and Winnie 2005). Solitary prey can exploit resources in the absence of competition, but may also incur foraging costs by not aggregating in higher-quality foraging patches. Group sizes in many taxa appear to be determined by trade-offs or interactions between food availability, intra-specific competition for food, and predation risk (Heard 1992, Molvar and Bowyer 1994, Grand and Dill 1999, Parrish and Edelstein-Keshet 1999, Buckel and Strona 2004, Semeniuk and Dill 2004), with the most advantageous group size reflecting the balance between the costs and benefits of the competing demands for each group member. Theoretically, this

optimal size would offer maximum fitness to each group member and may vary for any given individual, environment, or situation (Sibly 1983, Pulliam and Caraco 1984, Heard 1992, Higashi and Yamamura 1993, Krause and Ruxton 2002).

Determining if an optimal group size exists for large herbivores is difficult because available forage and predation risk are often highly variable in both space and time and difficult to quantify. Variability in forage biomass due to heterogeneous landscapes, changes in plant phenology (and thus plant quality), and changes in availability of forage due to herbivory and snow pack conditions all result in group size varying predictably over seasons and among different types of plant communities (Heard 1992, Jędrzejewski et al. 1992, Borkowski and Furubayashi 1998). In a seasonal environment where the main predator is absent and snow limits access and availability to forage for a large proportion of the year, individuals should adopt an efficient and predictable grouping strategy that minimizes physiological costs (Messer et al. 2009). If a system includes highly-mobile, coursing predators such as wolves, then predation risk could be highly variable at a fine temporal scale because predators could frequently enter and leave areas occupied by prey. Considering the constraints imposed during winter, staying in a large group for a sustained period is costly to the individual. However, remaining solitary or in a small aggregation provides limited protection in the event the group is detected by predators. Thus, it is highly unlikely that one single group size is optimal to balance the demands of energy conservation while minimizing predation risk. Instead, individuals may aggregate into groups to reap the anti-predator behavior benefits during times of high predation risk, but disperse when there is not an imminent threat or as the level of individual risk diminishes (Lima and Bednekoff 1999, Sih et al. 2000, Sih and McCarthy

2002). If risk changes over the course of hours or even minutes, then a sustained response may not occur. Rather, a more ephemeral response may be evident, with frequent fragmenting and combining of groups as the level of risk changes.

It is generally accepted that animals reduce their risk of predation by associating with other herd members and, as a result, larger aggregations of large herbivores should be observed as predator abundance increases (Fryxell 1991, 1995, Jędrzejewski et al. 1992). However, there is only limited support for this prediction from recent studies of elk-wolf systems in the northern Rocky Mountains (Hebblewhite and Pletscher 2002, Creel and Winnie 2005, Gude et al. 2006). Varied grouping responses by elk in these different systems suggest predation alone is not wholly responsible for changes in group sizes and precludes generalizing one optimal grouping strategy by large herbivores in the presence of predators. These findings also indicate additional research is needed to evaluate competing hypotheses concerning the mechanisms driving grouping behavior in large herbivores.

The goal of this study was to improve understanding of the mechanisms driving grouping behavior in large herbivores by initially evaluating how elk in the Madison headwaters area of Yellowstone National Park responded to environmental conditions in the absence of predators and, subsequently, evaluating how their behavior changed when wolves were added to the system in 1995 and 1996. Data were collected for 5 years prior to 1995 when wolves were entirely absent from the system and for 11 years after wolf reintroduction. Information-theoretic model selection techniques were used to evaluate the strength of evidence in the data for the competing predictions that elk would either aggregate in response to increasing wolf presence or form smaller groups or become

more solitary once wolves re-colonized the area. The prediction that elk would exhibit greater variation in group size as the level of predation risk varied was also evaluated.

Methods

The grouping behavior of elk in the Madison headwaters area was recorded during 15 November through 30 April for 16 consecutive winters (1991-92 through 2006-07) by repeatedly sampling 20-35 adult female elk per year fitted with radio collars (i.e., approximately 4-10% of the population). Sampling of collared individuals followed a stratified random sampling regime, which ensured that sampling times were randomly distributed during daylight hours to capture daily variation in group size and composition. For this sampling regime the study area was divided into geographically defined drainages (i.e., the Madison, Firehole and Gibbon drainages), which were further stratified into areas within each of the three drainages. Radio-collared elk that inhabited the selected strata were located by randomly determining the order with which they were to be sampled and all groups within the study area were sampled once before re-sampling occurred. Hand-held telemetry equipment and homing procedures were employed to obtain direct observations of collared individuals (Garrott et al. 2009a) and obtain group locations, total group counts and compositions (i.e., calf, cow, yearling bull, adult bull), and identify the primary habitat occupied (meadow, thermal, unburned forest, burned forest, riparian).

These data were used to develop three response variables related to different elements of elk grouping behavior: group size, group size variation, and typical group size. Group size was defined as a single animal or individuals “that remain together for a period of

time while interacting with one another to a distinctly greater degree than with other conspecifics" (Wilson 1975:585). Group size variation was derived by calculating the absolute difference between a given group size and the mean group size for that particular year, and was used to assess the frequency of aggregation and dispersion of groups. Typical group size was defined as the size of the group in which the average animal finds itself and calculated as $\sum G_i^2 / \sum G_i$, where G_i is the size of the *ith* group (Jarman 1974). This metric of individual behavior is a descriptive statistic which, in addition to mean group size, could provide more information for discerning the effects of predation on prey behavior and the consequences of prey aggregation on the predator. Mean group size is often sensitive to the number of records of solitary animals and consequently can underestimate the size of the group that is experienced by the individual animal. In contrast, typical group size is less sensitive to the number of records of solitary animals and less sensitive to the commonly observed mean group size frequency distribution (a lot of small groups at the far left of the distribution, with few larger groups representing the right tail) (Heard 1992, Lingle 2003). Mean group size is therefore an "observer-centered" measure that provides useful information about how an outsider (i.e. an observer or a predator) views the group (Lingle 2003), whereas the typical group size is an "animal-centered" measure that provides insight into the group size than an individual chooses to occupy (Jarman 1974). Typical group size has been used in other studies that have evaluated large herbivore aggregation patterns (Heard 1992, Heard and Ouellet 1994, Lingle 2003, Mao 2003, Festa-Bianchet and Côte 2008) and would appear particularly useful when assessing grouping behavior in a predator-prey framework. Because selection acts upon the individual, not the group (Heard 1992), this metric was

used to describe the evolving behavior between predator and prey. Because typical group size is derived from the sum of an assemblage of groups over a determined time period, we calculated this metric using 10-day sampling intervals through the winter season at the study area level (16 periods per winter).

Non-Wolf Covariates of Elk Grouping Behavior

The influence of landscape attributes on elk grouping tendencies was explored using estimates of snow pack and habitat type. Snow pack and habitat type influence resource availability which, in turn, could play a vital role governing how large herbivores aggregate (Heard 1992, Jędrzejewski et al. 1992, Borkowski and Furubayashi 1998). A validated snow pack simulation model for the central Yellowstone region (Watson et al. 2008) was used to construct a covariate that represented the average snow water equivalent value (SWE_L) on the elk winter range (landscape SWE) for each day that radio-collared elk were observed. This metric described the mean water content of the snow (Farnes et al. 1999) and provided an index of resource availability because higher values reflected decreased forage accessibility and higher energetic costs (Parker et al. 1984). A snow heterogeneity metric (SNH_L) was also developed to index the continuity of snow cover across the landscape. This metric was used as a surrogate for snow melt, which creates patches of available forage during spring. In addition, a categorical habitat covariate (HBT) was defined and classified each elk observation into meadow, burned forest, unburned forest, thermal, or riparian categories based on field observations of the plant communities the animals occupied at the time of the observation.

SWE_L and time period (SEASON) were considered as the non-wolf covariates in the typical group size analyses. SWE_L represented the average daily snow water equivalent value for the 10 day period. SEASON was a continuous variable from 1-16 representing the consecutive 10-day intervals within each winter season. Foraging dynamics likely reflect the seasonal variation in the quality and quantity of available forage (Craighead et al. 1973, Green and Bear 1990, Ager et al. 2003), so this covariate was used to evaluate seasonal trends in typical group size because larger groups of elk occurred in openings during spring green up.

Covariates of Predation Risk

The presence of wolves was detected and quantified in the Madison headwaters from 15 November to 30 April during the winters of 1996-97 to 2006-07. National Park Service biologists captured wolves to maintain radio-collared animals in each pack (Smith 2005, Smith et al. 2009), and wolf presence and their locations were monitored using ground-based telemetry, snow tracking, and visual observations of collared and un-collared individuals. Each drainage was intensively monitored for wolf presence daily with crews of 3-4 people using snowmobiles, vehicles, snowshoes, and high points in the landscape to facilitate telemetry and observations. When packs with radio-collared wolves were detected, telemetry locations were estimated using triangulation (White and Garrott 1990) and multiple locations were obtained throughout the day. Snow tracking, visual observations, and counts during aerial monitoring by National Park Service biologists provided estimates of the number of animals per pack and aid in the daily assessments of wolf presence or absence (Becker et al. 2009a, Smith et al. 2009).

Detection of un-collared wolves was facilitated by opportunistic observations of tracks and wolves by field personnel that were working throughout the study area on elk and bison investigations (Bruggeman et al. 2009, Garrott et al. 2009a, White et al. 2009). The total number of wolves present in each drainage each day was estimated based on the information obtained from the various wolf monitoring techniques and was quantified in the form of wolf-days (i.e., the number of individual wolves known to be present in each of the drainages each day).

Using these data on wolf presence, three wolf covariates were developed to assess the hypotheses about the influence of predation risk on aggregation behavior by elk. The covariate $WOLF_{period}$ categorized wolf presence within each drainage into three periods: before wolf reintroduction, during wolf colonization, and after wolf establishment. Pre-reintroduction occurred during the initial years of the study (1991-92 through 1995-96), prior to wolf reintroduction when no wolves were present in the study area. To account for the potential transitory behavioral dynamics due to the initial naïveté of the prey (Berger et al. 2001), the colonizing period was defined as the time immediately following wolf reintroduction, when elk were initially exposed to wolf predation risk, but no wolf pack (≥2 animals) was routinely detected in the drainage. The established wolf presence period began the first winter that a pack was consistently detected in a drainage. Wolves became established in different drainages during different winters (Firehole: 1997-98; Gibbon: 2000-01; Madison: 2001-02; Smith et al. 2009) therefore the $WOLF_{period}$ covariate was drainage-specific. The level of wolf predation risk for elk occupying each drainage was highly variable among winters, and it was suspected that the magnitude or frequency of any behavioral responses would be scaled to predation risk. Thus, wolf

presence data was used to construct a continuous wolf covariate, $WOLF_{days}$, that indexed the prevalence of wolf activity in each drainage each day. For the group size and group size variation analyses, $WOLF_{days}$ was calculated as the estimated number of wolves within that drainage on any particular day. Wolf days were assigned to multiple drainages if wolves traveled between drainages during any one day. For the typical group size analysis, $WOLF_{days}$ was calculated as the total number of wolf days in the study area during the 10-day period. The covariate $WOLF_{period}$ could not be used for this analysis because the study area encompassed drainages at different stages of wolf colonization or establishment. For all three analyses, a third wolf metric, KILLS, was developed that represented the number of wolf-killed ungulates discovered in each drainage on a given day (for methodology see Becker et al. 2009a, Smith et al. 2009), or in the case of the typical group size analyses, the total number of wolf-killed ungulates detected in the study area over the 10-day period.

Statistical Analyses

Analysis of Variance (ANOVA) and Tukey multiple comparisons with unequal sample size (Kutner et al. 2005: 750) were used to evaluate the change in mean elk group size and identify differences in the means between the three time periods defined by the predictor variable wolf presence ($WOLF_{period}$). The data were *ln*-transformed and diagnostic residual plots were used to evaluate the assumption of constant variance and normality of residuals. I used 95% confidence intervals to quantify uncertainty in parameter estimates.

Mixed-effects linear models (Pinheiro and Bates 2000) were used to evaluate competing *a priori* models for assessing group size and group size variation, which treated the covariates SWE_L, HBT, and $WOLF_{period}$ as fixed effects. Individual animal identity (ID) was treated as a random effect (i.e., intercept-only) because these datasets included observations of the same individual through time, and it was suspected that individuals tended to repeatedly choose similar size groups. This covariate allowed for the variation in group size preference between individuals (intercept) and within an individual (residual) to be partitioned and it could be determine how much of the variation in group size was accounted for by the fixed and random effects. I used multiple regression analyses with the covariates SWE_L, SEASON and $WOLF_{days}$ to evaluate competing *a priori* models for assessing typical group size because this dataset did not include repeated measures sampling. Combinations of the covariates were included in the additive form or as an interaction for all analyses. I predicted a fixed rate of change in the response variable per unit change in the predictor variable (i.e., linear form). Diagnostic plots were evaluated to assess the assumptions of normality and constant variance of residuals for all three response variables, and the group size and typical group size response variables were transformed using the natural log to conform to linear models assumptions. All continuous covariates were centered and scaled to facilitate comparisons and interpretations of covariate coefficients. Variance inflation factors (VIF), which measure multi-colinearity among variables, were calculated for all additive and interactive combinations of predictors. Those models that included predictor combinations with VIF <6 were retained in the model list. This was a conservative approach because VIF in excess of 10 implies multi-colinearity (Kutner et al. 2005: 409).

Correlation coefficients were also calculated to further check for multi-colinearity between the predictor variables. Akaike Information Criteria (AIC) was used to rank models given the data and compare the relative ability of each model to explain variation in the data (Burnham and Anderson 2002, 2004). Akaike model weights (w_i) were used to address model selection uncertainty, and model-averaged coefficient estimates for each covariate were computed across all models (Burnham and Anderson 2002) when no clear support for a single model was found. Covariate coefficients and variance of the random effects were estimated using restricted maximum likelihood. Comparable AIC values were calculated using maximum likelihood estimation (Pinheiro and Bates 2000). All statistical analyses were performed using the R statistical package (R Development Core Team 2006).

A Priori Model Suites and Predictions

Hypotheses representing the relationships between elk grouping behavior and covariates were expressed as suites of candidate *a priori* models for group size (6 models), group size variation (6 models), and typical group size (6 models). Every model in the group size and group size variation suites contained the covariates snow and habitat (Hirth 1977, Heard 1992, Bender and Haufler 1995), as well as the individual random effect. A null model was also included into each suite which hypothesized constant grouping behavior for the respective response variable.

I predicted the covariate estimates for the response variables group size and group size variation would be negatively correlated with the landscape snow covariate and positively correlated with open habitat types. While there is empirical evidence that

group size in large herbivores is positively correlated with snow depth (Heard 1992, Jędrzejewski et al. 1992), I predicted the opposite would be observed for elk in the heterogeneous landscape of the Madison headwaters area. Group size is positively influenced by the size of the food patch (Berger et al. 1983) and if snow limits forage availability (Telfer and Kelsall 1984, Jenkins and Wright 1987) by reducing the number and size of available food patches, then the resulting small foraging areas would be unlikely to support large aggregations of elk. In addition, I predicted open habitat types (i.e., meadow and thermal) would promote a foraging response and have a positive effect on group size. Social ungulates regularly form larger groups in more open areas that contain more abundant, high-quality forage than closed habitat types (Jarman 1974, Hirth 1977, Clutton-Brock et al. 1982, Creel and Winnie 2005, Gude et al. 2006). Thus, habitat type often serves as a surrogate for relative forage biomass that is available in different plant communities.

There is strong evidence that group sizes of large herbivores increase with predator density or predation pressure (Fryxell 1991, Heard 1992, Jedrzejewski et al. 1992, Molvar and Bowyer 1994, Mao et al. 2005). Thus, I predicted that elk group size would increase from pre-wolf to colonizing to established wolf periods if elk adopted the “many eyes” strategy (Pulliam 1973) in an attempt to benefit from risk dilution and better detection of predators (Bertram 1978, Dehn 1990, Lima 1995). However, groups of large herbivores have also been empirically shown to disperse in response to predation presence (Creel and Winnie 2005). Thus, a competing hypothesis predicted that a higher frequency of smaller aggregations and solitary elk would be observed as the system

transitioned from pre-wolf through to the established period if elk tried to remain elusive during times of high predation risk (Creel and Winnie 2005).

It was predicted that the influence and strength of the response of elk group size to snow would vary by habitat type (e.g., a SWE_L * HBT interaction), with more elk congregating in geothermally-warmed areas as snow pack increased in other areas (Messer et al. 2008). Models with a $WOLF_{period}$* HBT interaction were also included into the *a priori* suite because anti-predator strategies may be determined by habitat characteristics (Molvar and Bowyer 1994, White and Berger 2001). If elk aggregate in open areas as an anti-predator strategy, then groups should be even larger in the presence of predators. However, if elk aggregate in open areas as a foraging response (rather than a direct response to predation; Clutton-Brock et al. 1982, Creel and Winnie 2005), then aggregations should become smaller in open areas and larger in closed habitat types as predation risk increases. If elk are reacting to wolf presence differently in different habitat types, then the effect of wolf predation pressure on elk group size should be intensified in particular habitat types. I predicted a larger response (either positive or negative) in thermal areas and meadows because wolf kills often occur in these habitat types (Bergman et al. 2006).

The same suite of *a priori* candidate models were used to evaluate the importance of specific ecological factors causing elk groups to vary in size. I predicted increasing SWE_L would result in more stable groups because snow reduces variation in food resources, while making movement between patches more difficult (Sweeney and Sweeney 1984). I also predicted there would be more frequent aggregation and dispersion of groups as elk adjusted to spatial and temporal variations in predation risk

(Lima and Bednekoff 1999, Sih et al. 2000). For the effects of wolves on typical group size, I adopted the competing hypotheses described previously for the group size response variable. It was also predicted that typical group size would be negatively correlated with snow pack, but positively correlated with SEASON because elk aggregate in larger groups during spring green up (Craighead et al. 1973, Ager et al. 2003).

Based on the outcome of the *a priori* model-selection results, *post hoc* exploratory analyses were conducted to generate hypotheses for future work. $WOLF_{period}$ was substituted with $WOLF_{days}$ in the group size and group size variation analyses to evaluate if a finer-temporal scale metric indexing the frequency of encounter with wolves described grouping behavior better than the defined multi-year wolf presence covariate. SWE_L was substituted with snow heterogeneity (SNH_L), to evaluate if this covariate made an improvement over the *a priori* model, and it was hypothesized that elk would aggregate into larger groups as the snow pack became more heterogeneous. For all three of the analyses, the covariate KILLS was added to the top-ranked model to evaluate if elk responded to successful predation events by wolves. Changes in AIC scores were used to evaluate if models were improved with the covariate additions and substitutions.

Results

Temporal Trends in Elk Group Size

A total of 8,373 random elk group sizes were obtained from repeated sampling of a total of 115 radio-collared, adult, female elk during the winters 1991-92 through 2006-07. Group size ranged from 1 to 128 (mean = 7.2, se = 0.09). There was a 56 % increase (P = 0.001) in mean group size as the system transitioned from no wolves (n = 3103, mean =

5.58, se = 0.17), to wolf colonization (n = 1810, mean = 7.55, se = 0.09) and, eventually, to established wolf packs (n = 3460, mean = 8.70, se = 0.17). Transformed group sizes differed between the pre-wolf and colonization ($\hat{D}_{\text{ln(colonizing)-ln(pre-wolf)}}$ = 0.297; 95% CI: 0.230, 0.364; P < 0.001) and established wolf periods ($\hat{D}_{\text{ln(established)-ln(pre-wolf)}}$ = 0.299; 95% CI: 0.243, 0.355; P< 0.001), but were similar during the colonization and established wolf periods ($\hat{D}_{\text{ln(established)-ln(colonizing)}}$ = 0.002; 95% CI: -0.064, 0.068; P = 0.998). However, untransformed mean group sizes were significantly different ($\hat{D}_{\text{established-colonizing}}$ = 1.152; 95% CI: 0.602, 1.701; P < 0.001) between the colonization and established wolf periods (Figure 3.1) (Note: $\hat{D}$ defines the difference in transformed or untransformed mean group size between two wolf periods). There was also a shift in group size distribution between the colonization and established wolf periods (Figure 3.2). Thus, the lack of a significant difference in group size on a natural log scale between the colonizing and established periods likely reflects higher variance in group sizes during the established wolf period compared to the pre-wolf and colonization periods. An advantage of log transformations is that the results can be interpreted on the original scale of the variable (Ramsey and Schafer 2002). So by taking the exponent of the difference in the mean log (Y) between two time periods a multiplicative value for the change in the median (Y) between the time periods can be obtained. Consequently the median group size for the established period was exp (0.299) = 1.349 times bigger than the median group size for the pre-wolf period (95% CI: 1.275, 1.426). Similarly the median group size during the colonizing period was 1.346 times bigger than the median group size for the pre-wolf period (95% CI: 1.259, 1.439), while the median group size

for the established period and colonizing period were quite similar (1.000, 95% CI: 0.938, 1.073).

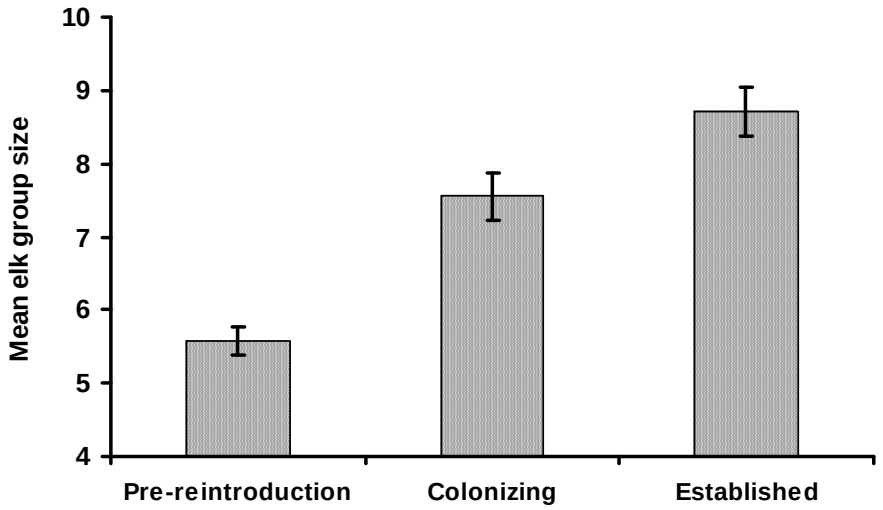

Figure 3.1 Changes in mean elk group size before wolf reintroduction, during wolf colonization, and after wolf establishment in the Madison headwaters area of Yellowstone National Park during the winters of 1991-92 through 2006-07. The plotted values are based on the untransformed data, with error bars representing standard errors.

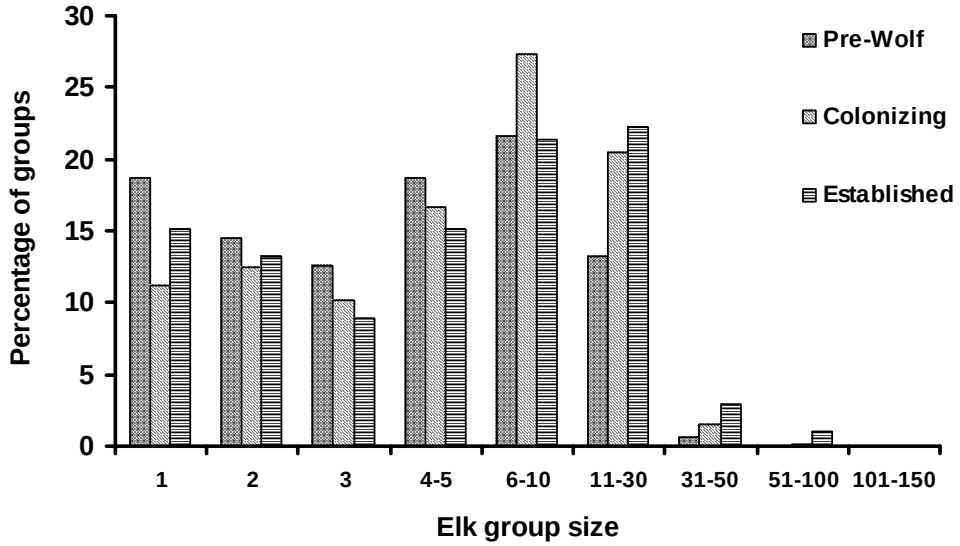

Figure 3.2 Changes in the distribution of elk group size (percentage of groups) before wolf reintroduction, during wolf colonization, and after wolf establishment in the Madison headwaters area of Yellowstone National Park during the winters of 1991-92 through 2006-07.

Model Selection Results

Wolves were absent from the Madison headwaters area prior to reintroduction in 1995-96. Thereafter, the total number of wolf days increased from 55 in 1996-97 to a peak of 3657 in 2004-05. The Firehole drainage experienced high wolf use immediately following reintroduction, while the Madison and Gibbon drainages did not experience wolf use until several years later and never reached the magnitude of use observed in the Firehole (see Chapter 2; Figure 2.1). Pack size and number of packs also varied both spatially and temporally (Smith et al. 2009).

Model selection results for the group size analysis supported one top model that received all of the model weight and contained the covariates SWE_L, HBT, $WOLF_{period}$, and a HBT*$WOLF_{period}$ interaction (Table 3.1). As predicted, snow had a negative effect on elk group size and, in the absence of wolves, larger groups were evident in meadow and thermal areas compared to other habitat types. Elk group size was positively correlated with wolf presence, but its influence was dependent on habitat type. Elk in meadows and riparian habitats were aggregated into larger groups during the colonization and established wolf periods compared to the pre-wolf period. Elk in forested habitats aggregated into larger groups during the colonization period than the pre-wolf period, but did not appear to differ in the established period. Elk groups in the thermal habitat remained similar or became slightly smaller as wolf presence increased (Table 3.2).

Table 3.1 Model selection results for elk group size, group size variation, and typical group size multiple regression analyses. All models are ranked according to AIC and presented along with the number of parameters (*k*), the ΔAIC value (the change in AIC value relative to the best model), and the Akaike weight (w_i). The AIC value for the top model for the *ln* (group size), group size variation, and *ln* (typical group size) were 21120, 52631 and 213 respectively. Abbreviations are (group size and group size variation): SWE_L (landscape-scale snow water equivalent), HBT (habitat), $WOLF_{period}$ (pre-reintroduction, colonizing, and established); (typical group size): SEASON (time period), SWE_L (average landscape-scale snow water equivalent for the 10-day period), $WOLF_{days}$ (total number of wolf days within the study area for the 10-day period).

Model Structure	*k**	ΔAIC	*w*i
***ln* (Group size)**			
SWE_L + HBT + $WOLF_{period}$ + (HBT * $WOLF_{period}$)	18	0.00	1.00
SWE_L + HBT + $WOLF_{period}$ + (SWE_L * HBT)	14	20.16	0.00
SWE_L + HBT + $WOLF_{period}$	10	35.26	0.00
SWE_L + HBT + (SWE_L * HBT)	12	35.80	0.00
SWE_L + HBT + $WOLF_{period}$ + (SWE_L * $WOLF_{period}$)	12	38.18	0.00
SWE_L + HBT	8	50.16	0.00
NULL	3	564.17	0.00
Group size variation			
SWE_L + HBT + $WOLF_{period}$ + (SWE_L * HBT)	14	0.00	0.98
SWE_L + HBT + $WOLF_{period}$ + (SWE_L * $WOLF_{period}$)	12	7.71	0.02
SWE_L + HBT + $WOLF_{period}$	10	13.30	0.00
SWE_L + HBT + $WOLF_{period}$ + (HBT * $WOLF_{period}$)	18	16.50	0.00
SWE_L + HBT + (SWE_L * HBT)	12	130.00	0.00
SWE_L + HBT	8	141.00	0.00
NULL	3	353.63	0.00
***ln* (Typical group size)**			
SEASON + $WOLF_{days}$	4	0.00	0.60
$Wolf_{days}$	3	1.59	0.27
SWE_L + $WOLF_{days}$	4	3.04	0.13
SWE_L + SEASON	4	52.16	0.00
SWE_L	3	71.61	0.00
SEASON	3	73.40	0.00
NULL	2	77.27	0.00

*Residual error from the mixed modeling accounts for 1 parameter value for the *ln* (group size) and group size variation analyses.

Table 3.2 Coefficient estimates and 95% confidence limits for the factors influencing *ln* (group size) and group size variation. All covariate levels are compared to the intercept reference level which is the meadow habitat type in the pre-reintroduction $WOLF_{period}$. Bold font denotes coefficient estimates with 95% confidence limits that do not span zero.

	ln (Group size)			Group size variation		
Covariate	Estimate	Lower CI	Upper CI	Estimate	Lower CI	Upper CI
Intercept	**1.631**	**1.510**	**1.752**	**4.684**	**4.215**	**5.152**
SWE_L	**-0.261**	**-0.312**	**-0.210**	**-2.388**	**-2.963**	**-1.813**
HBT-Riparian	**-0.499**	**-0.657**	**-0.341**	**-1.837**	**-2.426**	**-1.249**
HBT - BF	**-0.292**	**-0.381**	**-0.203**	**-1.440**	**-1.805**	**-1.075**
HBT - UF	**-0.326**	**-0.422**	**-0.230**	**-1.584**	**-1.982**	**-1.186**
HBT - TH	-0.040	-0.150	0.070	**-1.194**	**-1.712**	**-0.676**
$WOLF_{period}$ - Col	**0.213**	**0.100**	**0.326**	**1.717**	**1.304**	**2.130**
$WOLF_{period}$ - Est	**0.245**	**0.130**	**0.360**	**2.488**	**2.061**	**2.914**
Riparian*Col	0.077	-0.158	0.313			
BF*Col	-0.062	-0.192	0.069			
UF*Col	-0.132	-0.283	0.019			
TH*Col	**-0.254**	**-0.447**	**-0.060**			
Riparian*Est	-0.199	-0.400	0.001			
BF*Est	**-0.302**	**-0.418**	**-0.187**			
UF*Est	**-0.358**	**-0.489**	**-0.227**			
TH*Est	-0.125	-0.279	0.029			
SWE_L*Riparian				0.818	-0.428	2.063
SWE_L*BF				**1.486**	**0.778**	**2.194**
SWE_L*UF				**1.483**	**0.658**	**2.307**
SWE_L*TH				0.355	-0.774	1.485

On the log scale, heterogeneity of group size preference between ($\hat{\sigma}^2_B$) and within ($\hat{\sigma}^2_W$) individual females was relatively high ($\hat{\sigma}^2_B = 0.18$ and $\hat{\sigma}^2_W = 0.70$, respectively). Individual elk did not routinely seek larger or smaller groups, and their choice of group sizes was quite variable (i.e. there was considerable variation between different elk, and each elk displayed considerable variation in their group size choice). *Post hoc* exploratory analyses revealed that substituting $WOLF_{days}$ for $WOLF_{period}$, and SNH_L (snow heterogeneity) for SWE_L, did not improve models. However, the addition of KILLS to the original top model improved the model by 17.96 AIC units. The estimated

coefficient for KILLS was 0.339 (95% CI = 0.191, 0.489) and was a strong predictor of elk group size. Adding KILLS changed the coefficients for the best *a priori* model only slightly.

Model selection results for the group size variation analysis supported one model that included the covariates SWE_L, HBT, and $WOLF_{period}$, and a SWE_L*HBT interaction which received an Akaike weight of 0.98 (Table 3.1). Overall, models that contained the $WOLF_{period}$ covariate accounted for all of the model weights. Similar to the group size analysis, snow had a negative affect on group size variation. Variation in group size also appeared to be habitat specific and, for an average snow pack, groups were more stable in riparian, thermal, and forested habitats compared to meadows. After wolf reintroduction, grouping behavior by elk became more dynamic and as predicted, more group size variation was observed during the colonization and established wolf periods (Table 3.2). The interaction term SWE_L*HBT indicated that more variation in grouping behavior was observed under deep snow conditions in the forested habitat types. No females had a specific tendency to aggregate and disperse more frequently than others ($\hat{\sigma}^2_B = 1.25$), and variation in grouping behavior was very inconsistent within individual elk ($\hat{\sigma}^2_W = 30.84$). *Post hoc* exploratory analyses revealed that adding KILLS to the original top model improved the model by 19.6 AIC units. The estimated coefficient for KILLS was 2.33 (95% CI = 1.35, 3.31) and was a strong predictor of elk group size variation. Adding KILLS changed the coefficients for the best *a priori* model only slightly. Substituting $WOLF_{days}$ and SNH_L for $WOLF_{period}$ and SWE_L, respectively, did not improve models. The sizes of elk aggregations and associated variation matched the trend in wolf-days

among years (Figure 3.3), suggesting a response to predation risk at an intermediate temporal scale.

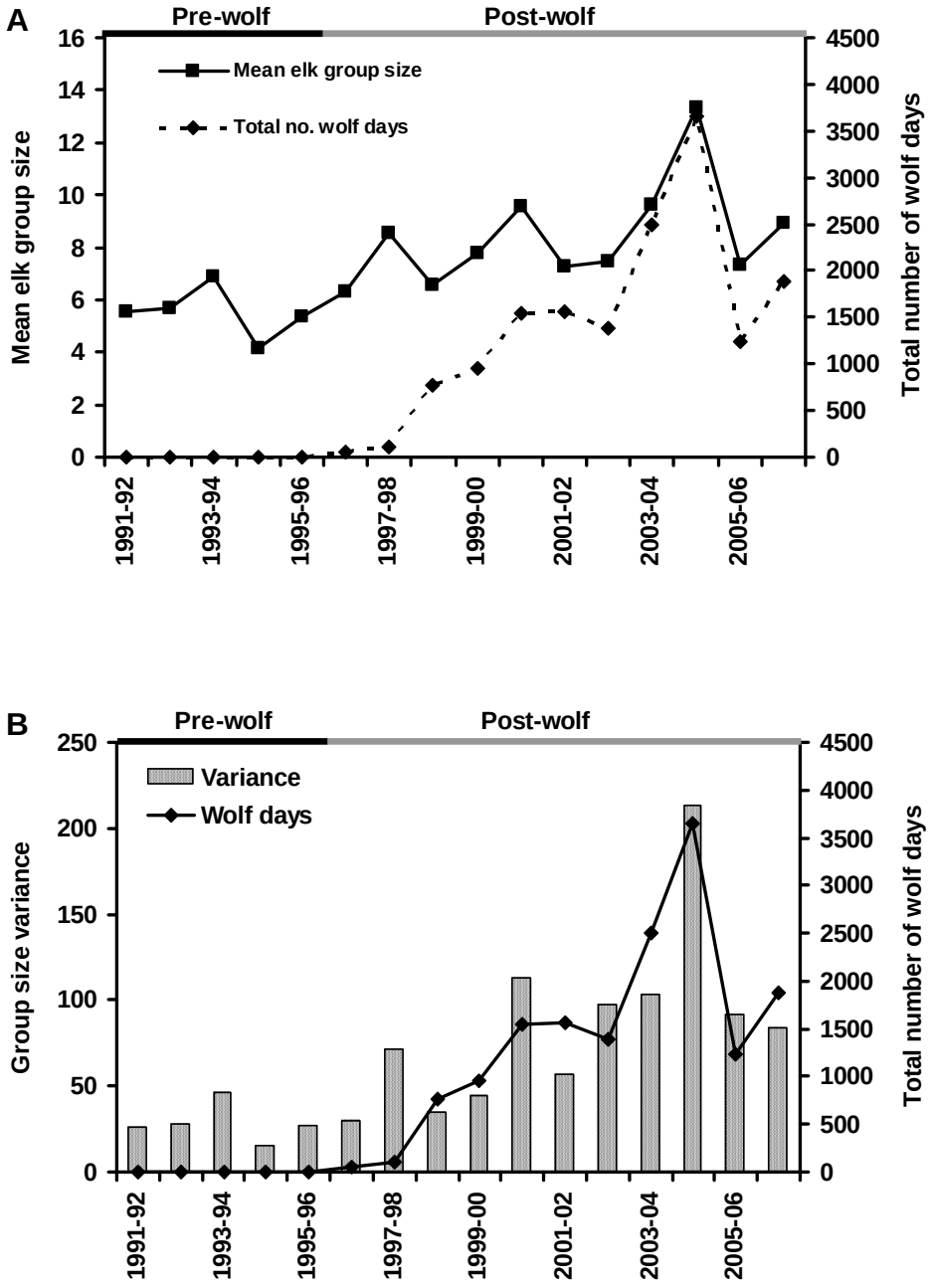

Figure 3.3 Changes in mean elk group size (**A**) or the variance in elk group size (**B**) and the total number of wolf days in the Madison headwaters area of Yellowstone National Park during the winters of 1991-92 through 2006-07. Mean annual group size showed a strong correlation with the total number of wolf days for the study area ($R^2_{adj} = 0.75$, $F_{1,14} = 47.86$, $P < 0.001$). Mean annual group size is shown with error bars representing standard errors (**C**).

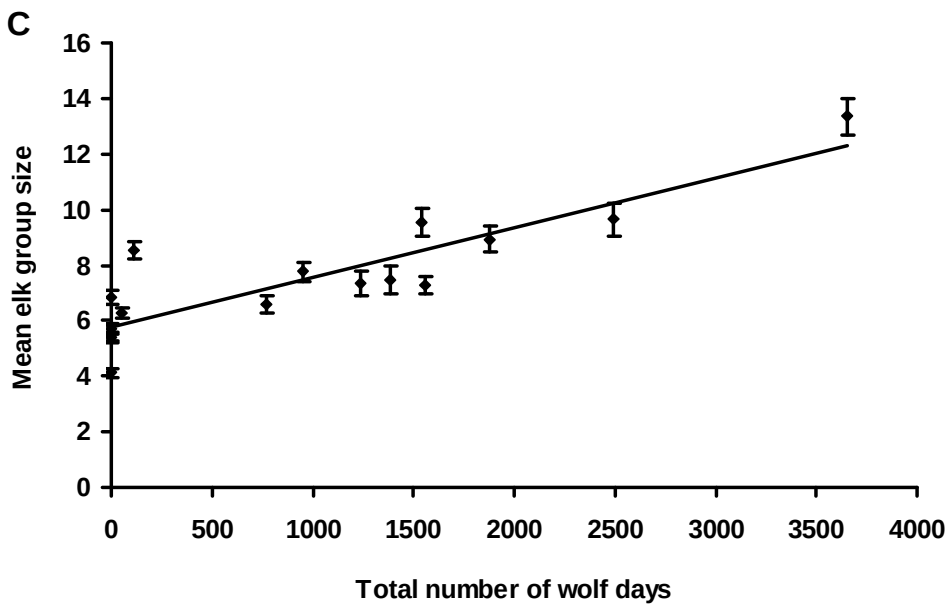

Figure 3.3 Continued. Changes in mean elk group size (**A**) or the variance in elk group size (**B**) and the total number of wolf days in the Madison headwaters area of Yellowstone National Park during the winters of 1991-92 through 2006-07. Mean annual group size showed a strong correlation with the total number of wolf days for the study area ($R^2_{adj} = 0.75$, $F_{1,14} = 47.86$, $P < 0.001$). Mean annual group size is shown with error bars representing standard errors (**C**).

Typical group size was substantially larger than mean group size (Figure 3.4), which is always the case when the variance of mean group size is larger than zero (Heard 1992). Model selection results for the typical group size analysis supported two top models (Table 3.1). The most- supported model included the covariates SEASON and $WOLF_{days}$ and received an Akaike weight of 0.60 ($R^2_{adj} = 0.30$, $F_{2,217} = 48.48$, $P < 0.001$). The second-ranked model included only $WOLF_{days}$ and received an Akaike weight of 0.27 ($R^2_{adj} = 0.29$, $F_{1,218} = 92.31$, $P < 0.001$). Models with the $WOLF_{days}$ covariate accounted for all the model weight, indicating that models incorporating the effect of wolf activity received more support from the data than the non-wolf models when explaining differences in typical group size. There was support for the predictions of larger typical group sizes as wolf activity increased and, also, that a slight increase in typical group size

would occur throughout winter (Table 3.3). Adding KILLS to the top model during *post hoc* exploratory analyses provided no improvement to *a priori* models.

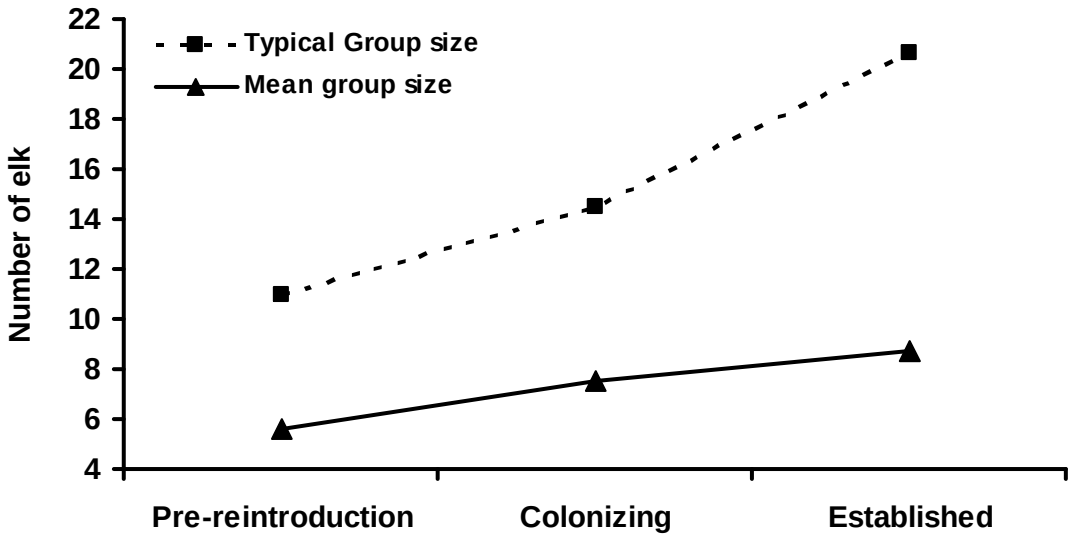

Figure 3.4 Temporal trends in mean elk group size and typical group size before wolf reintroduction, during wolf colonization, and after wolf establishment in the Madison headwaters area of Yellowstone National Park during the winters of 1991-92 through 2006-07.

Table 3.3. Coefficient estimates and 95% confidence limits for covariates affecting *ln* (typical group size). Bold font denotes coefficient estimates with 95% confidence limits that do not span zero. Coefficients for the typical group size are based on model averaged results.

	ln (Typical group size)		
Covariate	Estimate	Lower CI	Upper CI
SWE_L	-0.049	-0.181	0.082
$WOLF_{days}$	**0.517**	**0.409**	**0.625**
SEASON	0.090	-0.003	0.183

Discussion

Several investigations of the relationship between large herbivore behavior and predation risk have been conducted in the Greater Yellowstone Ecosystem, focusing on the behavior of naïve elk after wolves became established on the landscape (Laundré et al. 2001, Childress and Lung 2003, Wolff and Van Horn 2003). These studies documented elk behavior in accordance with general theories of prey responses to predation risk, forming larger group sizes and increasing vigilance as predation risk increased. However, empirical data documenting pre-wolf behavior was lacking and prevented comparisons between behaviors with and without a top predator, and in at least one of the previously published studies the investigators assumed low wolf presence in a drainage within the Madison headwaters study area where this study documented substantial wolf activity. Additional insights were gained by incorporating empirical data on elk grouping behavior before wolf reintroduction, during the colonizing stage, and when wolf packs were resident in the study area. Elk in the Madison headwaters area demonstrated changes in aggregation patterns that coincided with the reintroduction of wolves and provided strong support for the effects of wolves on elk grouping behavior. Larger aggregations were positively correlated with wolf presence, activity, and the number of kills in a drainage each day. Groups were also more variable in the presence of wolves relative to the pre-wolf period, and on days that wolves had been actively hunting the drainage and successfully killed prey. Models that contained only non-wolf covariates received little support from the data when compared to the models that incorporated a wolf covariate.

These results are similar to those of other studies reporting larger aggregations of large herbivores during times of high predation risk (Heard 1992, Jędrzejewski et al. 1992, Molvar and Bowyer 1994, Lingle 2001, Mao et al. 2005). However, these findings are in sharp contrast to two other recent studies of elk behavioral responses to wolf predation risk conducted in the Greater Yellowstone Ecosystem. Creel and Winnie (2005) studied elk-wolf interactions along the western border of Yellowstone National Park (approximately 75 km north of the Madison headwaters study area) and concluded elk formed smaller groups when wolves were in the same drainage compared to when wolves were absent. Also, Gude et al. (2006) reported that wolves had no detectable effect on the size of elk groups in the lower Madison Valley (40 km west of the Madison headwaters area). These equivocal results from studies in close geographic proximity suggest wolf predation may not be the only factor influencing elk group size and variation. The top model from our group size analyses contained a habitat*wolf presence interaction, by which grouping behavior in the presence of wolves was amplified in certain habitat types. However, the response was not uniform across all habitat types in the entire study area. Likewise, Kunkel and Pletscher (2000) reported that certain habitat and landscape features affected vulnerability to predation, and Bergman et al. (2006) found that predators are capable of selecting such vulnerable conditions, which may explain this habitat-specific response. Thus, differences in habitat, snow pack, and landscape features among sites in close proximity may influence elk grouping behavior in the presence of wolves. The Madison headwaters area is a highly heterogeneous landscape with burned and unburned forest patches, snow free thermal areas, steep rocky canyons, and small open meadow complexes along major river corridors. In contrast, the

Gallatin Valley is comprised of large expanses of sage scrub and grassland, with relatively continuous unburned stands of coniferous forest and some small riparian zones (Creel and Winnie 2005). The lower Madison Valley consists of expansive flat grassland and sage brush on low-elevation benches along the Madison River, with small riparian communities and west-facing slopes with coniferous forest and intermixed stands of aspen (Gude et al. 2006). Snow conditions also differ among the sites. Snow depths commonly exceeding 90 cm are typical for the Madison headwaters (Eberhardt et al. 1998), whereas in the lower Madison Valley snow may reach depths of 40 cm in wooded areas but rarely exceeds 10 cm in the grassland. Typically these large grassland/shrub areas are windblown and many areas remain snow free (Gude et al. 2006). The Gallatin Valley experiences intermediate snow conditions (Figure 3.5).

The heterogeneous nature of the landscape in the Madison headwaters area imposes numerous hard edges that can impede animal movement away from predators (Bergman et al. 2006). If animals occupy habitats where escape is not an effective anti-predator tactic or conditions such as deep snow make movement difficult, then forming groups rather than fleeing may be an effective alternative (Lima 1992). Elk in the Gallatin and lower Madison valleys were not as severely constrained by such landscape heterogeneity or deep snow conditions, which may explain why these elk adopted a strategy of moving instead of aggregating (Gude et al. 2006). The smaller aggregations of elk observed in forested areas of the Gallatin Valley when wolf predation risk was high may reduce the probability of being detected by predators (Creel and Winnie 2005) or, alternatively, may be a result of a bias due to the difficulty of accurately determining group size in dense forested environments. Regardless, landscape disparities among areas may strongly

influence the behavioral responses of elk to wolf presence, and the degree to which these behaviors are manifested. As Hebblewhite and Pletscher (2002) point out, prey grouping behavior could be a fundamental component affecting the detection and hunting success by wolves. As a result, grouping behavior could potentially influence the functional response of wolves and, consequently, elk population dynamics. We have evidence from our studies that this may have occurred as indicated by the negative correlation (R^2=0.66) between mean annual elk group size and mean annual wolf kill rates on elk (Becker et al. 2009b). Thus, if landscape differences dictate behavioral responses, then they could also alter the strength of top-down effects by predators on their prey and therefore sociality among prey may have important implications for stability in predator-prey dynamics (Fryxell et al. 2007).

Elk in the Madison headwaters area also responded to the presence of wolves at short time scales, when wolves were actively hunting and killing in a given drainage. These findings suggest elk may adopt risk allocation in their grouping behavior to some degree, raising the baseline level of anti-predator behavior in the presence of predation risk and demonstrating the greatest level of anti-predator behavior during brief, but infrequent, high risk situations (Lima and Dill 1990, Lima and Bednekoff 1999, Sih et al. 2000, Sih and McCarthy 2002, Gude et al. 2006; Figure 3.6). After wolves became established in the Madison headwaters area, the moderately stable aggregations of elk observed during the pre-wolf period changed to more dynamic aggregations with frequent variations in the aggregation and dispersion of groups. Such variations in group size may be an effective anti-predator strategy because unpredictable behavior can reduce predator efficiency (Bowyer et al. 1999). Also, because predator-prey feedback mechanisms are governed

by the way an individual (rather than a group) responds, these results may better explain evolutionary forces that shape prey and predator behavior over time.

Another explanation for dynamic grouping behavior in the presence of predators could be that animals are trying to balance competing demands. Costly anti-predator behavior is adopted during bouts of elevated predation threat and relaxed when the immediate threat of predation subsides (White and Berger 2001, Wolff and Van Horn 2003). These data support this interpretation, particularly considering the extreme temporal and spatial variation in wolf presence exhibited within our study tract. The relatively modest variation in elk group size before wolf reintroduction may reflect elk adopting a single feeding strategy solely based on energy conservation and food acquisition. During the colonizing and established wolf periods, however, elk aggregated ephemerally when wolf predation risk was high, and then reverted to smaller aggregations similar to the pre-wolf period as the immediate risk subsided. An alternative interpretation for the higher variation observed during the colonization and established wolf periods is that the threat of predation makes the baseline group size larger, which then fragments and disperses when the group is attacked. This would also explain the increased variation observed on days when wolves had been successful in making a kill. Clearly the response is temporally dependent and the temporal scale to which the response is observed may yield different insights.

In the absence of wolves, elk were less aggregated with increasing snow conditions. The Madison headwaters area is a mosaic of small foraging patches during winter that likely cannot support large aggregations of elk for long periods of time. Thus, the small group sizes that were observed when snow pack was high likely reflect elk using smaller

foraging patches with reduced snow. Deep snow also restricts elk movements and increases the effective distance between suitable feeding areas (Heard 1992); thereby inducing elk to conserve energy and remain in stable groups. Because snow pack severity has been related to the risk of predation for large herbivores in numerous studies (Mech 1970, Jędrzejewski et al. 1992, Huggard 1993, Becker et al. 2009a and b), it was surprising to find no support from the data for an interaction between snow and wolf presence in these analyses.

A positive correlation between group size and population density has been reported for several large ungulate species (Clutton-Brock et al. 1982, Hebblewhite and Pletscher 2002, Krause and Ruxton 2002). Population estimates for elk in the Madison headwaters area indicate a decreasing trend in abundance since 1998 (Garrott et al. 2009b). Though population size was not included as a covariate in any of the models due to correlations with the wolf covariates, an obvious expectation would be that decreasing population size should produce smaller aggregations of elk. This was not the case because group size increased as population size decreased. Similar findings were reported for red deer in response to human hunting (Jędrzejewski et al. 2006) and Gude et al. (2006) observed the large elk herds in the lower Madison valley fragmented as a response to human hunters, suggesting that predation in any form can have an effect on elk grouping behavior regardless of density.

Garrott et al. (2005) stressed that the effects of wolves on the demographics of ungulate prey populations should not be generalized between areas and, based on these findings, I extend this caution to the behavior of prey at different sites. Variations in the behavior of subpopulations in close proximity have been previously documented

(Brashares and Arcese 2002), and geographic variation in behavior has been widely discussed in relation to evolutionary theory (Foster 1999, Foster and Endler 1999). Behavior is an important component of the way animals adapt to local conditions (Foster and Endler 1999), so it is not unexpected that differentiation in anti-predator behavior between locations occurs. As a result, ecologists are becoming increasingly aware that behavioral and physiological changes resulting from anti-predator constraints should be considered in predator-prey models (Beckerman et al. 1997, Schmitz 1997, 1998, Brown et al. 1999, Hebblewhite and Pletscher 2002, Denno et al. 2003, Nelson et al. 2004, Preisser et al. 2005, Eshel et al. 2006, Mchich et al. 2006, Creel and Christianson 2008).

While it could be argued that animals aggregate to form stable optimal groups (Giraldeau and Gillis 1985), results from this study suggest the contrary. Optimal group size is what would be expected under stable conditions, whereby every individual member's fitness is maximized. However, this study highlights that the theoretically optimal group size is unlikely to be met under most natural conditions because of temporal and spatial variation, uncertainty in prey knowledge of predation risk, and the ephemeral nature of animal groups (Sibly 1983, Pulliam and Caraco 1984). Individuals must aggregate in a manner that maximizes their individual fitness at a specific location or circumstance. They do this by individually selecting to be part of the typical group size (Jarman 1974) which could essentially be defined as a composite of individual decisions made to maximize individual fitness. Therefore, typical group size consists of an aggregation of animals where every member in the group strives for, but potentially falls short of maximizing their fitness because of variation in the environment. As such "typical group size" would appear to be a more realistic definition to describe the most

advantageous group to be a part of rather than the “optimal group size”. Typical group size seems to be an underused metric in most behavioral studies, however it would appear to be a valuable and more realistic metric to use when variable environmental conditions prevail.

I documented changes in elk behavior that can be interpreted as responses to the reestablishment of predation risk due to the reintroduction of wolves into the Yellowstone Ecosystem. Specifically, elk have adapted to coping with predation risk from wolves by individually increasing their typical group size. With these prey aggregation responses, how wolves perceive the vulnerability of their prey must also differ, and predators must now face the challenge of adjusting their behavior accordingly. In summary, results from this study show how elk respond to the newly established wolf population and the consequent risk of predation. What we would now expect to see is an adjustment in wolf behavior to compensate for this prey behavioral response, and we would expect that optimality and stability in prey behaviors will not occur as this continuous process of predator and prey responding to one another continues to evolve in this study system.

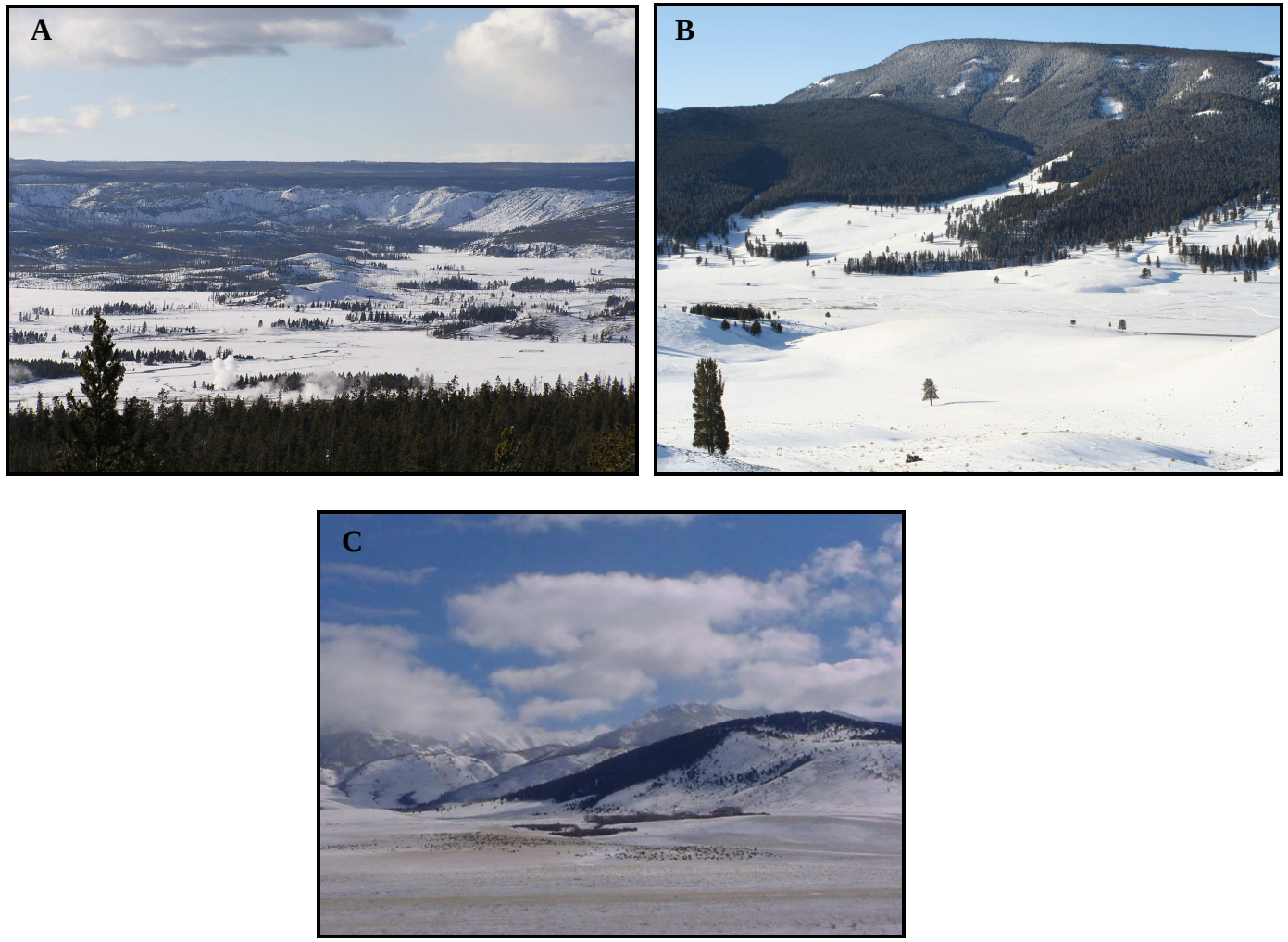

Figure 3.5 Characteristic landscape and topography of the Madison headwaters (**A**), Gallatin Valley (**B**), and lower Madison Valley (**C**). The grouping behavior of elk in response to wolf predation risk was studied at each of these sites which are in close geographic proximity to one another, but quite divergent results were found. The large group of elk in the lower Madison Valley photo is typical of this windswept grassland/shrub winter range that contrasts with the much smaller groups that are typical of the Madison headwaters study site (Photos by Matthew Becker -**A**, David Christianson -**B**, Justin Gude -**C**).

Figure 3.6 Elk aggregating in response to wolves in the Madison headwaters. Elk remained clumped and vigilant as a single wolf approached near Biscuit basin in the Firehole drainage (**A**) and were often observed fleeing into deep spots in the river when wolves were close (**B**). Elevated behavioral alertness and tight aggregation were maintained when a predation threat was imminent, but elk often resumed feeding just a short period of time after wolves left the immediate vicinity (Photos by Claire Gower).

Summary

1. Since wolves were reintroduced to Yellowstone in 1995-96 a considerable amount of research has contributed to our understanding of prey behavior in response to this newly established top carnivore. I extended this work by adding a pre-wolf component which allowed me to evaluate how these behaviors have changed following reintroduction. Collectively these studies provide a comprehensive synthesis of elk grouping behavior over a wide ecological range. This allowed for possible disparities to be identified, and the mechanisms responsible could be explored.
2. A total of 8,373 randomly-selected elk groups were sampled during 16 consecutive winters between 1991-92 and 2006-07 to compare group sizes before wolf reintroduction, during colonization, and after wolf establishment. With these data the non-wolf and wolf covariates influencing elk group size, group size variation, and typical group size were evaluated.
3. It was determined that group size and group size variation were negatively correlated with snow pack severity and positively correlated to the presence of wolves under certain habitat conditions. Elk altered their grouping behavior at multiple temporal scales, including among years, within winters, and daily depending on wolf presence and if a kill had occurred in a given drainage.
4. The relatively modest variation in group size before wolf restoration can be interpreted as a consequence of elk adopting a single feeding strategy based solely on energy conservation and food acquisition. During the wolf colonization and

establishment periods, a substantial increase in group size variation that I suggest was due to animals trying to balance the conflicting demands of minimizing predation risk and maximizing food acquisition.

5. While I have documented elk aggregating into larger groups in response to wolf predation risk, studies similar to this study, and in close geographic proximity to this study site, have documented both no detectable change in elk group size and elk aggregating into smaller groups in the presence of wolf predation risk. These differences in prey behavioral responses can be attributed to substantial differences in landscapes attributes such as snow pack severity and habitat types, complexity, and patch size that influence predation risk and dictate different prey behavioral responses.
6. Prey individuals can adjust their behavior rapidly to the presence or absence of predators and site-specific situations. Ultimately, how individual animals aggregate and the influence of these aggregation responses on the risk of predation, could influence predator-prey dynamics at the community level.

Acknowledgements

Collaboration with Bob Garrott, P.J. White, Steve Cherry, and Nigel Yoccoz was fundamental for the successful completion of this manuscript. R. Garrott provided endless guidance and advice throughout the entire process, S. Cherry and N. Yoccoz guided me through the analyses and always made time for discussions regarding the statistical procedures and interpretation of results. I am thankful to R. Garrott and P.J. White for the months that they invested into discussing ideas and editing this manuscript.

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CHAPTER 4

ELK FORAGING BEHAVIOR: DOES PREDATION RISK REDUCE TIME FOR FOOD ACQUISITION?

Abstract

Large herbivores that inhabit seasonal environments face considerable challenges when trying to balance the conflicting demands of satisfying physiological requirements and avoiding predation. The harsh environment imposes strong nutritional constraints which influence activity patterns and foraging strategies. In addition, the need to evade predators strongly determines the way in which prey behave. To evaluate how elk (*Cervus elaphus*) managed food acquisition and predation risk the behavior of elk in the Madison headwaters area of Yellowstone National Park was observed during 15 consecutive winter field seasons (1991-2006). Using approximately 3100 hours of behavioral data before and after wolf (*Canis lupus*) reintroduction, logistic and negative binomial regression were used to evaluate factors affecting the likelihood of a foraging bout and the scanning behavior of elk. It was determined that the likelihood of a foraging bout was influenced by snow, time of day, and habitat type. Also, the likelihood of foraging was marginally higher following wolf establishment. This increase may reflect a strategy of sacrificing foraging for predator vigilance or avoidance during the high-risk nighttime period, but increasing foraging during the day to compensate for this loss. It was also determined that elk infrequently scanned the environment when foraging during the day, and scans were short in duration and often occurred concurrently when processing food. Results from other areas of this long term study suggest little apparent

reduction in the nutritional status of elk following wolf reintroduction. I therefore propose that the ability of elk to mitigate predation risk with only minimal or no effects on food acquisition and nutrition is due to their highly acute senses and their ability to simultaneously scan the environment for predators and process food. Additionally, if a range of anti-predator behaviors can collectively be adopted at appropriate temporal scales, then the trade-off between food acquisition and predation risk may be somewhat reduced. Therefore, from this study it can be proposed that high plasticity in prey behaviors may balance the need to forage and minimize risk, thereby allowing prey to remain in an environment that provides adequate forage resources but also poses a high threat of predation.

Introduction

Animals should make decisions regarding their foraging behavior by selecting strategies that ultimately maximize long-term fitness (Pyke et al. 1977, Pyke 1984, Kie 1999). For animals that are not constrained by predation this strategy would theoretically appear quite simple and decisions would be based predominately on energetic considerations (Parker et al. 2005, Loe et al. 2007). When predation risk becomes an additional selective force, an individual must attempt to minimize their vulnerability to predators while still obtaining the necessary food resources for survival. Optimization theory predicts that animals will maximize their fitness by modulating their behavior to balance energy gain and predator avoidance (Abrams 1984). The response often observed reflects an individual's nutritional state (Stephens and Krebs 1986, Lima 1998a, Winnie and Creel 2007), the relative frequency of predation risk (Lima and Bednekoff

1999a, Sih et al. 2000, Sih and McCarthy 2002, Laurila et al. 2004), and the range of possible compensatory behaviors (Lind and Cresswell 2005, Ajie et al. 2007, Watson et al. 2007).

Increased visual awareness by prey, commonly referred to as vigilance, is a universal behavioral response among many different taxa (Elgar 1989, Treves 2000). In the presence of predators, prey will increase their level of behavioral alertness to facilitate early detection of predators which may reduce their probability of being attacked and ultimately killed (Elgar 1989, Quenette 1990, Hunter and Skinner 1998, Lima and Bednekoff 1999b, Treves 2000, Caro 2005). Probability of survival may be enhanced if early predator detection allows prey to find an effective escape route, seek protection from landscape features in close proximity that serve as refuges (Lima 1992, Berryman and Hawkins 2006), and/or congregate with conspecifics for defense (Caro 2005) and dilution of risk (Hamilton 1971, Bertram 1978, Dehn 1990). However, anti-predator responses aimed at reducing predation risk may have measurable fitness costs, particularly if the responses interrupt other fitness-enhancing activities such as feeding (Fitzgibbon and Lazarus 1995). Scanning the environment for predators may reduce nutrition which, in turn, could translate into non-lethal costs, or even indirect lethal effects if predator presence is severe enough to cause starvation in prey (Lima and Dill 1990, Lima 1998b).

The threat of predation affects a greater number of individuals than those that are killed. Therefore, there is increasing interest to more fully understand predator intimidation and quantify the non-consumptive effects predators inflict on their prey (Nelson et al. 2004, Bolnick and Preisser 2005, Preisser et al. 2005, Creel et al. 2007,

Creel and Christianson 2008). Experimental manipulations in a laboratory or field setting have revealed behavioral shifts in foraging as a result of predation threat (Beckerman et al. 1997, Schmitz 1997, 1998), but trying to empirically quantify individual-level foraging responses in large mammal systems presents a far more challenging task. In most large herbivore systems, it is notoriously hard to study the effects of predation threat on prey behavior, particularly if there is a heavy human influence that causes confounding effects. Protected areas in Africa provide conducive systems to study behavioral alertness under varying levels of risk due to the lack of any significant human disturbance and tolerance of human observers by both predators and prey (Underwood 1982, Hunter and Skinner 1998). However, few systems exist in North America where prey are tractable and/or the system has an intact predator guild and human influence is negligible. Recently, vigilance levels of elk have been compared in areas with and without the presence of wolves, or following reintroduction of wolves into Yellowstone National Park in 1995 and 1996 (Laundré et al. 2001, Childress and Lung 2003, Wolff and Van Horn 2003, Lung and Childress 2006, Winnie and Creel 2007, Halofsky and Ripple 2008, Liley and Creel 2008). These studies empirically documented noticeable changes in vigilance levels as the threat of predation risk by wolves increased. While there were differences among the studies, they demonstrated strong relationships between variation in vigilance with group size, sex and age class, and maternal state. In a few cases, a corresponding decrease in the proportion of time foraging with increasing vigilance was also observed (Laundré et al. 2001, Childress and Lung 2003, Wolff and Van Horn 2003, Winnie and Creel 2007). However, whether increased vigilance actually results in any detrimental consequence for the prey remains uncertain.

Vigilance is normally addressed by measuring the proportion of time prey spend scanning the environment for predators. This is often considered time that would otherwise be invested in searching for and consuming food (Quenette 1990). While this is a reasonable assumption when foraging and scanning are mutually exclusive behaviors, it is not always the case for prey that can simultaneously conduct both activities. The extent to which foraging opportunities are compromised and, thus, the cost of vigilance, consequently depends on how much visual attention is required when searching for and handling food (Studd et al. 1983, Lima 1988, Cowlishaw et al. 2003, Cresswell et al. 2003, Fortin et al. 2004 a, b; Caro 2005). Therefore, it is more difficult to directly assign a cost of vigilance for prey animals that can process their food and survey their surroundings at the same time because vigilance does not necessarily imply that feeding activities are interrupted. Large herbivores often perform additional activities such as scanning their immediate surroundings, while simultaneously searching for, chewing, and physiologically processing food (Owen-Smith and Novellie 1982). Illius and Fitzgibbon (1994) theoretically proposed that this efficient use of time can enable large herbivores to essentially forage cost free, and Fortin et al. (2004b) empirically showed that if the two behaviors somewhat overlap, the foraging costs can be reduced.

While there have been many investigations addressing the anti-predator behavior of prey, few can draw unequivocal conclusions about the fitness consequences associated with the behavioral response (Lind and Cresswell 2005). This is particularly true for studies of vigilance in large mammal predator-prey systems that assumed vigilance was conducted at the exclusion of foraging. While many of these studies have been able to correlate changes in vigilance behaviors with perceived variation in predation risk,

assessments of potential reductions in foraging as a consequence of increased vigilance could only be suggested or inferred.

To avoid the inherent and subjective difficulty of discerning if foraging is actually interrupted while being vigilant, this study focused on quantifying foraging behavior directly and correlating variation in the time devoted to foraging with varying levels of predation risk. The likelihood of changes in foraging activity by elk associated with varying levels of perceived predation risk before, during, and after wolf colonization of the Madison headwaters area in Yellowstone National Park were evaluated. Due to the tractable nature of the elk occupying this area, it was possible to accurately quantify elk behavior and wolf predation risk simultaneously at relatively fine temporal and spatial scales. Working with a non-hunted, non-migratory herd provided a rare opportunity to isolate the effects of wolf predation on elk foraging behavior where the confounding effects of human hunting were absent. It was predicted that elk would respond to wolves by altering their level of behavioral alertness and modifying the time devoted to foraging activities. It was also predicted that foraging behavior would be strongly influenced by environmental conditions that also vary substantially at relatively fine spatial and temporal scales.

Methods

The winter foraging behavior of non-migratory elk in the Madison headwaters area was recorded over 15 consecutive winters from 1991-92 through 2005-06, during which time a VHF radio-collared population of 20-35 adult cow elk per year (i.e., approximately 4-10% of the herd) was maintained. The collared individuals were repeatedly sampled

annually from November 15 to April 30 using a stratified random sampling regime to select the focal collared cow to be monitored for behavioral data (Garrott et al. 2009a). This sampling design also ensured that daily variation in elk behavior was captured because sampling times were randomly distributed through the daylight hours. For this sampling regime the study area was divided into geographically defined drainages (i.e., the Madison, Firehole and Gibbon drainages), which were further stratified into areas within each of the three drainages. Radio-collared elk that inhabited the selected strata were located by randomly determining the order with which they were to be sampled and all groups within the study area were sampled once before re-sampling occurred. Hand-held telemetry equipment and homing procedures were employed to locate the selected animal. When the focal animal was observed, a Universal Transverse Mercator (UTM) location, total group count and composition of the herd (calf, cow, yearling bull, adult bull), the predominant habitat type used through the majority of the observation (meadow, thermal, unburned forest, and burned forest), and if the focal animal was positively identified to have a calf were recorded. A 30-minute continuous behavioral observation (Altmann 1974) was then conducted. Focal animal watches were typically carried out from a distance of 20-300 m to avoid disturbing the animal's normal activities, with the observation bout terminated if the animal walked out of view or if its behavior was altered by an anthropogenic disturbance. Observation bouts with <15 minutes of data were censored from all analyses. Often observations were conducted on more than one collared elk in the same group, but to retain independence of the data only one observation per group was used in all analyses.

For each observation period, the time the focal animal spent in each of five discrete behavioral states: foraging; bedded; standing; traveling; and grooming/socializing was quantified. A number of specific behaviors were included into our classification of a foraging bout including cropping plant material, displacing snow to access forage, traveling short distances at a slow pace with lowered head, and brief periods when the animal would raise its head apparently surveying its surroundings. These ephemeral look-resume behaviors were often performed while the animal masticated plant material prior to swallowing and, thus, this behavior was considered to be part of a foraging bout. However, the number of times this behavior occurred during the observation was also recorded. If the head-up posture was maintained more than momentarily, then the behavior was recorded as standing. These data were used to develop two response variables, including the proportion of time foraging and the total number of look-resume behavioral scans that an animal made during a foraging bout. The proportion of time spent foraging was the product of time spent searching for and consuming food divided by the total length of the observation. This metric provided an estimate of the proportion of the daytime activity allocated to maintaining physiological condition during winter. The total number of look-resume behavioral scans that the animal made during a foraging bout was not mutually exclusive from processing food (masticating or swallowing plant material), so it merely provided an index of the amount of time extracted from searching for and cropping plant material. The number of look-resume behavioral scans was only evaluated for 30-minute behavioral observations that were exclusively composed of foraging behaviors. Using the term “vigilance” was intentionally avoided because it is often associated with the assumption that other ongoing activities are interrupted

(Quenette 1990) or that surveillance is directed specifically towards predator detection. Due to the uncertainty surrounding these two assumptions, I refrained from using this terminology and contend the term “behavioral scan” was more appropriate. There is the potential for an observer effect and confounding variables of other human presence during any behavioral study. However, elk in this study area exhibited habituation to humans (White et al. 2009a), so there was no reason to suspect this would be confounded with any wolf influence.

Landscape, Temporal, and Social Covariates of Elk Foraging Behavior

Three landscape, three temporal, and one social covariate that were suspected to influence large herbivore foraging behavior during winter were considered. Snow is a fundamental factor limiting the availability of forage in temperate and high latitude environments. Thus, a validated snow pack simulation model for the central Yellowstone region (Watson et al. 2009) was used to construct two covariates that captured important attributes of snow pack. The mean snow water equivalent (SWE, water content of snow) of all 28.5 m x 28.5 m pixels within a 100-m radius of the elk location (SWE_A (m)) was calculated and was specific to the day the radio-collared elk was observed. The standard deviation of all pixels within a 100-m radius of each elk location was also calculated as a metric of snow heterogeneity across the local landscape (SNH_A). Different habitat types offer different feeding opportunities for large herbivores (Craighead et al. 1973, Hobbs et al. 1981). Thus, a categorical habitat covariate (HBT) was defined and classified each elk observation into meadow, burned forest, unburned forest, or thermal based on field observations of the plant communities the animals were predominately using at the time

of the observation. Meadow habitat type was used as the reference category with which to compare foraging behavior in other habitat types.

Covariates were generated at three temporal scales that literature suggested may be biologically meaningful with respect to foraging behavior. The covariate YEAR was constructed, which was a continuous variable from 1-15 representing the successive winters from 1991-92 through 2005-06. Extensive wildfires burned approximately 48% of the study area in 1988 (Newman and Watson 2009). Thus, this metric was used to index the temporal trend in forest succession and potential changes in forage availability for large herbivores post-fire (Houston 1973, Knight and Wallace 1989, Pearson et al. 1995). It was hypothesized that the effect of fires would only influence foraging behavior in the burned forest habitat type. Thus, the covariate YEAR was only included as a YEAR*BF interaction (BFYR). Foraging behavior is also likely influenced by seasonal variation in the quality and quantity of available plant material (Craighead et al. 1973, Green and Bear 1990, Ager et al. 2003) and changes in body condition and physiological requirements of elk. To capture this within season variability, the covariate SEASON was generated, which was a continuous variable from 1-167 (168 in leap years) and represented the day within the season starting from November 15. Because large herbivores have daily behavioral cycles or rhythms (Green and Bear 1990, Ager et al. 2003), the covariate $TIME_{day}$ was developed. This metric was a continuous variable, calculated as the number of hours and proportion of the hour between 6:00 am and the time the behavioral observation was initiated. Finally, the covariate GROUP was included to define the size of the group the focal animal occupied during the time of the observation. Foraging behavior may be affected by intra-specific competition for

resources (Ranta et al. 1993, Fritze and De Garne-Wichatitsky 1996, Rita et al. 1996), attraction towards conspecifics in foraging patches (Clark and Mangel 1984, Valone 1989, Ruxton et al. 1995), and anti-predator behaviors such as vigilance (Elgar 1989, Kie 1999). While others have reported adult, female elk showing elevated anti-predator responses if they are accompanied by young (Hunter and Skinner 1998, Laundré et al. 2001, Childress and Lung 2003, Wolff and Van Horn 2003), I did not include maternal status in these analyses because it was often difficult to discern how long a female retained a calf. Also, once calves become part of the herd they must learn to avoid danger independently and there is often little assistance provided by the mother (Geist 2002). Adult, female elk in the Madison headwaters were often observed fleeing when approached by wolves, without waiting for their calves to join them. Thus, there was no reason to suspect maternal status would be an important covariate in these analyses.

Covariates of Predation Risk

The presence of wolves was detected and quantified in the Madison headwaters from November 15 to April 30 during the winters of 1996-97 through 2005-06. Each drainage was intensively monitored daily for wolf presence using ground-based telemetry, snow tracking, and visual observations of collared and un-collared individuals. When packs containing radio-collared wolves were detected telemetry locations were estimated using triangulation (White and Garrott 1990) and multiple locations were obtained through the day. Snow tracking, visual observations, and counts during aerial monitoring by National Park Service biologists were used to provide estimates of the number of animals per pack and aid in the daily assessments of wolf presence or absence (Becker et al. 2009, Smith et

al. 2009). Detection of un-collared wolves was facilitated by opportunistic observations of tracks and wolves by field personnel that were working throughout the study area on elk and bison investigations (Bruggeman et al. 2009, Garrott et al. 2009a, White et al. 2009b). The total number of wolves present in each drainage each day was estimated based on the information obtained from these various wolf monitoring techniques.

These data on wolf presence were used to develop three wolf covariates, reflecting different temporal scales, and were used to assess the hypotheses about the influence of predation risk on elk foraging behavior. The covariate $WOLF_{period}$ categorized the 15-year data set into three periods: before wolf reintroduction, during wolf colonization, and after wolf establishment. The $WOLF_{period}$ covariate was drainage-specific because wolves established in different drainages during different winters (Firehole: 1997-98; Gibbon: 2000-01; Madison: 2001-02; Smith et al. 2009). No wolves were present in the study area during the initial years of the study (1991-92 through 1995-96). To account for the potential transitory behavioral dynamics due to the initial naïveté of the prey (Berger et al. 2001), a colonizing period immediately following wolf reintroduction was defined when elk were initially exposed to wolf predation risk, but no wolf pack (≥2 animals) was routinely detected in the drainage. The established wolf presence period began during the first winter that a pack was consistently detected in a drainage. Wolves were wide-ranging, routinely moving among drainages and in and out of the study area (Becker et al. 2009, Smith et al. 2009). Thus, a dichotomous covariate, $WOLF_{presence}$, was also developed to indicate whether or not wolves were present in a drainage on a given day (0 = absent, 1 = present). To evaluate if surviving elk responded to successful hunting and killing by wolves, a third wolf metric, KILLS, was developed that

represented the number of wolf-killed ungulates discovered in each drainage on a given day (Becker et al. 2009, Smith et al. 2009).

Statistical Analyses

Analysis of Variance (ANOVA) was used to evaluate the change in mean proportion of time foraging by elk during winter and Tukey multiple comparisons with unequal sample size (Kutner et al. 2005: 750) was used to identify differences in the means between the pre-wolf, colonizing, and established wolf periods ($WOLF_{period}$). The response variable, the proportion of an observation bout that an elk was engaged in foraging behaviors, was transformed using the logit transformation: logit (P) = $\log_e \frac{P}{1-P}$. Because logit transformations cannot be applied to proportions of exactly zero or one, the proportions were adjusted using the following equation; $P' = \frac{F+0.5}{N+1}$ (Fox 1997: 80), where F is the frequency of the focal category (e.g., the number of minutes foraging) and N is the total number of minutes included in the observation bout. The adequacy of the logit transformation was evaluated using diagnostic residual plots to assess the assumption of constant variance. The diagnostic plots showed that assumption of normality of the residuals was not met. However, ANOVA is robust to the assumption of normality, particularly when evaluating average values and the sample size is large (Gelman and Hill 2007: 46). I used 95% confidence intervals to quantify uncertainty in parameter estimates.

The ANOVA analysis that assessed differences in the mean proportion of time elk spent engaged in foraging behaviors among the three time periods was complimented

with a regression analysis to gain further insight into the potential influences of wolf predation risk on foraging behavior. A large number of observations were comprised of animals either feeding through the entire observation period or not feeding at all. These long sequences of a single behavior prevented the use of a generalized linear model with the logit link and binomial error structure on the proportions directly because they violated the assumptions of independence. This lack of independence was consistent with the extremely large over-dispersion parameter ($\hat{c} = 29$). Therefore, a dichotomous response variable was created from these data by coding observation bouts where the elk spent 0-25% of the observation time in foraging behaviors as zero, and bouts where the elk spent 75-100% of the observation time engaged in foraging behaviors as one. Fifteen percent of the observation bouts with intermediate foraging proportions (0.26-0.74) were censored (Figure 4.1). Thus, each observation bout included in the analysis was classified as either a foraging or non-foraging bout which allowed for the use of logistic regression (logit link, assuming binomial error structure) to estimate the log odds. These odds were then used to generate the odds ratios (*exp* (log odds)) which were used to define the ratio of probability of the event occurring to the probability that it does not occur (Agresti 1996), thereby providing a ratio of the likelihood of foraging under certain conditions. Odds ratios lie between zero and ∞, with values larger than one indicating higher probability of an event occurring, values less than one indicating lower probability of an event occurring, and values of one indicating equal probability of an event occurring. Log odds lie between $-\infty$ and $+\infty$, so the coefficient values from the logistic regression provided an interpretation of the strength and direction of the relationship (Agresti 1996).

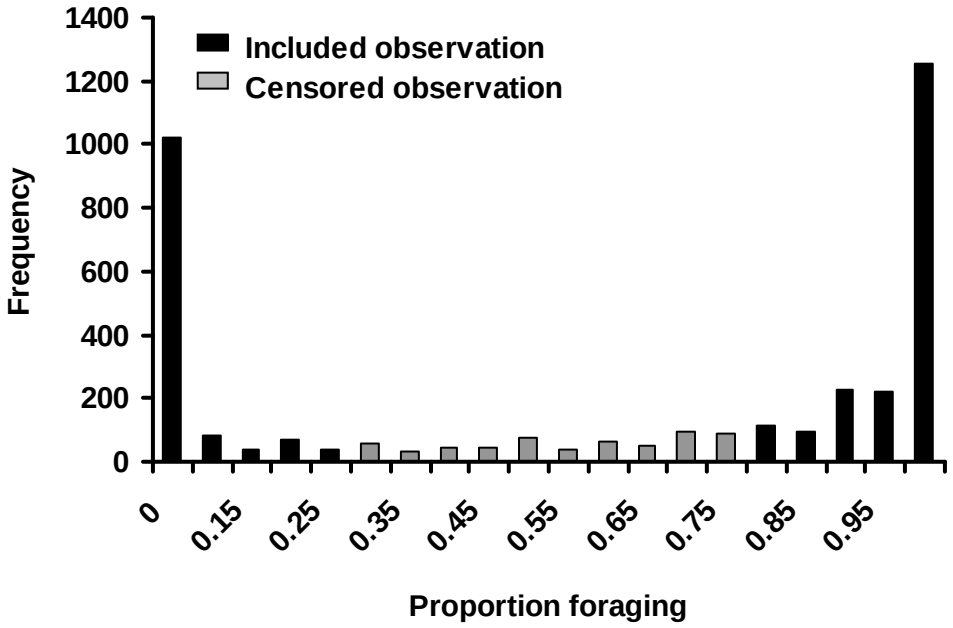

Figure 4.1 Frequency distribution of the proportion of an observation bout that radio-collared, adult, female elk in the Madison headwaters of Yellowstone National Park engaged in foraging behaviors. Note the bimodal distribution of these data.

A subsidiary analysis was conducted on a subset of the data (1998-99 through 2005-06) to evaluate if the frequency of look-resume behavioral scans was influenced by the daily presence or absence of wolf predation threat. This data set included only 30-minute behavioral observations that were entirely composed of foraging and occurred during the colonizing and established wolf periods. I did not feel comfortable using the complete 15-year data set due to potential inconsistencies with how we recorded look-resume behavioral scans in the field prior to 1998-99. The data set was based on counts (i.e., total number of scans in 30 minutes), and made up of a large proportion of zero's (53%). While the distribution showed a large proportion of the observations at the left tail and

few high counts representing the right tail, it was not Poisson distributed. The dispersion of the data was larger than expected for a Poisson distribution, but histograms of the expected versus observed showed a good fit to the negative binomial distribution. Therefore, a model assuming a negative binomial distribution and a log link (Venables and Ripley 2000) was used to evaluate the scanning behavior of elk during and after wolf colonization. Such a model assumes an over-dispersion compared to a Poisson distribution described by the relationship variance = mean + mean^2 / θ, rather than variance = mean, as would be expected with the Poisson distribution.

Competing hypotheses that were expressed as suites of *a priori* candidate models were developed for both the logistic and negative binomial regression and Akaike Information Criteria (AIC) was used to rank models given the data and compare the relative ability of each model to explain variation in the data (Burnham and Anderson 2002, 2004). Akaike model weights (w_i) were used to address model selection uncertainty, and evidence ratios (ratio of wi/wj) were used to measured the relative likelihood of model pairs (Burnham and Anderson 2002).

The same collared elk were repeatedly sampled through a winter and frequently over numerous consecutive winters. Thus, for the logistic regression analysis the over-dispersion parameter, *c*, was calculated to assess potential violations of the assumption of independence in the data (Burnham and Anderson 2002). *C* was calculated by dividing the residual deviance of the most general model by the deviance degrees of freedom (McCullagh and Nelder 1989). Because this is a biased-high estimate of the true over-dispersion (White 2002), I also estimated *c* using the Pearson's residuals (Faraway 2006). Goodness of fit for the most general model was evaluated using the le Cessie's test for

binary response variables (le Cessie and van Houwelingen 1991, Hosmer et al. 1997). This was conducted using the lrm function in the design library in R (R Development Core Team 2006). The negative binomial takes into account over-dispersion through the extra parameter θ. Therefore, it was not necessary to evaluate over-dispersion for this analysis. All continuous variables were centered and scaled prior to analyses to facilitate interpretation of the coefficient estimates and to alleviate problems with correlation among covariates. Variance inflation factors (VIF), which measure multi-colinearity among variables, were calculated for all combinations of predictors. Those models that included predictor combinations with VIF <6 were retained in the model list. This was a conservative approach because VIF in excess of 10 implies multi-colinearity (Kutner et al. 2005: 409). Correlation coefficients were also calculated to further check for multi-colinearity between the predictor variables. All statistical analyses were performed using the R statistical package (R Development Core Team 2006).

A Priori Model Suites and Predictions

To evaluate the likelihood of a foraging bout, two restricted *a priori* model suites of additive models were formulated which were based on literature and field knowledge of the study system. One suite of 14 models represented the non-wolf hypotheses and, also, included a null model (constant likelihood of a foraging bout), while the second suite of 13 models had the same structure, but with the addition of the $WOLF_{period}$ covariate (Appendix 4.1). Every model contained the covariate indexing mean snow pack in the vicinity of the elk, SWE_A, and the habitat covariate, HBT due to their importance in the foraging ecology of large herbivores during winter. Competing hypotheses regarding the

effects of snow on the probability of foraging by elk were proposed. It was hypothesized that the probability of foraging would be negatively correlated with SWE_A because increasing snow pack diminishes forage availability (Jenkins and Wright 1987) and increases energetic costs associated with locomotion and displacing snow to expose forage (Fancy and White 1985). Alternatively, it was predicted that elk would need to spend more time searching and displacing snow for forage when snow conditions are high. Because foraging was being defined as the product of time invested into searching and actually consuming forage, the absolute time required to obtain the baseline level of food would be amplified when elk foraged under high snow pack conditions. Feeding and other activities are often related to specific habitat types (Craighead et al. 1973, Collins and Urness 1983, Green and Bear 1990), with grasses and shrubs typically constituting the winter diet of elk (Kufeld 1973, Hobbs et al. 1981, 1983; Christianson and Creel 2007, White et al. 2008c). Because elk intensively use areas of high herbaceous biomass while foraging, it was predicted that the probability of observing a foraging bout would not be uniform across all habitat types, but observations of elk in open habitats (meadow and thermal) would reflect a higher probability of foraging than in the less productive forested habitats. It was suspected that in the initial years after the extensive 1988 wildfires high quantity and quality of forage may have been available in the burned forests (Hobbs and Spowart 1984, Pearson et al. 1995), but that the reestablishment of lodgepole pine saplings gradually reduced forage quantity and quality over the duration of this study. Since this potential effect would be limited to the burned forest habitat type, a YEAR*BF interaction was considered and I predicted the

probability of a foraging bout in burned forest habitat would gradually decrease over the period of this study.

Foraging dynamics reflect seasonal fluctuations in the quantity and quality of available forage (Hobbs et al. 1981, Green and Bear 1990), and changes in physiological demand (Clutton-Brock et al. 1989) that occur over winter. Therefore, SEASON was expressed as a quadratic function predicting that the odds of foraging would be highest during the late autumn and early spring periods of reduced snow pack and higher forage availability (Craighead et al. 1973, Georgii and Schröder 1983, Green and Bear 1990, Ager et al. 2003). It was hypothesized that the odds of foraging would not be uniform across the daytime hours, but feeding bouts would coincide with sunrise and sunset and extended periods of rest would occur during the day (Georgii and Schröder 1983, Green and Bear 1990, Ager et al. 2003). Therefore, $TIME_{day}$ was also expressed as a quadratic function to capture crepuscular foraging activity. It was also hypothesized that if larger groups are formed as a foraging response (Creel and Winnie 2005), then the odds of foraging would be positively correlated with GROUP.

Finally, competing hypotheses regarding the effects of wolf period on the likelihood of a foraging bout were proposed. If elk in the Madison headwaters cannot simultaneously forage and scan for predators (McNamara and Houston 1987), then anti-predator vigilance should carry a cost of reduced foraging time. Thus, the odds of a foraging bout would be lower during wolf colonization and establishment than the pre-wolf period. Alternatively, if a large proportion of foraging time is at night or during the crepuscular hours (Green and Bear 1990, Ager et al. 2003), coinciding with the most active hunting time for wolves (Mech 1970, Peterson and Ciucci 2003, Becker et al.

2008), then it was predicted that elk would trade-off foraging when wolves are most active and adopt a strategy of increased foraging during the daytime hours when predation risk was lower. Therefore, the odds of a daytime foraging bout would increase from the pre-reintroduction to the established wolf period. Lastly, it was proposed that there would be no effect of the covariate $WOLF_{period}$ on the probability of a foraging bout by elk due to digestive system constraints and the ability of large herbivores to remain vigilant while still foraging (Illius and Fitzgibbon 1994, Fortin et al. 2004 a, b).

Based on the outcome of the *a priori* model-selection results, *post hoc* exploratory analyses were conducted to generate hypotheses for future work. In the top model for both the non- wolf and wolf suite, the mean snow water equivalent covariate, SWE_A, was replaced with the snow heterogeneity covariate, SNH_A, hypothesizing that elk would spend a greater proportion of their time foraging with increased heterogeneity of snow pack. The $WOLF_{period}$ was replaced with the $WOLF_{presence}$ covariate to evaluate if a metric indexing daily presence or absence described variation in foraging behavior better than the coarse temporal scale of $WOLF_{period}$. The possibility that elk behavioral responses to daily wolf presence differed when predation risk was a relatively novel phenomenon during wolf colonizing period compared to latter years after wolves had been established in the system was also explored. To accomplish this both $WOLF_{presence}$ and $WOLF_{period}$ main effects and their interaction were included. The covariate KILLS was added to the top wolf model to evaluate if the likelihood of foraging by surviving elk was influenced by successful predation events by wolves. Though it was suspected that SWE_A and HBT would contribute heavily to the best supporting model because of the importance these covariates play in the winter ecology of large herbivores, I removed

them and their associated interactions from the top models to verify their importance. Similarly, other covariates were removed from the top model to verify their significance.

To evaluate scan behavior, an *a prior*i model suite was formulated with a null model (hypothesizing constant number of scans) and 23 models that included the covariates GROUP, HBT, TIME, $WOLF_{presence}$, and KILLS independently or in the additive form (Appendix 4.2). Competing hypotheses were proposed for the effect of group size on the scanning behavior of elk. First it was predicted that a decrease in the frequency of scans within a 30-minute foraging bout would be observed with larger groups. This would support the assumption of reduced individual vigilance (Pulliam 1973, Elgar 1989), which is suspected to be one of the principal benefits of group living. Alternatively, larger groups would facilitate more scans which were directed towards con-specifics within the group (Quenette 1990, Beauchamp 2001, Lung and Childress 2006). It was suspected that the number of scans would increase in closed habitats where visibility is impaired (Underwood 1982) or the ability to escape is hindered (Halofsky and Ripple 2008). It was also predicted that there would be an increase in the number of scans in the morning and evening to coincide with the main hunting times for wolves. Thus, the covariate $TIME_{day}$ was included in the model in the quadratic form. Finally, it was predicted that elk would increase their level of behavioral alertness on a given day that wolves were present within the same drainage as the elk (Liley and Creel 2008), or if a kill had been made within the drainage. Thus, the number of scans would be positively related to the $WOLF_{presence}$ and KILLS covariates.

Results

A total of 186,823 minutes (3114 hours) of behavioral data (6428 observation bouts) were accrued through repeated sampling of a total of 108 radio-collared, adult, female elk during the winters 1991-92 through 2005-06. To retain independence of the data for analyses only one radio-collared animal was included per observation bout, thus reducing data to 113,806 minutes (1897 hours) of observations accrued during 3749 independent behavioral observation bouts (mean = 249 observations annually; range = 115-553, se = 26.6; range 15-180 minutes per observation, mean = 30.4 minutes, se = 0.11). A total of 1700 independent observation bouts were conducted prior to wolf reintroduction, 657 bouts during wolf colonization, and 1392 bouts after wolf packs were established in the area. Feeding comprised a mean proportion of 0.58 (se = 0.007) of elk activity budgets, compared to bedding (0.33; se = 0.007), standing (0.05; se = 0.002), traveling (0.03; se = 0.001), and grooming/socializing (0.01; se = 0.001). Only modest variation in the proportions of each of these behaviors was recorded among the pre-reintroduction, colonizing, and established time periods defined by $WOLF_{period}$ (Figure 4.2). The proportion of time spent foraging was the only behavioral category that demonstrated a consistent trend across the three periods, with indications of a slight increase in time devoted to foraging from the pre-reintroduction to the established periods (Figure 4.3). Results of the ANOVA analysis of the logit transformed adjusted proportion of time foraging (logit (P')), indicated no significant difference in the proportion of time spent foraging between the pre-reintroduction and wolf colonization period ($\hat{D}_{\text{colonizing-prewolf}}$ = 0.292; 95% CI: -0.056, 0641; P = 0.12) or between the colonizing and established wolf

periods ($\hat{D}_{\text{established-colonizing}}$ = 0.115; 95% CI: -0.244, 0.474; P = 0.73). However, a significant difference was detected between the pre-reintroduction and established wolf periods ($\hat{D}_{\text{established-prewolf}}$ = 0.408; 95% CI: 0.133, 0.682; P < 0.001). The lack of a significant difference in the proportion of time foraging on a logit scale between the colonizing and the established periods, or between the colonizing and pre-wolf period likely reflects higher variance during the colonizing wolf period compared to the other two periods. $\hat{D}$ defines the difference between the logit transformed mean proportion of time foraging between two wolf periods.

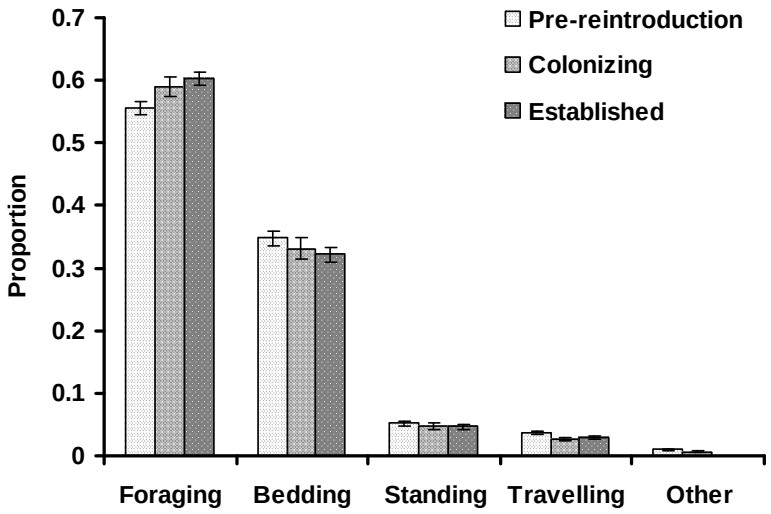

Figure 4.2 Variation in daytime activity budgets for elk in the Madison headwaters of Yellowstone National Park during periods before, during, and after wolf colonization. Data were collected over 15 consecutive winters (1991-92 through 2005-06) from November 15 to 30 April annually. Proportion represents the mean proportion of all observation time, with error bars representing standard errors.

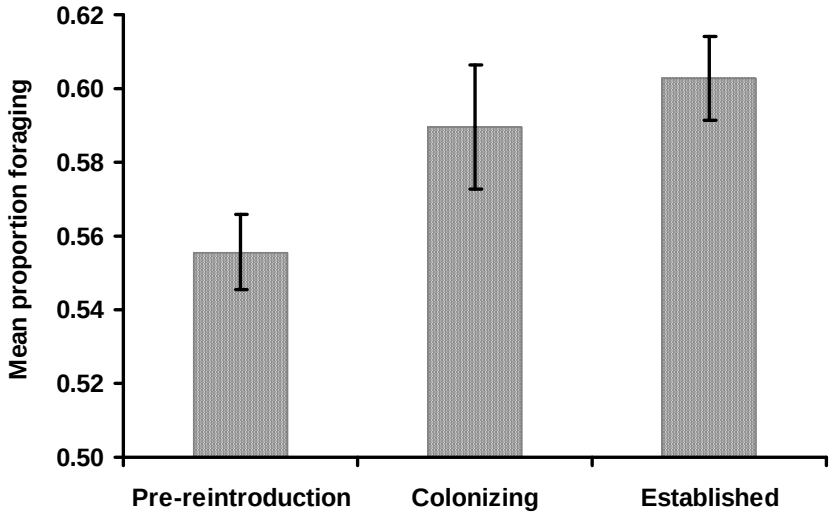

Figure 4.3 Changes in the mean proportion of time radio-collared, adult, female elk in the Madison headwaters of Yellowstone National Park engaged in foraging behaviors before, during, and after wolf colonization. The plotted values are based on the untransformed data with error bars representing standard errors.

Model Selection Results

Wolves were absent from the Madison headwaters area prior to reintroduction in 1995-96. Thereafter, the total number of wolf days increased from 55 in 1996-97 to a peak of 3657 in 2004-05. The Firehole drainage experienced high wolf use immediately following reintroduction, while the Madison and Gibbon drainages did not experience wolf use until several years later and never reached the magnitude of use observed in the Firehole (see Chapter 2: Figure 2.1) . Pack size and number of packs varied both spatially and temporally (Smith et al. 2008).

Conversion of the observation data to a dichotomous response variable resulted in classifying 1925 foraging observation bouts (foraging proportion 0.75-1.0), 1248 non-foraging bouts (foraging proportion 0-0.25), and 576 observation bouts with intermediate foraging proportions (0.26-0.74) that were censored. Thus, a total of 3173 behavioral

observations of ≥15 minutes in length were used to evaluate the *a priori* logistic regression model suites. The residual deviance/degrees of freedom for the most general model suggested slight over-dispersion ($\hat{c} = 1.32$), but the Pearson's test indicated no evidence of over-dispersion ($\hat{c} = 1.01$). Because the deviance/degrees of freedom method yields estimates of *c* which are usually biased high, and because this method is as well approximated as the Pearson's method for large sample sizes (White 2002), there was no reason to suspect over-dispersion was a concern. The goodness of fit tests revealed the most general model from the wolf suite fit the data only reasonably well (*P* = 0.042), but because of the large sample size, I felt comfortable that this was a satisfactory fit.

Model selection results for the non-wolf suite supported two top models that received approximately 0.85 of the model weight (Table 4.1). As predicted, the SWE_A coefficient was negative, with the odds of a foraging bout being less likely with increasing SWE_A (Table 4.2*a*). Also as predicted, the odds of a foraging bout in burned forest and unburned forest were 0.79 and 0.61 times, respectively, lower than the odds of a foraging bout in meadow habitats, while the odds of foraging in geothermal was not significantly different from meadow. These results suggest that open habitats rather than closed forested habitats types offered better foraging opportunities and hence, higher probability of elk foraging bouts. There was strong support for the hypothesis that elk in the Madison headwaters exhibited crepuscular foraging behavior as illustrated by the predicted temporal curves from the top-ranked model when other coefficients were fixed at their means (Figure 4.4). Also, the likelihood of a foraging bout decreased with increasing elk group size. While the seasonal and year by burned forest interaction

covariates were included in top-ranked models, confidence intervals of coefficient estimates spanned zero. Thus, there was no strong evidence supporting an effect of season or forest succession in predicting the probability of a foraging bout.

Table 4.1. Model selection results for the most-supported logistic regression models (non-wolf and wolf suites) examining the likelihood of a foraging bout by elk in the Madison headwaters area of Yellowstone National Park during 1991-92 through 2005-06. All models are ranked according to AIC values, and presented along with the number of parameters (*k*), ΔAIC value (change in AIC value relative to the best model), and the Akaike weight (w_i). AIC values for the top non-wolf model and top wolf model were 4195.03 and 4191.22, respectively. Among-suite ΔAIC values were calculated based on the difference in AIC value from the top wolf model (AIC value of 4191.22). Abbreviations are: SWE_A (local-scale snow water equivalent), HBT (habitat), BFYR (burned forest*year interaction), SEASON (day within the season), $TIME_{day}$ (time of day), GROUP (elk group size), and $WOLF_{period}$ (pre-reintroduction, colonizing, and established).

Model structure	Within Suite			Among Suite	
	k	**ΔAIC**	w_i	**ΔAIC**	w_i
Non-wolf models					
SWE_A + HBT + $TIME_{day}$ + $TIME_{day}^2$ + SEASON + $SEASON^2$ + GROUP	10	0.00	0.55	3.81	0.08
SWE_A + HBT + BFYR + $TIME_{day}$ + $TIME_{day}^2$ + SEASON + $SEASON^2$ + GROUP	11	1.23	0.30	5.05	0.04
SWE_A + HBT + BFYR + $TIME_{day}$ + $TIME_{day}^2$ + GROUP	9	3.56	0.09	7.38	0.01
SWE_A + HBT + BFYR + $TIME_{day}$ + $TIME_{day}^2$ + SEASON + $SEASON^2$	10	5.60	0.03	9.41	0.00
SWE_A + HBT + $TIME_{day}$ + $TIME_{day}^2$	7	7.03	0.02	10.84	0.00
Wolf-models					
SWE_A + HBT + $TIME_{day}$ + $TIME_{day}^2$ + SEASON + $SEASON^2$ + GROUP + $WOLF_{period}$	12	0.00	0.60	0.00	0.52
SWE_A + HBT + BFYR + $TIME_{day}$ + $TIME_{day}^2$ + SEASON + $SEASON^2$ + GROUP + $WOLF_{period}$	13	1.72	0.26	1.72	0.22
SWE_A + HBT + BFYR + $TIME_{day}$ + $TIME_{day}^2$ + GROUP + $WOLF_{period}$	11	3.24	0.12	3.24	0.10
SWE_A + HBT + BFYR + $TIME_{day}$ + $TIME_{day}^2$ + SEASON + $SEASON^2$ + $WOLF_{period}$	12	8.52	0.01	8.52	0.01
SWE_A + HBT + $TIME_{day}$ + $TIME_{day}^2$ + $WOLF_{period}$	9	8.68	0.01	8.69	0.01

Table 4.2*a*. Coefficient estimates (log odds) and 95% confidence limits for the best supported logistic regression model from the *a priori* non-wolf model suite examining the factors affecting the probability of a foraging bout by elk in the Madison headwaters area of Yellowstone National Park during 1991-92 through 2005-06. All covariate levels are compared to the Meadow habitat type. Bold font denotes coefficient estimates with 95% confidence limits that do not include zero. Abbreviations are explained in Table 4.1.

Covariate	**Estimate**	**L.CI**	**U.CI**	**Odds ratio**
SWE_A	**-0.099**	**-0.175**	**-0.024**	**0.905**
HBT - BF	**-0.239**	**-0.431**	**-0.048**	**0.787**
HBT - UF	**-0.499**	**-0.719**	**-0.279**	**0.607**
HBT - TH	0.190	-0.050	0.430	1.209
GROUP	**-0.095**	**-0.171**	**-0.020**	**0.909**
$TIME_{day}$	**0.119**	**0.045**	**0.193**	**1.126**
$TIME_{day}^2$	**0.117**	**0.037**	**0.197**	**1.124**
SEASON	-0.001	-0.003	0.001	0.999
$SEASON^2$	**0.075**	**0.002**	**0.148**	**1.078**

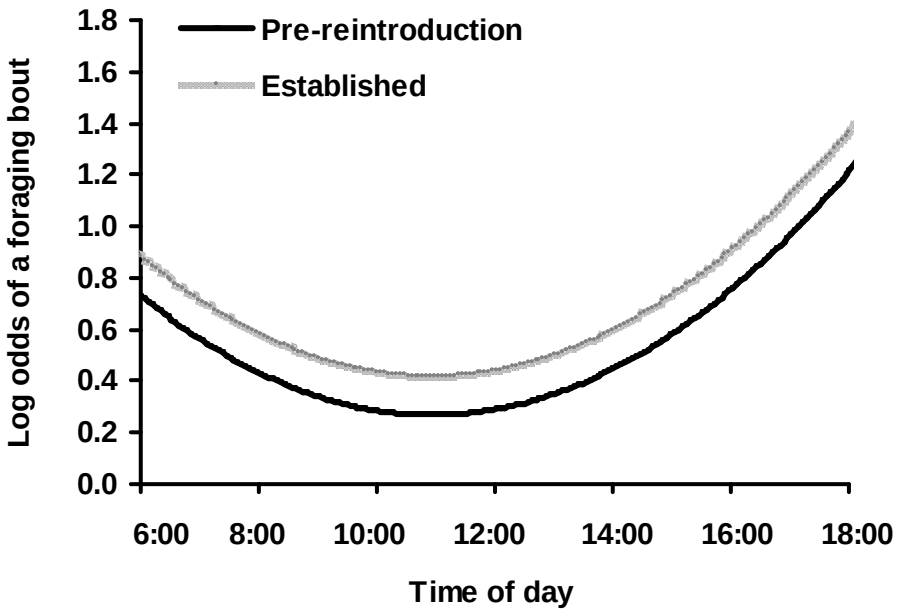

Figure 4.4 The estimated log odds of a foraging bout during the day for radio-collared, adult, female elk in the Madison headwaters of Yellowstone National Park before and after wolf colonization. Predicted values are based on the top wolf model (Tables 4.1 and 4.2*b*) for elk foraging in meadow habitat type.

Within and between model suite comparisons made it possible to evaluate if models with the wolf covariate were more supported by the data. The inclusion of the wolf period covariate improved the model performance for almost all model pairs, with evidence ratios suggesting that the top model from the wolf suite was approximately seven times more supported than the top non-wolf model. Model selection results for the wolf suite supported two top models that received approximately 0.86 of the model weight (Table 4.1). The most parsimonious models for the wolf suite consisted of SWE_A, HBT, $TIME_{day}$ and $TIME_{day}^2$, SEASON and $SEASON^2$, BFYR, GROUP, and $WOLF_{period}$, with coefficient values and confident intervals changing little for the landscape and temporal covariates between the non-wolf and wolf suite (Table 4.2*b*).

The coefficients for the wolf covariate indicated that the likelihood of a foraging bout was slightly higher in the colonizing and established period compared to the pre-wolf period, thus the baseline level of the likelihood of a foraging bout was raised following reintroduction (Figure 4.4). None of the *post hoc* exploratory analyses provided improvements over the top *a priori* models and the decision to include both SWE_A and the HBT covariates in all *a priori* models was supported because dropping either of these covariates singly or in combination resulted in increases of 5.1 to 34.6 AIC units. Dropping TIME from the top model resulted in an increase of 15.3 AIC units, which further highlighted the importance of time of day in the foraging behavior of elk.

Table 4.2*b*. Coefficient estimates (log odds) and 95% confidence limits for the best supported logistic regression model from the *a priori* wolf model suite (and best among-suite model) examining the factors affecting the probability of a foraging bout by elk in the Madison headwaters area of Yellowstone National Park during 1991-92 through 2005-06. All covariate levels are compared to the Meadow habitat type, pre-reintroduction. Bold font denotes coefficient estimates with 95% confidence limits that do not include zero. Abbreviations are explained in Table 4.1.

Covariate	**Estimate**	**L.CI**	**U.CI**	**Odds ratio**
SWE_A	**-0.108**	**-0.188**	**-0.029**	**0.897**
HBT - BF	**-0.223**	**-0.415**	**-0.031**	**0.800**
HBT - UF	**-0.468**	**-0.689**	**-0.247**	**0.627**
HBT - TH	0.229	-0.012	0.471	1.258
GROUP	**-0.116**	**-0.193**	**-0.039**	**0.891**
$TIME_{day}$	**0.103**	**0.027**	**0.178**	**1.108**
$TIME_{day}^2$	**0.136**	**0.054**	**0.218**	**1.146**

Table 4.2*b*. Continued. Coefficient estimates (log odds) and 95% confidence limits for the best supported logistic regression model from the *a priori* wolf model suite (and best among-suite model) examining the factors affecting the probability of a foraging bout by elk in the Madison headwaters area of Yellowstone National Park during 1991-92 through 2005-06. All covariate levels are compared to the Meadow habitat type, pre-reintroduction. Bold font denotes coefficient estimates with 95% confidence limits that do not include zero. Abbreviations are explained in Table 4.1.

Covariate	**Estimate**	**L.CI**	**U.CI**	**Odds ratio**
SEASON	-0.040	-0.116	0.035	0.960
$SEASON^2$	0.070	-0.003	0.143	1.073
$WOLF_{PERIOD}$ - COL	**0.256**	**0.044**	**0.469**	**1.292**
$WOLF_{PERIOD}$ - EST	**0.196**	**0.024**	**0.369**	**1.217**

From 1998-99 through 2005-06 (i.e., the post-wolf reintroduction period), 435 independent observations of 30 minutes in length which were made up entirely of foraging (217.5 hours of observation time) were classified. Overall, the number of behavioral scans performed by an individual while feeding was extremely low, and in the majority of the observations (53%), the individuals did not look up from foraging once (n = 435, mean = 1.6, se = 0.15, range = 0 to 23). Though this data set did not incorporate observations from the entire colonization period, there was still a sufficient sample of observations that could be compared between wolf colonization (n = 75) and establishment (n = 360). Using the negative binomial distribution, a significant difference between the two time periods ($P < 0.001$) was observed with a mean number of scans increasing from 0.47 (se = 0.15, range = 0 to10) to 1.92 (se = 0.17, range = 0 to 23) as the system transitioned from colonizing to establishment. There was also a significant difference in the number of scans made when wolves were detected in the

same drainage as the elk compared to days where there was a high probability that no wolves were using the drainage (P = 0.03). When there was no detection of wolves in the drainage, elk scanned the environment on average 1.4 times during a 30-minute foraging bout (n = 255, se = 0.18, range = 0 to 21), with 58% of the observations not including a single scan response. Even when wolves were present in the same drainage as the collared elk, 46 % of the observations showed that an animal did not actively scan the surroundings once, and the mean number of look-resume scans was only 2.05 which is still low for a 30-minute foraging bout (n =180, se = 0.25, range = 0 to 23).

Model selection results from the negative binomial regression analysis supported one top model that contained the covariates GROUP and $\text{WOLF}_{\text{presence}}$, receiving approximately 0.57 of the model weight (Table 4.3). As predicted, GROUP was negatively correlated with the behavioral scan response ($\hat{\beta}_{GROUP}$ = -0.234, 95% CI = -0.416, -0.053) and there was an increase in the number of scans when wolves were present in a drainage ($\hat{\beta}_{WOLFpresence}$ = 0.397, 95% CI = 0.054, 0.741). Predictor weights showed that the most important predictors were GROUP and $\text{WOLF}_{\text{presence}}$, receiving a weight of 0.95 and 0.75, respectively. The covariates HBT, TIME_{day}, and KILLS were not influential predictors and received predictor weights of 0.09, 0.13, and 0.07, respectively.

Table 4.3. Model selection results for the best-supported negative binomial linear regression models to evaluate factors affecting the scanning behavior of elk in the Madison headwaters area of Yellowstone National Park during 1998-99 through 2005-06. All models are ranked according to AIC values and presented along with the number of parameters (*k*), ΔAIC value (change in AIC value relative to the best model), and the Akaike weight (w_i). AIC value for the top model was 1447.8. Abbreviations are: GROUP (elk group size), HBT (habitat), $TIME_{day}$ (time of day), $WOLF_{presence}$ (presence or absence of wolves within a drainage on a given day), and KILL (number of wolf-killed ungulates within a drainage on a given day).

Model structure	***k****	**ΔAIC**	w_i
GROUP + $WOLF_{presence}$	4	0.00	0.57
GROUP	3	3.15	0.12
GROUP + $TIME_{day}$ + $TIME_{day}^2$ + $WOLF_{presence}$	6	3.87	0.08
GROUP + HBT + $WOLF_{presence}$	7	4.60	0.06
GROUP + KILL	4	5.13	0.04

* Extra parameter to account for the θ distribution

Discussion

A prediction of foraging theory is that animals will alter their feeding behavior under the risk of predation (Lima and Dill 1990), which has been demonstrated empirically in a wide variety of predator-prey systems (Sih 1980, Edwards 1983, Brown et al. 1988, Kohler and McPeek 1989, Schmitz 1997, Abramsky et al. 2002). One of the predominant behavioral responses that is enhanced during times of high predation threat is vigilance (Lima 1987). This response has lead to the assumption that increased vigilance will decrease foraging consumption (Lima and Dill 1990, Brown 1999) which, in turn, could lead to reduced growth and decreased survival and reproduction (Lima 1998a). In recent years, there has been a substantial amount of research investigating vigilance levels of elk following the re-introduction of wolves to Yellowstone National Park (Laundré et al. 2001, Childress and Lung 2003, Wolff and Van Horn 2003, Lung and Childress 2006,

Winnie and Creel 2007, Halofsky and Ripple 2008, Liley and Creel 2008). As expected, these studies documented that elk expressed a high level of awareness when wolves were present in the system. Several of these studies also demonstrated less time foraging in areas that contained wolves compared to wolf-free sites. While these studies support the majority of theoretical predator-prey models of vigilance, which assume that foraging by prey will be sacrificed at the expense of remaining behaviorally aware for predators, I present results indicating the risk of predation may not reduce time for food acquisition to any detrimental degree. Because recent literature questions the traditional foraging-vigilance trade-off, particularly in large herbivores where these two behaviors can be conducted simultaneously (Caro 2005: 117), I proposed a different method that used a direct measure of foraging (i.e., likelihood of a foraging bout) to provide additional insights regarding the effects predators have on large herbivore feeding strategies.

Results from the logistic regression analysis provided strong evidence that the likelihood of a foraging bout was influenced by the presence of wolves. The direction of this response supported the *a priori* prediction that elk would manifest a strategy of increasing the frequency and length of foraging bouts in the presence of wolves. These analyses also corroborated the results of the ANOVA analysis in which the proportion of time foraging marginally increased as wolves colonized and eventually became established in the Madison headwaters. In addition, these results suggested that elk did not excessively allocate time to scanning the environment during a foraging bout when wolves were colonizing the Madison headwaters area or after they were well established in the system. In fact, there was a high prevalence of complete observation periods where elk never looked up from feeding. In accordance with my predictions, the level of

scanning subtly increased when wolves were present within the drainage, but I suspect this modest increase did not inflict any foraging costs.

It was observed that wolves in the Madison headwaters were most often found on a kill at dawn and spent a large proportion of the diurnal period resting (Becker et al. 2009), a pattern also documented by others (Mech 1970, Peterson and Ciucci 2003). This implied that the majority of hunting occurred at night or during early morning. Thus, one explanation for the increase in the likelihood of a foraging bout following wolf reintroduction could be that elk were forced to compromise feeding during the night when wolves were actively hunting, but increased forage during the diurnal period to compensate for this loss. Elk likely remained acutely aware during the main hunting period and increased the intensity or number of foraging bouts during the diurnal period when wolves were typically not hunting and, as a result, relative risk of predation was lower.

The modest increase in the likelihood of a foraging bout that was associated with increased wolf predation risk would initially imply that these results were in sharp contrast to other studies that observed increased vigilance when wolves were associated with the observed elk (Laundré et al. 2001, Childress and Lung 2003, Wolff and Van Horn 2003, Lung and Childress 2006, Winnie and Creel 2007, Liley and Creel 2008). However, this study evaluated whether or not a foraging bout occurred during each observation. Thus, although it would appear that elk in the Madison headwaters were not trading-off foraging time for anti-predator awareness, the way that “foraging” was recorded in this study meant that short duration vigilance was incorporated into this “foraging” category. Even if vigilance levels were elevated in the presence of wolves,

there would not necessarily have been any observable change in the likelihood of a foraging bout in this study. This limitation in the methodology precludes making a strong conclusion regarding whether changes in the likelihood of a foraging bout came with any nutritional costs. Similarly the inherent ability of ruminants to routinely overlap behaviors (Illius and Fitzgibbon 1994, Fortin et al. 2004a,b), which would allow a large herbivore to essentially continue foraging without interruption while other activities are simultaneously being carried out (Fig. 4.5), highlights that using vigilance as a metric comes with its own set of limitations. Thus, it is very challenging for observational studies of this kind to provide a quantitative measure that associates predation and foraging, and this becomes more of a task when behavioral observations are being conducted at a time when the threat of predation on prey is relatively reduced (i.e., daylight hours).

These results suggest that there is no obvious reduction in diurnal foraging by elk, but one can speculate that wolves may still have induced a cost which these analyses were unable to detect. For example, costs could have been derived if foraging and scanning did not completely overlap and consequently animals would be less effective at gaining adequate nutrition (Fortin et al. 2004a). Similarly, elk may have been scanning for predators through the observation while at the same time masticating forage. While they may have partially compensated by increasing the length or number of foraging bouts in a day, when wolves were in the system, if interruptions were abundant, bouts may have been less efficient and elk could have sustained a foraging cost. These costs would have most likely occurred due to a reduction of the harvest rate of forage, which was too fine a behavioral response to capture with the methodology in this study. However, I suspect

these costs were inconsequential because the minimal number of look-resume scans that were recorded during foraging bouts would not have equated to any significant cost.

If elk were trading vigilance behavior at the expense of reduced foraging at night when relative risk was high, then they may have incurred costs which were only partially offset by increased foraging during the day. Heightened behavioral alertness is an obvious behavioral response when the threat of attack by a predator is imminent (Chapter 3; Figures 3.6a and 4.5a). Loss of foraging would be expected during or immediately following a direct encounter between a predator and its prey. However, elk are in poor nutritional condition over winter (Cook 2002) and we suspect this interruption of feeding only was sustained for a short duration following a predation event. The main hunting period for wolves occurred outside the sampling period of this study, which could explain why I was unable to empirically or statistically detect any apparent change in the likelihood of a foraging bout by elk.

One could also speculate that foraging costs could have been incurred by elk if they were forced into safer but poorer quality habitats in the presence of wolves. This is a commonly adopted strategy by prey in many aquatic and terrestrial systems (Sih 1980, 1982, Brown et al. 1988, Werner and Hall 1988, Beckerman et al. 1997, Schmitz 1997, 1998, Lima 1998*b*). In some wolf-ungulate systems, prey have shifted habitats to reduce their level of predation risk (Creel et al. 2005) and sustained a decrease in diet quality as a consequence (Edwards 1983, Hernández and Laundré 2005). However, Mao et al. (2005) and Kauffman et al. (2007) did not show any significant changes in resource selection by northern Yellowstone elk due to wolves. Similarly, other work conducted in the Madison headwaters study area provides no evidence to indicate that elk were moving

to nutritionally less profitable habitats or that costs were being accrued via this mechanism. On the contrary, resource selection was relatively stable before and after wolf colonization (Messer et al. 2009, White et al 2009b), with no definitive changes in the nutritional status of elk during this time (White et al. 2009c, d).

These results suggest that elk maintain the same level of foraging time, and retain a relatively constant level of nutrition, by adopting other behaviors to mitigate indirect predation costs. Results from this system, and other wolf-elk systems, demonstrated many responses to predation risk such as changes in aggregation patterns (Hebblewhite and Pletcher 2002, Creel and Winnie 2005, Chapter 3), habitat shifts (Creel et al. 2005), and distribution and movement (Fortin et al. 2005, Gude et al. 2006, Hebblewhite and Merrill 2007, White et al. 2009b, Chapter 2). Increased group size by elk after wolf colonization of the Madison headwaters was accompanied by a decrease in the number of behavioral scans. Thus, these additional behavioral modifications may be balancing trade-offs between resource acquisition and vigilance (White et al. 2009c, d). If plasticity in behavioral responses allowed elk to forage efficiently in the presence of wolves, then these findings support the work of Lind and Cresswell (2005), Ajie et al. (2007), and Watson et al. (2007) who suggest that predation costs can be mitigated if prey integrate multiple behavioral responses collectively. Most studies correlate a single behavior with the apparent fitness cost of predation, but addressing collective responses simultaneously may provide a more realistic understanding of the fitness costs that predators inflict on their prey (Lind and Cresswell 2005, Ajie et al. 2007).

Integrating anti-predator behaviors in a multiplicative fashion, rather than considering these behaviors as additive could provide another explanation for the ability of prey to

maintain adequate foraging activities in the presence of predation risk. Frid (1997) explored the possibility that vigilance will increase as group sizes decrease, but this relationship will not be as strong if prey are close to a refuge. Vigilance in Dall's sheep (*Ovis dalli dalli*) was negatively correlated with group size, but the magnitude of the response decreased as they foraged closer to steep cliffs. This implied that animals did not redundantly invest in anti-predator behavior when risk was perceived as low (i.e. close to a refuge), even if they were in a small group. Alternatively, animals did not need to employ strong vigilance with increasing distance to a refuge when they were in larger groups. Following wolf reintroduction, a redistribution of elk in the Madison headwaters was observed, which can be attributed to differences in vulnerability within the heterogeneous landscape of this study system (Garrott et al. 2009b, White et al. 2009b). If elk select safe areas on the landscape to enhance their survival (i.e., refuge habitat such as rivers; Garrott et al 2009b, White et al. 2009b), then the integration of anti-predator behaviors could effectively reduce predation risk while maintaining foraging activities in the presence of wolves. Thus, remaining close to refugia may be more profitable and less costly than sustaining vigilance for long periods of time. In the Madison headwaters, this would appear even more attractive because the majority of the meadows are adjacent to rivers and increased vigilance is likely an unnecessary adjustment if elk can continue to feed, or conduct other daily activities, and simply flee into the river upon detection of wolves (Chapter 3; Figure 3.6 b).

Figure 4.5 The typical definition of vigilance assumes mutually exclusive behaviors. Thus, all other behaviors are interrupted while animals respond to an external stimulus (**A**). However, large herbivores have the capacity to conduct multiple behaviors simultaneously. This elk calf in the Madison headwaters of Yellowstone National Park continues to process forage while remaining aware of its surroundings (**B**). Also, a bedded bull elk surveys the area while masticating a bolus of regurgitated forage (**C**). Further, an adult, female elk masticates a bolus of regurgitated forage while walking and scanning in the direction of her travel (**D**) (Photos **A, B**, and **D** by Kevin Pietrzak. Photo **C** by Claire Gower).

In addition to adopting behavioral compensation to mediate the effects of wolves, it appears elk adaptively manage their foraging strategy to cope with environmental and temporal conditions - both in the presence and absence of wolves. These results supported predictions that the decision to forage was heavily influenced by depth and density of the local snow. On days when levels of local SWE_A at a specific location were high, the likelihood of foraging by elk was strongly reduced. Deep snow impedes access to forage and induces high energetic costs of searching for and moving between foraging patches (Sweeney and Sweeney 1984, Fancy and White 1985, Jenkins and Wright 1987). Thus, periods of reduced activity would be typical of animals attempting to minimize energy expenditure (Craighead et al. 1973). Due to the duration and the severity of the winter, however, high levels of local SWE_A persist for long periods of time and elk cannot give up feeding for extended periods. Thus, it seems elk attempted to minimize the detrimental effects of snow by selecting sites with reduced local SWE_A (Messer et al. 2008). In the absence of predation, elk generally selected low elevation meadows and geothermal areas (Messer et al. 2009), which coincided with the areas that a foraging bout was most likely to occur. This supported the prediction that these open habitat types were selected because they permit easier locomotion and access to relatively high quality forage than the closed habitat types (Craighead et al. 1973). The strength of selection for these sites increased after wolf reintroduction (White et al. 2009b), implying elk did not adopt the strategy of permanently moving to different habitats in the presence of predators (Mao et al. 2005, Kauffman et al. 2007). Rather, elk continued to forage in these areas at similar rates to that documented during the pre-wolf period. Even though these areas were heavily selected for by wolves (Bergman et al. 2006), they clearly

possessed foraging attributes which would appear essential to elk during these time of nutritional hardship.

Surprisingly, there was no evidence to support the prediction that the effect of forest succession would alter foraging by elk in the burned forest. Rather the consistently low likelihood of foraging among years in this habitat type may have been because sapling regeneration curbed the benefits of foraging several years after the initiation of this study. Also, a large proportion of the burned forests were on slopes or higher elevation plateaus, offering very little opportunity to forage without substantial energetic costs. Contrary to the predictions, the probability of foraging did not appear to coincide with periods of higher quantity and quality of forage, low snow pack during autumn and spring, or times of high nutritional demand (Craighead et al. 1973, Georgii and Schröder 1983, Green and Bear 1990). These results suggested that the likelihood of foraging remained constant through winter. This is not surprising in an environment like the Madison headwater where both the quantity and quality of forage biomass were lowest during winter and elk need to forage consistently through winter to avoid starvation. Time of day also played a significant role determining the likelihood of foraging by elk, with the likelihood of foraging coincided with dawn and dusk (Craighead et al. 1973, Green and Bear 1990, Ager et al. 2003). It has been suggested that these feeding patterns may be linked to maximizing energy intake rates, but could also be in response to predators (Leuthold 1977, Loe et al. 2007). If crepuscular foraging was linked solely to predation it would not explain why we observed crepuscular foraging pre-wolf reintroduction, though this inherent behavior evolved in the system with an intact predator guild and likely may not

be lost over the short evolutionary time span since anthropogenic activities have altered large predator abundance.

These studies provided insights into the adaptive behavioral strategies of elk to accommodate harsh environmental constraints during winter. Complementary components of this study (White et al. 2009b, d, Chapters 2 and 3) provide additional evidence that wolf colonization of the system may not necessarily be contributing detrimentally to these constraints. There was no evidence that foraging bouts were decreasing with wolves, and during the colonizing and the established periods elk did not scan the environment at a level that would contribute to any significant decrease of forage intake. The level of scanning did not substantially increase when wolves were present, and did not increase on days when a kill had been made within the drainage. Also, there was no evidence that elk selected poorer quality food in the presence of wolves (White et al. 2009b) or that nutrition was substantially lower when wolves occupied the system (White et al. 2009d). These results can be interpreted as evidence that large herbivores have evolved to live and forage efficiently in the presence of predators. I suspect this ability to apparently minimize nutritional costs of predator detection may at least partially be due to numerous senses elk may employ for predator detection (Hudson and Haigh 2002, Mech and Peterson 2003). Sight is just one of several senses that large herbivores employ to detect predators, as their acute auditory and olfactory senses would also allow them to forage and remain aware at the same time. In addition, the ability of large herbivores to simultaneously process food and be visually aware (Illius and Fitzgibbon 1994, Fortin et al. 2004a, b), and the development of a complex and sophisticated range of possible compensatory behaviors exhibited by large herbivores (White et al. 2009b,

Chapters 2 and 3), would provide elk with the capacity to cope with environmental constraints and lessen the effects of predation risk simultaneously (Figure 4.5).

While I did not directly observe any indication that nutritional costs are being derived via predation in the Madison headwaters, I do not doubt that the addition of wolves to central Yellowstone is an added complication to an already strained foraging strategy of elk. Contrary to other studies that have inferred quite significant reductions in foraging time due to wolves (Laundré et al. 2001, Childress and Lung 2003, Wolff and Van Horn 2003, Winnie and Creel 2007), this study concluded that potential detriments of predation pressure on foraging and nutrition were not substantially realized in Madison headwaters elk. These unequivocal results between studies likely reflect emphasis on differing behavioral activities, the subjective nature in classifying behaviors such as vigilance, and monitoring of elk that are in different physiological states. Also, the potential for several behaviors to occur simultaneously, the range of possible compensatory behaviors, and the types of sampling designs and statistical analyses employed by various studies will contribute to these disparities. These complicating factors demonstrate that employing observational studies to assess the indirect effects of predation in wolf-ungulate systems and obtain insights about this potentially important component of predator-prey interactions is fundamentally challenging.

Summary

1. Throughout the duration of this study 113,806 minutes of independent behavioral observations were collected from 108 individual radio-collared, adult, female elk during daytime in the Madison headwaters of Yellowstone National Park, to evaluate

changes in the proportion of time elk devoted to foraging before, during, and after wolf colonization.

2. The results showed that the likelihood of a foraging bout by elk was marginally higher in the presence of wolves. This finding may reflect that wolves actively hunted primarily during the crepuscular and nighttime periods, but were relatively inactive during the day. Thus, elk could sacrifice foraging for predator vigilance or avoidance during the high-risk nighttime period, but compensate by increasing foraging during the relatively low-risk daytime hours.
3. Elk never looked up during a high proportion of observation periods, even after wolves were established in the system. Behavioral scans by elk were short in duration and often occurred while the animals were chewing food prior to swallowing. Thus, there was little apparent reduction in foraging efficiency.
4. Elk can likely mitigate predation risk with only minimal effects on food acquisition due to their highly acute senses, ability to simultaneously scan the environment for predators and process food, and high plasticity in their behaviors.
5. In contrast to other studies, this study found little evidence that vigilance during foraging significantly reduced foraging efficiency. However, the literature is conflicting because different studies emphasize different behavioral activities, classifying vigilance behavior is subjective, foraging and vigilance behavior can occur simultaneously, and prey could compensate by employing other behaviors. Thus, studies of anti-predator behaviors come with limitations when trying to assess the foraging costs that wolves inflict on their ungulate prey.

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Appendices

Appendix 4.1 Complete model suite for the non-wolf and wolf models used in the logistic regression analysis to evaluate the factors influencing elk foraging behavior in the Madison headwaters area of Yellowstone National Park during 1991-92 through 2005-06. Abbreviations are: SWE_A (local-scale snow water equivalent), HBT (habitat), BFYR (burned forest*year interaction), SEASON (day within the season), $TIME_{day}$ (time of day), GROUP (elk group size), and $WOLF_{period}$ (pre-reintroduction, colonizing, and established).

Model number*	**Model structure - non-wolf models**
0	NULL
1	SWE_A + HBT
2	SWE_A + HBT + BFYR
3	SWE_A + HBT + SEASON + $SEASON^2$
4	SWE_A + HBT + $TIME_{day}$ + $TIME_{day}^2$
5	SWE_A + HBT + GROUP
6	SWE_A + HBT + BFYR + SEASON + $SEASON^2$
7	SWE_A + HBT + BFYR + $TIME_{day}$ + $TIME_{day}^2$
8	SWE_A + HBT + BFYR + GROUP
9	SWE_A + HBT + BFYR + $TIME_{day}$+ $TIME_{day}^2$ + SEASON +$SEASON^2$
10	SWE_A + HBT + BFYR + $TIME_{day}$ + $TIME_{day}^2$+ GROUP
11	SWE_A + HBT + BFYR + SEASON + $SEASON^2$ + GROUP
12	SWE_A + HBT + BFYR + $TIME_{day}$ +$TIME_{day}^2$ + SEASON + $SEASON^2$ + GROUP
13	SWE_A + HBT + $TIME_{day}$ +$TIME_{day}^2$ + SEASON + $SEASON^2$ + GROUP

Appendix 4.1 Continued. Complete model suite for the non-wolf and wolf models used in the logistic regression analysis to evaluate the factors influencing elk foraging behavior in the Madison headwaters area of Yellowstone National Park during 1991-92 through 2005-06. Abbreviations are: SWE_A (local-scale snow water equivalent), HBT (habitat), BFYR (burned forest*year interaction), SEASON (day within the season), $TIME_{day}$ (time of day), GROUP (elk group size), and $WOLF_{period}$ (pre-reintroduction, colonizing, and established).

Model number*	**Model structure - wolf models**
14 (1)	SWE_A + HBT + $WOLF_{period}$
15 (2)	SWE_A + HBT + BFYR + $WOLF_{period}$
16 (3)	SWE_A + HBT + SEASON + $SEASON^2$ + $WOLF_{period}$
17 (4)	SWE_A + HBT + $TIME_{day}$ + $TIME_{day}^2$ + $WOLF_{period}$
18 (5)	SWE_A + HBT + GROUP + $WOLF_{period}$
19 (6)	SWE_A + HBT + BFYR + SEASON + $SEASON^2$ + $WOLF_{period}$
20 (7)	SWE_A + HBT + BFYR + $TIME_{day}$ + $TIME_{day}^2$ + $WOLF_{period}$
21 (8)	SWE_A + HBT + BFYR + GROUP + $WOLF_{period}$
22 (9)	SWE_A + HBT + BFYR + $TIME_{day}$ + $TIME_{day}^2$+ SEASON + $SEASON^2$ + $WOLF_{period}$
23 (10)	SWE_A + HBT + BFYR + $TIME_{day}$ + $TIME_{day}^2$ +GROUP + $WOLF_{period}$
24 (11)	SWE_A + HBT + BFYR + SEASON + $SEASON^2$+ GROUP + $WOLF_{period}$
25 (12)	SWE_A + HBT + BFYR + $TIME_{day}$ + $TIME_{day}^2$ + SEASON + $SEASON^2$ + GROUP + $WOLF_{period}$
26 (13)	SWE_A + HBT + $TIME_{day}$ + $TIME_{day}^2$ + SEASON + $SEASON^2$ + GROUP + $WOLF_{period}$

* Model number in parentheses represents the associated non-wolf model pair.

Appendix 4.2. Complete model suite for the models used in the negative binomial regression analysis to evaluate the factors influencing the scanning behavior of elk in the Madison headwaters area of Yellowstone National park 1998-99 through 2005-06. Abbreviations are: GROUP (elk group size), HBT (habitat), $TIME_{day}$ (time of day), $WOLF_{presence}$ (presence or absence of wolves within a drainage on a given day), and KILL (number of wolf-killed ungulates within a drainage on a given day).

Model number	**Model structure**
0	NULL
1	GROUP
2	HBT
3	$TIME_{day} + TIME_{day}^2$
4	$WOLF_{presence}$
5	KILL
6	GROUP + HBT
7	GROUP + $TIME_{day} + TIME_{day}^2$
8	GROUP + $WOLF_{presence}$
9	GROUP + KILL
10	HBT + $TIME_{day} + TIME_{day}^2$
11	HBT + $WOLF_{presence}$
12	HBT + KILL
13	$TIME_{day} + TIME_{day}^2 + WOLF_{presence}$
14	$TIME_{day} + TIME_{day}^2$ + KILL
15	GROUP + HBT + $TIME_{day} + TIME_{day}^2$
16	GROUP + HBT + $WOLF_{presence}$
17	GROUP + HBT + KILL

Appendix 4.2. Continued. Complete model suite for the models used in the negative binomial regression analysis to evaluate the factors influencing the scanning behavior of elk in the Madison headwaters area of Yellowstone National park 1998-99 through 2005-06. Abbreviations are: GROUP (elk group size), HBT (habitat), $TIME_{day}$ (time of day), $WOLF_{presence}$ (presence or absence of wolves within a drainage on a given day), and KILL (number of wolf-killed ungulates within a drainage on a given day).

Model number	**Model structure**
18	$HBT + TIME_{day} + TIME_{day}^2 + WOLF_{presence}$
19	$HBT + TIME_{day} + TIME_{day}^2 + KILL$
20	$GROUP + TIME_{day} + TIME_{day}^2 + WOLF_{presence}$
21	$GROUP + TIME_{day} + TIME_{day}^2 + KILL$
22	$GROUP + HBT + TIME_{day} + TIME_{day}^2 + WOLF_{presence}$
23	$GROUP + HBT + TIME_{day} + TIME_{day}^2 + KILL$

CHAPTER 5

SYNTHESIS, DIRECTIONS FOR FUTURE RESEARCH, AND MANAGEMENT AND CONSERVATION IMPLICATIONS

Synthesis

Long-term monitoring of the Madison headwaters elk population since 1991 has resulted in an extensive database to assess demographic changes of elk before and after the reestablishment of wolves (Garrott et al. 2009a, b). Direct off-take by wolves was high and significantly contributed to a decrease in the elk population due to relatively high wolf kills rates and heavy selection on elk (Becker et al. 2009a, b). In addition to the significant direct lethal consequences of wolves on the Madison headwaters elk population, there is also evidence to document that elk appeared to respond behaviorally to the presence of wolves, presumably to mediate these direct lethal effects.

Relative to the pre-wolf observation period, elk in the Madison headwaters responded to wolves by altering their behavior in several different ways. Some behaviors changed only subtly while others were modified quite dramatically. Several modifications in elk space use (Chapter 2) were observed relative to the pre-wolf reintroduction period, including subtle increases in home range size and small reductions in annual site fidelity. Based on empirical observations in the field, the change in both of these parameters appears to reflect an increase in fine-scale movement within the animals' range. This would seem characteristic of animals using the landscape and the associated habitat components to balance competing demands. More dramatic spatial shifts were also

exhibited after wolves became an established component of the landscape. Long-distance sallies of short duration (1-3 days) were documented immediately, or shortly after, consecutive predation events upon a sub-herd. Also, long-distance movements (up to 63 km) were observed subsequent to a year with high wolf predation pressure within the animals' typical range. These range shifts lasted for an entire winter or resulted in permanent dispersal away from the Madison headwaters. In addition, some animals that had exhibited strong sedentary behavior when wolf predation pressure was low, adopted seasonal range shifts after reintroduction, and occupied a different winter range where the relative magnitude of wolf use was lower. These long-distance movements and shifts from sedentary to migratory behavior were only documented during the second half of the study and occurred only in areas where the magnitude of wolf use was high. This strongly suggests that spatial modifications could be attributed to the presence of wolves. Changes in aggregation patterns were also observed following wolf reintroduction (Chapter 3). The general trend showed a slight increase in group size compared to the average pre-wolf group size, and there was a rather strong correlation between the annual number of wolf days and annual mean elk group size. Finally, from this research I documented very little change in the way elk foraged with and without the presence of wolves on the landscape (Chapter 4). While I acknowledge that I was unable to quantify foraging cost that may have been incurred during the nighttime hours, I was able to conclude that there is very little evidence that wolves were causing any daytime foraging loss in this study. On the contrary, the number and frequency of foraging bouts may have actually increased after reintroduction, which suggests that elk may have been compensating for nighttime foraging loss when wolves were most actively hunting.

Regardless, in concert with other components of this study (White et al. 2009a) it would appear that the overall nutritional costs of predation were negligible.

A higher level of variation was associated with many of the behavioral responses after wolf reintroduction, suggesting that elk may have been adjusting their behavior at a fine temporal scale. The high energetic limitations of surviving in an environment with severe snow-pack allows limited flexibility for large herbivores to invest into anti-predator behavior for sustained periods. Therefore, I suspect that this more dynamic behavior reflected the need to balance competing demands, a reasonable explanation considering elk in the Madison headwaters are working within the confines of a severe winter environment. Additionally, the Madison headwaters is an environment where wolf predation pressure varies spatially and temporally, so maintaining prolonged anti-predator behavior may lead to excessive energetic costs. Similarly, there appeared to be discrete differences in the same behavioral response between elk herds at different geographical locations within close proximity. Group size in particular, seemed to vary quite significantly among sites (Chapter 3, Creel and Winnie 2005, Gude et al. 2006) and these differences in prey behavioral responses can be attributed to substantial differences in landscapes attributes such as snow pack severity and habitat types, complexity, and patch size that influence predation risk and dictate different prey behavioral responses. This illustrates that we cannot expect to generalize a uniform behavioral response. Rather, it would seem plausible that landscape attributes set the scene for the type of behavioral response that we would expect to see.

The benefit of anti-predator behavior is to reduce the risk of predation, but it is very hard to assess how effective these strategies are at reducing predation rates. The

functional response of the predator can be defined as the rate of prey captured by a predator as a function of prey abundance (Solomon 1949). Therefore, any action that reduces either the prey's relative availability, and/or increases predator capture efficiency or handling time will reduce the rate of being captured and consumed. Using long-term trend data on predator kill rates provides a crude measure with which to evaluate the efficacy of these behavioral responses, especially if there is some kind of association between increased anti-predator behavior and change in kill rate over time. In the Madison headwaters, it appeared that even though wolves were causing a substantial decrease in the elk population size (Garrott et al. 2009b), behavioral perturbations appeared to be affecting the efficiency in the way wolves successfully killed their prey. Larger groups of elk effectively seemed to curb the consumption rate of wolves in our system as shown by the negative correlation between mean annual elk group size and mean annual wolf kill rates on elk (Becker et al. 2009b). Also, effective use of habitat attributes within our study system may have been one reason for the lower kill rates in the Madison drainage (White et al. 2009b). Collectively, changes in behavior and changes in prey density due to direct mortality would both contribute to a change in the functional response of wolves. Creel and Creel (2002) described that an individual's risk of predation is not just defined at one stage of the predator sequence, but the probability of risk occurs at many different stages. Therefore, it seems plausible that different behaviors act to reduce the probability of being killed at different stages. If prey can adopt plasticity in their behaviors to alter the detection efficiency, encounter rate, the hunting and handling time of the predator, and/or results in the dilution of risk, it would allow prey to reduce the combined probability of the direct lethal effects.

Conversely, while risk effects are most commonly referred to as non-lethal, there is extensive literature expressing that defensive behavior of prey may have lethal ramifications, and can play a central role in shaping prey population demography and predator-prey dynamics (Lima and Dill 1990, Lima 1998, Bolnick and Preisser 2005, Preisser et al. 2005, Schmitz 2005). If indirect lethal consequences transpire, then anti-predator behavior may not alleviate the effects on prey communities. Rather, they may exacerbate the total predation effect. Work by Werner et al. (1983), and more recently by Schmitz (1998) and Nelson (2004), were able to quantify the direct effects of the predator from the trait-mediated indirect effects in small vertebrate and invertebrate systems. This approach showed that the demographic and developmental costs associated with predation risk could be quite substantial because the threat of predation alone could be responsible for reduced growth and maturation rates in prey. Reduced survivorship and subsequent reductions in prey population growth could also occur due to the loss of feeding opportunities and/or shifts to less productive habitat type. Additionally, reduced fecundity could contribute to population level decreases if prey sacrifice mating opportunities in risky environments, and/or redirect resources from reproduction to chemical or structural defenses.

Creel et al. (2007) discuss these same demographic and reproductive perturbations in relation to large herbivore systems, specifically linking anti-predator responses to reduced pregnancy and juvenile recruitment in elk. Creel and Christianson (2008) expand on this work by conceptually partitioning the indirect costs that are associated with the risk effects, from the direct mortality costs of predation; they draw upon an empirical case study to exemplify their point. This work provides an innovative view of

predation costs, clearly illustrating that it is misleading to assume that risk effects are totally benign to prey populations. It also presents new hypotheses pertaining to the strength of the risk effects in predator-prey systems. However, the lack of any empirical data showing reduced pregnancy rates in elk from the Madison headwaters study (Garrott et al. 2009b), and other studies in close geographical proximity (Hamlin et al. 2009), preclude any generalization of these indirect lethal effects in wolf-elk systems. Also, there are many gaps in our knowledge base concerning the mechanisms of these physiological effects, and so many confounding factors that could also be responsible for these demographic changes, that strong conclusions regarding these indirect lethal effects cannot easily be made.

Direction for Future Research

Future work will need to confront these discrepancies that have been identified between wolf-elk studies, and additional research using longer term datasets within and between locations is needed to test the hypotheses of Creel and Christianson (2008). Trying to quantify indirect costs of anti-predator behaviors will be a daunting task considering that each different behavioral response likely comes with a different cost. Behaviors also seem to change at short temporal scales and prey can adopt interacting responses at the same time. If additional research does support these predictions, however, then we can make stronger inferences regarding behavior and consequences at the individual and population levels.

Unlike direct mortality, population losses that arise from indirect lethal effects do not provide any consumptive benefits to the predator, and do not result in any increase in

predator numbers (Ives and Dobson 1987). Also, if prey adopt anti-predator behaviors that reduce the chance of predators actually capturing these extremely wary prey, it would seem rather unprofitable for predators to induce such strong, persistent, and costly behaviors in prey, such that their rate of consumption actually decreases. Instead, it would seem more advantageous for the predator to manage the behavior of their prey in such a way that the indirect lethal consequences are small and prey relax their anti-predator behavior when the threat of being killed is reduced – such relaxed behavior may in fact assist predators to capture unsuspecting prey (Brown et al. 1999, Lima 2002, Roth and Lima 2007). Therefore, while I have predominantly discussed prey behavior in this dissertation, we could gain some valuable insights by evaluating the predator's behavior as well. Indeed, the behaviors of each should not be considered independent from one another, but we should expect predators to strategically respond to the behavior of their prey, which in turn would likely further affect the anti-predator decision making of the prey (Lima 2002). Expanding the focus of this dissertation to develop hypotheses relating to the predator-prey shell games theory may provide important new insights into predator-prey dynamics. It is a relatively new area of research which needs to be more extensively explored in an empirical setting, and may help us to more fully understand the important link between individual ecology and population biology of both predator and prey.

Management and Conservation Implications

In general, these results show that elk do respond quite strongly to the presence of wolves, with these modifications having potential implications for management of both species. Probably one of the most widely discussed modifications is the changing spatial patterns of large herbivores and the strong ecological relevance pertaining to trophic cascades. This work and the work of others (Fortin et al. 2005, Gude et al. 2006) suggest that elk will manifest a more dynamic movement behavior as wolves course the landscape looking for prey. If elk no longer adopt the strategy of predictably feeding at one site, but are constantly moving to reduce further encounters with wolves, then predation may facilitate the dilution of foraging pressure on plant communities. Subsequently, these distributional changes could in turn have significant implications for resource managers because of the changes in ecosystem dynamics (Ripple et al. 2001, Beschta 2003, Smith et al. 2003, Fortin et al. 2005). Similarly, how elk aggregate and move across the landscape could have important implications when managing elk at the landscape level. Knowledge from an elk-wolf system could be applied into elk-human systems whereby human hunting pressure could be manipulated to encourage movement of large concentrations of elk that are seeking refuge on private patches adjacent to public lands. In fact, the recent work by Proffitt et al. (In press) quantified the effects of humans and wolves on elk behavior, with the effect of humans being more substantial on elk aggregation patterns and movement than the effects of wolves.

State agencies that manage large ungulate populations should also be aware that hunter opportunities could be affected if larger groups of elk are harder for hunters to

successfully harvest. Conversely, wolves may be responsible for moving elk out of Yellowstone National Park to areas where they become part of the harvestable population, leading to an increase in the opportunities for hunters adjacent to wildlife preserves such as parks. The accuracy of annual population estimates may also be affected if smaller aggregations of elk, and/or shifts to more closed habitat types impede the accuracy of aerial counts. Conversely, if elk are clumped in larger aggregations and/or use open meadow complexes when predators are present, counting could be facilitated. Additionally, decreasing ungulate populations may be confused with distributional shifts.

Finally, the seminal publication by Paine (1966) discussed the ecological consequences of keystone species on ecosystem structure and function, and points out the implications of predator removal on food web complexity and species diversity in an intertidal marine system. More recently, Heithaus et al. (2008) furthered this work and discussed the wider ecological consequences of the decrease of top marine predators, outlining both the direct and indirect consequences of marine predator loss. From this work it is evident that density and risk-driven ecological processes are both important mechanisms due to the cascading effects top predators have on entire marine communities. Prior to wolf reintroduction to Yellowstone, there was much uncertainty regarding the effects wolves would have on their prey, but their direct impacts have been well documented since their establishment (White et al. 2003, Vucetich et al. 2004, White and Garrott 2005a, b, Becker et al. 2009b, Garrott et al. 2009b, Hamlin et al. 2009). While there is certainly some debate regarding the additive contribution wolves play in population-level decreases, it is widely acknowledged that the direct demographic effects

have been larger than initially expected. Understanding the behavioral aspects of predator-prey dynamics contributes significantly to this body of ecological knowledge, and while this is certainly not a new concept, understanding the behavioral consequences of elk to wolves raises our understanding of the wider ecological role that top carnivores play in terrestrial environments. Insights from this study, and similar work elsewhere in the Greater Yellowstone Ecosystem, can be used to evaluate and predict the broader implications of future eradication and reintroduction programs, and can be applied to current and future conservation work.

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