APPLYING PREDATOR-PREY THEORY
TO EVALUATE LARGE MAMMAL DYNAMICS:
WOLF PREDATION IN A NEWLY-ESTABLISHED MULTIPLE-PREY SYSTEM

by

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ABSTRACT

I studied wolf prey selection and kill rates during 1996-97 through 2006-07 winters in a newly established two-prey system in central Yellowstone National Park. Prey differed substantially in their vulnerability to wolf (*Canis lupus*) predation and wolves preyed primarily on elk (*Cervus elaphus*) but also used bison (*Bison bison*) to varying degrees within and among winters and packs. Winter severity, wolf abundance, distribution, and prey selection varied during the study, concurrent with variations in the demography, distribution, and behavior of elk and bison. A total of 759 wolf-killed ungulates were detected and prey selection by wolves was influenced by the absolute and relative abundance of prey types, the abundance of predators, and the duration of snow pack. Wolves strongly preferred elk calves relative to all other prey types, and elk calf abundance was inversely related to the occurrence of bison in wolf diets. Increasing wolf numbers also broadened prey selection from elk calves, and predation on bison and adult elk increased with increasing snow pack accumulation and duration, likely due to its long-term debilitating influence. Elk abundance and wolf pack size best explained variation in kill rates for elk while bison calf abundance and snow pack duration best explained kill rates of bison. The functional response of wolves for elk was best described by a Type II ratio-dependent model, indicating significant predator dependence. Prey-switching evaluations indicated increasing selection of bison with increasing bison:elk ratios, however no concurrent decrease in elk predation occurred. Increased bison predation is not solely dependent on relative abundance of the two prey species; therefore it is unlikely at this time that wolf prey-switching will stabilize the system.

CHAPTER 1

INTRODUCTION TO DISSERTATION

Introduction

One of the most fundamental and dramatic interactions in nature is that of an animal capturing, killing, and consuming another. Perhaps due both to its importance and to the intrigue associated with it, predation has received considerable attention in ecological investigations, arguably as much or more than any other topic (Berryman 1992). Consequently, decades of productive research on predator-prey dynamics have revealed an immense complexity of direct and indirect demographic, behavioral, and spatial effects associated with predation in ecosystems (Holt 1977; Taylor 1984; Lima and Dill 1990; Schmitz et al. 2000; Sinclair and Krebs 2002; Creel and Christianson 2008; Heithaus et al. 2008).

Due to these complexities however, clear insights into predator-prey dynamics are often best gained with rigorous experimental designs that control for the abundance of confounding variables prevalent in natural systems. Thus, smaller taxa and systems more conducive to experimentation, such as invertebrates, fish, and small mammals, have comprised the majority of investigations (Solomon 1949; Holling 1959; Hassell 1978; Akre and Johnson 1979; Elliot 2006). These studies form the basis of predator-prey theory (Garrott et al. 2007) and their insights have found a myriad of practical applications for researchers, managers, and society at large to such issues as biological control, commercial harvesting, and wildlife and endangered species management (Yodiz 1994; Sinclair et al. 1998; Dixon 2000).

Large mammals assume prominent roles in most ecosystems, with large herbivores exerting considerable effects on the structuring of plant communities, species diversity, nutrient cycling, energy transfer, fire regimes, hydrology and soil erosion (McNaughton 1985; Frank and McNaughton 1992; Hobbs 1996; Collins et al. 1998). Large predators in turn, with their direct and indirect effects on prey and ecosystems, can exert equally important influences, and therefore understanding the mechanisms by which populations of prey and predators are limited or regulated in natural systems is essential to effective conservation and management of species and the processes they engender. Extirpation of top predators has been a pervasive human impact on ecosystems worldwide, with reintroduction recently becoming a widely accepted conservation practice. The effects of returning predators to systems in which they have been absent for several decades have been controversial however, largely because little information exists on these large mammal systems prior to predator removal and rigorous experimentation is not typically possible. Consequently, insights gained from studies of smaller taxa are typically used to predict the dynamics of large mammal predator-prey systems (Garrott et al. 2007).

While much of predator-prey theory is directly applicable to these systems there is evidence that some aspects may be worthy of more research to clarify their applicability. Recent investigations demonstrate the considerable influence that life history characteristics of both predator and prey can exert on ecosystem dynamics and the subsequent strength of "top-down" and "bottom-up" forces (Moran et al. 1996; Denno et al. 2002; Woodward and Hildrew 2002; Rosenheim et al. 2004). Given these insights it seems likely that differences in life history characteristics could result in differences in dynamics between large mammals systems and those that are typically the focus of investigations (Garrott et al. 2007). Not only do large mammals differ from smaller taxa in that they are larger, longer-lived, and slower to reproduce, but they can also differ fundamentally in the respective characteristics of predator and prey, as large mammalian prey are typically larger than their predators, have slower reproductive capacity, and are equipped with an array of sophisticated and dangerous defenses (Mech 1970; Kruuk 1972; Schaller 1972; Creel and Creel 2002; Garrott et al. 2007).

Actually evaluating the effects of these differences in natural systems not only necessitates the slow accumulation of observational data across a range of different case studies in order to make generalizations, but also requires that systems are studied across a range of predator and prey densities, something that is not typically possible without incredibly long time series that allow for perturbations (Garrott et al. 2007). However, large predator reintroduction provides a unique opportunity to effectively evaluate these dynamics across a potentially wide range of variation in predator and prey abundance, diversity, and distribution if predators exert a strong "top-down" influence on ecosystems (Garrott et al. 2007). One such valuable opportunity was the reintroduction of wolves into Yellowstone National Park in 1995, effectively reestablishing a top predator into multiple-prey systems that had not experienced wolf predation for nearly seven decades.

The objective of this dissertation research was to evaluate predator-prey dynamics in a newly-established wolf-elk-bison system in the Madison headwaters area of central Yellowstone National Park by applying several fundamental concepts in predator-prey theory to wolf predation data collected from 1996-97 to 2006-07. Chapter 2 explores sources of variation in wolf prey selection, evaluating the concepts of preference and vulnerability in a system where the prey types differ dramatically in abundance, size, defenses, behavior, and their responses to variability in climate and landscape features. I describe trends in prey selection within and among winters from nearly 800 wolf-killed elk and bison, analyze the potential drivers of variability in these trends, and ultimately test whether the stabilizing effect of prey-switching is occurring in the system. Chapter 3 describes wolf kill rates from 1998-99 to 2006-07 across a wide range of predator and prey densities and climatic variation, evaluating factors affecting variability in kill rates for elk and bison, as well as total kill rates, before determining the shape of the functional response for elk. Chapter 4 provides a synthesis of the research, discusses the applicability of current predator-prey theory for large mammal systems, and provides suggestions for future work based on these findings and the present trajectories of the Madison headwaters system.

Study Area

The Madison headwaters is approximately 31, 000-ha located in the west-central portion of Yellowstone National Park, Wyoming, USA (Fig. 1.1). Unlike most wolf predation studies, we did not follow wolf packs throughout their entire home range, but rather confined our investigations to the primary winter range of the two ungulate prey species present in the system. A non-migratory elk herd and migratory central bison herd defines the study area which is centered along the Madison, Firehole, and Gibbon river drainages (Garrott et al. 2008*b,c*; Bruggeman et al. 2008). Concurrent investigations of both bison and elk, and the accessibility of the study site, allowed us to evaluate wolf predation in a tractable area with a well-described ungulate prey base. The climate of the Madison headwaters is characteristic of mountainous areas in the region, with elevations ranging from 2250 to 2800 m and snow typically accumulating in late October and beginning to melt in early March (Watson et al. 2008*a*). Snowpack, measured in snow-water equivalents (SWE), ranges from 58 to 113 cm at peak (Natural Resource Conservation Service SNOTEL data, *available online*). SWE measures the amount of water in a column of snow, thus accounting for differences in snowpack density.

The landscape is characterized by a mosaic of river drainages and meadow complexes bordered by higher elevation forested plateaus (Newman and Watson 2008). River drainages are heavily influenced by geothermal features (Watson et al. 2008*b*), resulting in open water throughout the winter and concentration of ungulates in the resultant low-snow areas afforded by geothermal habitats. Meadow complexes are either wet and primarily comprised of sedges and marsh reedgrass (*Calamagrostis* spp.) or dry and composed of primarily tufted hairgrass (*Deschampsia caespitosa*) and grasses (*Festuca idahoensis, Poa* spp.) (Despain 1990). The predominant vegetation type in the system is lodgepole pine (*Pinus contorta*) which is present in various stages of mature and regenerating forest resulting from the 1988 fires burning approximately 50% of the area (Newman and Watson 2008).

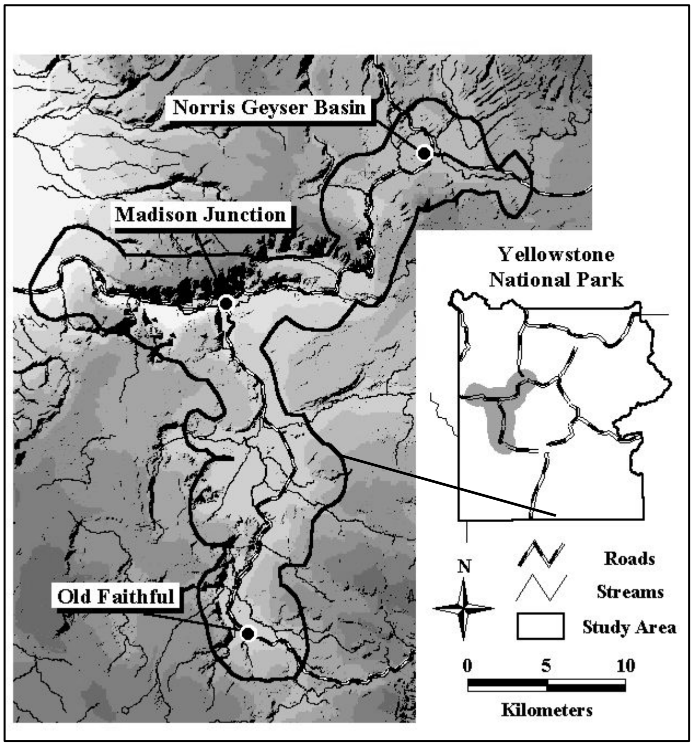

Figure 1.1 The Madison headwaters system in central Yellowstone National Park, USA, generally defined by the approximate boundaries of the elk winter range (from Messer 2003).

The ungulate prey base varied in abundance and composition both within and across winters, as the bulk of the central bison herd migration occurred mid-winter (Bruggeman et al. 2008). The Madison headwaters elk herd consisted of 200-600 animals during the course of the study, with a significant population decline evidenced in the latter years (Garrott et al. 2008*c*), while the central bison herd estimates for the study area ranged from 200-1500 animals and populations remained steady or increasing (Bruggeman et al. 2008; Fuller et al. 2008). Wolf reintroduction to Yellowstone National

Park occurred in 1995 and wolves were soft-released into the study area via acclimatization pens in three reintroduction efforts from 1996 to 1998 before a pack established a winter range in the study area in 1998-99 (Smith et al. 2008).

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CHAPTER 2

WOLF PREY SELECTION IN AN ELK-BISON SYSTEM: CHOICE OR CIRCUMSTANCE?

Introduction

In single predator systems predator-prey dynamics can be broadly classified by whether they are single prey or multiple prey systems. Predator diets can be relatively simple when only one prey type is present and few options exist. However, what a predator eats when given choices is a fundamental question germane to the multiple prey assemblages characteristic of most natural predator-prey systems. During the predatory sequence of encountering, attacking, and killing prey, most predators are assumed to select prey types based on abundance, thereby typically relying on encounter rates that are assumed to be random (Holling 1959). Once encountered, prey are frequently selected by sex, age, size, condition and behavior when individuals differ in their vulnerability to predation (Errington 1946; Morse 1980; Pastorok 1981; Greene 1986; Stephens and Krebs 1986; Quinn and Cresswell 2004). Selection across prey species can also differ based on their absolute or relative abundances and the life history characteristics of both predator and prey as manifested in morphology, defenses, and behavior. Thus, all of these variables have the potential to dramatically influence the dynamics of multiple-prey systems (Murdoch 1969; Moran et al. 1996; Denno and Peterson 2000; Denno et al. 2002; Rosenheim et al. 2004; Fitzgibbon and Lazarus 1995). While the physical vulnerability of a species or individual is of considerable importance in predatory interactions, environmental attributes can also influence vulnerability. Variables such as heterogeneity in climate, habitat structure, and landscape attributes can act alone or in concert with physical vulnerability to influence a predator’s diet (Smuts 1978; Peckarsky and Penton 1989; Hunter and Price 1992; Langellotto and Denno 2004; Hopcraft et al. 2005; Garrott et al 2008*a*).

Prey selection by predators in multiple-prey systems can have fundamental positive or negative effects on community stability and prey diversity (Oaten and Murdoch 1975; Murdoch and Bence 1987; Holt and Lawton 1994; Bonsall and Hassell 1997; Synder and Ives 2001). When a predator consumes a prey item disproportionately to its abundance it is said to exhibit a preference (Begon et al. 1996). Many predators have strong preferences for a certain prey type regardless of its abundance (i.e., specialist), and this strong preference is typically viewed as destabilizing to a predator-prey system (Andersson and Erlinge 1977; Hanski et al. 1991; Turchin and Hanski 1997; Eubanks and Denno 2000). Conversely, other predators consume a wide variety of prey, with changes in prey availability strongly affecting their patterns of selection (i.e., generalist). Prey switching behavior is typically associated with generalist predators and occurs when attacks are disproportionately frequent when a prey species is abundant and disproportionately infrequent when a prey species is rare (Murdoch 1969). Switching behavior by predators is generally viewed as stabilizing to a system because a predator can have a regulating influence through density-dependent predation on both prey species (Oaten and Murdoch 1975; Fryxell and Lundberg 1994). Thus, the patterns of prey selection a predator exhibits can have dramatically different ecological consequences (Paine 1966; Holt 1977; Caswell 1978; Hanski et al 1991; Fryxell and Lundberg 1994; Krivan and Eisner 2003).

Studies of predation and its effects on ecosystem stability are difficult because, even in experimental settings, disentangling the myriad factors influencing prey selection is quite complicated. Nevertheless, decades of investigations have increased our understanding of these processes (Murdoch 1969; Oaten and Murdoch 1975; Post et al. 2000; Krebs et al. 2001; van Balaan et al. 2001; Prugh 2005). Relative to investigations of smaller taxa, intensive long-term studies of prey selection and stability in large mammal systems are hindered by the logistic and financial constraints imposed by the broad spatial and temporal scale of investigations. However, large mammal systems have the potential to yield significant insights because the life history characteristics of top predators and large herbivores with strong ecological influences differ substantially from those of smaller taxa typically used in prey selection studies (Temple 1987; McNaughton 1985; Frank and McNaughton 1992; Hobbs 1996; Terborgh et al. 2001; Garrott et al. 2007). Unlike systems of smaller taxa where prey typically rely on avoiding detection, large herbivore prey species are formidable and diverse in their array of defenses and behaviors they can employ once encountered and attacked. These defenses preclude large predators from killing all types of prey with equal effort and subject the predator to constant risk of severe injury and even death (Makacha and Schaller 1969; Mech 1970; Kruuk 1972; Schaller 1972; Carbyn and Trottier 1987; Creel and Creel 2002; Mech and Peterson 2003; Smith et al. 2003; MacNulty et al. 2007). As a result, substandard or vulnerable individuals are frequently selected. This vulnerability often depends on attributes of the prey (e.g., age, size, physiological condition, behavior), environmental attributes, prey density, encounter rates, and the availability of alternative prey (see Mech and Peterson 2003 for review).

An impressive body of work has been compiled on wolf prey selection during the last several decades. Wolves are typically considered consummate generalists—opportunistic coursing predators taking advantage of whatever vulnerable prey are available within their territories (Mech 1970; Mech and Peterson 2003). However, virtually all wolf-ungulate investigations in multiple-prey systems have also demonstrated a clear selection for a particular prey species relative to other species in an assemblage (Carbyn 1983; Huggard 1993*a*; Dale et al. 1995; Jędrzejewski et al. 2000; Hebblewhite et al. 2003; Smith et al. 2004). Also, within a prey species wolves generally select certain age classes such as young-of-the-year (Mech 1970; Mech et al. 1995; Jaffe 2001; Smith et al. 2004) that could be considered different prey types due to differences in vulnerability. The dynamics of multiple-prey systems, and the mechanisms and conditions whereby wolf prey selection affects community stability and diversity have not been extensively investigated (Dale et al. 1995) and should yield insights into predation processes and the dynamics of large-mammal predator-prey systems.

Furthermore there is a need to formally evaluate prey switching for wolves (Dale et al. 1994), because switching has often been incorporated into models of wolf-ungulate dynamics and used to describe simple changes in predator diet composition rather than density-dependent predation (Garrott et al. 2007). Wolves exhibit many of the attributes common to predators that switch prey, including typically hunting by sight, cueing into the different areas where each prey species can be found (Bergman et al. 2006), and testing and evaluating individual prey (Murie 1944; Carbyn et al. 1993; MacNulty et al. 2007). Thus, it is feasible wolves could exhibit prey switching under some conditions. However, if prey preference for a particular species is strong, perhaps due to differences in vulnerability, then switching is unlikely to occur (Murdoch 1969; Murdoch and Marks 1973).

In addition to the ecological complexity inherent in studies of predation, comparative investigations are further complicated by the frequent use of terminology without consistent and explicit definitions and distinctions. Specifically, the concepts of prey selection, vulnerability, prey preference and prey switching are ubiquitously employed in predator-prey literature, but typically without concise definitions or differentiation. Prey selection is often considered to be what a predator eats when given choices, with no reference to the abundances of the various prey types available. Fundamental to this choice is the concept of differential vulnerability, or the factors that make an individual more susceptible to predation than other animals in a system. Vulnerability is considered to be of overriding importance in many predator-prey systems, especially those involving large mammals (Ivlev 1961; Mech 1970; Menge 1972; Power et al. 1992; Sinclair and Arcese 1995). However, precise definitions of vulnerability are infrequent and highly variable, ranging from the product of encounter rates and attack probabilities (Pastorok 1981; Greene 1986), “a combination of capture efficiency and profitability relative to risk” (Mech and Peterson 2003:140), to comprising “all of the behaviors that a prey can adopt to modify its risk of being targeted and caught when attacked" (Lind and Cresswell 2005:946). Disparities in definitions owe to the fact that quantifying vulnerability in most natural systems is extremely difficult because it is influenced by physical, behavioral, and environmental factors, and can vary among individuals, populations, species, and landscapes (Garrott et al 2008*a*).

Consequently, defining and quantifying prey preference is equally fraught with difficulties and most ecologists employ what Taylor (1984) terms the "black box" definition of preference, defined as when a predator selects a prey type disproportionately to its occurrence in the environment (but see Scheel 1993; Creel and Creel 2002). This interpretation is frequently employed in analyses because it serves as an umbrella for data that are rarely available in natural systems, encapsulating every decision a predator makes based on the myriad physical, behavioral, and environmental factors acting upon all stages of the predatory encounter, attack, and capture (Taylor 1984). Lastly, the definition of prey switching comes from Murdoch (1969) where "the number of attacks on a species is disproportionately large when the species is abundant relative to the other prey, and disproportionately small when the species is relatively rare." This indicates a preference that is not constant across all levels of abundances of the prey types but changes across a gradient of relative prey abundances, with a predator having a preference for the most abundant prey. Evaluations of dynamics in multiple-prey systems suffer from a lack of consistency in using the term "prey switching," with some investigators employing it to indicate a density-dependent change in predator preference (Murdoch 1969), while others use it to simply describe changes in predator diet composition.

I evaluated prey selection by wolves in a newly-colonized, bison-elk prey system in the Madison headwaters area of Yellowstone National Park during the winters of 1996-97 through 2006-07. Wolf numbers varied between 2-50 wolves in 1-5 packs after they were reintroduced and colonized the area beginning in 1995-96 (Smith et al. 2008). Elk were resident throughout the year, but their numbers decreased from approximately 600 to 174 following wolf establishment (Garrott et al. 2008*c,d*). In contrast, bison were seasonally migratory with numbers increasing through each winter (200-1500) until they exceeded elk numbers by several orders of magnitude in late winter (Bruggeman et al. 2008*a*,*b*). The dramatic contrasts in life history characteristics, movements, and abundance between these two prey species, coupled with variations in snow pack and wolf abundance, offered a unique opportunity to evaluate prey selection. Elk are smaller in size and prone to flight as an anti-predator behavior, while bison are larger and tend to employ sophisticated group defenses (Carbyn 1974; Carbyn and Trottier 1987; Carbyn et al. 1993; MacNulty et al. 2007). Our objectives were to (1) characterize wolf prey selection over time and among packs, (2) evaluate the drivers of wolf prey selection at the species- and age-class levels, and (3) evaluate if wolves switched from elk to bison in this multiple-prey system.

Methods

Detecting and Identifying Wolf Kills

We conducted intensive predation investigations in the primary winter ranges of bison and elk in the Madison headwaters area (31,000 ha), with concurrent investigations of these prey species allowing collection of wolf predation data in a tractable area with a well-described ungulate prey base. We documented prey selection by wolves during November 15 through April 30 each winter from 1996-97 through 2006-07. Our sampling unit was radio-collared wolf packs that used the study area as part of their territory. Wolves were aerially darted from helicopters by National Park Service biologists and equipped with VHF telemetry collars. A total of 37 wolves from four packs were collared during the course of the study (Smith et al. 2008).

The number and sizes of wolf packs using the study area were dynamic within and among winters. Thus, we used ground observations, snow-tracking, and aerial counts during tracking flights by park biologists to estimate the wolf population. I defined two metrics, wolf days and pack days, as one wolf or one pack in the study area for one day, respectively (Smith et al. 2008). I also defined multiple pack days as the number of days when more than one pack was present in the study area. We used roads traversing each river drainage in the study area (Newman and Watson 2008) to sample for wolf presence daily throughout the winter. Sampling began at dawn with ground crews of 3-4 people covering all roads by snowmobile or vehicle, and using strategic high points in the landscape to facilitate telemetry triangulations (White and Garrott 1990) and observations of wolves. When possible, multiple locations were obtained in early morning and evening each day. We also recorded any uncollared wolves detected opportunistically via tracks or observations to aid in the estimation of the wolf population using the study area. In addition, biologists studying elk and bison routinely covered backcountry areas to assist with wolf detection.

When wolves were located, we used visual scans and monitoring of avian scavengers in the vicinity to detect kills. Ravens preferentially associate with wolves in winter, and an average of 28.6 ravens (*Corvus corax*) were present at fresh wolf kills in the Northern range of Yellowstone Park (Stahler et al. 2002), with slightly lower averages in the Madison headwaters area (D. Stahler, National Park Service, personal communication). This association facilitated the detection of kills. We also conducted extensive snow-tracking after wolves departed the area to further facilitate kill detection (Huggard 1993*a*; Dale et al. 1995; Jędrzejewski et al. 2000; Jaffe 2001; Hebblewhite et al. 2003). We necropsied ungulate carcasses to determine cause of death, species, sex, age, and condition. Wolf kills were inferred from collective evidence of subcutaneous hemorrhaging indicative of injuries sustained before death, signs of struggle or chase at the kill site, blood trails, signs of predator presence, and our knowledge of wolf movements and activities. We documented frequent spring grizzly bear (*Ursus arctos*) predation on bison during the latter years of the study. Thus, when both bears and wolves were present on a kill, we classified it based on the patterns of injury and subcutaneous hemorrhaging. Bears typically attacked the head and spine, while wolves attacked the hindquarters and flanks. Similarly, mountain lion (*Puma concolor*) kills of elk were determined based on characteristics of the kill site and patterns of injury. Kills were sexed using the presence of genitalia, horns, antlers, or pedicels, and aged based on size and patterns of tooth eruption and replacement (Fuller 1959; Hudson et al. 2002). When available, an incisor or canine was removed from adult ungulates and aged using cementum annuli (Moffitt 1998; Hamlin et al. 2000). Marrow fat from the femur or humerus was assessed visually based on color and consistency, and classified as: 1) solid and white; 2) 50-75% solid with red spots; 3) 25-50% solid, reddish; and 4) 0-25% solid, gelatinous and red (Cheatum 1949). We also classified the extent of fluoride toxicosis and necrosis (0 = none, 1 = mild, 2 = moderate, 3 = severe) in jaws from adult animals because these ailments were relatively common due to the strong geothermal influence (Shupe et al. 1984; Garrott et al. 2002; Garrott et al. 2008*b*).

Observed patterns of wolf predation can be biased by differing rates of detection for various prey types, with smaller prey such as calves consumed faster and, thus, potentially detected less frequently (Fuller and Keith 1980; Fuller 1989; Hebblewhite et al. 2003). While this bias is more likely in aircraft-based studies or studies that do not use snow-tracking (Fuller 1989; Dale et al. 1995), recent studies have considered kill detection efficiency in ground-tracking (Jędrzejewski et al. 2000; Jaffe 2001; Smith et al. 2004; Hebblewhite et al. 2003). We empirically evaluated our efficiency in detecting kills and concluded our methods provided accurate data on wolf prey selection patterns (Jaffe 2001).

Factors Influencing Wolf Prey Selection

The probability of a prey animal being consumed by a predator is the product of the probability of being encountered by the predator, the probability of the predator attacking the prey once encountered, and the probability that the attack is successful (Endler 1991). I did not assess encounter rates and attack rates, but recognized that bison and elk calves could be considered separate prey items given their dramatic differences in vulnerability compared to adults (Fig. 2.1, Mech 1970; Carbyn and Trottier 1987; Mech et al. 1995).

Thus, I identified four main prey types available to wolves (i.e., elk calves, elk adults, bison calves, bison adults) in the Madison headwaters area.

Studies of prey selection in natural systems where encounter and attack rate data are unavailable typically employ selection indices (Lechowicz 1982), whereby the occurrence of a prey type in the predator's diet is compared to its abundance in the system. Thus, I calculated selection indices for the four prey types using Chesson's (1978) alpha method across early-, middle-, and late-winter periods from the establishment of resident packs in winter 1998-99 through 2006-07 to determine whether wolves selected any prey types disproportionately to their abundance.

Figure 2.1. An elk calf and bull bison feeding along the banks of the Firehole river. Elk calves and bull bison represent the extremes in prey sizes and defenses confronting wolves (Photo by Kevin Pietrzak).

However, selection indices in this context are limited to prey abundance questions. Therefore, I employed a multinomial logit analysis (Menard 2002) to evaluate the relative importance of prey abundance, predator abundance, and environmental variables on selection across prey species and age classes. I modeled four response categories corresponding to the four main prey types available to resident wolf packs. Each kill comprised an observation and I used elk calves as the base model because wolves tended to select them when available (Jaffe 2001, Smith et al. 2004). Three logits were modeled as $L_a(x) = \log[\pi_a(x)/\pi_0(x)](a = 1,2,3)$, where $\pi_0(\mathbf{x})$, $\pi_1(\mathbf{x})$, $\pi_2(\mathbf{x})$, and $\pi_3(\mathbf{x})$ were the probabilities of a calf elk, adult elk, calf bison, and adult bison response, respectively. $\pi_0(\mathbf{x})$ was the denominator (i.e., baseline response) of each odds ratio and $\mathbf{x} = (x_1, x_2, \ldots, x_p)$ was a vector of model covariates. A suite of covariates corresponding to prey, predator, and snow pack variables to evaluate factors influencing prey selection by wolves was developed and chosen based on our knowledge of the system and variables reported to significantly influence prey vulnerability and selection by wolves in other systems. I estimated covariates for the date that each wolf kill occurred.

Wolf population structure consisted primarily of territorial packs, each occupying a particular territory, though often with considerable overlap (Smith et al. 2008). Prey abundance also varied temporally and spatially, with bison prone to frequent large-scale movements between drainages (Bruggeman et al. 2008*a,b*). Thus, all prey in the study area were not equally available to all wolf packs, and such disproportionate abundance could affect wolf diets. Therefore, I estimated prey abundance at a scale contained within the river drainages (Madison, Gibbon, Firehole) of each pack’s respective territory. I determined the drainages used by each pack each winter by constructing 95% fixed kernel territories from ground locations collected from November 15 through April 30 each winter (Smith et al. 2008). I excluded temporary probes by packs into other drainages from these calculations as they were rare and their inclusion would likely overestimate prey abundance for wolf territories.

I estimated abundance covariates ($\mathrm{ELK}_{\mathrm{calf}}$, $\mathrm{ELK}_{\mathrm{adt}}$, $\mathrm{BISON}_{\mathrm{calf}}$, and $\mathrm{BISON}_{\mathrm{adt}}$) for the four prey types within each drainage by decomposing the 167-day winter field season into three approximately 8-week periods corresponding to early, middle, and late winter. The non-migratory elk population (Craighead et al. 1973, Garrott et al. 2003) was not subject to the dramatic fluctuations in abundance characteristic of migratory populations, and typically only experienced decreases across winter due to starvation and predation, particularly of calves (Garrott et al 2008*c,d*). Consequently, I estimated the abundance of adult elk and calves during early, middle, and late winter using mark-resight techniques and age composition data (Garrott et al 2008*c,d*). We conducted multiple mark-resight surveys in late winter (n =10-33) when elk were concentrated in meadow complexes. We also estimated calf:cow ratios during early and late winter using the respective first and last 100 random elk groups obtained from telemetry sampling (Garrott et al 2008*c,d*). I then estimated adult elk abundance ($\mathrm{ELK}_{\mathrm{adt}}$) for the early- winter period by multiplying the previous spring's mark-resight population estimate by a pooled summer survival rate of 0.95 derived from telemetry data (Garrott et al 2008*c,d*). I assumed 85% of the adult population was females (Garrott et al 2008*c,d*) and multiplied the early-winter adult female estimate by the early-winter calf:cow ratio to obtain an early-winter calf ($\mathrm{ELK}_{\mathrm{calf}}$)

estimate. Similarly, I multiplied the adult cow estimate by the late-winter calf:cow ratio to obtain the number of elk calves remaining in the late-winter period. A late-winter adult elk estimate was then calculated by subtracting the late-winter calf estimate from the total late-winter mark-resight population estimate. I averaged the respective means of the early- and late-winter estimates to approximate the abundance of both adult and calf elk for the mid-winter period. While elk distribution among the three drainages varied among winters (White et al 2008*c*), there was little elk movement between drainages within winters (Gower et al. 2008*c*). Thus, I multiplied our estimates by the proportion of the elk population observed within each drainage during the spring mark-resight surveys to estimate the abundance of both prey types within each of the three drainages. Lastly, I estimated a covariate for the total abundance of elk (ELK) by summing the adult and calf estimates.

We estimated bison adult and calf abundance ($\mathrm{BISON}_{\mathrm{adt}}$ and $\mathrm{BISON}_{\mathrm{calf}}$, respectively) by conducting ground counts through the winter range every 10-16 days, with observers recording the number, location, sex, and age class of all observed bison. Each drainage was subdivided into discrete survey units and bison totals for each drainage were calculated by summing the respective unit totals. Because substantial changes in bison abundance could occur between surveys, I interpolated between estimates to derive the bison abundance estimates for the date of each wolf kill. I also estimated a total bison abundance covariate (BISON) by summing the adult and calf estimates. In addition, I calculated the ratio of bison to elk abundance (BISON.ELK) by dividing the bison estimate by the elk estimate.

The high density ungulate winter range of the Madison headwaters experienced considerable wolf use despite comprising a relatively small area. Following the establishment of multiple packs in the system there was a substantial increase in wolf abundance, spatial and temporal territory overlap, and inter-pack strife (Smith et al. 2008). These dynamics, coupled with increases in elk anti-predator responses to increasing wolf numbers (Gower et al. 2008*a,b,c*; White et al. 2008*c*) and decreasing elk numbers (Garrott et al 2008*d*), were negatively related to kill rates for wolves using the system (Chapter 3) and likely affected prey selection. Thus I developed three covariates to index the strength of these competitive interactions: the wolf:ungulate ratio (WOLF:UNG); the wolf:elk ratio (WOLF:ELK); and multiple pack days ($\mathrm{PACK}_{\mathrm{mult}}$). I estimated each of these as population level indices for early-, middle-, and late-winter periods across the entire study area because wolf territories often overlapped extensively, pack territories often included more than one drainage, and adjacent packs likely influenced each others' movements and behaviors (Smith et al. 2008). I calculated the wolf:ungulate and wolf:elk ratios by dividing the total wolf days estimated for the time period by the number of days in the period, and then dividing by the mean elk and bison estimates. I estimated multiple pack days by summing the total number of days in a period during which more than one pack was detected in the study area.

Snow pack substantially decreases ungulate mobility and increases their vulnerability to wolf predation (Peterson 1977; Parker et al. 1984; Nelson and Mech 1986; Huggard 1993*b*). Snow depth, density, and crusting can impede escape for ungulates that employ flight as an anti-predator tactic. Snow depth is not an accurate integrator of snow pack attributes due to differences in density, crust conditions, and layers. Thus, I described the temporal and spatial dynamics of snow pack using a validated snow model (Watson et al. 2008) to estimate mean daily snow-water equivalents (i.e., the amount of water in a column of snow; SWE_{mean}), for the Firehole, Gibbon, and Madison drainages during October 1 through April 30. When a pack's territory encompassed more than one drainage, I calculated mean snow pack metrics across the two drainages. SWE_{mean} was estimated for the date of each wolf kill to provide an indirect measure of prey escape ability.

The nutrition and condition of ungulates in mid- to high-latitude systems decrease through the winter because most forage is senescent and animals must forage and travel through snow (White et al. 2008*a,b*). Consequently, the accumulation and duration of snow pack can have a long-term weakening influence on ungulate physiological condition that can ultimately be lethal in severe winters (Murie 1944; Severinghaus 1947; Jędrzejewski et al. 1992; Garrott et al. 2003). I estimated the sum of daily snow-water equivalent values beginning on October 1 each winter (SWE_{acc}; Garrott et al. 2003) for the date of each kill to provide an indirect measure of ungulate physiological condition.

I developed and evaluated *a priori* hypotheses to estimate the relative influence of prey abundance, snow pack, and wolf competition on wolf prey selection of ungulate species and age classes. Our *a priori* hypotheses were expressed in four main model structures incorporating prey abundance and other potential covariates of snow pack and wolf competition (Appendix A). For each covariate, I then identified the metrics I believed were appropriate for estimation. I developed 84 candidate models in the form of multinomial logit equations to evaluate our hypotheses. Three logit equations were generated for each candidate model, describing (1) the probability of an elk adult kill compared to an elk calf kill, (2) the probability of a bison calf kill compared to an elk calf kill, and (3) the probability of a bison adult kill compared to an elk calf kill.

For comparison of coefficient estimates, I scaled and centered each covariate prior to analysis by subtracting the dataset's midpoint from each covariate value and dividing them by the dataset's midrange. This restricts each covariate's values to fall within -1 and 1, inclusively. I assessed potential colinearity between covariates using variance inflation factors and did not use covariates with values >6 in the same model (Neter et al. 1996). Covariates that were not used in the same model due to strong colinearity were $\text{BISON}_{\text{adt}}$ and $\text{BISON}_{\text{calf}}$, SWE_{mean} and SWE_{acc}, and combinations of MULTPK, WOLF:UNG, or WOLF:ELK. I fitted all models in R version 2.4.1 using the function multinom in the nnet package (R Development Core Team 2006). Models were compared using Akaike's Information Criterion corrected for small samples (AIC_c; Burnham and Anderson 2002). I calculated Akaike weights and evaluated the importance of each covariate by its predictor weight (w_p), which I calculated by summing the Akaike weights for all models containing the covariate in the final model suite (Burnham and Anderson 2002). Our model selection followed a stepwise procedure within each suite, whereby I first fit all candidate models, calculated AIC_c and model weights and then determined for a given model structure which metric best estimated a given covariate. For example, if the three top models had identical structure and differed only by their inclusion of a different metric of wolf competition (WOLF:UNG, WOLF:ELK, MULTPK), then I determined which model was best-supported and removed the other two models from among suite comparisons. Among suites, I then recalculated model weights for the reduced set of models once I had determined the best metric for a given model structure.

Because elk are considerably more vulnerable to wolf predation than bison (MacNulty 2002), I predicted that covariates of bison abundance ($\text{BISON}_{\text{adt}}$, $\text{BISON}_{\text{calf}}$, BISON, BISON.ELK) would have no effect on the probability of wolves eating adult versus calf elk. I also predicted that elk abundance covariates (ELK_{adt}, ELK_{calf}, ELK) would be negatively related to the probability of wolves eating a bison adult or bison calf given that low elk abundance (absolute and relative to bison) would likely compel wolves to kill bison with increasing frequency. In addition, I predicted the probability that wolves would kill bison compared to elk calves would increase with the relative and absolute numbers of bison because the number of vulnerable individuals in the bison population would likely increase with the influx of migrating animals during winter.

I predicted that winters with more severe snow pack, as indexed by SWE_{acc}, would be positively correlated with wolves killing both bison age classes and adult elk because the larger and less vulnerable species and age classes would become weakened and relatively more vulnerable. Given that elk and bison differ in their responses to wolves when encountered and attacked, with elk typically employing flight and bison resorting to group defense (Carbyn 1974; Carbyn and Trottier 1987; MacNulty 2002), the two snow pack metrics could have different effects on vulnerability across species. Specifically SWE_{mean} could be more influential in predation of elk, as increasing values of SWE_{mean} equate to decreased mobility, while SWE_{acc} could be more influential in predation of bison by weakening their ability to defend themselves against attack. In addition, I predicted that competition imposed by multiple wolf packs (indexed by MULTPK, WOLF:UNG, and WOLF:ELK) would have a positive influence on the probability of wolves taking bison because packs competing for limited and decreasing elk resources would likely need to pursue other prey species to persist. Similarly, I predicted increasing wolf competition would result in increased selection for adult elk as wolves expanded through the study area.

Cooperative-hunting large carnivores often exhibit a positive relationship between group size and prey size (Rosenzweig 1966; Gittleman 1989; Creel and Creel 1995). However, the relationship between pack size and prey size for wolves is unclear (Mech and Boitani 2003). I did not expect pack size to be positively correlated with prey size, but added a pack size covariate ($WOLF_{pk}$) to the best-supported *a priori* models to determine if the covariate improved model fit.

Prey Switching

Evaluating if wolves are capable of prey switching, or have a strong preference for elk regardless of bison abundance, cannot be determined by examining diet composition alone (Garrott et al. 2007). Thus, I evaluated wolf preference and potential prey-switching by relating the relative availability of bison and elk in the study system with the ratio of the two prey species in the wolves' diet. Murdoch (1969) provided the classic equation that relates the ratio of two prey types eaten by a predator (g_1/g_2) to the ratio of the prey types available to the predator (N_1/N_2). I evaluated the existence and extent of wolf prey switching by regressing the ratio of bison and elk in wolf diets to the ratio of bison and elk available in the population and evaluating the subsequent form (i.e., linear or nonlinear) of the relationship (Murdoch 1969; Garrott et al. 2007). I used Murdoch's (1969) selection coefficient where the ratio of the two prey types eaten is denoted by:

$$\frac{g_{bison}}{g_{elk}} = c\frac{N_{bison}}{N_{elk}} \tag{1}$$

The left-hand side of Equation 1 is the ratio of bison to elk in wolf diets and N_{bison}/N_{elk} is the ratio of bison to elk in the population. The proportionality constant, *c*, measures "the bias in the predator's diet to one prey species" and relates the ratio of prey eaten to their relative abundance (Murdoch 1969:337). If wolves exhibit a high plasticity in their diet, then prey selection would likely change depending on the relative availability of the two prey types as determined by their abundance, vulnerability, and actual predator preference (Garrott et al. 2007). This dynamic nature of *c* can be incorporated by modifying the equation to allow changes in diet with changes in relative availability of elk and bison:

$$\frac{g_{bison}}{g_{elk}} = \left(c\frac{N_{bison}}{N_{elk}}\right)^{b} \tag{2}$$

The variable *b* is a measure of the extent of prey switching, bounded by zero and with values greater than one denoting switching (Greenwood and Elton 1979; Elliot 2004). If wolves preferred elk proportional to relative abundance ratios of the two prey, then I would expect the relationship between diet and abundance ratios to be linear (Murdoch 1969; Garrott et al. 2007) because wolves would continue to prefer elk over all ranges of relative abundance ratios, even when elk were rare relative to bison (Fig. 2.2). However, if wolves exhibit prey-switching then the relationship should be curvilinear and indicate a diet switch to the more abundant prey with increasing bison:elk ratios (Murdoch 1969; Garrott et al. 2007).

Obtaining sufficient data on the ratio of bison to elk in wolf diets required a time-scale of three winter periods of approximately eight weeks each, during which time bison abundance varied substantially among drainages (Bruggeman et al. 2008*a,b*). To account for this, I estimated prey abundance for the entire study system each winter period and calculated the ratio of the two prey species in wolf diets by pooling all wolf-killed elk and bison detected during the respective periods and deriving a ratio of bison to elk (g_{bison}/g_{elk}). Relative abundance ratios of prey (N_{bison}/N_{elk}) were estimated by calculating mean bison population estimates from surveys conducted during the early-, middle-, and late-winter periods and dividing by elk population estimates for these periods. Elk estimates by winter period were calculated similarly to the multinomial model. Twenty-seven data points were generated corresponding to nine years of three winter periods each. To determine the form of the relationship between the wolf diet ratio and the ratio of prey abundance, I fit Equation 2 to these data and estimated parameter coefficients using the nls function from the nlme package in R version 2.4.1 (R Core Development Team 2006).

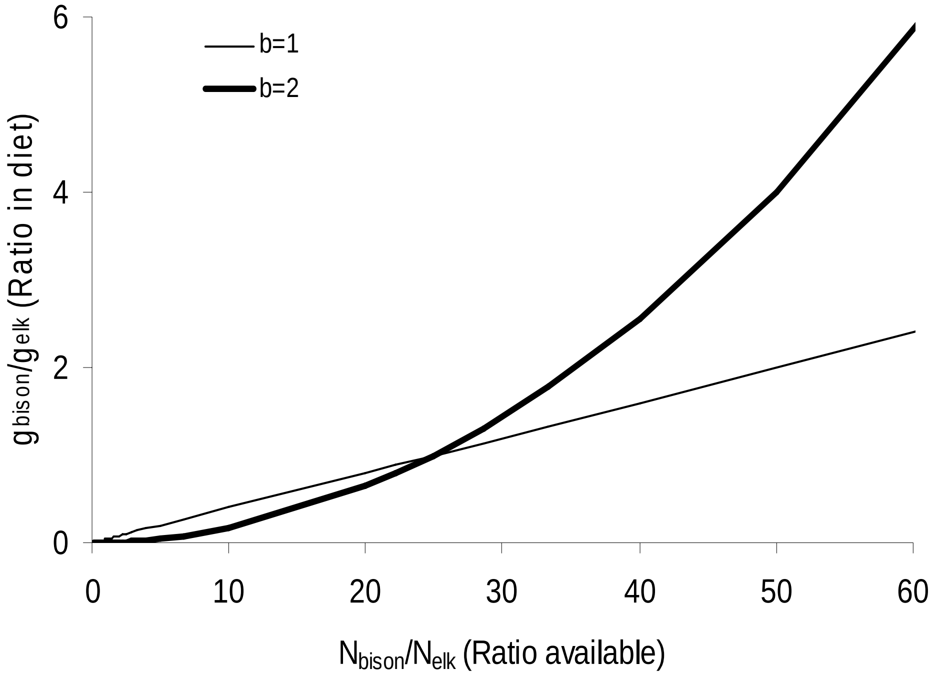

Figure 2.2. Theoretical relationship between the ratio of bison to elk in wolf diets versus the ratio of bison to elk available in the population. Curves for the scenarios for no prey switching (b = 1) and prey switching (b = 2) are depicted (Murdoch 1969; Garrott et al. 2007).

Results

Wolves were detected in the study area on 1306 days of the 1837 day study period, comprising a total of 16,801 wolf days, 1872 pack days, and 437 multiple pack days. We obtained 1369 telemetry locations, 534 visual locations, and 4175 km of backtracking. Approximately 6600 person days were spent in the field, and an estimated 368,000 kilometers were logged on snowmobiles and vehicles.

Wolf presence during the 167-day winter field season ranged from 60-3964 wolf days, with pack days and multiple pack days ranging from 19-383 and 0-128, respectively. Established packs ranged in size from 2-22 wolves (mean = 9.6; 95% CI = 9.4, 9.8), and the percentage of days wolves were detected during the field season ranged from 19-96%. Ten different wolf packs used the Madison headwaters area to varying degrees over the course of the study, with wolves first detected during the winter of 1996-97 when several itinerant wolves used the area and the Nez Perce pack was soft released into the Firehole drainage (Smith et al. 2008). The Nez Perce pack became established in the study area during 1998-1999, and was the only resident pack until the winter of 2002-03 when the Cougar pack and another uncollared pack in the Gibbon drainage used portions of the study area. Two more packs became established in the study area during 2003-04, and wolf presence peaked in 2004-05 with up to five packs totaling approximately 45 wolves using the study area (Smith et al. 2008). The wolf population decreased precipitously during winter 2005-06 to primarily one pack, before increasingly to primarily three packs and an estimated 21 wolves the following winter (Smith et al. 2008).

Elk population estimates for the study area ranged from 290-664 in autumn to 174-577 in spring, with the population decreasing 5-42% during winter. A progressive decrease in the elk population began in 2003-04 and continued through spring 2007 when the population was estimated at 174 animals (Garrott et al 2008*d*). Elk were equally distributed among the three drainages until the winter of 2000-01 when the proportion of animals in the Madison drainage abruptly increased, accompanied by the virtual elimination of elk in the Gibbon drainage, and a gradual decrease in the Firehole drainage to a low of 28 animals (16% of the population) by the end of the study (Gower et al.

2008*c*; White et al. 2008*a*). The proportion of elk in the Madison drainage gradually increased to 84% of the population in late-winter 2006-07. Calf abundance also decreased 48-98% during each winter (Garrott et al 2008*d*). Elk abundance estimates within pack territories ranged from 28-331 total animals, 0-84 calves, and 28-271 adults.

We conducted 114 ground distribution surveys of bison from 1997-98 to 2006-07, with abundance ranging from 205-1538 animals using the study area. Bison abundance generally increased as winter progressed and animals migrated into the study area from the Hayden and Pelican Valleys (Bruggeman et al. 2008*a,b*). Estimated bison abundance in pack territories ranged from 20-1108 animals, with 3-271 calves and 17-952 adults. With fluctuating populations of both prey and predator within and across seasons, we also documented considerable variation in the ratios of bison:elk, wolf:ungulate, and wolf:elk. Estimates ranged from 0.10-29.57 for bison:elk ratios, 0.003-0.038 for wolf:ungulate ratios, and 0.006-0.100 for wolf:elk ratios, respectively.

Snow pack accumulation in the study area typically began in late October (Watson et al. 2008) and increased until late March when spring melt began, particularly in the lower-elevation meadows and drainages. Snow pack during the course of the study was below historical averages, with annual maximum SWE_{acc} values ranging from 1023-3612 cm days and averaging 2044 cm days (95% CI = 2038, 2050). Maximum SWE_{mean} values ranged from 9.8-31.9 cm and averaged 18.8 cm (95% CI = 14.0, 23.6).

A total of 759 wolf-killed ungulates and 21 canids were detected during the study period. Ungulate kills were comprised of elk (79.8%, *n* = 606), bison (19.9%, *n* = 151), moose (0.1%, *n* = 1), and mule deer (*Odocoileus hemionus*; 0.1%, *n* = 1), while wolf-killed canids consisted of coyotes (71.4%, *n* = 15), wolves (23.8%, *n* = 5), and red fox (4.8%, *n* = 1). Detected kills varied from 14-106 among winters, with a mean of 81.0 kills (sd=16.8) following wolf establishment in 1998-99. Elk were the primary prey species for wolves, with calves and adult females comprising 38% (*n* = 292) and 32% (*n* = 241) of total kills, respectively (Table 2.1).

Table 2.1. Numbers of bison and elk carcasses killed by wolves and detected in the Madison headwaters area of Yellowstone National Park during 1996-97 through 2006-07.

Winter	**Total Elk**	**Total Bison**	**Elk Calves**	**Elk Cows**	**Elk Bulls**	**Bison Calves**	**Bison Cows**	**Bison Bulls**
1996-97	13	1	5	5	0	1	0	0
1997-98	15	0	11	4	0	0	0	0
1998-99	51	12	31	11	8	12	0	0
1999-00	49	3	28	19	2	1	1	0
2000-01	71	2	39	30	1	2	0	0
2001-02	75	16	32	33	10	9	5	2
2002-03	61	14	30	23	5	5	6	3
2003-04	82	24	30	41	11	12	9	3
2004-05	61	33	31	19	11	16	7	9
2005-06	47	37	22	21	4	26	11	0
2006-07	81	9	33	35	12	3	4	2
Totals	**606**	**151**	**292**	**241**	**64**	**87**	**43**	**19**

Note: Age class and sex totals do not include kills that could not be categorized by age.

The percentage of bison in the pooled diets of resident wolf packs increased from zero soon after wolf recolonization to 53% (*n* = 29) in winter 2005-06, when bison comprised the primary prey species (Fig. 2.3). However, the proportion of bison in wolf diets decreased to 15% during winter 2006-07 (*n* = 9). Prey selection by wolves was predictably variable within winters, with elk calves primarily killed in early-middle winter, bison killed during middle-late winter, and adult elk killed throughout winter

(Fig. 2.4). Selection indices calculated for early-, middle-, and late-winter periods from 1998-99 through 2006-07 demonstrated a strong preference only for elk calves (mean=0.82, sd=0.12) throughout every winter, with selection by winter period summarized in Table 2.2.

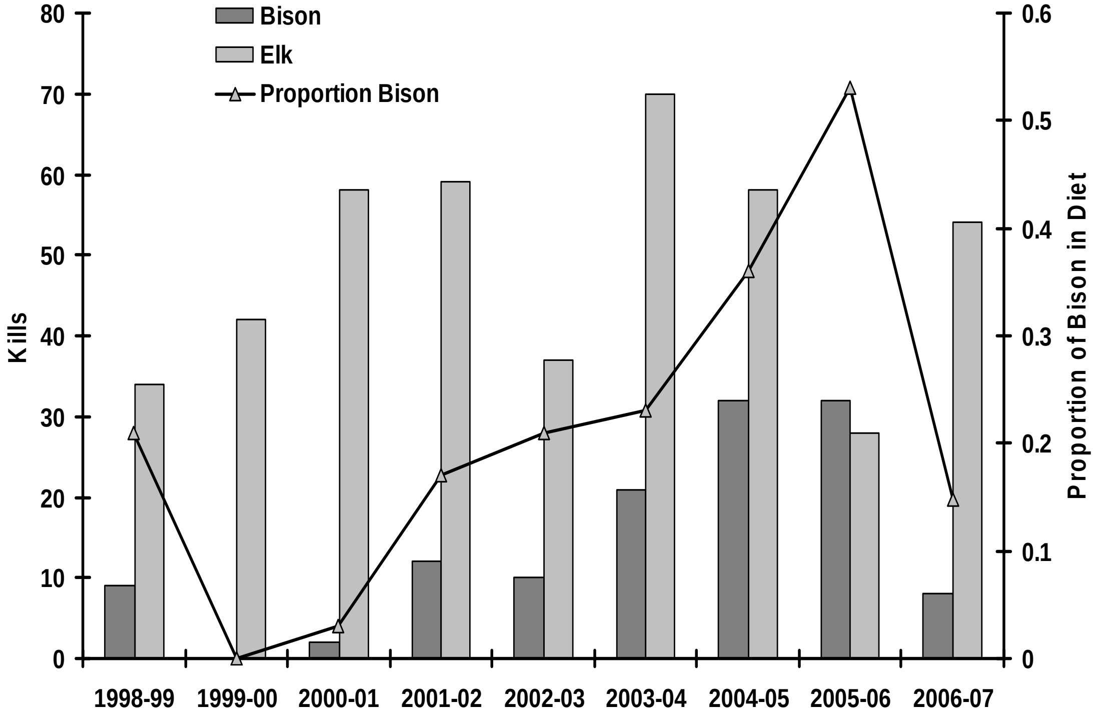

Figure 2.3. Wolf-killed elk and bison from resident packs in the Madison headwaters area of Yellowstone National Park during 1998-99 through 2006-07 (n = 566). Bison steadily increased in the diet until the mild winter of 2006-07 when considerably more elk were killed despite a substantial decrease in elk abundance.

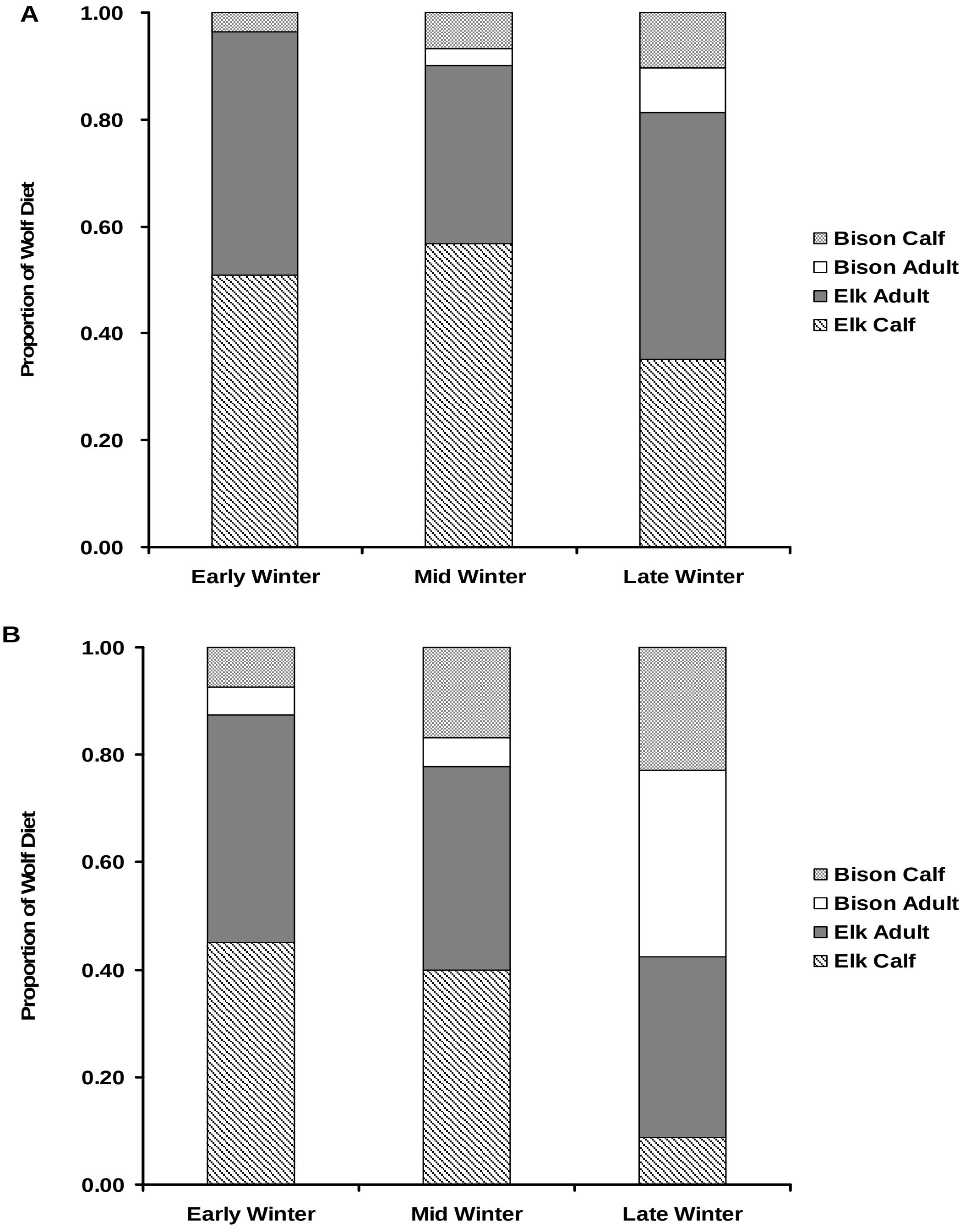

Figure 2.4. Winter trends in pooled diet composition from resident wolf packs in the Madison headwaters area of Yellowstone National Park during (a) 1998-99 through 2002-03 (*n* = 262) and (b) 2003-04 through 2006-07 (*n* = 302). Kills were classified by species, age class, and winter period (early = November 15-January 10; middle = January 11-March 6; late =March 7-April 30).

Table 2.2. Selection indices (Chesson 1978) for four prey types from resident wolf pack kills during winters 1998-99 through 2006-07.

	Index of Selectivity		
Prey Type	**Early Winter**	**Middle Winter**	**Late Winter**
Elk Calf	0.752	0.827	0.816
Elk Adult	0.176	0.094	0.098
Bison Calf	0.059	0.073	0.070
Bison Adult	0.013	0.006	0.016

Note: Kills were classified by species, age class, and winter period (early = November 15-January 10; middle = January 11-March 6; late = March 7-April 30). For *m* prey types a value greater than 1/*m* (i.e. 0.25) indicates a preference.

Marrow samples from 121 bison (52 adults, 69 calves) and 481 elk (275 adults, 206 calves) indicated condition decreased from early- to late-winter periods (Fig. 2.7). Of the 120 elk jaws that were rated for necrosis, 50% (*n* = 60) showed no signs of necrosis, 18% (*n* = 21) were mild, 16% (*n* = 19) moderate, and 17% (*n* = 20) severe. Eleven bison jaws were rated, with 55% (*n* = 6) showing no signs of necrosis, 36% (*n* = 4) moderate, and 9% (*n* = 1) severe.

Mean ages of adult elk (*n* = 280) and bison (*n* = 44) killed by wolves were 8.3 years (95% CI = 7.8, 8.8) and 10.0 years (95% CI = 8.4, 11.6), respectively. Adult female elk killed by wolves were older than males, with a mean female age of 9.1 years (*n* = 220; 95% CI = 8.6, 9.7) and a mean male age of 5.6 years (*n* = 58; 95% CI = 4.6, 6.5). Ages of adult bison killed by wolves were older for females compared to males, with a mean age of 11.0 years (*n* = 31; 95% CI = 9.3, 12.6) and 7.7 years (*n* = 13; 95% CI = 4.3, 11.1) respectively, with considerably more variability for males. Wolves killed all age classes of adult bison and elk, but the highest proportion of kills was in the older age classes (Figs. 2.5 and 2.6). The proportion of elk kills in the older age classes was higher during winters 2002-03 through 2006-07 when the number of resident packs and wolves increased compared to winters 1998-99 through 2002-03 when Nez Perce was the primary resident pack (Fig 2.6). 2002-03 (*n* = 262) and (b) 2003-04 through 2006-07 (*n* = 302). Kills were classified by species, age class, and winter period (early = November 15-January 10; middle = January 11-March 6; late = March 7-April 30).

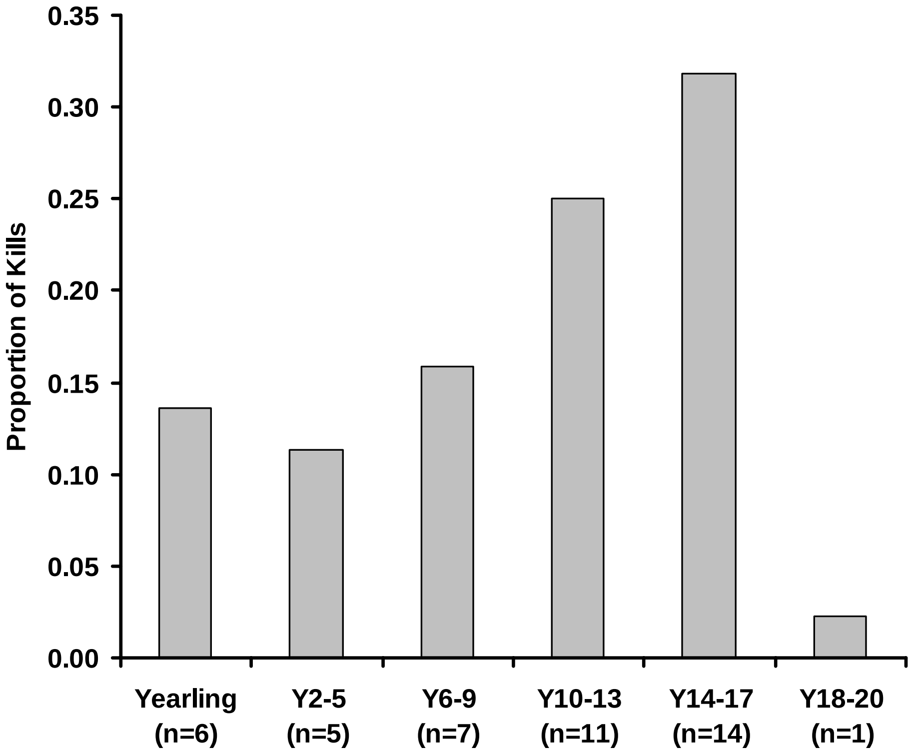

Figure 2.5. Age distribution of adult bison killed by wolves in the Madison headwaters area of Yellowstone National Park during 1996-97 through 2006-07 (n = 41).

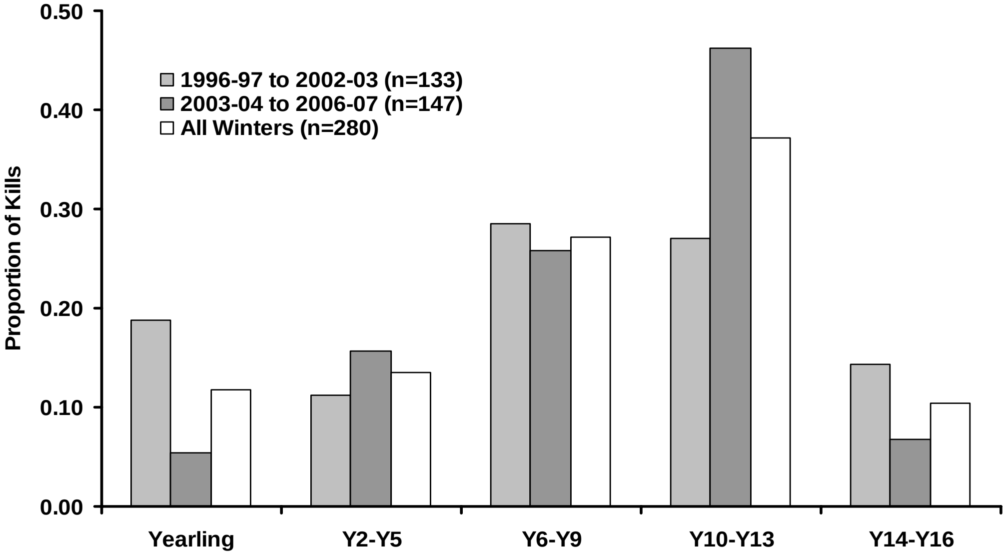

Figure 2.6. Age distribution of adult elk killed by wolves in the Madison headwaters area of Yellowstone National Park during 1996-97 through 2002-03 and 2003-04 through 2006-07. Reductions in younger age classes during the latter time period reflect lack of recruitment.

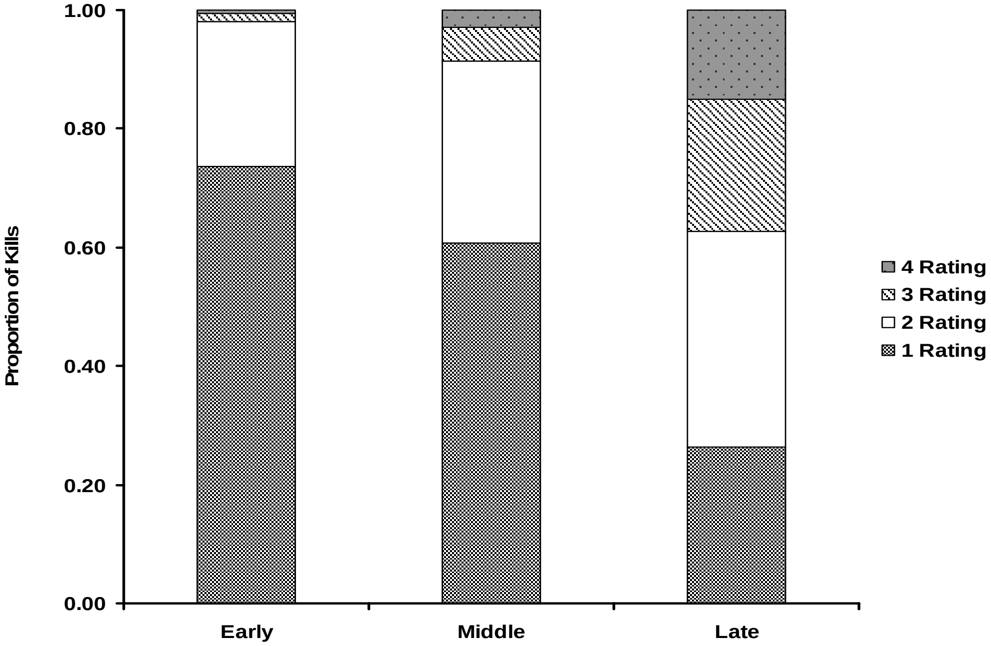

Figure 2.7. Marrow classifications for ungulates killed by wolves in the Madison headwaters area of Yellowstone National Park during early, middle, and late winter, 1996-97 through 2006-07 (n = 602).

Factors Influencing Wolf Prey Selection

I fitted 84 models from three *a priori* suites to data from 564 kills (216 elk calves, 223 elk adults, 69 bison calves, 56 bison adults) by resident wolf packs during 1998-99 through 2006-07. Model selection results supported two top models within $2\Delta AIC_c$ of each other and Akaike model weights (w_k) of 0.70 and 0.28, respectively (Table 2.3). The covariates ELK_{calf}, $BISON_{calf}$, WOLF:UNG, and SWE_{acc} were included in each of these models, with predictor weights (w_p) of 0.99, 0.99, 0.99, and 1.00, respectively. The structure of the two models differed only in the inclusion of ELK_{adt} in the top model, with $w_p = 0.71$. All other models had $\Delta AIC_c > 8.5$ and differed in structure from the best-supported models by their lack of inclusion of the WOLF:UNG covariate. An exploratory analysis adding wolf pack size ($WOLF_{pk}$) to the two best-supported models did not improve the top model, but improved the second best model's AIC_c to 1259.56, with a resultant ΔAIC_c of 0.31.

Elk abundance was negatively related to the probability that wolves would kill bison of both age classes relative to elk calves and, in particular, the abundance of elk calves was strongly negatively correlated with predation of adult bison (Table 2.4). The abundance of bison calves was positively related to the probability of wolves killing a bison calf relative to an elk calf. This relationship was similar for bison adults, though confidence intervals for the coefficient estimates spanned zero. In contrast to our hypotheses, bison abundance was negatively correlated with the probability that adult elk would be killed relative to calf elk. The wolf:ungulate ratio was positively correlated with the predation probability of all other prey types relative to elk calves, but was strongest for the bison adult logit (Table 2.4). There was not a significant positive relationship between pack size and prey size, and there was a negative correlation with the probability of predation of bison calves relative to elk calves. The effect of SWE_{acc} was strongly positive for all logit equations, indicating that increasing snow pack resulted in increased probability of predation for all prey types relative to elk calves (Table 2.4).

Table 2.3. A priori model structure and results from top models within and among suites for multinomial logit analyses of winter prey selection by resident wolf packs in a bison-elk system in the Madison headwaters area of Yellowstone National Park during 1998-99 through 2006-07.

		Within Suite			Among Suites	
Model Structure	***K***	**AIC_c**	**ΔAIC_c**	**w_k**	**ΔAIC_c**	**w_k**
Prey Suite						
ELK_{calf}+$BISON_{calf}$	3	1284.6	0.00	0.74	25.35	0.00
ELK_{calf}+ELK_{adt}+$BISON_{calf}$	4	1286.8	2.14	0.26	27.49	0.00
ELK_{calf}	2	1298.9	14.29	0.00	39.65	0.00
Prey + Wolf Competition Suite						
ELK_{calf}+$BISON_{calf}$+WOLF:ELK	4	1283.4	0.00	0.43	24.15	0.00
ELK_{calf}+$BISON_{calf}$+MULTPK	4	1284.9	1.51	0.20	†	
ELK_{calf}+ELK_{adt}+$BISON_{calf}$+WOLF:ELK	5	1285.7	2.28	0.14	26.43	0.00
ELK_{calf}+$BISON_{calf}$+WOLF:UNG	4	1286.0	2.57	0.12	†	
ELK_{calf}+ELK_{adt}+$BISON_{calf}$+WOLF:UNG	5	1287.2	3.84	0.06	†	
ELK_{calf}+ELK_{adt}+$BISON_{calf}$+MULTPK	5	1287.6	4.16	0.05	†	
ELK_{calf}+WOLF:UNG	3	1300.2	16.77	0.00	40.91	0.00
Prey + Snow Pack Suite						
ELK_{calf}+ELK_{adt}+$BISON_{calf}$+SWE_{acc}	5	1267.8	0.00	0.65	8.54	0.01
ELK_{calf}+$BISON_{calf}$+SWE_{acc}	4	1269.1	1.33	0.34	9.87	0.01
ELK_{calf}+ELK_{adt}+SWE_{acc}	4	1277.5	9.67	0.01	18.21	0.00
ELK_{calf}+ SWE_{acc}	3	1279.5	11.70	0.00	20.24	0.00
Prey + Wolf Competition + Snow Pack Suite						
ELK_{calf}+ELK_{adt}+$BISON_{calf}$+WOLF:UNG+SWE_{acc}	6	1259.3	0.00	.56	0.00	0.70
ELK_{calf}+$BISON_{calf}$+WOLF:UNG+SWE_{acc}	5	1261.1	1.86	0.22	1.86	0.28
ELK_{calf}+ELK_{adt}+$BISON_{calf}$+WOLF:ELK+SWE_{acc}	6	1263.1	3.86	0.08	†	
ELK_{calf}+ $BISON_{calf}$+WOLF:ELK+SWE_{acc}	5	1263.7	4.48	0.06	†	
ELK_{calf}+ELK_{adt}+$BISON_{calf}$+MULTPK+SWE_{acc}	6	1265.0	5.71	0.03	†	
ELK_{calf}+$BISON_{calf}$+ MULTPK +SWE_{acc}	5	1265.0	5.76	0.03	†	
ELK_{calf}+ELK_{adt}+WOLF:UNG+SWE_{acc}	5	1269.5	10.20	0.00	10.20	0.00

Note: Covariate codes are the abundance of elk adults (ELK_{adt} , ELK_{calf}), bison calves ($BISON_{calf}$), accumulated snow pack (SWE_{acc}), wolf:elk ratio (WOLF:ELK), wolf:ungulate ratio (WOLF:UNG), and multiple pack days (MULTPK).
†Values not included in among suite evaluations due to identical model structure differing only in wolf competition metric.

There were significant increases in the odds of elk adult, bison calf, and bison adult kills with increases in bison calf abundance, wolf:ungulate ratios, and SWE_{acc} (Table 2.4). The odds of predation by wolves for adult elk were 0.57 lower for every 134 animal increase in bison calf abundance, 1.7 times greater for every 0.018 increase in wolf:ungulate ratios, and 6.5-7.6 times higher for each 1800 cm days increase in SWE_{acc}. The odds of predation for bison calves decreased 0.32 and 0.38 times with every 42 animal and 122 animal increase in elk calf and elk adult abundance, respectively. The odds of predation for bison calves increased 2.21-2.67 times per 134 animal increase in bison calf abundance and 4.6-11.8 times per 1800 cm days increase in SWE_{acc}. The odds of predation for adult bison were 6.6-6.9 times greater for each 0.018 unit increase in wolf:ungulate ratio, 17.7-23.9 times greater for each 1800 cm days increase in SWE_{acc}, and 0.03-0.05 times greater for every 42 animal increase in elk calf abundance.

Wolf Prey Switching with Murdoch's Equation

There was a positive relationship between the ratios of bison to elk in wolf diets and the population (Fig. 2.8). Fitting a non-linear model of Murdoch's equation to the data indicated a curvilinear relationship, with *c* and *b* values of 0.229 (95% CI = 0.203, 0.254) and 2.091 (95% CI = 1.175, 3.007), respectively. The majority of this relationship was supported by data collected during the winters of 2001-02 through 2006-07, in particular two points corresponding to the late-winter periods of 2004-05 and 2005-06 appeared to have considerable influence on the shape of the relationship (Fig. 2.8). To evaluate the effect of these points I removed them and refit the models. The estimated values of *c* and *b* decreased to 0.15 (95% CI=0.08, 0.22) and 1.27 (95% CI=0.60, 1.94) respectively, while the standard error of each estimate increased, and thus the confidence interval of *b* included values less than 1 (Table 2.5).

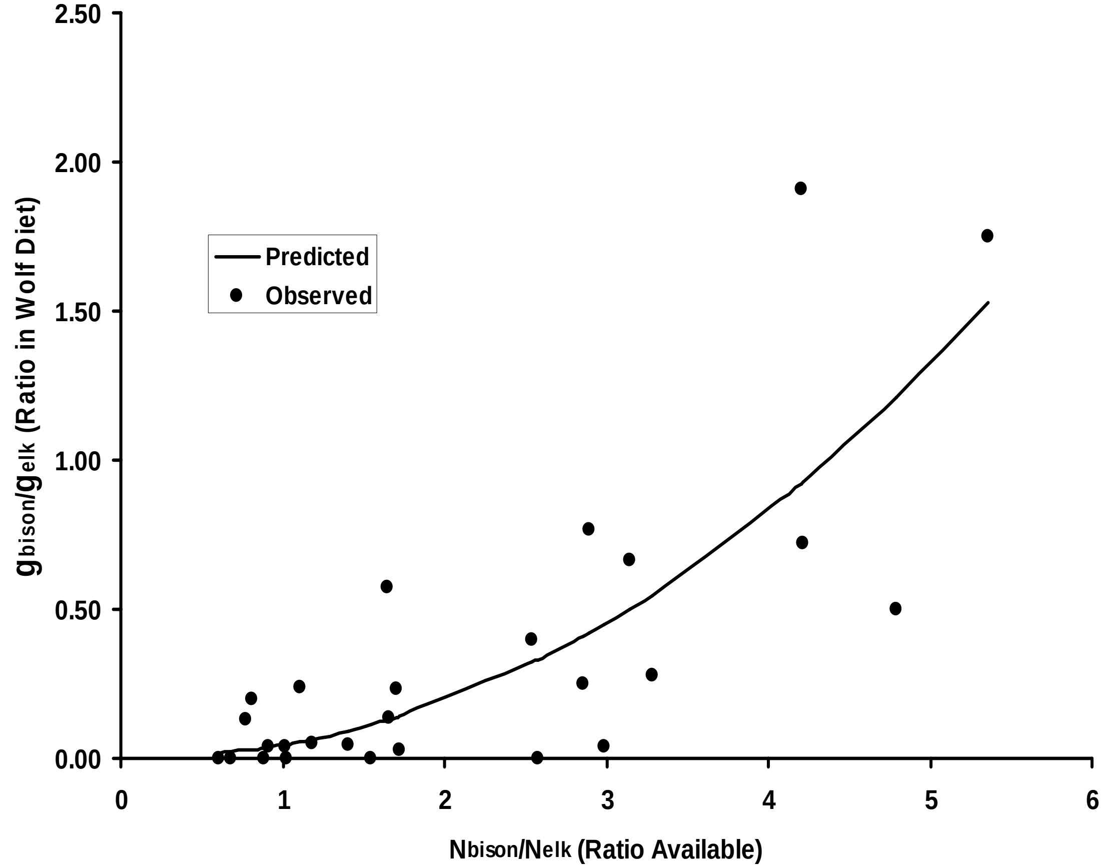

Figure 2.8. Observed versus predicted relationships between the ratio of bison:elk wintering in the Madison headwaters area of Yellowstone National Park and the ratio of bison:elk in wolf diets during 1998-99 through 2006-07.
Predicted coefficients for fitted line are *c* = 0.23 and *b* = 2.09.

Table 2.4. Models identified through AIC model comparison techniques for prey selection by resident wolf packs on bison and elk in the Madison headwaters area of Yellowstone National Park during1998-99 through 2006-07.

	Model	ELK$_{calf}$ $w_p = 0.99$	ELK$_{adt}$ $w_p = 0.71$	BISON$_{calf}$ $w_p = 0.99$	SWE$_{acc}$ $w_p = 1.00$	WOLF:UNG $w_p = 0.99$	WOLF$_{pack}$ †
Elk adult	PSW15	0.21	-0.21	**-0.56**	**2.03**	**0.51**	
		(-0.38, .80)	(-0.68, 0.26)	**(-1.10, -0.02)**	**(1.13, 2.93)**	**(0.01, 1.02)**	
		1.23	0.81	**0.57**	**7.60**	**1.67**	
	PSW41	0.06		-0.51	**1.87**	0.48	
		(-0.44, 0.56)		(-1.04, 0.02)	**(1.03, 2.72)**	(-0.02, 0.98)	
		1.07		0.60	**6.51**	1.61	
	PSW41w	0.07		-0.52	**1.89**	0.49	0.03
		(-0.43, 0.57)		(-1.08, 0.05)	**(1.01, 2.77)**	(-0.02, 0.99)	(-0.46, 0.51)
		1.07		0.60	**6.62**	1.62	1.03
Bison calf	PSW15	-0.31	**-0.96**	0.70	**2.47**	0.55	
		(-1.49, 0.87)	**(-1.64, -0.27)**	(-0.01, 1.42)	**(1.25, 3.68)**	(-0.41, 1.51)	
		0.73	**0.38**	2.02	**11.76**	1.73	
	PSW41	**-1.13**		**0.79**	**1.89**	0.52	
		(-2.20, -0.06)		**(0.08, 1.50)**	**(0.75, 3.03)**	(-0.40, 1.44)	
		0.32		**2.21**	**6.60**	1.68	
	PSW41w	-1.06		**0.98**	**1.52**	0.55	**-0.85**
		(-2.13, 0.02)		**(0.24, 1.73)**	**(0.35, 2.70)**	(-0.36, 1.45)	**(-1.57, -0.12)**
		0.35		**2.67**	**4.59**	1.73	**0.43**
Bison adult	PSW15	**-3.00**	-0.41	0.37	**3.17**	**1.93**	
		(-5.32, -0.69)	(-1.14, 0.32)	(-0.43, 1.17)	**(1.83, 4.52)**	**(0.94, 2.93)**	
		0.05	0.67	1.45	**23.90**	**6.91**	
	PSW41	**-3.46**		0.40	**2.87**	**1.89**	
		(-5.53, -1.39)		(-0.39, 1.19)	**(1.64, 4.11)**	**(.90, 2.89)**	
		0.03		1.49	**17.70**	**6.65**	
	PSW41w	**-3.34**		0.36	**3.05**	**1.89**	0.29
		(-5.38, -1.30)		(-0.47, 1.19)	**(1.71, 4.38)**	**(0.90, 2.88)**	(-0.62, 1.20)
		0.04		1.43	**21.07**	**6.61**	1.34

Note: Coefficient values (B_i), lower and upper 95% confidence intervals (in parentheses), and odds ratios for the three best approximating models identified through AIC model comparison techniques for prey selection by resident wolf packs on bison and elk in the Madison headwaters area of Yellowstone National Park during 1998-99 through 2006-07. Covariate codes are the abundance of elk calves and adults (ELK$_{calf}$, ELK$_{adt}$), bison calves (BISON$_{calf}$), accumulated snow pack (SWE$_{acc}$), wolf:ungulate ratio (WOLF:UNG), and wolf pack size (WOLF$_{pack}$). Boldface type indicates confidence intervals do not span zero.

Table 2.5. Coefficient values and lower and upper 95% confidence intervals from analyses of prey switching by wolves in a bison-elk system in the Madison headwaters area of Yellowstone National Park during 1998-99 through 2006-07.

	Parameter Estimates	
Model Structure	***c***	***b***
(c*BISON:ELK)^b	0.23 (0.20, 0.25)	2.09 (1.18, 3.01)
Outliers Removed	0.15 (0.08, 0.22)	1.27 (0.60, 1.94)

Note: Boldface type indicates confidence intervals do not span zero. The constant *c* measures the bias in a predator's diet (Murdoch 1969), with values less than one indicating a preference for elk. The constant *b* measures the extent of prey-switching, with values greater than one indicating switching. The covariate code BISON:ELK measures the relative abundance of bison and elk in the system.

Discussion

In this study prey selection was influenced by the absolute and relative abundance of prey types, the abundance of predators, and the duration of snow pack. Prey abundance, particularly elk calf and bison calf abundance, was important because wolves strongly preferred elk calves relative to all other prey types and elk calf abundance was inversely related to the predation of bison calves and adults. While wolves preferred elk to bison, their patterns of selection were also driven by the relative abundance of the two prey species with wolves killing disproportionately more bison at high bison:elk ratios, and the curvilinear form of Murdoch's equation indicating prey switching. In addition to prey abundance, the wolf:ungulate ratio resulted in a broadening of wolf prey selection from elk calves, with increasing probabilities of different prey types in the diet with increasing predation pressure. Lastly, I demonstrated that the probability of predation on both bison age classes and adult elk increased dramatically with increasing snow pack duration and accumulation. The profound influence of snow pack illustrates the important role of environmental variables on prey selection in wolf-ungulate systems.

Preference for elk calves was strong within and among all years, presumably due to their small size and lack of defenses relative to other prey types. Unlike most small taxa, ungulates pose considerable injury risk to predators, and anti-predator defenses vary among species and age classes (Nelson and Mech 1981; Bergerud et al. 1984; Carbyn and Trottier 1987; Dale et al. 1995). Therefore, the ability of prey individuals to repel an attack can substantially influence large mammal predator-prey dynamics (Garrott et al. 2007). Elk typically employed flight as a primary anti-predator tactic when encountered and attacked and, as a result, elk calves did not benefit from group protection strategies such as those used by bison (Carbyn and Trottier 1987, Carbyn et al. 1993). Elk adults are more capable of effective flight compared to calves and are more capable of inflicting injury on wolves due to their larger size, strength, experience, and the presence of antlers on bulls. However, wolves also killed elk from all other age classes, with the proportion of older adult elk in wolf diets increasing in the latter years of the study due to the effects of consistently low recruitment on the age structure of the population (Garrott et al 2008*d*).

While wolves preferred elk calves over adults they also preferred elk over bison presumably due to differences in vulnerability, and selected both age classes of bison less than expected given their abundance. As in other studies (Carbyn et al. 1993; Smith et al. 2000;

MacNulty et al. 2007), bison constituted an extremely formidable and dangerous prey to wolves due to their physical and behavioral defenses. We documented numerous instances of wolves seriously injuring bison and returning to kill and feed on them later (Carbyn et al. 1993). We also frequently witnessed bachelor and cow-calf herds continually defending injured or weak animals under attack by wolves (Carbyn and Trottier 1987; MacNulty et al. 2007). The majority of bison predation occurred in late winter when ungulates are likely in their most substandard physiological condition (Fig. 2.9, White et al. 2008a) and in the latter years of the study when bison were most abundant relative to elk (Bruggeman et al. 2008*a,b*). The smallest bison prey with the fewest defenses, calves, comprised the majority of bison kills, followed by cows and bulls, respectively (Table 2.1). Bison adults of both sexes were likely weakened in late winter, but cows had increased energetic demands because they were at or nearing parturition (Geremia et al. 2008). Bison were more abundant than elk during all years of our study, and were predictably found feeding in the open meadow complexes (Bruggeman et al 2008*a*,*b*). Therefore encountering bison was unlikely to be a limiting factor influencing wolf predation on bison, even if a group was considered the unit of encounter (Huggard 1993*a*). Thus, while general models of predator behavior typically focus on encounter rates (Taylor 1984) I support the caution of Dale et al. (1995) against wolf predation models incorporating only encounter rates given the dramatic differences in vulnerability and risk of injury ungulates pose when attacked.

(A)

(B)

Figure 2.9. Winter-starved bull bison (A) and calf bison (B) in the Firehole River drainage. Late winter starvation was the primary source of mortality for both elk and bison prior to wolf recolonization and the weakening influence of snow pack made formidable prey such as bison considerably more vulnerable to wolf predation (Photos by Jeff Henry and Matt Becker).

While absolute and relative prey abundance and life history characteristics were influential, the effect of snow pack duration and accumulation, as indexed by SWE_{acc}, had an overwhelming influence on predation by wolves among the four prey types. Though snow depth has been frequently attributed to increased vulnerability due to its inhibition of movement in a predation event and its longer-term weakening influence on ungulates (Nelson and Mech 1986; Huggard 1993*b* ; Mech and Peterson 2003), the relative importance of each has not been analyzed for specific predator-prey systems and prey species. While both metrics have important and interacting influences, the mean snow pack on the ground at the time of a kill (SWE_{mean}) explained much less variation in prey selection than the duration and accumulation of snow up to that date (SWE_{acc}). Physical condition of wolf-killed ungulates decreased through each winter, consistent with nutritional profiles of the elk population (White et al. 2008a), and winter starvation mortalities were the predominant source of mortality for both elk and bison prior to wolf recolonization (Garrott et al. 2008*c,d*). The odds of wolf predation on bison increased many orders of magnitude with increasing accumulation and duration of snow pack, presumably weakening bison such that they were less able to defend themselves or their calves. While we did observe bison being killed in deep snow, observations of wolves attacking bison in late winter typically occurred in low snow meadow complexes and defense sometimes lasted several hours, as wolves continually attempted to isolate and injure vulnerable individuals. An animal in a weakened state is likely much less able to sustain such defense in the face of an attack. Snow pack is also highly influential in driving broad-scale movements of bison, such as their winter migrations into the Madison headwaters area and movements among drainages (Bruggeman et al 2008*a*, *b*).

Snow pack also increased wolf predation on adult elk both by weakening their condition and impeding their escape during flight. Because of their habitat selection and anti-predator defenses elk are likely more susceptible to environmental vulnerability in the form of hard habitat edges, structure, and changes in snow pack that can impede flight (Bergman et al. 2006). We frequently found wolf-killed elk that had been either encountered and killed in deep snow and complex forest structure or chased into it and killed. Thus, environmental vulnerability (Garrott et al 2008*a*) can assume considerable importance in wolf-ungulate interactions given the severe weakening influence of snow pack on prey animals, the potential for snow pack effects to differ among prey species depending on their life history characteristics, and the potentially negative effect of edge and the accompanying differences in habitat structure.

In addition to prey and snow pack variables, the ratio of wolves to ungulates was influential in wolf prey selection within and among species, likely due to a combination of wolf competition and elk anti-predator behavior. The transition from a one-wolf-pack system to a multiple-wolf-pack system resulted in wolves occupying the entire study area and overlapping extensively, with inter-pack strife the main cause of wolf mortality (Smith et al. 2008) and wolf functional responses to elk best described as a Type II ratio-dependent response, indicating significant predator dependence (Chapter 3). Although the winter range comprised a relatively small area, wolf pack territories spatially overlapped and packs did not exhibit temporal avoidance in their use of the system, as they were routinely detected in the same drainages, though they typically avoided direct encounters (Smith et al. 2008). However, despite this intense use there was typically one dominant pack which appeared to displace smaller packs to more marginal areas of the study system. For example, the majority of the Biscuit Basin and

Nez Perce pack territories overlapped with each other during winters 2003-04 and 2004-05; however when both packs were detected in the same drainage Nez Perce appeared to occupy the main hunting areas while Biscuit Basin was often displaced. Similar dynamics were apparent with the Hayden pack and dominant Gibbon pack in 2006-07. Packs whose territories included large areas of marginal foraging based on the paucity of elk (e.g., Gibbon drainage, White et al 2008*c*) also preyed on adult elk and bison considerably more than packs occupying areas with relatively abundant elk, and the saturation of the system with wolves likely resulted in fewer places for adult elk to avoid encounters, such as bulls that often resided in minor drainages away from the main meadow complexes. This competition likely intensified as the elk population and the per-capita availability of calves decreased concurrent with a substantial distribution change within and among the three drainages (Gower et al. 2008*c*; White et al. 2008*c*). While wolves killed elk calves throughout all winters, high wolf numbers in the system resulted in nearly all elk calves being killed by late winter in several of the latter years (Garrott et al 2008*d*). While wolf pack size did not appear to affect selection, we are not aware of other studies that demonstrated the influence of wolf population numbers on prey selection. This may be because most of these analyses were confined to a single prey species or prey item, established wolf-ungulate systems do not typically undergo the dramatic changes in predator and prey populations that accompany newly-established systems, or the spatial and temporal dynamics of wolf territoriality in this system are unusual due to the high prey density of the Madison headwaters relative to the surrounding areas.

The significance of the wolf:ungulate ratio was also likely related to elk anti-predator responses. The elk population experienced a substantial decrease and re-distribution following wolf restoration, with 84% of the population residing in the Madison drainage by the end of the study period compared to approximately equal proportions distributed among the three major drainages before wolves (White et al 2008*c*). In addition, elk increased the variability of their group sizes, changed their movements, and intensified their selection for habitats with high snow heterogeneity and possible escape terrain in response to increasing wolf numbers (Gower et al. 2008*a,b,c*, White et al. 2008*c*). Under the behavioral resource depression hypothesis (Charnov et al. 1976), increasing predator presence should decrease the ability of individual predators, in this case packs, to capture prey due to increased wariness (and therefore decreased vulnerability) of prey (Chapter 3). Whether such elk responses were elicited by spatial variation in risk (White et al. 2008*c*), temporal variation in risk (Gower et al. 2008*b*) or a combination of the two (Creel et al. 2008) is unclear given the dramatic changes in elk abundance, distribution and behavior following wolf recolonization. Behavioral responses by elk in this system may have been manifested by a strategy of risk allocation (Lima and Bednekoff 1999) in response to temporal pulses of predation risk, with animals displaying the greatest amount of anti-predator behavior during the infrequent but high risk periods of wolf encounters and attacks (Gower et al. 2008a, *b*); however the frequency and duration of these risky periods increased with increasing wolf numbers in the system such that behavior was perhaps better characterized by a decrease in anti-predator behavior during infrequent pulses of safety. Regardless, prey-switching is typically thought to result in prey persistence because the relative rarity of the primary prey results in lower encounter and kill rates and, as a result, the predator switches to the more abundant prey (Murdoch 1969). However, rarity alone is likely insufficient for prey persistence and has not been well-demonstrated (Matter and Mannan 2005). In systems where large predators are being restored, changes in prey selection and the potential for prey-switching may be driven in part by a shift in prey behaviors as species adopt more effective anti-predator strategies to reduce their vulnerability rather than changes in predator preference.

Virtually all studies of predation in large mammal multiple-prey systems report strong selection for certain prey species (Carbyn 1974; Potvin et al. 1988; Dale et al. 1995; Karanth and Sunquist 1995; Kunkel et al. 1999; Jędrzejewski et al. 2000; Creel and Creel 2002; Sinclair et al. 2003; Hayward et al. 2006). However, this selection is not consistent among studies or species assemblages. For example, wolves primarily select caribou in some systems and not in others (Dale et al. 1995; Wittmer et al. 2005). Likewise, our documentation of elk as the primary prey of wolves was consistent with some investigations in other multiple-prey systems containing elk (Carbyn 1974; 1983; Huggard 1993; Weaver 1994; Hebblewhite et al. 2003; Husseman et al. 2003; Smith et al. 2004) and contrary to others (Kunkel et al. 1999). These apparent contrasts have led some investigators to conclude that use of the term "preference" to describe wolf prey selection is inappropriate because wolves select individuals of whatever species are most profitable with the least risk (i.e. the most vulnerable; Mech and Peterson 2003).

Defining preference as what a predator eats when all prey types are equally abundant and available confines investigations to the sophisticated cafeteria feeding trial experiments used on smaller taxa (Rodgers 1990). Thus, it is admittedly infeasible to determine if wolves have an inherent preference for a particular prey species. However, investigations of prey selection patterns in the context of natural multiple-prey systems, where preference is defined relative to the prey species assemblage available and influenced by the backdrop of landscape and climate variables upon which these interactions occur, have the potential to significantly advance our understanding of wolf-prey dynamics and help explain the prey selection contrasts observed among different systems (Garrott et al. 2007). I used data on wolf diet composition and relative abundance ratios to evaluate whether wolves switched from preying primarily on elk to bison. Murdoch (1969) demonstrated that values of $c < 1$ are indicative of preference, while values of $b > 1$ indicate switching. Based on this equation our analyses indicate that wolves in the Madison headwaters area had a strong preference for elk relative to bison ($c = 0.229$), but switched to bison at high bison:elk ratios ($b = 2.091$). Garrott et al. (2007) estimated Murdoch's selection coefficient by decomposing c into vulnerability (v), preference (s), and biomass (m) to account for the profound differences in morphology and anti-predator defenses across ungulate prey species. Based on attack rate and attack success data on elk and bison in the northern portion of Yellowstone and the Pelican Valley (MacNulty 2002); Garrott et al. (2007) estimated the product of svm as 0.04, considerably lower than what I estimated by fitting Murdoch's equation to our data. This discrepancy may illustrate the difficulty of obtaining sufficient data on attack rates and success when decomposing c into svm, as well as the potential differences among wolf-elk-bison systems. Elk vastly outnumber bison on the northern range of Yellowstone, while the Pelican Valley prey base is primarily one bison herd of ≤150 animals (MacNulty 2002). Thus, it is reasonable to assume that differences in attack rates on the two prey species might differ as well among the three systems. While the utility of decomposing c into svm may primarily be confined to systems where such data are more readily collected (e.g., Scheel 1993; Creel and Creel 2002; MacNulty et al. 2007), simply estimating c and b for a given system can be accomplished with data on wolf diet composition and relative prey abundance (Garrott et al. 2007).

The significance of distinguishing between Murdoch's (1969) definition of prey switching and using prey switching to simply describe changes in diet ultimately concerns the possible regulatory effects of a predator. By having a preference for the more abundant prey and thereby presumably lessoning predation on the less abundant prey at the same time, the predator can exert strong stabilizing density-dependent effects on the system (Murdoch and Oaten 1975, Oaten and Murdoch 1975). However, much of the experimental work on switching assumes constant predator and prey abundance (Murdoch 1969; Messier 1995). Thus theoretical and empirical treatments of switching that do not consider a numerical response (Messier 1995) or that assume a constant handling time do not address situations where predators respond numerically or can decrease their handling time under certain circumstances when prey become more available. When these equations are applied to natural systems with these characteristics a curvilinear relationship can be derived, yet a predator can take disproportionate amounts of the relatively more abundant prey without diminishing their take of the relatively less abundant prey. In this situation, predators will not exert a stabilizing influence on the less abundant and preferred prey species and consequently the switching evaluations recommended by Garrott et al. (2007) require further refinement to account for potentially common scenarios in natural settings.

Though Murdoch's (1969) equation suggested wolves in the Madison headwaters switched to bison at high bison:elk ratios, I did not detect a concurrent switch away from their preferred prey, elk, and I did not have constant abundances for either wolves or ungulates. Variations in wolf kill rates on elk were not negatively related to bison abundance and the effect of increasing bison abundance and increasing snow pack duration and accumulation was simply to increase the total wolf kill rate and the wolf kill rate on bison rather than reduce the kill rate on elk (Chapter 3). Furthermore, carcass consumption was negatively related to total kill rates and bison kill rate variation was best explained by snow pack or bison calf abundance (Chapter 3). The curvilinear relationship indicating switching was also heavily leveraged by two points comprising the late winter periods of 2004-05 and 2005-06 respectively. Disproportionate bison selection by wolves in late winter 2004-05 occurred during the peak of wolf abundance in the study area, with calf elk abundance decreasing to an estimated six animals by winter's end. Peak snow pack accumulation was below average for the study period, but substantial numbers of bison relative to elk and high wolf abundance likely resulted in increased selection for bison. In contrast the winter of 2005-06 followed a dramatic decrease in wolf abundance coupled with an above-average snow pack accumulation and high numbers of bison relative to elk, resulting in the highest proportion of bison killed during the study period. Nevertheless, elk continued to be preferred during the final winter of the study (2006-07), when elk numbers were at their lowest and the bison.elk ratios were near their highest. This was further corroborated by selection indices indicating continued high preference for elk calves with declining elk availability both within and among winters. Thus, it appears that wolf prey selection in this system is driven by a strong preference for the most vulnerable prey items (i.e., elk and elk calves in particular) and changes in prey selection are driven largely by circumstance (i.e. high bison:elk ratios; high wolf abundances; severe winters) rather than by a density-dependent change in wolf preference. Consequently the ecological relevance of prey-switching, namely its density-dependent stabilizing effects, do not appear to be present in this system at this time, perhaps best evidenced by a continued decline of elk due to wolf predation (Garrott et al. 2008*a,d*). Most natural systems with wolves, whose abundance has a strong positive relationship to prey biomass (Fuller

1989), are unlikely to have constant predator or prey abundance and stochastic processes can contribute to variable handling time. Thus I suggest continued refinement of prey-switching evaluations to account for this variability, and that evaluations with the definition provided by Murdoch (1969) should also consider whether there is a concurrent decrease in predation on the formerly more abundant and preferred prey, as herein lies the density-dependent stabilizing effect that is of primary ecological interest.

Prior to reintroduction investigators predicted wolves would reduce the Yellowstone bison population by <15% (Boyce and Gaillard 1992; Boyce 1993). Bison predation park-wide was actually considerably less (<1%) during 1995-2000 (Smith et al. 2004). However Boyce (1995) did predict that prey switching from elk to bison could possibly occur in the Madison headwaters area in late winter. While we observed increased wolf predation on bison in late winter, it was unclear prior to our analyses whether this trend was driven by circumstance or by prey-switching to the increasing bison population and concurrently switching away from elk. Wolves are capable of subsisting almost exclusively on bison as evidenced in Wood Buffalo National Park (Carbyn et al. 1993). However, at this time wolves appear to primarily kill bison at high relative abundance ratios, particularly in severe winters and in times of high wolf abundances, with no indication that preference for elk has changed. Given this strong preference for elk it seems likely that elk numbers in the Madison headwaters area will continue to decrease to a low equilibrium, depending on their ability to escape predation via behavior or use of refuges (Creel et al. 2005; Hebblewhite et al. 2005; Garrott et al. 2008*a,d*; Gower et al. 2008*a,b,c*; White et al. 2008*c*) that could produce pronounced switching away from elk and elk calves in particular. It is even possible that local extirpation of the Madison headwaters elk population could occur (Garrott et al 2008*a*). However, the dynamics of wolves, elk, and bison in the Madison headwaters area are still those of a developing system, with wolves present for little over a decade. Understanding patterns of prey selection, preference, and the presence or absence of prey-switching and their effects on community stability and persistence will require subsequent years of study to distinguish between transitory phenomena and the myriad influences of predator, prey, and environment in a newly-established large mammal system.

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CHAPTER 3

WOLF KILL RATES: PREDICTABLY VARIABLE?

Introduction

The role of a predator in regulating or destabilizing prey populations is widely believed to depend on the form of its functional response (Murdoch and Oaten 1975; Oaten and Murdoch 1975; Hassell 1978). There are three general forms of the functional response (Holling 1959). A predation rate increasing linearly with prey density is know as a Type I response, which is considered unrealistic for most predators due to lack of constraints in handling time or the time needed to capture and subdue a prey item. Consequently, Type I responses are most likely confined to predators with few handling constraints such as filter feeders (Jeschke et al. 2004). A more plausible description of predation behavior is the Type II response, which exhibits a decelerating predation rate with increasing prey density reflective of predator satiation and the constraints of handling time (Holling 1959). This form of predatory behavior is thought to be common in natural systems consisting of a single prey species or a specialist predator (Peckarsky 1984) and is considered destabilizing because it is inversely density-dependent (Oaten and Murdoch 1975; Hassell 1978; Hassell 2000). However, Fryxell et al. (2007) argue that, while Type II responses can be destabilizing in the solitary prey and predator systems from which most predator-prey theory has been developed and refined, such a response can also be stabilizing if prey and predators aggregate in groups. The sigmoidal Type III functional response can also be exhibited when more than one prey type exists and a predator is plastic in its foraging (Holling 1959). A Type III functional response can be generated by a variety of factors such as prey-switching (Murdoch 1969), selective foraging and learning by the predator (Tinbergen 1960; Real 1979), or use of refuges by prey (Taylor 1984). Because a Type III response implies density-dependent predation, such behavior is considered to have a stabilizing influence on ecosystems (Oaten and Murdoch 1975).

Due largely to the dramatically different ecosystem trajectories that can ensue with different predator behaviors, an immense body of work has been performed on determining the drivers of kill rates. Kill rates are influenced by encounter rates and prey density (Holling 1959), the presence of alternative prey (Murdoch 1969), environmental factors (Thompson 1978; Anderson 2001), and prey distribution (Real 1979; Cosner et al. 1999; Pitt and Ritchie 2002). However, the causal factors driving the ultimate form of the functional response have been the subject of considerable debate. The long-standing belief that forms were driven by prey density alone ("prey-dependence") has been challenged by the idea that predator density can also appreciably influence per-capita consumption ("predator dependence"). Strong predator density, typically denoted by the ratio of predators to prey ("ratio-dependence") has been vigorously debated as an alternative to the prey dependent functional response (Arditi and Ginzburg 1989; Berryman 1992; Abrams 1994; Akcakaya et al. 1995; Abrams and Ginzburg 2000). While this debate has not been resolved, it is likely that both prey and predator numbers influence predation and more empirical studies are needed (Abrams and Ginzburg 2000; Schenk et al. 2005).

Wolf-ungulate systems have received substantial attention in studies of kill rates, largely due to the strong scientific and societal interest in assessing the effects of wolves on prey populations. Kill rates of wolves are extremely variable and influenced by prey density, pack size, and snow pack (see reviews in Hebblewhite et al. 2003; Mech and Peterson 2003). There is considerable disagreement regarding the nature of wolf foraging behavior, but few studies of functional responses due to the difficulties inherent in data collection (Mech and Peterson 2003). Thus, various scientists have advocated that wolf kill rates were best described as constant (Eberhardt 1997), ratio-dependent (Vucetich et al. 2002; Jost et al. 2005), or prey dependent (Messier 1994; 1995; Messier and Joly 2000; Varley and Boyce 2006). Recent analyses from the long-term wolf-moose dataset of Isle Royale indicated that ratio-dependence best described the nature of wolf predation in this system (Vucetich et al. 2002; Jost et al. 2005), and that the inclusion of a ratio-dependent functional response in kill rate analyses may provide significant insights into discrimination between types of predation.

Disagreement also stems, in part, from the inherent difficulty in accurately assessing kill rates in wolf-ungulate systems. These metrics are so difficult to measure that some scientists question the appropriateness and/or feasibility of estimating the functional response for describing wolf-ungulate systems (Eberhardt 1997; Marshal and Boutin 1999; Person et al. 2001; Mech and Peterson 2003) while others contend that distinguishing between functional response forms is not ecologically critical (Dale et al. 1994; Van Ballenberghe and Ballard 1994). Instead, some scientists suggest monitoring cause-specific mortality and recruitment rates of prey species (Kunkel et al. 2004) or changes in ungulate carrying capacity (Bowyer et al. 2005). In addition, the methods and metrics used to calculate kill rates vary widely. Thus, comparisons between systems and methods are often not possible (Hebblewhite et al. 2003). Lastly, the estimation of kill rates is subject to variable observer effort, weather conditions, and movement of wolves. Only recently have investigators attempted to account for these sources of variability (Jaffe 2001; Hebblewhite et al. 2003; Smith et al. 2004).

I evaluated drivers of kill rates and the forms of wolf functional response using long-term predation data collected during winters 1998-99 through 2006-07 from a tractable wolf-elk-bison system in the Madison headwaters area of Yellowstone National Park that experienced substantial seasonal and annual variation in prey abundance, predator abundance, and snow pack. Data on wolf numbers and kills were collected daily for each winter (November 15-April 21) of the study period. There are various ecological justifications for employing several different metrics to evaluate wolf kill rates. Metrics employing kills as the unit of measure are likely more appropriate than biomass for evaluating the effects of wolf predation on ungulate prey populations (Hayes et al. 2000; Hayes and Harestad 2000). Furthermore, it is useful to distinguish between kills per pack and kills per wolf because wolves are group hunting predators with a rigid social hierarchy and the pack is typically the hunting unit rather than individual wolves (Mech 1970). Questions concerning wolf population dynamics and their food acquisition are better addressed using a metric of biomass (Mech and Peterson 2003). Consequently, I calculated metrics of kills/pack/day, kills/wolf/day, and kg/wolf/day for each pack. Our objectives were to: 1) describe temporal trends in kill rates within and among winters and wolf packs; 2) determine the primary factors driving trends in total wolf kill rates, as well as kill rates for elk and bison for various metrics; and 3) assess the form of wolf functional response for elk. I predicted that kill rates would be positively influenced by the abundance of elk and bison and negatively influenced by wolf abundance. Also, I predicted that kill rates would be positively related to pack size when calculated per pack, and negatively related to pack size when calculated per wolf. Further, I predicted wolf functional responses would be best described by ratio dependence due to the strong potential for predator dependence.

Methods

Wolf Tracking and Kill Detection

We conducted intensive kill rate investigations in the primary winter ranges of bison and elk in the Madison headwaters area (31,000 ha), with concurrent investigations of these prey species allowing collection of wolf predation data in a tractable area with a well-described ungulate prey base. We documented wolf kill rates during November 15 through April 21 each winter from the establishment of a resident pack in 1998-99 (Smith et al. 2008) through 2006-07. Our sampling unit was radio-collared wolf packs that incorporated the study area as part of their territory. Wolves were aerially darted from helicopters by National Park Service biologists and fitted with VHF telemetry collars. A total of 37 wolves from four packs were collared during the course of the study (Smith et al. 2008).

The number and sizes of wolf packs using the study area were dynamic within and among winters (Smith et al. 2008). Thus, we used ground observations, snow-tracking, and counts during aerial tracking flights by park biologists to estimate the wolf population. We estimated the wolf population in wolf days, defined as one wolf in the study area for one day. We used roads traversing each river drainage in the study area (Newman and Watson 2008) to rapidly sample for wolf presence daily through the winter. Sampling began at dawn with ground crews of three to four people covering all roads by snowmobile or vehicle and using strategic high points in the landscape to facilitate telemetry triangulations (White and Garrott 1990) and observations of wolves. When possible, multiple locations were obtained in early morning and evening each day. We also recorded any uncollared wolves detected opportunistically via tracks or observations to aid in the estimation of the wolf population using the study area. In addition, biologists studying elk and bison routinely covered backcountry areas to assist with wolf detection.

When wolves were located, we used visual scans and monitoring of avian scavengers in the vicinity to detect kills. Ravens preferentially associate with wolves in winter, and an average of 28 ravens (*Corvus corax*) were present at fresh wolf kills on the northern elk winter range in Yellowstone National Park (Stahler et al. 2002), with slightly lower averages in the Madison headwaters area (D. Stahler, National Park Service, personal communication). This association facilitated the detection of kills. We also conducted extensive snow-tracking after wolves departed the area to further facilitate kill detection (Huggard 1993; Dale et al. 1995; Jedrzejewski et al. 2000; Jaffe 2001; Hebblewhite et al. 2003; Bergman et al. 2006). We necropsied ungulate carcasses to determine cause of death, species, sex, age, condition, and percent consumed. Wolf kills were inferred from collective evidence of subcutaneous hemorrhaging indicative of injuries sustained before death, signs of struggle or chase at the kill site, blood trails, signs of predator presence, and our knowledge of wolf movements and activities. We documented frequent spring grizzly bear (*Ursus arctos*) predation on bison during the latter years of the study. Thus, when both bears and wolves were present on a kill, we classified it based on the patterns of injury and subcutaneous hemorrhaging. Bears typically attacked the head and spine, while wolves attacked the flanks, hindquarters, and underside of the neck. Similarly, mountain lion (*Puma concolor*) kills of elk were determined based on characteristics of the kill site and patterns of injury. Kills were sexed using the presence of genitalia, horns, antlers, or pedicels, and aged based on size and patterns of tooth eruption and replacement (Fuller 1959; Hudson et al. 2002). When available, an incisor or canine was removed from adult ungulates and aged using cementum annuli (Moffitt 1998, Hamlin et al. 2000).

Kill Rate Estimation

Daily estimates of wolf numbers and kills detected for the wolf population at large and for each pack were used to estimate minimum kill rates each winter and for three winter periods of approximately eight weeks each that corresponded to early (November 15-January 6), middle (January 7-February 27), and late winter (February 28-April 21), ending near the mean pack denning date, after which packs were considerably less cohesive (Jaffe 2001, Smith et al. 2008). The kills/pack/day metric was calculated by dividing the number of kills by the number of days in the sampling period in which the respective pack was detected, while the kills/wolf/day metric was calculated by dividing the number of kills by the estimated wolf days for a given pack for each period. Winter and winter period estimates of kills/wolf/day for the entire population were calculated from pooled estimates of wolf days and kills for a given period or winter. Estimates for kg/wolf/day were derived by summing the biomass of all kills for a given pack and dividing by the estimated wolf days for that period. We classified all kills into species, sex, and age, and used biomass estimates for elk and bison obtained from Murie (1951) and Meagher (1973), respectively. Elk bulls, cows, and calves were estimated at 287 kg, 236 kg, and 116 kg, respectively, while bison adults and calves were estimated at 500 kg and 136 kg, respectively. Bison adult age classes of both sexes can vary dramatically in weight depending on age (Berger and Peacock 1988). Thus, I did not use separate categories for males and females in biomass estimation. I assumed 75% edible biomass for each prey item (Peterson 1977), but did not account for scavenger loss or incomplete consumption of carcasses. Therefore, the kg/wolf/day metric was considered an index rather than an absolute measure of consumption per wolf. For each pack, I estimated total kill rates and separate kill rates for elk and bison using all three kill rate metrics for each winter period. I also estimated these kill rates using the same metrics for the entire wolf population during each winter and winter period.

Evaluating Kill Rate Variation

I used multiple linear regression techniques (Neter et al. 1996) to evaluate factors affecting variation in wolf kill rates within and among winters and packs Because the Madison headwaters was a multiple-prey system with ungulate species differing substantially in abundance and defenses (Garrott et al. 2007), I evaluated variations in kill rates for each wolf pack using three separate response variables: total kill rates; kill rates for elk; and kill rates for bison. For each response variable, I calculated three kill rate metrics (kills/wolf/day, kills/pack/day, and kg/wolf/day) during a given winter period, comprising nine analyses in total. I developed eight covariates to evaluate the influences of prey abundance, wolf pack size, and snow pack. These covariates were judiciously selected from factors reported to be influential in the kill rate literature, as well as from our knowledge of the study system.

I used six covariates to describe wolf prey abundance, including elk abundance (ELK_{all}), bison abundance ($BISON_{all}$), and the respective abundances of elk adults and calves (ELK_{adt}, ELK_{calf}) and bison adults ($BISON_{adt}$) and calves ($BISON_{calf}$). I estimated prey abundance for the entire study area rather than just the drainages encompassed by a particular pack's territory because multiple packs overlapped spatially and temporally, larger packs were more dominant (Chapters 15 and 16), and kill rates were estimated for each pack over nearly an 8-week period during which bison movement between wolf pack territories was considerable (Bruggeman et al.

2008*a,b*). I estimated the abundances of adult elk and calves during early, middle, and late winter using replicate mark-resight techniques and age composition data (Chapter 2, Garrott et al. 2008*c,d*). Estimates of bison abundance and age class were obtained via ground survey counts of the bison winter range in the study area. Surveys were conducted every 10-16 days during winter, with observers recording the number, location, sex, and age class of all bison sighted (Bruggeman et al. 2008*b*). The effect of snow pack on prey vulnerability was estimated using a metric of accumulated snow-water equivalents (SWE_{acc}, Garrott et al. 2003). I used a validated model describing snow pack dynamics (Watson et al. 2008) to estimate a mean daily SWE for the study area, and accumulated mean daily SWE values from the typical start of the first snowfall (October 1) until the end of a given winter period. By estimating the duration and severity of snow pack and its weakening effect on prey, I considered SWE_{acc} an indicator of prey physiological condition and SWE_{acc} explained substantially more variation in wolf prey selection in the Madison headwaters area than the mean SWE on the ground at the time of a kill (Chapter 2). Also, I calculated a mean wolf pack size ($WOLF_{pk}$) for each winter period from daily estimates of size for a given pack

I developed and evaluated *a priori* hypotheses in the form of 12 candidate models fitted to each of the kill rate metrics (Appendix B). Thus, I performed three separate analyses for total kill rates and kill rates of elk and bison. To facilitate comparison of coefficient estimates, all covariates were centered and scaled prior to analysis by subtracting the midpoint and dividing by half of the range, resulting in values between –1 and 1. I assessed potential colinearity between covariates using variance inflation factors and did not use covariates with values >6 in the same model (Neter et al. 1996). Covariates that were not used in the same model due to strong colinearity were $\mathrm{BISON}_{\mathrm{adt}}$ and $\mathrm{BISON}_{\mathrm{calf}}$, and all bison covariates with $\mathrm{SWE}_{\mathrm{acc}}$ because increasing snow pack resulted in increased bison migration into the study area (Bruggeman et al. 2008a). I fitted all models in R version 2.4.1 (R Development Core Team 2006). Models were compared using Akaike's Information Criterion corrected for small samples (AIC_c; Burnham and Anderson 2002). I calculated Akaike weights and evaluated the importance of each covariate by its predictor weight (w_p), which I calculated by summing the Akaike weights for all models containing the covariate (Burnham and Anderson 2002). Goodness of fit was evaluated using adjusted R-squared values for each model, and covariate coefficients were evaluated for direction (i.e. positive or negative) and stability among different models. Next, I fit moderated and pseudo-threshold forms to all prey covariates to determine if the fit was improved. Lastly, I performed exploratory analyses fitting kill rates to a "per-pack" scale, wherein prey abundance was estimated for each pack's territory, to determine if covariate relationships and model selection results were affected.

Elk were considerably more vulnerable to wolf predation than bison in the Madison headwaters, though wolves increasingly selected bison in late winter at high bison:elk ratios (Chapter 2). Thus, I predicted elk abundance would be positively related to elk kill rates and total kill rates, but negatively related to bison kill rates, for all three metrics. Similarly, I predicted bison abundance covariates would be negatively correlated with elk kill rates of all three metrics because the migration of bison into the system would provide a large alternative food source that could decrease kill rates of elk. I predicted that increasing abundance of either or both prey species would be positively related to total kill rates. In social predators such as wolves, pack size has an important influence on kill rates because larger packs can make more kills, but acquire less food per capita (Thurber and Peterson 1993, Schmidt and Mech 1997). Thus, I predicted pack size would be positively related to kills/pack/day, but negatively related to kills/wolf/day and kg/wolf/day for total kill rates and kill rates of elk and bison. Lastly, snow pack has a considerable debilitating influence on prey, both in their ability to escape from predation and on their physiological condition (Chapter 2). Thus, I predicted that SWE_{acc} would be positively related to kill rates of all three metrics (Appendix B).

Evaluating the Functional Response for Elk

Multiple regression analyses evaluated the influence of various prey, predator, and environmental influences on the kill rates of wolf packs within the study area. To describe the average rate of elk consumption per wolf (i.e., the functional response), however, I fit traditional functional response models (Holling 1959) to wolf kill rate data. Functional response curves were fit for the metric of elk kills/wolf/day estimated at a winter range scale, whereby a single elk kill rate for the study area during a given winter period was estimated by pooling all elk kills and dividing by the estimated wolf days in the period. Bison and elk abundance covariates were then estimated for the entire study area for each period as described for the kill rate variation analyses, and wolf abundance was estimated by dividing the total wolf days for a given winter period by the number of days in the period. While wolves killed bison to varying degrees within and among winters, this change in diet appeared to be heavily moderated by circumstances that increased bison vulnerability, such as severe winters and high wolf:ungulate ratios (Chapter 2) I also did not have sufficient kill rates on bison across a wide range of bison densities and therefore did not fit a wolf functional response for bison.

I fit elk kill rate data to seven *a priori* models to evaluate the form of wolf functional responses. The models were categorized into four groups, namely a null model of constant kill rate, prey-dependent Type II and Type III responses, ratio-dependent Type II and Type III responses, and prey- and ratio-dependent Type III responses with two prey. The generalized prey-dependent Type II and Type III equations (1a and 1b respectively) from Holling's (1959) disk equation were:

$$\frac{\alpha N}{1+\alpha h N} \tag{1a}$$

$$\frac{\alpha N^2}{1+\alpha h N^2} \tag{1b}$$

where α is the elk attack rate, h is the handling time of a single prey item, and N is elk abundance. While prey abundance is certainly of essential importance in kill rates, there are a growing number of findings demonstrating the importance of predator dependence (Reeve 1997; Vucetich et al. 2002; Jost et al. 2005; Schenk et al. 2005; Tschanz et al. 2007). Thus, I used the Type II and Type III ratio-dependent models (2a and 2b respectively) from Arditi and Ginzburg (1989) denoted as:

$$\frac{\alpha N}{P+\alpha h N} \tag{2a}$$

$$\frac{\alpha N^2}{P+\alpha h N^2} \tag{2b}$$

where P is wolf abundance. Different functional responses can be exhibited for different species in multiple prey systems (Messier 1995), and indirect effects can exist between prey species sharing a predator (Holt 1977). Thus, I fit Type III prey-dependent and ratio-dependent functional responses that incorporated the abundances of both elk and bison. The structures of these models were adapted from Garrott et al. (2007), with Type III prey-dependent and ratio-dependent equations (3a and 3b) as:

$$g_1 = \frac{\alpha N_1}{1 + \alpha \ N_2 h \ c^b m \ \left(N_2/N_1\right)^{b-1} + \alpha \ N_1 h} \tag{3a}$$

$$g_1 = \frac{\alpha N_1}{P + \alpha \ N_2 h \ c^b m \ \left(N_2/N_1\right)^{b-1} + \alpha \ N_1 h} \tag{3b}$$

Where subscripts 1 and 2 denote elk and bison respectively, the proportionality constant, *c*, measures "the bias in the predator's diet to one prey species" and relates the ratio of prey eaten to their relative abundance (Murdoch 1969:337), and *b* is the extent of prey switching (Chapter 1). A value of *c* less than one indicates a preference for that prey, a value of *b* greater than one indicates prey switching (Greenwood and Elton 1979; Elliot 2004), and *m* is the biomass ratio between bison and elk. Values of *b* are bounded at the lower limit by zero. I estimated fixed quantities of *c* and *b* from prey selection data in the Madison headwaters to be 0.229 and 2.091 respectively (Chapter 2), with *m* = 2. A complete explanation of these equations is available in Appendix C.

Determining *a priori* the appropriate scale at which to evaluate functional responses can be difficult (Jost et al. 2005). However, I considered the effects of predator abundance and interference reflected in ratio dependence to be most pronounced on a population scale, where predator abundance was not pack size but rather wolf numbers. Thus, I fit models on a study area-wide scale. Elk populations typically declined modestly from fall to spring (Chapter 2, Garrott et al. 2008*d*) and therefore division into winter periods of approximately eight weeks each minimized the possibility of prey depletion bias (Jost et al. 2005). I fitted models and estimated parameter coefficients using the nls function from the nlme package in R version 2.4.1

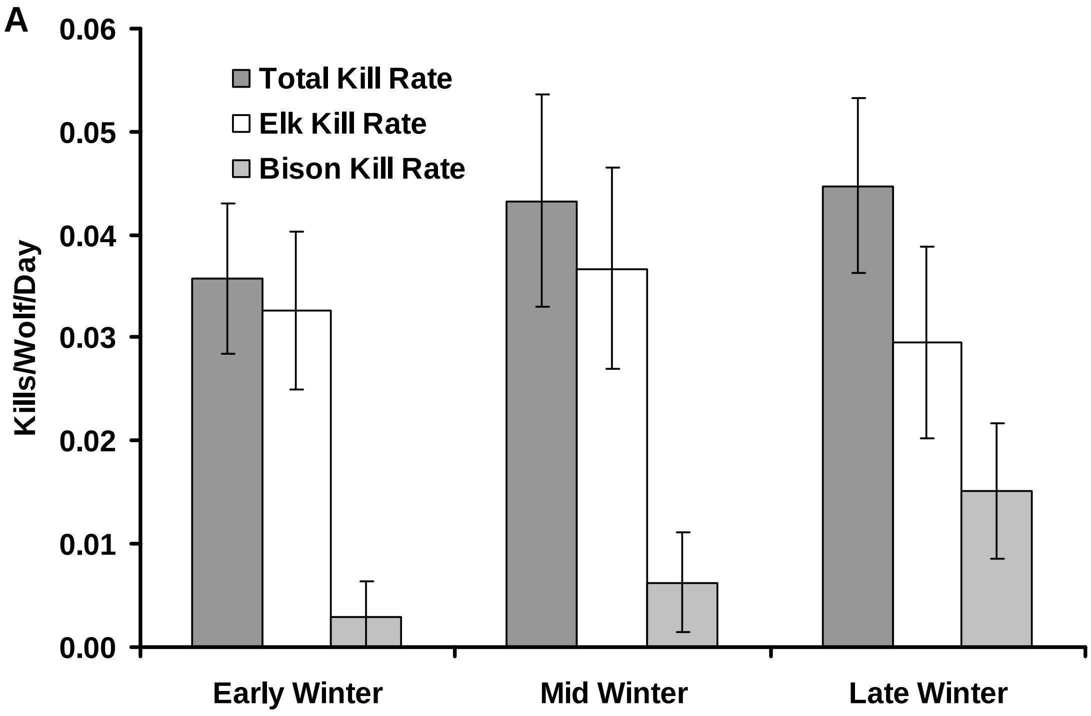
(R Core Development Team 2006). I determined model and predictor weights and employed diagnostics similar to the multiple linear regression analysis. Based on previous empirical evaluations of wolf functional responses from Isle Royale (Vucetich et al. 2002; Jost et al. 2005), I predicted that ratio-dependent models would be more supported than prey-dependent models, and that the elk:wolf ratios would be positively related to wolf per capita kill rates on elk.

Results

We detected and followed each radio-collared pack for an average of 35.1 days (95% CI = 31.6, 38.6) during each winter period, or approximately 66% of the time. Wolves were not detected in the Madison headwaters study area during the remainder of the time. We detected 688 ungulates (i.e., 274 elk calves, 276 elk adults, 79 bison calves, 59 bison adults) killed by wolf packs during the winters of 1998-99 through 2006-07. The mean number of kills per period for each pack was 13.9 (range = 2-37, sd = 7.1) and mean pack size for which I estimated kill rates was 10.4 (range = 3.6-21.1, sd = 4.4). I censored kill rate estimates from four wolf packs for five predation periods that had inadequate tracking efficiencies due to wolves spending little time in the study area or poor tracking conditions.

Elk population estimates for the study area ranged from 290-664 in autumn to 174-577 in spring, with the population decreasing 5-42% during winter. Dramatic changes in elk distribution and abundance occurred over the course of the study (White et al. 2008*c* and Garrott et al. 2008*d*), with a progressive decrease beginning in 2003-04 and continuing through 2006-07. The distribution of elk also changed from approximately equal proportions in each drainage prior to 1997-98 to 84% of the population residing in the Madison drainage by the end of 2006-07 (White et al. 2008*c*). I detected no discernible trend in bison abundance over the 9-year study. However, pronounced seasonal trends were evident with bison numbers generally increasing as winter progressed as animals migrated into the study area from the Hayden and Pelican Valleys (Bruggeman et al. 2008*a,b*). The mean numbers of bison recorded in the study area for the three periods used to estimate kill rates each year ranged from 234-1356. The wolf population increased steadily from seven wolves during the first winter to a peak of approximately 45 animals in multiple packs during winter 2004-05, followed by an abrupt decrease in wolf abundance in the ensuing winters (Smith et al. 2008).

We collected kill rate data from four main radio-collared wolf packs during 26 winter predation periods, for a total of 36 measures of kill rate for each metric during 1998-99 through 2006-07. Total kills/wolf/day ranged from 0.020 to 0.083 (mean = 0.042; 95% CI = 0.037, 0.048), with elk kills/wolf/day ranging from 0.007-0.074 (mean = 0.033; 95% CI = 0.028, 0.039) and bison kills/wolf/day ranging from 0.000-0.045 (mean = 0.009; 95% CI = 0.013, 0.005). Total kills/pack/day ranged from 0.125 to 0.810 (mean = 0.400; 95% CI = 0.346, 0.450), while elk kills/pack/day ranged from 0.070 to 0.810 (mean = 0.320; 95% CI = 0.260, 0.381), and bison kills/pack/day ranged from 0.000 to 0.265 (mean = 0.076; 95% CI = 0.049, 0.103). Total kg/wolf/day ranged from 1.7-19.1 (mean = 6.6; 95% CI = 5.6, 7.7), while elk kg/wolf/day ranged from 1.1 to 9.4 (mean = 4.6; 95% CI = 3.9, 5.4), and bison kg/wolf/day ranged from 0.0 to 16.3 (mean = 2.0; 95% CI = 1.0, 3.0). Mean total kill rates did not significantly differ from mean elk kill rates across winter periods for all metrics except the late winter kg/wolf/day estimates, while mean bison kill rates increased from early to late winter (Fig. 3.1). Mean elk kill rates were similar across all winter periods and were higher than mean bison kill rates for early and middle winter periods. However, the two kill rates had overlapping confidence intervals for the late winter period (Fig. 3.1). I pooled kill rate data across all wolf packs to estimate total kills/wolf/day and elk kills/wolf/day for each winter period and winter, providing 26 and nine measures of kill rates, respectively. Winter range kill rate estimates for each winter exhibited steady decreases, with the lowest kill rate corresponding to peak wolf abundance in 2004-05, before sharply increasing in 2005-06 and decreasing again in 2006-07 (Fig. 3.2). There was also an inverse relationship between kill rates and consumption among winters, with the highest carcass consumption and lowest variance occurring in 2004-05 when wolf numbers peaked and kill rates were at their lowest, and the lowest carcass consumption occurring when wolves first established in the system in 1998-99 (Smith et al. 2008, Fig. 3.3). Aside from these two extremes, carcass consumption did not vary substantially among winters.



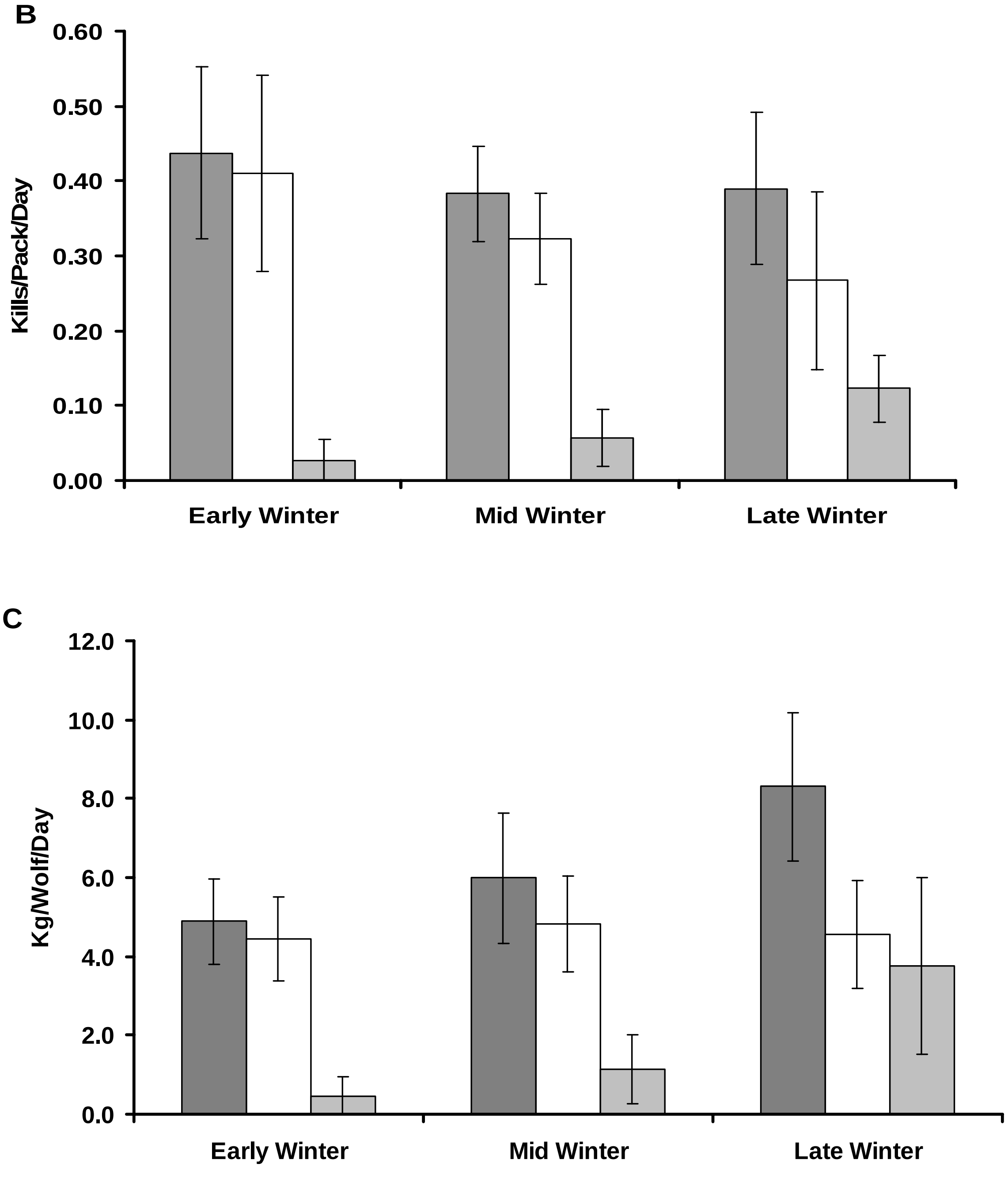


Figure 3.1. Kill rate summaries and 95% confidence intervals by winter period (early = November 15-January 6; middle = January 7-February 27; late = February 28-April 21) for wolves in the Madison headwaters area of Yellowstone National Park during 1998-99 through 2006-07 using the following metrics: A) kills/wolf/day; B) kills/pack/day; and C) kg/wolf/day.

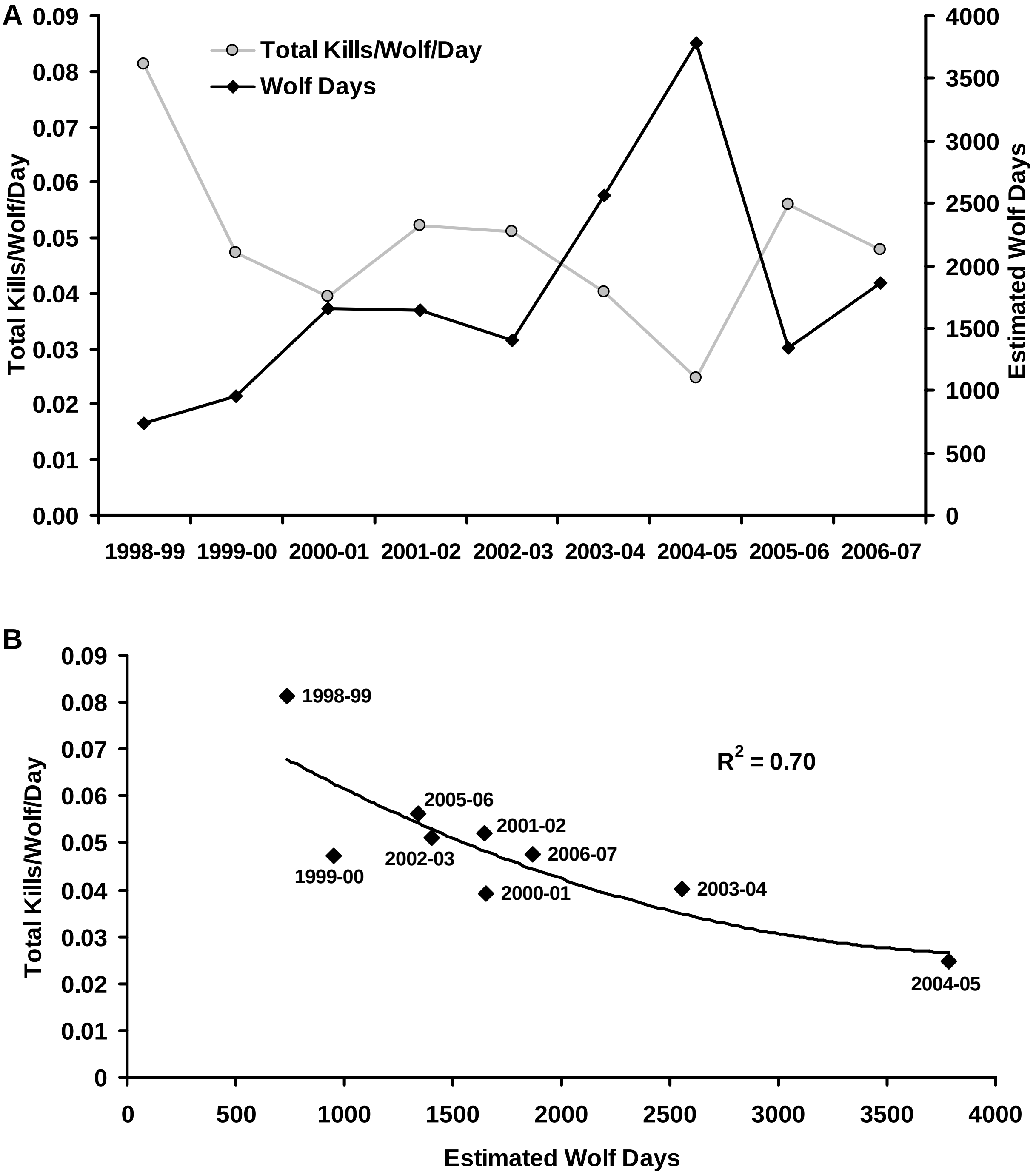


Figure 3.2 (A) Observed trends in estimated wolf days and winter kill rates (kills/wolf/day) in the Madison headwaters area of Yellowstone National Park during winters 1998-99 through 2006-07, and (B) the correlation between the two metrics.

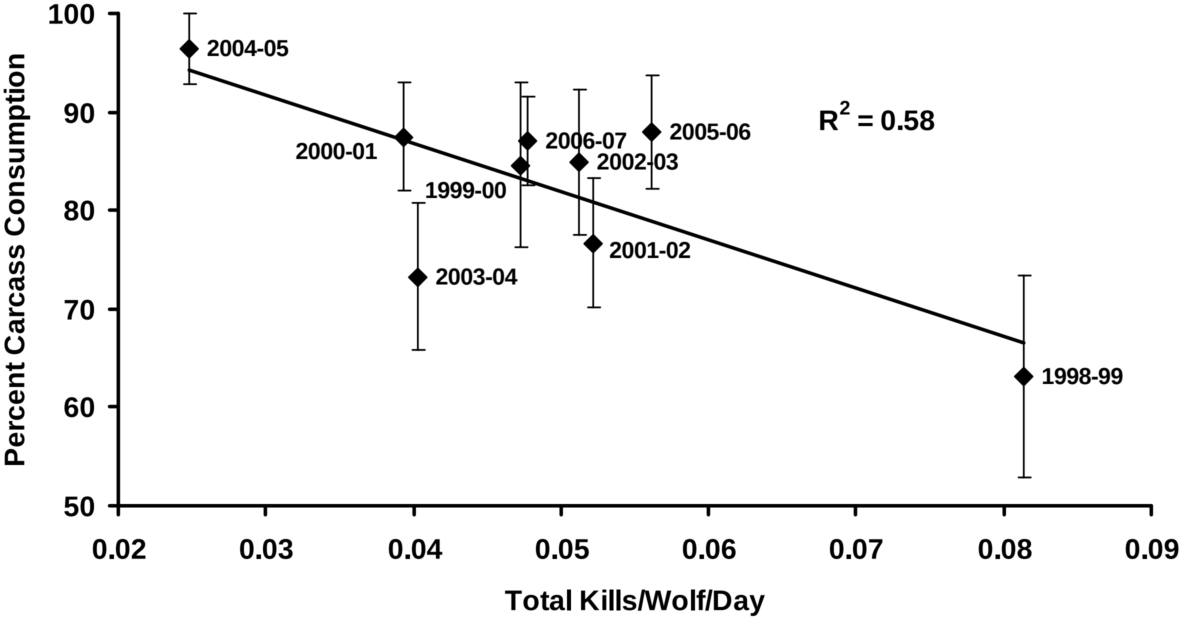


Figure 3.3 Relationship between total wolf kill rates and percent of carcass consumption with 95% confidence intervals for the Madison headwaters area of Yellowstone National Park during winters 1998-99 through 2006-07. Peak carcass consumption occurred in winter 2004-05 and corresponded to peak wolf numbers, decreasing elk abundance, and low kill rates. The lowest carcass consumption occurred in winter 1998-99 when wolves first became established in the Madison headwaters, elk were most abundant, and kill rates peaked.

Variations in Elk Kill Rate

I fitted 12 *a priori* models to 36 elk kill rate estimates of kills/wolf/day, kills/pack/day and kg/wolf/day, respectively, from resident wolf packs across nine winters. Model selection results supported one top model for both the kills/wolf/day and kills/pack/day metrics, with Akaike model weights (w_k) of 0.46 and 0.40, respectively (Table 3.1). The most-supported model structure was identical for both metrics, consisting of covariates for total elk abundance ($\mathrm{ELK}_{\mathrm{all}}$) and pack size ($\mathrm{WOLF}_{\mathrm{pack}}$). For both metrics, all other models had $\Delta\mathrm{AIC}_c > 2$ and primarily differed in the substitution of elk age class covariates ($\mathrm{ELK}_{\mathrm{ad}}$ and $\mathrm{ELK}_{\mathrm{calf}}$) for total elk abundance, though confidence intervals for elk calves overlapped zero (Table 3.3). Several models also included covariates for bison abundance, wolf population, and snow pack, but coefficient estimates overlapped zero. Predictor weight for total elk abundance (ELK_{all}) for kills/wolf/day and kills/pack/day was 0.70 and 0.68, respectively, while the predictor weight for wolf pack size ($WOLF_{pack}$) was 0.99 and 0.86, respectively. Elk abundance was significant in all models because models estimating elk abundance by age class accounted for the remaining predictor weights (0.29 and 0.30 for kills/wolf/day and kills/pack/day, respectively; Table 3.3). Model results for kg/wolf/day were less clear, with three most-supported models differing primarily in whether total elk abundance or age class abundance was used (Table 3.1) and one model including snow pack (SWE_{acc}). Additional predictors aside from elk abundance and wolf pack size (predictor weights of 0.66 and 0.97, respectively) contributed little explanatory power (Tables 3.1 and 3.3). Consistent with our predictions, the elk abundance covariates ELK_{all} and Elk_{ad} were positively related to kill rates of all three metrics. Wolf pack size was negatively related to kills/wolf/day and kg/wolf/day, but positively related to kills/pack/day (Table 3.3). Coefficients for significant top model covariates were stable and fitting modified and pseudo-threshold forms to prey abundance covariates did not improve model fits. Substantially more variation was explained by the most-supported model for elk kills/pack/day than the top models of kills/wolf/day and kg/wolf/day (r^2_{adj} of 0.51 versus 0.37 and 0.36, respectively).

Table 3.1. *A priori* model structure and results from top models for multiple linear regression analyses of elk kill rates by resident wolf packs in the Madison headwaters area of Yellowstone National Park during 1998-99 through 2006-07.

Model structure and metric	**ΔAIC_c**	**w_k**	**r^2_{adj}**
Elk kills/wolf/day			
$ELK_{all} + WOLF_{pack}$	0.00	0.46	0.37
$ELK_{ad} + ELK_{calf} + WOLF_{pack}$	2.44	0.13	0.38
$ELK_{ad} + ELK_{calf} + BISON_{calf} + WOLF_{pack}$	2.53	0.13	0.35
$ELK_{all} + WOLF_{pack} + SWE_{acc}$	2.67	0.12	0.35
$ELK_{all} + BISON_{all} + WOLF_{pack}$	2.71	0.12	0.36
$ELK_{ad} + ELK_{calf} + WOLF_{pack} + SWE_{acc}$	5.31	0.03	0.33
ELK_{all}	10.22	0.00	0.12
Elk kills/pack/day			
$ELK_{all} + WOLF_{pack}$	0.00	0.40	0.51
$ELK_{ad} + ELK_{calf} + WOLF_{pack}$	2.33	0.12	0.50
$ELK_{all} + WOLF_{pack} + SWE_{acc}$	2.64	0.11	0.49
$ELK_{all} + BISON_{all} + WOLF_{pack}$	2.71	0.10	0.49
$ELK_{ad} + ELK_{calf} + BISON_{calf} + WOLF_{pack}$	2.87	0.09	0.51
$ELK_{ad} + ELK_{calf} + WOLF_{pack} + SWE_{acc}$	4.47	0.04	0.49
ELK_{all}	4.73	0.04	0.41
$ELK_{ad} + ELK_{calf} + SWE_{acc}$	5.58	0.02	0.45
$ELK_{ad} + ELK_{calf} + BISON_{calf}$	5.64	0.02	0.45
$ELK_{all} + SWE_{acc}$	5.87	0.02	0.42
$ELK_{ad} + ELK_{calf}$	6.81	0.01	0.40
$ELK_{all} + BISON_{all}$	7.20	0.01	0.40
Elk kg/wolf/day			
$ELK_{all} + WOLF_{pack}$	0.00	0.39	0.36
$ELK_{ad} + ELK_{calf} + WOLF_{pack}$	1.63	0.17	0.36
$ELK_{all} + WOLF_{pack} + SWE_{acc}$	1.74	0.16	0.36
$ELK_{all} + BISON_{all} + WOLF_{pack}$	2.53	0.11	0.34
$ELK_{ad} + ELK_{calf} + BISON_{calf} + WOLF_{pack}$	2.68	0.10	0.37
$ELK_{ad} + ELK_{calf} + WOLF_{pack} + SWE_{acc}$	4.36	0.04	0.34
$ELK_{all} + SWE_{acc}$	11.53	0.00	0.11

Note: Covariate codes are total numbers of elk and bison ($ELK_{all,}$, $BISON_{all}$), numbers of adult elk and bison (ELK_{adt} , $BISON_{adt}$), numbers of calf elk and bison (ELK_{calf} ,$BISON_{calf}$), wolf pack size ($WOLF_{pk}$), and accumulated snow pack (SWE_{acc}).

Table 3.2. A priori model structure and results from top models for multiple linear regression analyses of bison kill rates by resident wolf packs in the Madison headwaters area of Yellowstone National Park during 1998-99 through 2006-07.

Model structure and metric	**ΔAIC_c**	**w_k**	**r^2_{adj}**
Bison kills/wolf/day			
SWE_{acc}	0.00	0.29	0.39
$BISON_{calf}$	0.72	0.20	0.38
$BISON_{calf}$ + $WOLF_{pack}$	0.73	0.20	0.40
ELK_{all} + SWE_{acc}	0.89	0.18	0.40
ELK_{all} + SWE_{acc} + $WOLF_{pack}$	3.52	0.05	0.38
ELK_{ad} + ELK_{calf} + $BISON_{calf}$	4.29	0.03	0.37
ELK_{ad} + ELK_{calf} + SWE_{acc} + $WOLF_{pack}$	4.87	0.03	0.39
ELK_{ad} + ELK_{calf} + $BISON_{calf}$ + $WOLF_{pack}$	5.89	0.02	0.37
$BISON_{all}$ + $WOLF_{pack}$	12.01	0.00	0.18
Bison kills/pack/day			
$BISON_{calf}$	0.00	0.58	0.39
$BISON_{calf}$ + $WOLF_{pack}$	2.31	0.18	0.37
ELK_{ad} + ELK_{calf} +$BISON_{calf}$	3.88	0.08	0.37
SWE_{acc}	5.42	0.04	0.29
ELK_{ad} + ELK_{calf} +$BISON_{calf}$ + $WOLF_{pack}$	5.53	0.04	0.37
ELK_{all} + SWE_{acc}+ $WOLF_{pack}$	5.70	0.03	0.34
ELK_{all} + SWE_{acc}	6.26	0.03	0.30
ELK_{ad} + ELK_{calf} + SWE_{acc}+ $WOLF_{pack}$	8.12	0.01	0.33
$BISON_{all}$	10.09	0.00	0.19
Bison kg/wolf/day			
$BISON_{calf}$	0.00	0.50	0.34
$BISON_{calf}$ + $WOLF_{pack}$	1.59	0.22	0.34
ELK_{ad} + ELK_{calf} +$BISON_{calf}$	2.21	0.16	0.35
ELK_{ad} + ELK_{calf} + $BISON_{calf}$ + $WOLF_{pack}$	5.06	0.04	0.33
ELK_{all} + SWE_{acc}	5.67	0.03	0.26
SWE_{acc}	5.92	0.03	0.22
ELK_{all} + SWE_{acc}+ $WOLF_{pack}$	8.35	0.01	0.23
$BISON_{all}$	9.81	0.00	0.13

Note: Covariate codes are defined in Table 3.1.

Table 3.3. Elk kill rates by resident wolf packs in the Madison headwaters area of Yellowstone National Park during 1998-99 through 2006-07.

Metric and model	**ELK$_{all}$**	**ELK$_{adt}$**	**ELK$_{calf}$**	**BISON$_{all}$**	**BISON$_{calf}$**	**WOLF$_{pk}$**	**SWE$_{acc}$**
Elk kills/wolf/day							
Predictor weight	0.70	0.29	0.29	0.12	0.13	0.99	0.15
ELK$_{all}$+WOLF$_{pk}$	**0.020** **(0.011, 0.029)**					**-0.019** **(-0.028, -0.009)**	
Elk kills/pack/day							
Predictor weight	0.68	0.30	0.30	0.11	0.11	0.86	0.19
ELK$_{all}$+WOLF$_{pk}$	**0.161** **(0.115, 0.207)**					**0.131** **(0.037, 0.225)**	
Elk kg/wolf/day							
Predictor weight	0.66	0.31	0.31	0.11	0.10	0.97	0.20
ELK$_{all}$+WOLF$_{pk}$	**2.19** **(0.97, 3.41)**					**-2.87** **(-4.18, -1.56)**	
ELK$_{adt}$+ELK$_{calf}$+WOLF$_{pk}$		**2.19** **(0.82, 3.56)**	0.06 (-1.57, 1.68)			**-2.91** **(-4.22, -1.60)**	
ELK$_{all}$+WOLF$_{pk}$+SWE$_{acc}$	**2.20** **(0.98, 3.40)**					**-2.62** **(-4.03, -1.21)**	0.67 (-0.73, 2.06)

Note: Coefficient values (B_i), lower and upper 95% confidence intervals (in parentheses), and predictor weights (w_p) for the best approximating models for each kill rate metric identified through AIC model comparison techniques. Boldface type indicates confidence intervals do not span zero. Covariate codes are defined in Table 3.1.

Table 3.4. Bison kill rates by resident wolf packs in the Madison headwaters area of Yellowstone National Park during 1998-99 through 2006-07.

Metric and model	Covariate						
	ELK_{all}	ELK_{adt}	ELK_{calf}	$\text{BISON}_{\text{all}}$	$\text{BISON}_{\text{calf}}$	WOLF_{pk}	SWE_{acc}
Bison kills/wolf/day							
Predictor weight	0.23	0.08	0.08	0.00	0.45	0.30	0.55
SWE_{acc}							**0.015** **(0.009, 0.021)**
$\text{BISON}_{\text{calf}}$					**0.013** **(0.007, 0.019)**		
$\text{BISON}_{\text{calf}}$+$\text{WOLF}_{\text{pk}}$					**0.011** **(0.005, 0.017)**	-0.005 (-0.011, 0.001)	
ELK_{all}+SWE_{acc}	-0.003 (-0.009, 0.003)						**0.015** **(0.009, 0.021)**
Bison kills/pack/day							
Predictor weight	0.07	0.13	0.13	0.00	0.88	0.26	0.11
$\text{BISON}_{\text{calf}}$					**0.094** **(0.055, 0.133)**		
Bison kg/wolf/day							
Predictor weight	0.04	0.20	0.20	0.00	0.92	0.27	0.07
$\text{BISON}_{\text{calf}}$					**3.44** **(1.89, 4.99)**		
$\text{BISON}_{\text{calf}}$+$\text{WOLF}_{\text{pk}}$					**3.23** **(1.62, 4.84)**	-0.85 (-2.61, 0.92)	

Note: Coefficient values (B_i), lower and upper 95% confidence intervals (in parentheses), and predictor weights (w_p) for the best approximating models for each kill rate metric identified through AIC model comparison techniques. Boldface type indicates confidence intervals do not span zero. Covariate codes are defined in Table 3.1.

Variations in Bison and Total Kill Rates

I fitted 12 *a priori* models to 36 bison kill rate estimates of kills/wolf/day, kills/pack/day, and kg/wolf/day, respectively, from resident wolf packs across nine winters. Model selection results supported four top models for kills/wolf/day, one top model for kills/pack/day, and two top models for kg/wolf/day (Table 3.2). Akaike model weights (w_k) for the most-supported kills/wolf/day models were SWE_{acc} (0.29), $BISON_{calf}$ (0.20), $BISON_{calf}$ and $WOLF_{pack}$ (0.20), and Elk_{all} and SWE_{acc} (0.18; Table 3.2). Model weight for the most-supported kills/pack/day model with a single covariate structure, $BISON_{calf,}$ was 0.58. Model weights for the most-supported models for kg/wolf/day were $BISON_{calf}$ (0.50) and $BISON_{calf}$ and SWE_{acc} (0.22; Table 3.2). For kills/wolf/day, confidence intervals for only the SWE_{acc} and $BISON_{calf}$ coefficients did not overlap zero. Similarly, coefficient estimates for kills/pack/day and kg/pack/day indicated that $BISON_{calf}$ was the only significant predictor (Table 3.4). Predictor weights for SWE_{acc} and $BISON_{calf}$ in kills/wolf/day analyses were 0.55 and 0.45, respectively, while the predictor weight for $BISON_{calf}$ was 0.88 and 0.92 for kills/pack/day and kg/wolf/day, respectively. Consistent with our predictions, bison calf abundance and increasing snow pack were positively related to kill rates of all three metrics (Table 3.4). Coefficients for significant top model covariates were stable and fitting modified and pseudo-threshold forms to prey abundance covariates did not improve model fits. The top models for kills/wolf/day and kills/pack/day explained similar amounts of variation relative to kg/wolf/day (r^2_{adj} of 0.40 and 0.39 versus 0.34, respectively).

Top models for total kill rates primarily reflected the top elk kill rate models with the addition of SWE_{acc} (Appendix B). There was one most-supported model for kills/wolf/day with a weight of 0.73 and the structure of ELK_{all}, $WOLF_{pack}$, and SWE_{acc}. There were three top-ranking models for kills/pack/day that differed in their inclusion of SWE_{acc} and the covariates for elk abundance, with model weights of 0.32, 0.19, and 0.17, respectively. The kg/wolf/day analysis supported an identical top model to the analysis for kills/wolf/day, with a weight of 0.61. All predictors for these two analyses had coefficient estimates with confidence intervals that did not overlap zero, while confidence intervals for ELK_{calf} and SWE_{acc} coefficient estimates in the kills/pack/day analysis included zero (Appendix B). Elk abundance and SWE_{acc} were positively related to kill rates of all metrics. Pack size was positively related to kills/pack/day and negatively related to kills/wolf/day and kg/wolf/day (Appendix B).

Functional Response

Fitting seven functional response models to 26 pooled wolf kill rate estimates for each winter period yielded overwhelming support for the Type II ratio-dependent model ($w_k = 0.70$), and ratio-dependent models comprised 0.92 of the model weights (Table 3.5). Coefficient values for estimated attack rate (α) and handling time (h) in the top model were 0.002 (95% CI = 0.001, 0.004) and 13.9 days (95% CI = 7.9, 19.9), respectively. The predicted functional response from the most-supported model increased rapidly at low elk:wolf ratios before gradually approaching an asymptote of approximately 0.058 kills/wolf/day (Fig. 3.4A). One value in the data appeared to be an extreme outlier that could potentially influence the asymptotic value and model results (Fig. 3.4A). Thus, I removed this data point and refit all models during an exploratory analysis. The asymptotic value decreased to 0.048 kills/wolf/day, coefficient values for attack rate and handling time changed to 0.004 (95% CI = 0.001, 0.007) and 18.79 (95% CI = 13.8, 23.8), respectively, and model selection results remained unchanged. The Type II functional response was also the most-supported prey-dependent model, but overall had little support and no clear asymptote as elk abundance increased (Fig. 3.4B). The two-prey functional response models for both prey-dependent and ratio-dependent models were not supported by the data.

Table 3.5. Results from functional response analyses of wolf kill rates on elk during 1998-99 through 2006-07 in the Madison headwaters area of Yellowstone National Park.

Model	**Structure**	**ΔAIC$_c$**	**w_k**
Type II ratio-dependent	$\frac{\alpha N}{p + \alpha h N}$	0.00	0.70
Type III ratio-dependent	$\frac{\alpha N^2}{p + \alpha h N^2}$	2.49	0.20
Type II prey-dependent	$\frac{\alpha N}{1 + \alpha h N}$	6.47	0.03
Type III prey-dependent	$\frac{\alpha N^2}{1 + \alpha h N^2}$	6.94	0.02
Two-prey prey dependent Type III	$g_1 = \frac{\alpha N_1}{1 + \alpha\ N_2 h\ c^b m\ (N_2/N_1)^{b-1} + \alpha\ N_1 h}$	7.00	0.01
Two-prey ratio dependent Type III	$g_1 = \frac{\alpha N_1}{P + \alpha\ N_2 h\ c^b m\ (N_2/N_1)^{b-1} + \alpha\ N_1 h}$	7.88	0.01
Constant	α	8.27	0.01

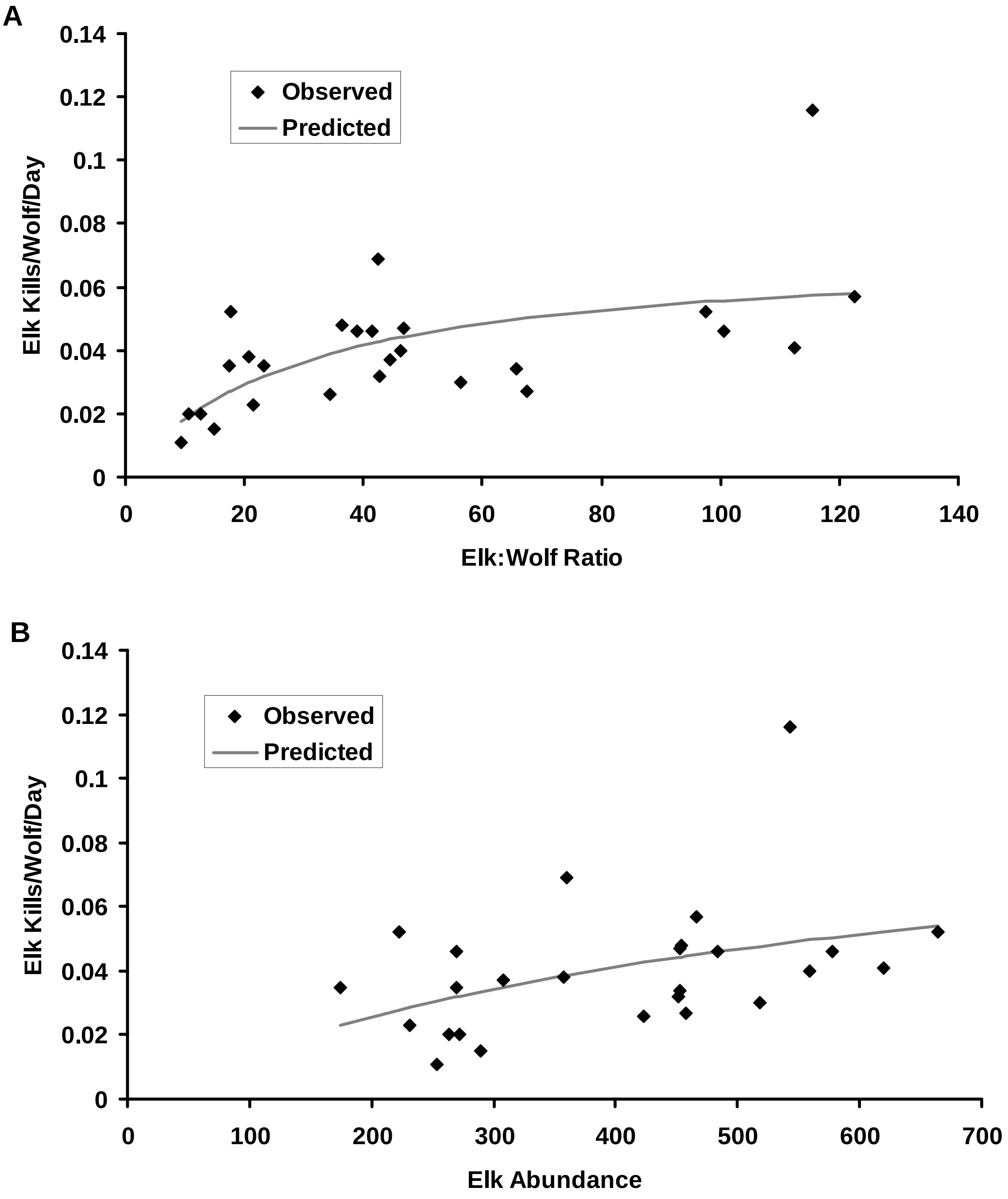


Figure 3.4 Predicted and observed functional response curves for elk from wolf predation data in the Madison headwaters area of Yellowstone National Park during winters 1998-99 to 2006-07, including (A) a Type II ratio-dependent curve; and (B) a Type II prey-dependent curve.

Discussion

Adding a top predator to an ecosystem can result in profound demographic, spatial, and behavioral changes in prey and predator populations (Taylor 1984, Berger et al. 2001). Evaluating these dynamics requires descriptions of a predator's per-capita consumption for a particular prey (Abrams and Ginzburg 2000). Thus, the functional response is a critical component embedded in virtually every predator-prey model. While prey abundance is essential for these descriptions, the influence of predator abundance on kill rates and functional responses is controversial because prey-dependent and predator-dependent models often make considerably different predictions about ecosystem dynamics (Abrams and Ginzburg 2000). I demonstrated that factors driving variation in wolf kill rates on elk and bison in the Madison headwaters area of Yellowstone differed between prey species. Kill rates on elk were primarily influenced by elk abundance and wolf pack size, while kill rates on bison were primarily influenced by the abundance of bison calves and snow pack severity. The form of the wolf functional response for elk was strongly Type II ratio-dependent, further supporting the importance of satiation and predator dependence in wolf-ungulate systems (Vucetich et al. 2002, Jost et al. 2005).

Elk were the preferred and primary prey for wolves in the Madison headwaters area, even though bison were more abundant during winter (Chapter 2). Thus, elk abundance significantly influenced variations in both total kill rates and kill rates on elk, similar to findings from other multiple-prey systems where elk were the primary prey (Hebblewhite et al. 2003). Discriminating between adult and calf elk abundance did not improve model fit relative to overall elk abundance, even though wolves preferred elk calves and calves were consumed faster due to their smaller size. The significance of total elk abundance and adult elk abundance in explaining kill rate variation on elk was likely due to an overall decrease in the elk numbers during the latter years of the study, which included a substantial increase in adult mortality (Garrott et al. 2008*d*). Calf survival was strongly affected by wolves (Garrott et al. 2008*d*) and typically decreased through winter due to starvation mortality prior to wolf recolonization (Garrott et al. 2008*c*), perhaps explaining why calf abundance was a poor predictor of kill rate variation on elk.

The Madison headwaters supported a two-prey system, making complex, indirect effects possible between prey that share a predator (Garrott et al. 2008*a*). However, the abundance of alternative bison prey explained little variation in wolf kill rates on elk. Rather than decreasing elk kill rates, increasing bison abundance, particularly calves, was correlated with increased bison kill rates and total kill rates (Table 3.1, Fig. 3.1). Similarly, accumulated snow pack did not appear to explain variation in wolf kill rates on elk in our study system, contrary to findings from other studies (Mech et al. 2001, Hebblewhite et al. 2002).

I detected a significant relationship between pack size and kill rates across all metrics for elk kill rates, consistent with findings from other studies (Thurber and Peterson 1993, Schmidt and Mech 1997, Hayes et al. 2000). Larger packs killed more frequently than smaller packs and per capita kills and gross food availability decreased with increasing numbers of wolves in a pack. However, the importance of pack size on kill rates differs across systems. For example, in linear regression analyses Hayes et al.

2000 found that variability in kill rates was best explained by pack size, while in multiple regression analyses Jędrezewski et al. (2002) found it explained little variance relative to snow cover, though the size and range of pack sizes in their study was limited. In terms of total biomass acquired per wolf per day, our estimates were well above the minimum estimated intake of 1.6 kg/wolf/day (Mech 1970), particularly in late winter when kg/wolf/day was significantly higher due to the increased predation on bison. However, these estimates certainly reflect maximum intake because I did not account for scavenger loss or incomplete consumption (Fig. 3.3). While smaller packs had a higher kg/wolf/day kill rate, the net disparity between large and small packs may not have been great given that larger packs are less prone to scavenger loss (Vucetich et al. 2004) and grizzly bears were common at wolf kills in spring and frequently usurped wolf kills (Ballard et al. 2003; R. Garrott, unpublished data). Thus, while larger packs had lower gross per capita biomass at kills, they also were likely more effective at avoiding scavenger loss and increasing food acquisition (Vucetich et al. 2004) such that the difference in food intake was not as pronounced. Alternatively, smaller packs may have consumed less food at higher kill rates.

In contrast to kill rates on elk, wolf pack size poorly explained variation in kill rates on bison because larger packs did not kill bison more frequently. Kill rate variation on bison was best explained by the abundance of bison calves or by snow pack severity, but was not significantly affected by elk abundance. Due to the strong correlation between increasing snow pack and bison migration into the study system (Bruggeman et al. 2008a), we were unable to distinguish between the respective influences of snow pack and bison calf abundance. Wolves strongly selected for bison calves and predation coincided with increases in bison abundance and bison abundance relative to elk. Bison predation typically occurred in late winter when ungulates were likely in their worst physical condition due to prolonged nutritional deficits (Bruggeman et al. 2008*a*, Chapter 2, White et al. 2008*a,b*). Bison are considerably more formidable prey than elk in both defenses and anti-predator behaviors (MacNulty et al. 2007, Chapter 2). Thus, wolf predation was largely opportunistic and primarily occurred when bison vulnerability increased late winter. Social carnivores typically take larger prey with larger foraging groups (Rosenzweig 1966, Gittleman 1989, Creel and Creel 1995). However, bison selection by wolves in the Madison headwaters was negatively related to pack size because the largest packs (22 wolves) selected primarily elk, while smaller packs (six wolves) killed the most bison (Chapter 2). This likely does not reflect an opposite trend from that observed in other systems so much as favorable conditions for killing bison occurred for these packs. In the more severe winters many bison were in very poor nutritional condition and therefore very vulnerable to wolf predation (Chapter 2, Fig. 2.9), and this vulnerability was likely not substantially increased with more wolves in a pack. In addition several of the largest packs occurred in winters when elk were abundant and widely distributed throughout the system and wolf competition for them was low. An alternative explanation for this relationship is that particular packs learned how to kill bison more efficiently, which would also affect kill rates but would not be reflected in pack size. While I acknowledge that learning can assume an important role in predation, virtually all wolf packs had experience in killing bison and specific wolf packs did not exhibit a constant increase in bison kills as would be expected if they were simply improving their efficiency. For example, the Gibbon pack killed 63% bison in winter 2005-06, but only 15% in 2006-07 (Chapter 2).

Approximately 0.45-0.57 of the variation in total wolf kill rate was explained by the abundance of preferred prey, wolf pack size, and snow pack severity. While all of these factors have been identified as having important influences on wolf kill rates, we are not aware of other studies that conducted separate evaluations of factors affecting kill rates for multiple prey species. Nevertheless the most-supported models across all kill rate metrics for elk and bison explained 0.36-0.51 of the respective kill rate variation for each species (Tables 3.1, 3.2), leaving a substantial amount of kill rate variation unexplained. This finding likely reflects the complexities of a multiple-prey system wherein species differed substantially in their relative vulnerability to wolves and vulnerability differed among age classes (Chapter 2). Also, there were complex interactions between heterogeneous landscapes, climate, and multiple, overlapping packs that undoubtedly contributed to variations in kill rate. In addition to these complexities, the appropriate scale at which to analyze kill rates and functional response is often unclear. Strong arguments can be made for using a per-pack scale, whereby kill rates and prey abundance are estimated for each pack's respective territory. However, kill rates could also be evaluated at a "mixed" scale, where kill rates are estimated for each pack but prey abundance is estimated for the entire system, or at a study area scale, where kill rates and prey abundance are estimated for the entire wolf and ungulate populations (Jost et al. 2005). In exploratory analyses, I evaluated kill rates on the per-pack scale and results were quite similar to the study-area scale analyses presented in this chapter. However, the per-pack scale models explained substantially less variation in kill rates with less distinction between models, possibly because much of the variation was related to decreases in elk abundance in the system during the latter years. Thus, estimating prey abundance at the study-area scale served as an umbrella for describing these influences. In addition, the study-area scale was appropriate for evaluating the shape of the functional response given that it is a description of the average per capita consumption rate of wolves. Nevertheless, the potential for differing results at differing scales should be heeded.

It is essential to avoid biases in the detection efficiency of kills when evaluating variation in kill rates and the subsequent shape of the functional response. For example, one potential reason for the effect of pack size on per capita kill rates is purely methodological in that larger packs can consume prey faster and potentially make kills more difficult to detect (Mech and Peterson 2003). Kill detection probability can also be subject to substantial variation in observer effort, weather conditions, and wolf movement, which can translate into substantial differences in kill detection both within and among studies (Jaffe 2001, Hebblewhite et al. 2003, Smith et al. 2004). We were able to obtain accurate estimates of wolf kill rates by evaluating wolf kill rates in a relatively small, tractable area defined by a high density ungulate winter range and employing intensive ground-based monitoring and tracking on a daily basis through each winter. Jaffe (2001) evaluated kill detection efficiency in the Madison headwaters and determined that the methods were effective in detecting at least 75% of the kills made by wolf packs in the study area, and subsequent estimates have improved efficiency to approximately 85% (Garrott unpublished data). No systematic biases were detected across prey types or pack sizes that would indicate inaccurate estimates.

Similar to other studies of functional responses, wolves exhibited a Type II curve for elk (Dale et al. 1994, Hayes and Harestad 2000, Vucetich et al. 2002). One of the primary ways an asymptotic, Type II functional response can arise is through predator satiation. However, this response may also be more likely to occur if a prey item is preferred (Holling 1959, Messier 1995). If a prey item is preferred relative to an alternative prey, then the functional response can be destabilizing (Eubanks and Denno 2000). Thus, the incorporation of a Type III functional response for elk in modeling wolf predation for Greater Yellowstone systems (Boyce 1993, 1995, Varley and Boyce 2006) may underestimate the effects of wolf predation on a preferred prey if alternative prey are considerably less vulnerable (Garrott et al. 2008*a*). Alternatively, recent investigations advocate that a Type II response can be stabilizing with social predators and prey (Fryxell et al. 2007). However, the dynamic nature of elk grouping strategies on fine and coarse temporal scales in response to variability in predation risk and habitat in this system (Gower et al. 2008*b*) make application of this idea difficult. Using data from Dale et al. (1994) and Messier (1991, 1994), Eberhardt (1997) demonstrated that wolf Type II functional response curves for moose and caribou increased rapidly before reaching asymptotic values at approximately 0.021 and 0.089 kills/wolf/day, respectively, across a wide range of prey densities.

The asymptotic value for elk functional response curves in the Madison headwaters was approximately 0.058 kills/wolf/day, similar to the mean total kill rates (90% of which were elk) reported by Smith et al (2004) of 0.061 and 0.068 kills/wolf/day for wolf packs elsewhere in Yellowstone during winters 1995-96 through 1999-00. When the asymptotic value for wolf functional responses on elk in the Madison headwaters and caribou from Dale et al. (1994) are converted to moose equivalents (one moose equivalent to two elk or three caribou; Keith 1983), the resultant values are both 0.029 moose/wolf/day respectively, remarkably similar to the value calculated by Eberhardt (1997) for moose. Such consistency suggests a relatively uniform asymptotic wolf kill rate across a wide variety of wolf-ungulate systems and ungulate densities (Eberhardt 1997; Eberhardt et al. 2003). In the Madison headwaters, the functional response curve appears relatively constant across a wide range of values aside from an outlier (where wolves had a very high kill rate in the first winter of their establishment in the study area) and the three lowest values. High initial kill rates occurring on a naïve prey base and the extremely low elk:wolf ratios we recorded at peak wolf abundance (approximately one wolf per 10 elk) possibly represented transitory extremes in the system. Given the potential for a continuing decrease in elk abundance (Garrott et al. 2008*a,d*), additional estimates at very low elk:wolf ratios may be possible.

The multiple-species dependent models incorporating elk and bison abundance in describing elk functional response were not supported likely due to a variety of reasons. While it is possible that the model structure is inappropriate for these multiple-species interactions, bison did not appreciably influence variation in elk kill rates due to differences in vulnerability between the two prey species. Therefore, application of these models may be more appropriate in multiple prey systems where prey species do not differ so substantially (Garrott et al. 2008*a*). Alternatively, given that the Madison headwaters is still a developing two-prey system, the lack of fit may simply be due to a strong wolf preference for elk, with increased bison predation only under circumstances such as severe winters and high bison:elk ratios (Chapter 2); therefore additional estimates with continued decreases in elk abundance and increases in bison:elk ratios may provide better fits as wolves may increasingly kill bison (Garrott et al. 2008*a*). Regardless, I strongly advocate the continued development of multiple-species dependent functional response models to describe multiple-prey systems (Garrott et al. 2007; Tschanz et al. 2007).

Ratio-dependent models describe the functional response well for numerous predators and parasitoids (Arditi and Akcakaya 1990), and are supported by controlled experiments in natural settings (Reeve 1997) and field studies (Vucetich et al. 2002; Jost et al. 2005). The extensive long-term kill rate data from the Isle Royale wolf-moose system strongly indicated that the functional response for moose was best described by ratio dependence, and our investigations in a multiple prey system yielded similar results. Ratio dependence can arise through a variety of factors, including direct and hostile interference among predators, non-random foraging, the presence of prey refugia, changes in prey behavior resulting in less vulnerable prey with increasing predators, and differential vulnerability among the prey population (Charnov et al. 1976; Hassell 1978; Arditi and Ginzburg 1989; Abrams 1994). Elk were considerably more vulnerable than bison and preferred by wolves during our study. There was also differential vulnerability of prey across age classes (Chapter 2). In addition, wolves were territorial and inter-pack strife was the major cause of mortality (Smith et al. 2008). Wolves had specific patterns of foraging and aggregated disproportionately in the Madison headwaters relative to the rest of their territories (Smith et al. 2008) to target areas of high elk vulnerability (Bergman et al. 2006). Furthermore, landscape characteristics apparently created refugia in certain areas that contributed to a large-scale change in elk distribution within our study system (White et al. 2008*c*). Consequently, increases in wolf numbers and decreases in the elk:wolf ratios negatively affected elk kill rates by increasing competition and intra-specific strife between packs and increasing anti-predator behaviors by elk (Gower et al. 2008*a,b,c*).

While there is a vast literature on anti-predator behaviors in prey (Caro 2005), less is known about the effectiveness of this decision-making in actually reducing predation (Lima 2002), and elk demonstrate a variety of anti-predator responses to wolves (Hebblewhite and Pletscher 2002; Creel et al. 2005; Creel and Winnie 2005; Gude et al. 2006; Hebblewhite and Merrill 2007). I detected a strong correlation between mean winter group size for elk and wolf abundance, as well as an increase in elk group size variance with increasing wolf abundance, which I interpret as an elk behavioral response to increasing predation risk (Gower et al. 2008*b*). In addition, substantial changes in elk abundance, recruitment, and distribution occurred during the study period (Garrott et al. 2008*d;* White et al. 2008*c*), such that in the latter winters elk became more concentrated and predictable in areas that apparently provided refuge and escape habitat (White et al.

2008*c*). If an elk group is the unit of encounter rather than an individual (Huggard 1993), and herd sizes are variable on fine temporal scales as elk respond to immediate wolf threats by grouping and using escape terrain (Garrott et al. 2008*a*; Gower et al. 2008*b*; White et al. 2008*c*), then I would expect kill rates to decrease with increased wolf numbers due to prey depression, as fewer vulnerable individuals would be available despite being relatively predictable in their locations. There was a negative correlation between mean winter group size for elk and winter wolf kill rates on elk ($R^2 = 0.66$; Fig. 3.5), indicating that these behavioral responses may have been effective at reducing predation risk. Whether these adjustments were part of the transitory dynamics of a newly-established system with prey adapting to the novel presence of a top predator or whether such plasticity in prey responses can be expected as the system continues to develop is unknown. Regardless, wolf kill rates on large herbivores in the Madison headwaters area were likely strongly dependent on the physical, behavioral, and environmental vulnerability of their prey (Garrott et al. 2008*a*), in addition to encounter rates.

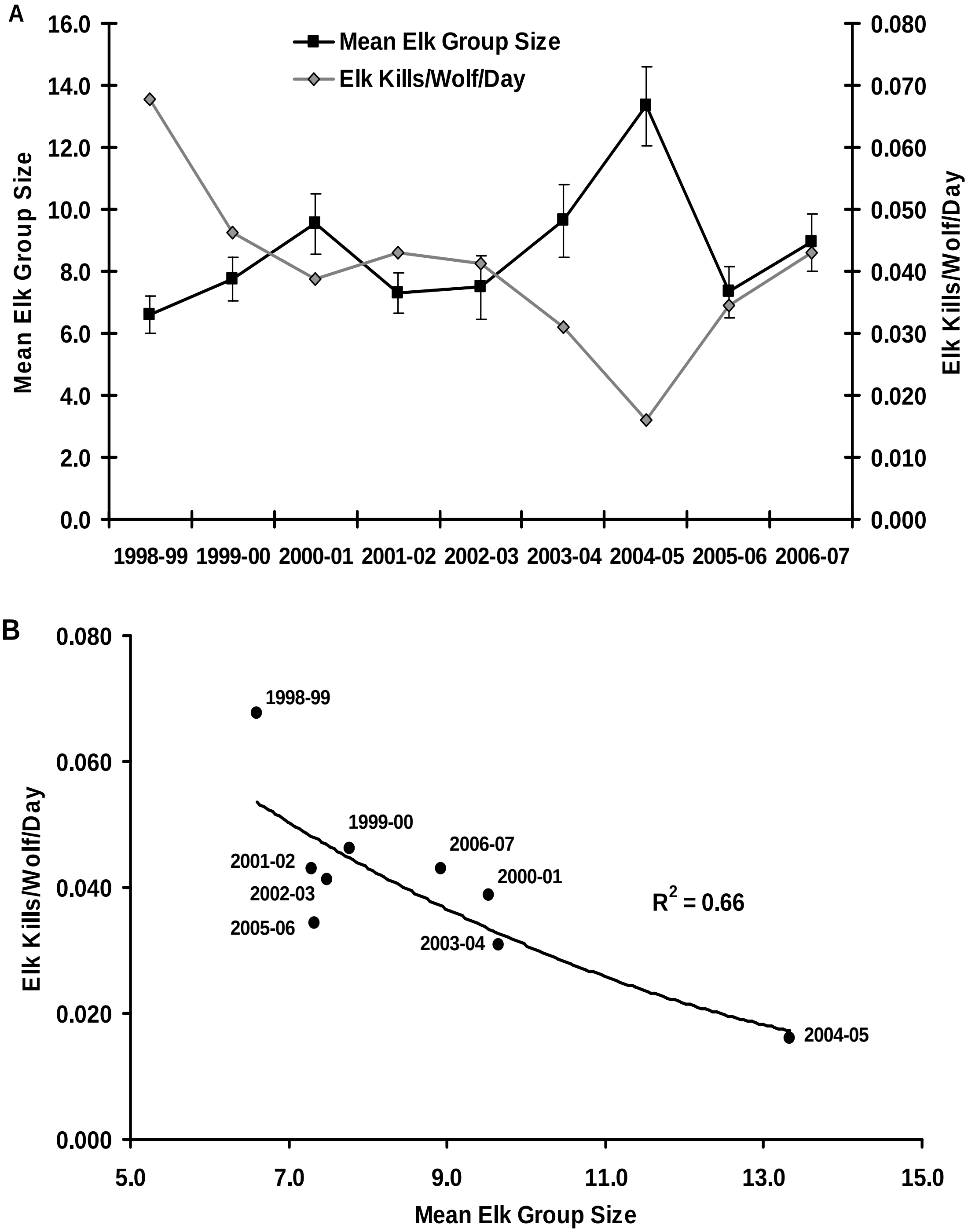


Figure 3.5. (A) Observed trends in mean winter elk group size (Gower et al. 2008a) and winter wolf kill rates (kills/wolf/day) on elk in the Madison headwaters area of Yellowstone National Park during 1998-99 through 2006-07, and (B) the correlation between the twp metrics.

Figure 3.6 Members of the Hayden pack scavenging on an adult, female bison carcass that was repeatedly revisited by wolves. Increased wolf use of the Madison headwaters area was strongly correlated with decreased kill rates and increased carcass consumption. Scavenging and revisitation of old kills also appeared to increase with decreased elk abundance and increased wolf use of the system (Photo by Shana Dunkley).

Though it is extremely difficult, if not impossible, to disentangle the respective influences of all these different factors into models of predator-prey interactions, I concur with other investigators that ratio-dependence is a parsimonious means of describing the effects of predator density on per-capita consumption rates (Jost et al. 2005, Fig. 3.4, Fig. 3.6). Precise ratio-dependence or prey dependence is likely rare in nature, and can change within systems (Abrams and Ginzburg 2000; Schenk et al. 2005; Tschanz et al. 2007). Thus, further studies are necessary before generalizations can be made. However, our evaluation of a newly-established large mammal predator-prey system further corroborates the importance of considering predator population density in understanding the nature of predation.

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CHAPTER 4

SYNTHESIS AND DIRECTIONS FOR FUTURE RESEARCH

Synthesis

Intensive long-term studies of recolonizing wolves in a temporally and spatially dynamic system provided valuable insights into large mammal predator-prey dynamics. In particular, the pervasive influence of differential vulnerability among prey species and age classes and its interactions with climate, landscape variables and predator abundance had pronounced effects on wolf prey selection, preference, kill rates, functional response, the propensity for prey-switching, and, ultimately, the likely trajectory of the Madison headwaters system.

Frequent and rigorous abundance estimates of all prey types for each season and winter, intensive monitoring of wolf packs and populations, and subsequent evaluations using selection indices and prey switching analyses indicated that wolves strongly preferred elk, particularly calves, to bison. Patterns of prey selection trends were strongly correlated to elk calf abundance. While wolves increasingly killed bison with increasing bison:elk ratios, snow pack duration, and wolf numbers, they did not appear to change their preference for elk. Similarly, variation in elk kill rates were not related to or reduced by increases in bison kill rates. The wolf functional response for elk was a Type II, indicative of a preferred prey, and strongly influenced by wolf abundance, as it was positively correlated with increased competition and anti-predator responses of elk.

Such predation patterns and their strong relationship to elk are likely due to the lower vulnerability of bison. Their larger size and imposing defenses made bison very formidable, while the flight responses of elk (in contrast to group defense typically employed by bison) rendered them much more vulnerable to environmental traps formed by landscape, habitat complexity and snow pack (Bergman et al. 2006; Garrott et al. 2008)**.** Thus, while changes in vulnerability occurred that resulted in increased wolf predation on abundant and nutritionally-deprived bison, this increase did not result in decreased predation on elk, but rather served to increase overall kill rates and likely subsidize a wolf numeric response that further depressed the elk population (Garrott et al. 2008). Consequently, although wolves were certainly very adept at killing vulnerable individuals of all species and age classes, inherent patterns of physical and behavioral vulnerability across species and age classes and their interactions with abiotic variables assumed considerably more importance in explaining the dynamics of this predator-prey system.

Such dynamics emphasize the need to evaluate concepts of predator preference and prey switching, and their impacts on the stability of large mammal systems, at a site-specific scale. Such an approach accounts not only for the absolute and relative abundance of the prey assemblage but also for the associated climatic and landscape features that can interact with life history characteristics of predators and prey to influence vulnerability. Although changes in preference have been well-demonstrated in laboratory experiments on invertebrates using Murdoch's (1969) equation (Elliot 2004), one fundamental disparity between these experiments and evaluating switching in natural systems is that experiments are typically performed using constant numbers of predators and prey (the latter simply changing in relative abundance), with no numerical response of the predator (Messier 1995). Such designs eliminate several fundamental properties of most predator-prey systems, namely that predators can respond numerically to prey and that relative and absolute prey abundances are rarely constant. Similarly one of the fundamental problems with defining switching as increases in predation with increases in relative abundance is that a predator population can increase predation on a more abundant prey but continue to predate a less abundant prey, thereby potentially destabilizing a system through apparent competition (Holt 1977). Lastly, while experimental studies of smaller taxa have elucidated key concepts and provided an immense amount of insights for predator-prey dynamics, arguably the most significant problems inherent in evaluating concepts such as predator preference and prey-switching relate to difficulties in quantifying vulnerability in natural systems. Because there are so many variables that potentially influence prey vulnerability it is likely to vary over very fine and broad temporal and spatial scales, making case studies in natural systems critical.

The reintroduction of wolves to Yellowstone National Park has resulted in a plethora of research and insights on wolf-ungulate dynamics, although there are fundamental disagreements as to the effect of wolves within and across systems that are in very close proximity to each other (Creel and Winnie 2005; Eberhardt et al. 2005; White and Garrott 2005; Vucetich et al. 2005; Creel et al. 2007; Hamlin et al. 2008). While differences in research methodology certainly exist which could assist in explaining these contrasts, it is also likely that there are variable effects of vulnerability created by the complex interactions of predators, prey species, landscape, and climate across systems. Even among systems with similar prey assemblages, intelligent and behaviorally responsive animals such as elk possess an array of sophisticated anti-predator strategies that can differ among systems. It is unlikely that populations in close proximity to each other are fundamentally different in behavior, but rather that certain behaviors are magnified or diminished in a system, reflecting a plasticity enabling prey species to adopt the best anti-predator strategies available to them given the constraints of the particular environment they reside in. Therefore, predator preference, prey vulnerability and, ultimately, the stability and persistence of large mammal predator-prey systems, are likely strongly related to the characteristics of the particular environment and its interactions with the characteristics of the animals themselves.

Management and Conservation Implications and Directions for Future Research

Reintroductions of top predators such as wolves can be expected to have significant effects on the abundance, distribution and behavior of prey species. The nature of these effects is likely dependent on the prey assemblage available and their respective characteristics, as well as on landscape, climate, and management variables that can also reduce or enhance prey vulnerability and wolf populations (Garrott et al. 2005; Garrott et al. 2008*a*; Hamlin et al. 2008). In areas where prey species are very similar in size, behavior and defenses, prey-switching might be expected to occur based on the relative abundances of the prey species. However, in systems where large differences exist in vulnerability between prey, strong preferences by predators and possibly apparent competition in the form of indirect amensalism might be expected (Garrott et al. 2008*a*). Similarly, interactions between physical, behavioral and environmental vulnerability of a prey species that enhance its predation risk can result in substantial distribution and abundance changes across systems.

A good example of this is the strong decrease documented in the resident Madison headwaters elk herd due to wolf predation (Garrott et al. 2008*b*). A non-migratory herd in this system may have arisen due to the absence of wolf predation for nearly seven decades that allowed colonization of a formerly risky area, as elk likely historically wintered outside of these high-risk areas (White et al. 2008; Garrott et al. 2008*a*). The return of top predators such as wolves therefore emphasizes the need for broad-scale management of landscapes to effectively maintain prey assemblages and allow species to successfully employ the defenses they evolved with, such as seasonal migrations to areas with lower snow pack, to buffer the effects of predation. Conservation of high-quality ungulate wintering ranges outside protected areas is therefore of paramount importance.

Similarly, potential changes in prey distribution and abundance have conservation implications for predators as well, because we can expect these prey changes to be mirrored by changes in wolf abundance and distribution. As systems in the Greater Yellowstone Area continue to transition following wolf reintroduction, it is possible that there will be reductions in wolf populations in protected areas if high snow pack and associated landscape variables eventually make these areas too risky for elk to occupy in winter. Changing elk dynamics within and outside some protected areas seem to indicate this possibility (Hamlin et al. 2008; Garrott et al. 2008*a*). With the eventual removal of wolves from the Endangered Species Act and the likely adoption of state-managed wolf harvests, considerable importance will undoubtedly be placed on source populations of wolves from protected areas. Reliance on high-elevation source populations that are still experiencing transitional dynamics themselves, such as Yellowstone National Park, is therefore a potentially problematic strategy for wolf management outside protected areas. Thus, continued research and monitoring of wolf-ungulate dynamics, coupled with continued management and conservation of landscapes that allow for predator-prey interactions to occur on broad scales, is likely the best approach to successfully maintaining assemblages of these species and the processes they affect.

Evaluations of prey preference and prey switching in natural systems are difficult and still in need of refining, but I advocate expanded research into wolf-multiple prey systems with continued refinement of Murdoch's (1969) switching equation and multiple species (or prey type) functional response models. Because of wolf preference for elk and a higher physical, behavioral, and environmental vulnerability of elk relative to bison, asymmetric apparent competition (Holt 1977; Chaneton and Bonsall 2000) appears increasingly likely in the Madison headwaters (Garrott et al. 2008*a*). In addition, potential continued declines in elk abundance due to wolf predation in the Madison headwaters could provide kill rate measures at very low elk numbers near the intercept, critical data that is extremely difficult to obtain in measures of functional response. Therefore, continued studies of prey-switching and apparent competition in this system and others in which wolves are recolonizing have the potential to yield significant insights. Similarly further investigations into the effect of life history characteristics on wolf-elk-bison dynamics and the effects of prey responses to predation risk, such as the use of refuges, on system stability will be particularly fruitful, and ongoing investigations into patterns of predator foraging and unpredictability will likely provide additional insights into these dynamics.

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APPENDICES

APPENDIX A

MULTINOMIAL MODEL LIST

Model Suite 1: Prey Models

P1=PREY~$\mathrm{ELK}_{\mathrm{calf}}$

P2=PREY~$\mathrm{ELK}_{\mathrm{calf}}$+$\mathrm{ELK}_{\mathrm{ad}}$

P3=PREY~$\mathrm{ELK}_{\mathrm{calf}}$+$\mathrm{ELK}_{\mathrm{ad}}$+$\mathrm{BISON}_{\mathrm{calf}}$

P4=PREY~ELK

P5=PREY~ELK+BISON

P6=PREY~BISON.ELK

P7=PREY~$\mathrm{ELK}_{\mathrm{calf}}$+$\mathrm{BISON}_{\mathrm{calf}}$

Model Suite 2: Prey+Snowpack Models

PS1=PREY~$\mathrm{ELK}_{\mathrm{calf}}$+$\mathrm{SWE}_{\mathrm{acc}}$

PS2=PREY~$\mathrm{ELK}_{\mathrm{calf}}$+$\mathrm{ELK}_{\mathrm{ad}}$+$\mathrm{SWE}_{\mathrm{acc}}$

PS3=PREY~$\mathrm{ELK}_{\mathrm{calf}}$+$\mathrm{ELK}_{\mathrm{ad}}$+$\mathrm{BISON}_{\mathrm{calf}}$+$\mathrm{SWE}_{\mathrm{acc}}$

PS4=PREY~ELK+$\mathrm{SWE}_{\mathrm{acc}}$

PS5=PREY~ELK+BISON+$\mathrm{SWE}_{\mathrm{acc}}$

PS6=PREY~BISON.ELK+$\mathrm{SWE}_{\mathrm{acc}}$

PS7=PREY~$\mathrm{ELK}_{\mathrm{calf}}$+$\mathrm{SWE}_{\mathrm{mean}}$

PS8=PREY~$\mathrm{ELK}_{\mathrm{calf}}$+$\mathrm{ELK}_{\mathrm{ad}}$+$\mathrm{SWE}_{\mathrm{mean}}$

PS9=PREY~$\mathrm{ELK}_{\mathrm{calf}}$+$\mathrm{ELK}_{\mathrm{ad}}$+$\mathrm{BISON}_{\mathrm{calf}}$+$\mathrm{SWE}_{\mathrm{mean}}$

PS10=PREY~ELK+$\mathrm{SWE}_{\mathrm{mean}}$

PS11=PREY~ELK+BISON+$\mathrm{SWE}_{\mathrm{mean}}$

PS12=PREY~BISON.ELK+$\mathrm{SWE}_{\mathrm{mean}}$

PS13=PREY~$\mathrm{ELK}_{\mathrm{calf}}$+$\mathrm{BISON}_{\mathrm{calf}}$+$\mathrm{SWE}_{\mathrm{acc}}$

PS14=PREY~$\mathrm{ELK}_{\mathrm{calf}}$+$\mathrm{BISON}_{\mathrm{calf}}$+$\mathrm{SWE}_{\mathrm{mean}}$

Model Suite 3: Prey+Wolf Competition Models

PW1=PREY~ELK$_{calf}$+MULTPK

PW2=PREY~ELK$_{calf}$+ELK$_{ad}$+MULTPK

PW3=PREY~ELK$_{calf}$+ELK$_{ad}$+BISON$_{calf}$+MULTPK

PW4=PREY~ELK+MULTPK

PW5=PREY~ELK+BISON+MULTPK

PW6=PREY~BISON.ELK+MULTPK

PW7=PREY~ELK$_{calf}$+WOLF:ELK

PW8=PREY~ELK$_{calf}$+ELK$_{ad}$+WOLF:ELK

PW9=PREY~ELK$_{calf}$+ELK$_{ad}$+BISON$_{calf}$+WOLF:ELK

PW10=PREY~ELK+WOLF:ELK

PW11=PREY~ELK+BISON+WOLF:ELK

PW12=PREY~BISON.ELK+WOLF:ELK

PW13=PREY~ELK$_{calf}$+ WOLF:UNG

PW14=PREY~ELK$_{calf}$+ELK$_{ad}$+WOLF:UNG

PW15=PREY~ELK$_{calf}$+ELK$_{ad}$+BISON$_{calf}$+WOLF:UNG

PW16=PREY~ELK+WOLF:UNG

PW17=PREY~ELK+BISON+WOLF:UNG

PW18=PREY~BISON.ELK+WOLF:UNG

PW19=PREY~ELK$_{calf}$+BISON$_{calf}$+MULTPK

PW20=PREY~ELK$_{calf}$+BISON$_{calf}$+WOLF:ELK

PW21=PREY~ELK$_{calf}$+BISON$_{calf}$+WOLF:UNG

Model Suite 4: Prey+Snowpack +Wolf Competition Models

PSW1=PREY~ELK$_{calf}$+MULTPK+SWE$_{acc}$

PSW2=PREY~ELK$_{calf}$+ELK$_{ad}$+MULTPK+SWE$_{acc}$

PSW3=PREY~ELK$_{calf}$+ELK$_{ad}$+BISON$_{calf}$+MULTPK+SWE$_{acc}$

PSW4=PREY~ELK+MULTPK+SWE$_{acc}$

PSW5=PREY~ELK+BISON+MULTPK+SWE$_{acc}$

PSW6=PREY~BISON.ELK+MULTPK+SWE$_{acc}$

PSW7=PREY~ELK$_{calf}$+WOLF:ELK+SWE$_{acc}$

PSW8=PREY~ELK$_{calf}$+ELK$_{ad}$+WOLF:ELK+SWE$_{acc}$

PSW9=PREY~ELK$_{calf}$+ELK$_{ad}$+BISON$_{calf}$+WOLF:ELK+SWE$_{acc}$

PSW10=PREY~ELK+WOLF:ELK+SWE$_{acc}$

PSW11=PREY~ELK+BISON+WOLF:ELK+SWE$_{acc}$

PSW12=PREY~BISON.ELK+WOLF:ELK+SWE$_{acc}$

PSW13=PREY~ELK$_{calf}$+ WOLF:UNG+SWE$_{acc}$

PSW14=PREY~ELK$_{calf}$+ELK$_{ad}$+WOLF:UNG+SWE$_{acc}$

PSW15=PREY~ELK$_{calf}$+ELK$_{ad}$+BISON$_{calf}$+WOLF:UNG+SWE$_{acc}$

PSW16=PREY~ELK+WOLF:UNG+SWE$_{acc}$

PSW17=PREY~ELK+BISON+WOLF:UNG+SWE$_{acc}$

PSW18=PREY~BISON.ELK+WOLF:UNG+SWE$_{acc}$

PSW19=PREY~ELK$_{calf}$+MULTPK+SWE$_{mean}$

PSW20=PREY~ELK$_{calf}$+ELK$_{ad}$+MULTPK+SWE$_{mean}$

PSW21=PREY~ELK$_{calf}$+ELK$_{ad}$+BISON$_{calf}$+MULTPK+SWE$_{mean}$

PSW22=PREY~ELK+MULTPK+SWE$_{mean}$

PSW23=PREY~ELK+BISON+MULTPK+SWE$_{mean}$

PSW24=PREY~BISON.ELK+MULTPK+SWE$_{mean}$

PSW25=PREY~ELK$_{calf}$+WOLF:ELK+SWE$_{mean}$

PSW26=PREY~ELK$_{calf}$+ELK$_{ad}$+WOLF:ELK+SWE$_{mean}$

PSW27=PREY~ELK$_{calf}$+ELK$_{ad}$+BISON$_{calf}$+WOLF:ELK+SWE$_{mean}$

PSW28=PREY~ELK+WOLF:ELK+SWE$_{mean}$

PSW29=PREY~ELK+BISON+WOLF:ELK+SWE$_{mean}$

PSW30=PREY~BISON.ELK+WOLF:ELK+SWE$_{mean}$

PSW31=PREY~ELK$_{calf}$+ WOLF:UNG+SWE$_{mean}$

PSW32=PREY~ELK$_{calf}$+ELK$_{ad}$+WOLF:UNG+SWE$_{mean}$

PSW33=PREY~ELK$_{calf}$+ELK$_{ad}$+BISON$_{calf}$+WOLF:UNG+SWE$_{mean}$

PSW34=PREY~ELK+WOLF:UNG+SWE$_{mean}$

PSW35=PREY~ELK+BISON+WOLF:UNG+SWE$_{mean}$

PSW36=PREY~BISON.ELK+WOLF:UNG+SWE_{mean}

PSW37=PREY~ELK_{calf}+$BISON_{calf}$+MULTPK+SWE_{acc}

PSW38=PREY~ELK_{calf}+$BISON_{calf}$+MULTPK+SWE_{mean}

PSW39=PREY~ELK_{calf}+$BISON_{calf}$+WOLF:ELK+SWE_{acc}

PSW40=PREY~ELK_{calf}+$BISON_{calf}$+WOLF:ELK+SWE_{mean}

PSW41=PREY~ELK_{calf}+$BISON_{calf}$+WOLF:UNG+SWE_{acc}

PSW42=PREY~ELK_{calf}+$BISON_{calf}$+WOLF:UNG+SWE_{mean}

APPENDIX B

A PRIORI MODEL LISTS FOR EVALUATING KILL RATE VARIATION

Total and Elk Kill Rates (Kill Rate is Kills/Wolf/Day, Kills/Pack/Day, or Kg/Wolf/Day)

S1. $\mathrm{KillRate}\sim\mathrm{ELK}_{all}$

S2. $\mathrm{KillRate}\sim\mathrm{ELK}_{all}+\mathrm{SWE}_{acc}$

S3. $\mathrm{KillRate}\sim\mathrm{ELK}_{all}+\mathrm{BISON}_{all}$

S4. $\mathrm{KillRate}\sim\mathrm{ELK}_{all}+\mathrm{WOLF}_{pk}$

S5. $\mathrm{KillRate}\sim\mathrm{ELK}_{all}+\mathrm{WOLF}_{pk}+\mathrm{SWE}_{acc}$

S6. $\mathrm{KillRate}\sim\mathrm{ELK}_{all}+\mathrm{BISON}_{all}+\mathrm{WOLF}_{pk}$

S7. $\mathrm{KillRate}\sim\mathrm{ELK}_{adt}+\mathrm{ELK}_{calf}$

S8. $\mathrm{KillRate}\sim\mathrm{ELK}_{adt}+\mathrm{ELK}_{calf}+\mathrm{SWE}_{acc}$

S9. $\mathrm{KillRate}\sim\mathrm{ELK}_{adt}+\mathrm{ELK}_{calf}+\mathrm{BISON}_{calf}$

S10. $\mathrm{KillRate}\sim\mathrm{ELK}_{adt}+\mathrm{ELK}_{calf}+\mathrm{WOLF}_{pk}$

S11. $\mathrm{KillRate}\sim\mathrm{ELK}_{adt}+\mathrm{ELK}_{calf}+\mathrm{WOLF}_{pk}+\mathrm{SWE}_{acc}$

S12. $\mathrm{KillRate}\sim\mathrm{ELK}_{adt}+\mathrm{ELK}_{calf}+\mathrm{BISON}_{calf}+\mathrm{WOLF}_{pk}$

Bison Kill Rates (KillRate is Kills/Wolf/Day, Kills/Pack/Day, or Kg/Wolf/Day)

S1. $\mathrm{KillRate}\sim\mathrm{BISON}_{all}$

S2. $\mathrm{KillRate}\sim\mathrm{SWE}_{acc}$

S3. $\mathrm{KillRate}\sim\mathrm{ELK}_{all}+\mathrm{BISON}_{all}$

S4. $\mathrm{KillRate}\sim\mathrm{BISON}_{all}+\mathrm{WOLF}_{pk}$

S5. $\mathrm{KillRate}\sim\mathrm{ELK}_{all}+\mathrm{BISON}_{all}+\mathrm{WOLF}_{pk}$

S6. $\mathrm{KillRate}\sim\mathrm{ELK}_{all}+\mathrm{SWE}_{acc}+\mathrm{WOLF}_{pk}$

S7. $\mathrm{KillRate}\sim\mathrm{ELK}_{all}+\mathrm{SWE}_{acc}$

S8. $\mathrm{KillRate}\sim\mathrm{BISON}_{calf}$

S9. $\mathrm{KillRate}\sim\mathrm{ELK}_{ad}+\mathrm{ELK}_{calf}+\mathrm{BISON}_{calf}$

S10. $\mathrm{KillRate}\sim\mathrm{BISON}_{calf}+\mathrm{WOLF}_{pk}$

S11. $\mathrm{KillRate}\sim\mathrm{ELK}_{adt}+\mathrm{ELK}_{calf}+\mathrm{BISON}_{calf}+\mathrm{WOLF}_{pk}$

S12. $\mathrm{KillRate}\sim\mathrm{ELK}_{adt}+\mathrm{ELK}_{cal}\mathrm{f}+\mathrm{SWE}_{acc}+\mathrm{WOLF}_{pk}$

Table B.1 Predictive table for multiple regression analyses of wolf kill rate variation.

Kill Rate and Metric	**Covariate**							
	ELK$_{all}$	**ELK$_{adt}$**	**ELK$_{calf}$**	**BISON$_{all}$**	**BISON$_{adt}$**	**BISON$_{calf}$**	**WOLF$_{pk}$**	**SWE$_{acc}$**
Elk								
Kills/Wolf/Day	+	+	+	-	-	-	-	+
Kills/Pack/Day	+	+	+	-	-	-	+	+
Kg/Wolf/Day	+	+	+	-	-	-	-	+
Bison								
Kills/Wolf/Day	-	-	-	+	+	+	-	+
Kills/Pack/Day	-	-	-	+	+	+	+	+
Kg/Wolf/Day	-	-	-	+	+	+	-	+
Total								
Kills/Wolf/Day	+	+	+	+	+	+	-	+
Kills/Pack/Day	+	+	+	+	+	+	+	+
Kg/Wolf/Day	+	+	+	+	+	+	-	+

Note: Covariate codes are total elk and bison abundance (ELKall,, BISONall), abundance of elk and bison adults (ELKadt , BISONadt) and calves (ELKcalf ,BISONcalf),

Table B.2. Total wolf kill rates by resident wolf packs in the Madison headwaters area of Yellowstone National Park during 1998-99 through 2006-07.

Model Structure and Metric	**ΔAIC_c**	**w_k**	**r^2_{adj}**
Total Kills/Wolf/Day			
$ELK_{all} + WOLF_{pack} + SWE_{acc}$	0.00	0.73	0.57
$ELK_{ad} + ELK_{calf} + WOLF_{pack} + SWE_{acc}$	2.95	0.17	0.55
$ELK_{ad} + ELK_{calf} + WOLF_{pack}$	5.88	0.04	0.49
$ELK_{all} + WOLF_{pack}$	6.08	0.03	0.47
$ELK_{all} + BISON_{all} + WOLF_{pack}$	7.18	0.02	0.47
$ELK_{ad} + ELK_{calf} + BISON_{calf} + WOLF_{pack}$	7.93	0.01	0.49
$ELK_{all} + SWE_{acc}$	15.14	0.00	0.31
Total Kills/Pack/Day			
$ELK_{ad} + ELK_{calf} + WOLF_{pack}$	0.00	0.32	0.53
$ELK_{all} + WOLF_{pack}$	1.05	0.19	0.50
$ELK_{all} + WOLF_{pack} + SWE_{acc}$	1.22	0.17	0.52
$ELK_{all} + BISON_{all} + WOLF_{pack}$	2.09	0.11	0.50
$ELK_{ad} + ELK_{calf} + WOLF_{pack} + SWE_{acc}$	2.64	0.08	0.52
$ELK_{ad} + ELK_{calf} + BISON_{calf} + WOLF_{pack}$	2.71	0.08	0.52
$ELK_{ad} + ELK_{calf}$	6.01	0.02	0.42
ELK_{all}	6.95	0.01	0.38
$ELK_{ad} + ELK_{calf} + SWE_{acc}$	7.76	0.01	0.42
$ELK_{ad} + ELK_{calf} + BISON_{calf}$	8.64	0.00	0.40
Total Kg/Wolf/Day			
$ELK_{all} + WOLF_{pack} + SWE_{acc}$	0.00	0.61	0.45
$ELK_{ad} + ELK_{calf} + WOLF_{pack} + SWE_{acc}$	2.66	0.16	0.44
$ELK_{ad} + ELK_{calf} + BISON_{calf} + WOLF_{pack}$	3.99	0.08	0.42
$ELK_{all} + SWE_{acc}$	4.35	0.07	0.35
$ELK_{ad} + ELK_{calf} + SWE_{acc}$	5.34	0.04	0.37
$ELK_{all} + BISON_{all} + WOLF_{pack}$	7.52	0.01	0.33
$ELK_{ad} + ELK_{calf} + WOLF_{pack}$	8.91	0.01	0.30
$ELK_{all} + WOLF_{pack}$	9.08	0.01	0.26
$ELK_{ad} + ELK_{calf} + BISON_{calf}$	12.89	0.00	0.22

Note: *A priori* model structure and results from top models for multiple linear regression analyses. Covariate codes are defined in Table 3.1.

Table B.3. Total kill rates by resident wolf packs in the Madison headwaters area of Yellowstone National Park during 1998-99 through 2006-07.

Metric and model	**ELK$_{all}$**	**ELK$_{adt}$**	**ELK$_{calf}$**	**BISON$_{all}$**	**BISON$_{calf}$**	**WOLF$_{pk}$**	**SWE$_{acc}$**
Total kills/wolf/day							
Predictor weight	0.78	0.22	0.22	0.02	0.01	1.00	0.90
ELK$_{all}$+WOLF$_{pk}$+SWE$_{acc}$	**0.018** **(0.012, 0.023)**					**-0.020** **(-0.029, -0.012)**	**0.013** **(0.005, 0.022)**
Total kills/pack/day							
Predictor weight	0.48	0.51	0.51	0.11	0.08	0.95	0.26
ELK$_{adt}$+ELK$_{calf}$+WOLF$_{pk}$		**0.160** **(0.074, 0.246)**	-0.043 (-0.145, 0.059)			**0.124** **(0.042, 0.205)**	
ELK$_{all}$+WOLF$_{pk}$	**0.130** **(0.051, 0.209)**					**0.128** **(0.043, 0.213)**	
ELK$_{all}$+WOLF$_{pk}$+SWE$_{acc}$	**0.131** **(0.054, 0.209)**					**0.154** **(0.064, 0.243)**	0.069 (-0.019, 0.158)
Total kg/wolf/day							
Predictor weight	0.70	0.29	0.29	0.01	0.08	0.88	0.88
ELK$_{all}$+WOLF$_{pk}$+SWE$_{acc}$	0.85 (-0.86, 2.56)					**-2.65** **(-4.62, -0.68)**	**3.51** **(1.56, 5.47)**

Note: Coefficient values (B_i), lower and upper 95% confidence intervals (in parentheses), and predictor weights (w_p) for the best approximating models for each kill rate metric identified through AIC model comparison techniques. Boldface type indicates confidence intervals do not span zero. Covariate codes are defined in Table 3.1.

APPENDIX C

DESCRIPTION OF MULTIPLE SPECIES FUNCTIONAL RESPONSE MODELS

I evaluate the relative availability of the bison and elk in the study system with the ratio of the 2 prey species in the wolves' diet. Murdoch (1969) provides the classic equation that relates the ratio of 2 prey types eaten by a predator (g_1/g_2) to the ratio of the prey types available to the predator (N_1/N_2):

$$\frac{g_1}{g_2} = \left(c \frac{N_1}{N_2} \right)^b , \qquad (1)$$

where subscripts 1 and 2 correspond to prey types 1 and 2, respectively; *g* is the functional response (prey killed.predator^{-1}.day^{-1}); *N* is the number of prey available, and *c* is a selection coefficient (Murdoch's 'proportionality constant') that measures the 'bias in the predator's diet to one prey species.' If $c = 1$, then there is no bias and the predator kills the 2 prey types in proportion to their availability. If $c > 1$, the predator kills prey type 1 disproportionately, and if $c < 1$ prey type 2 is killed disproportionately. The bias of a predator's diet could be quite malleable and, thus, *c* may not remain constant but change depending on the relatively availability of the two prey types and perhaps other factors (Elton 1927). The coefficient *b* is a measure of the extent of prey switching with values of $b > 1$ denoting prey switching (Greenwood and Elton 1979). Various relationships between the ratio of available prey and the ratio of prey types in the predator's diet using this equation. If both *c* and *b* equal 1 (i.e., no bias in the wolves' diet and no switching), then wolves simply consume prey in proportion to their availability and the relationship is linear with a slope of 1. If there is a bias in the wolves' diet ($c \neq 1$) and there is no prey switching ($b = 1$), the relationship will still be linear but the slope of the line will be <1. If switching occurs ($b > 1$), the relationship will be curvilinear.

The selection coefficient for two-prey systems can be influenced by a variety of factors, including differences in ungulate abundance, body size, anti-predator behaviors and defenses, and vulnerability, as well as variability in wolf preference for the two prey types. Thus, to capture inherent differences between bison and elk, I decompose *c* into three 3 components such that *c = svm,* where *s* is the differential preference for a predator to attack prey type 1 compared to type 2, *v* is the differential vulnerability of prey type 1 compared to type 2, and *m* is the relative nourishment of prey type 1 to type 2. . Estimates of c and b were derived from switching analyses in Chapter 16, while m estimates were based upon body mass, with bison being much larger than elk and providing approximately twice as much nourishment than elk to wolves when killed (*m* = 2, Murie 1951, Meagher 1973).

The first step toward this goal is development of functional response equations that incorporate 2 prey types and the potential for switching. For prey-dependence, following the structure proposed by Murdoch (1973), the functional response model for 2 prey types is:

$$g_1 = \frac{\alpha_1 N_1}{1 + \alpha_1 N_1 h_1 + \alpha_2 N_2 h_2};\ g_2 = \frac{\alpha_2 N_2}{1 + \alpha_1 N_1 h_1 + \alpha_2 N_2 h_2}, \qquad (2)$$

For ratio-dependence, the functional response model for 2 prey types is:

$$g_1 = \frac{\alpha_1 N_1}{P + \alpha_1 N_1 h_1 + \alpha_2 N_2 h_2};\ g_2 = \frac{\alpha_2 N_2}{P + \alpha_1 N_1 h_1 + \alpha_2 N_2 h_2}, \qquad (3)$$

where subscripts 1 and 2 correspond to prey types 1 and 2, respectively; *g* and *N* are defined as above; *P* is the number of predators; α is the 'attack rate' (i.e., instantaneous rate of discovering prey by one predator) in days^{-1}, and *h* is the 'handling time' (days.predator.prey killed^{-1}) taken by 1 predator for each prey killed. Switching can be incorporated into Eqs. 3 and 4 by defining $m = h_1/h_2$ and using Eqs. 1, 2, and 3 to derive an expression for α_1. It can be shown that Eq. 2 becomes:

$$g_1 = \frac{\alpha_2 N_1 (svm)^b (N_1/N_2)^{b-1}}{1+\alpha_2 N_1 h_2 (sv)^b m^{b+1} (N_1/N_2)^{b-1} + \alpha_2 N_2 h_2};$$

$$g_2 = \frac{\alpha_2 N_2}{1+\alpha_2 N_1 h_2 (sv)^b m^{b+1} (N_1/N_2)^{b-1} + \alpha_2 N_2 h_2}, \qquad (4)$$

and Eq. 3, for a ratio-dependent functional response, becomes:

$$g_1 = \frac{\alpha_2 N_1 (svm)^b (N_1/N_2)^{b-1}}{P+\alpha_2 N_1 h_2 (sv)^b m^{b+1} (N_1/N_2)^{b-1} + \alpha_2 N_2 h_2};$$

$$g_2 = \frac{\alpha_2 N_2}{P+\alpha_2 N_1 h_2 (sv)^b m^{b+1} (N_1/N_2)^{b-1} + \alpha_2 N_2 h_2}, \qquad (5)$$

From Chapter 2 I estimated variables *b* and *c*, and estimated *m* above. Thus rearranging the equations and substituting c=svm as well as values of b and m the new equations for two-prey functional for prey-dependent and ratio-dependent functional response models respectively are:

$$g_1 = \frac{\alpha N_1}{1+\alpha\ N_2 h\ c^b m\ (N_2/N_1)^{b-1} + \alpha\ N_1 h}$$

$$g_1 = \frac{\alpha N_1}{P+\alpha\ N_2 h\ c^b m\ (N_2/N_1)^{b-1} + \alpha\ N_1 h}$$