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Gray Wolf (*Canis lupus*) effects on Ecological Communities

by

Nathan Varley

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

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in
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Gray Wolf (*Canis lupus*) effects on Ecological Communities** submitted by **Nathan Varley** in partial fulfillment of the requirements for the degree of **Doctor of Philosophy in Ecology**.

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ABSTRACT

Wolves (*Canis lupus*) are being restored to many parts of their former range. With this, ecologists will have the opportunity to better understand the direct and indirect effects of wolves on communities. Simulation models can be used to predict direct effects of wolves on prey. A stochastic predator-prey model was used to predict the demographic outcome of wolf restoration on elk (*Cervus elaphus*) and human harvest of elk in Yellowstone National Park (YNP), USA. Wolf predation resulted in a moderate (14-21%) reduction in long-term elk abundance that was sufficient to maintain a conservative harvest. Together, wolf predation and hunter harvest provided a stabilizing influence that reduced the incidence of severe weather-driven population declines.

Spatial factors that influenced predation were investigated in YNP where landscape features influenced large-scale patterns of wolf predation. Landscape features defined distinct areas of risk and refuge for prey. In turn, wolves competed for prime hunting grounds that caused a shift in wolf distribution away from hunting grounds in order to avoid other wolves. This form of competition appears to contribute to density-dependent limitation of wolf population growth.

The influence of wolves on willow (*Salix* spp.) via their effects on elk (an indirect effect) was detected, although willow at 23 sites was predominately arrested due to chronic browsing. Elk consumed a mean of 49%, and up to 72% of available willow during winter 2003-2004. The indirect effect appears to be minor because winter elk density after wolf recovery remains sufficient to allow elk to consume willow and maintain the browse-suppressed state.

The high productivity of YNP may attenuate the top-down effect of wolves, leaving vegetation largely unchanged. Conversely, low productivity systems may tend to transmit large effects to vegetation thereby altering communities. Wolves, regardless of the magnitude of their effects, contribute to temporal and spatial heterogeneity in ecological communities through provisioning scavengers and other carnivores and reducing the impact of abundant herbivore populations. This trait allows wolves to be highly interactive in communities, a value that should be emphasized in management for ecological diversity.

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CHAPTER 1

GENERAL INTRODUCTION

Wolves (*Canis lupus*) are being restored to many parts of their former range around the world. In anticipation of this, ecologists have documented changes in community structure and function that would result from top-down trophic pathways. These direct and indirect effects in systems demonstrate that wolves may have keystone effects in many ecosystems.

With this dissertation, I have examined the magnitude and variation of direct and indirect effects of wolves in ecological systems. Specifically, I have examined the effects of wolf restoration on the ecosystem of Yellowstone National Park, Wyoming, USA, where wolves were reintroduced in 1995 after they had been absent for >70 years. These results were compared to results from other wolf systems to assess the magnitude of wolf effects reported across many systems.

With the return of wolves to YNP and other ecosystems, community effects may manifest at multiple trophic levels. The magnitude of these outcomes may hinge upon both biotic (e.g., prey abundance, prey diversity, and predator diversity) and abiotic (e.g., climate and productivity) components of the system. With these chapters, I sought to investigate the factors that influence both direct and indirect effects of wolves on systems, as well as, why these effects may vary among or within systems.

I first focused on the topic of predation effects on prey abundance, a direct effect, as a role of wolves in community ecology. In Chapter 2, the wolf-caused reduction in prey abundance in a multiple prey system was investigated. I updated a stochastic predator-prey model that simulated the population dynamics of wolves and elk (*Cervus elaphus*) in the YNP system. A version of this chapter has been published as Varley and Boyce (2006) in *Ecological Modelling* (193:315-339).

Many factors can mediate the direct effects of wolves on prey including multiple prey species, competing predator species, and the landscape upon which the interactions take place. In Chapter 3, the effects of wolf distribution, elk distribution, and landscape features influenced the likelihood that predation occurred at a particular location in YNP. A version of this chapter has been published as Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty and M. S. Boyce (2007) in *Ecology Letters* (11:690-700). Landscape influenced predation success resulting in distinct areas of risk and refuge for elk. Landscape-influenced predation rates also shaped the territorial patterns of wolves once high density was reached. Thus, a spatial mechanism for density-dependent limitation on wolf populations was revealed—as packs competed for the best hunting areas, mortality increased to limit density.

The magnitude of indirect effects of wolves on lower trophic levels was influenced by the degree to which wolf populations are self-limited, as well as, the degree to which wolf populations limit prey populations. In Chapter 4, I examined the indirect effects of wolves on willow (*Salix* spp.) in YNP. Specifically, the browsing rate of elk on willow was estimated to determine if wolves have significantly changed the state of willow on elk winter range. Long-term browsing resulting from decades of high elk density in YNP has left willow largely in a state of suppression. A variety of effects of wolves on prey and vegetation have been reported in other studies from YNP; in Chapter 4 also, wolves were found to mediate in part the browse rates of elk. The magnitude of these effects on communities appeared to be modest. Despite an effect of wolves, willow remained largely in a state of suppression indicated by architectural types of predominately an arrested form and browse rates that were moderate to high at most willow surveyed sites. Release from browsing in the summer may be negated by subsequent heavy use in the winter.

Following the results of Chapter 5, I investigated the effects wolves have had on ecosystems beyond YNP to evaluate the variable, but sometimes consequential, impacts wolves have on ecological communities. I synthesized direct and indirect effects that have been reported to occur in ecological communities after wolf restoration. Effects may be greater in low productivity systems possibly because in high productivity systems social and spatial limitations on wolf density, as detected in Chapter 3, prevent significant limitation of herbivore prey populations that would then cascade to lower trophic levels. Conversely, at low density prey may have less ability to compensate for predation, allowing for greater indirect effects of wolves in community dynamics.

Following this introduction to the dissertation, the remainder of this chapter is a description of the broader context for studies of trophic dynamics in community ecology. A discussion of the food web dynamics that led to the formulation of trophic regulation theories provides a suitable background for how wolf restoration and the associated community ecology research can contribute to the study of ecology.

TROPHIC CASCADES

The term “trophic cascade” appears frequently in ecological literature to indicate the outcome of changes in top-down influence on multiple trophic levels. Predators may be introduced to a system that then causes herbivores to decrease followed by an increase in producers. In concept, its origin can be traced back over forty years, and continues to be a topic of great interest to ecologists, theoreticians, and conservation biologists. Pioneers (e.g., Paine 1980, Carpenter et al. 1985, Fretwell 1987) have offered definitions that universally apply to cases of indirect effects of species at one trophic level on species at one or more nonadjacent, lower trophic levels. Traditionally, this was illustrated with the case of carnivores’ indirect effects on plants (e.g., Hairston et al. 1960). No one definition serves all cases of what is referred to as a trophic cascade, and with a term of increasing popularity, its definition derives less specification with widening use. In an appeal for clarity, Polis et al. (2000) differentiated two definitions, an “old” and a “new” one in which the latter referred to a significantly wider array of trophic interactions. Paine (1980) was credited by Polis et al. (2000) with the original usage of the term that serves as the “old” or traditional definition: a community-level interaction in which predators exert top-down control on herbivores and therefore indirectly control vegetation abundance. A cascade occurs when ecological changes among the predators bring ecological changes among the plants (Polis et al. 2000). The cascade referred to energy or biomass toppling from high levels through intermediate levels to lower levels, alternately affecting lower levels negatively and positively.

The “old” definition was adhered to from the 1960’s until about the 1990’s. A wave of trophic research brought about descriptions for interactions with trophic systems of more than 3 levels, and that exhibited perturbations both from the top-down and bottom-up, all of which were referred to as a trophic cascade. Pace et al. (1999) defined this more generally as strong interactions that restructure links and redistribute biomass in food webs. This updated definition encompassed a much wider array of trophic effects and reflected an increased effort to address the complexity of systems and the variation in influence on the entire system originating from any of the trophic levels. Hunter and Price (1992) broadened the meaning of the term to indicate the flow of interactions can cascade up or down trophic webs to determine species and patterns at any of the trophic levels. With that, the term was applied in ever-widening regard. Proliferation of research on this topic enjoyed much attention and acceptance in the last 15-20 years, making it a topic of primary importance to the study of ecological systems. With the more generally applied definition of a trophic cascade, many ecologists (e.g., Fretwell 1987, Hairston and Hairston 1993) suggest that cascading effects are the central topic in the context of food web dynamics.

A GREEN WORLD

The Green World Hypothesis (GWH) with its development in Hairston et al. (1960) is widely considered the theoretical underpinnings of trophic cascade research. Presented as a treatise on patterns of population regulation, the GWH assumed trophic control in ecosystems was governed by top-down mechanisms. Worldwide and in many different types of ecosystems, predators kept herbivore abundance relatively low and in so doing allowed primary production biomass to accumulate. The net effect was a green world—a world dominated by vegetation. The GWH makes use of the classic example of an indirect effect, i.e., predators determining vegetation abundance. Without predators the opposite tends to occur—a landscape largely devoid of vegetation after overabundant herbivores consume much of what is available. Pioneering observations of the like included Aldo Leopold's commentary on the poor state of vegetation on the Kaibab Plateau, Arizona, USA, where a deer population explosion occurred after humans exterminated wolves (Leopold 1949). Such observations shaped the GWH, which then became a focus of research and debate for the next five decades. Murdoch's (1966) critique of the GWH remains truthful of the study of ecology in general. He described the GWH as a flawed attempt to generalize across systems to describe patterns of how trophic regulation occurs. Given the variation found throughout systems in the world, attempts to draw these conclusions, while being the general charge of ecologists, rarely succeed in a lasting fashion (Murdoch 1966). Formulating grand abstraction in the patterns of nature is indeed among the primary, but often elusive, pursuits of ecologists.

The GWH may not be a testable theory, may contain errors of logic and deduction, and may be premised on ill-defined trophic levels (Murdoch 1966, Ehrlich and Birch 1966), so proving or disproving the GWH may be a moot endeavor. Ecologists have shifted to studying the conditions under which GWH predictions hold true. Therein it survives in evolving forms to explain structure and regulation in ecosystems. In the patterns of nature, evidence in both support and opposition continue to be found (Slobodkin et al. 1967), but the GWH has provided good direction in a debate that has delved deeper into the underlying mechanisms and conditions for which trophic interactions ultimately lead to structuring of whole communities and systems (Power 1992).

FOOD WEBS

After food chain trophodynamics had been first described (Lindeman 1942), Paine (1966) introduced the food web concept in a comparison of intertidal coastal ecosystems. Similar linkage concepts had appeared, but the food web, or interlinking of all community members through energy or interaction pathways, had not been widely used to advance the framework for describing ecosystems. Trophic levels within systems are chronically ill-defined (Murdoch 1966, Hanski 1987, Polis 1991, Power 1992) but through food webs the criticisms of the weakly aligned trophic levels of the GWH could be better defined. This framework allowed for trophic interactions to be clearly identified, their relative strength quantified, and trophic regulation to ultimately become more apparent. The food web of the coastal system of New Zealand consisted of sea-star (*Stichaster* spp.) predators that indirectly regulated numerous producers so that, following experimental removal of the sea-stars, mussels (*Perna* spp.) dominated and significantly decreased producer abundance (Paine 1966, 1980). This was one of the earliest demonstrations of a trophic cascade in which absence of predation caused some mussel species to emerge in competition and eliminate 19 other species in just 15 months. Monopolies by by dominant species that emerge in the absence of predation determined the species richness in this and other intertidal systems worldwide (Paine 1980). Predation tends to increase local diversity, and while anomalies occur (Menge 1994), predators explain the apparent absence of monopolies in diverse systems (Paine 1980). An analysis of a pelagic system using mathematical models led to a description of systems with >3 trophic levels (Smith 1969). Gradients of productivity in systems determined the number of trophic levels a system would support, e.g., 3, 4, 5, or 6 (Smith 1969; Rosenzsweig 1971, 1973; Menge and Sutherland 1987), and the number of trophic levels determined how each level would be effected, i.e., positively or negatively, when perturbations occurred in the system. For example, primary producers might be affected positively by top-down perturbations in 3- and 5-level aquatic systems but negatively in 4- and 6-level systems (Rosenzweig 1971, 1973).

Many studies (e.g., Wolkind 1976, Wiegert 1977, Pimm and Lawton 1977) inferred top-down regulation in food webs and described the mechanism as exploitive. Upper levels exploited lower levels to determine energy flow and biomass accumulation within the web. Descriptions as such were championed in a new paradigm, the Exploitive Ecosystem Hypothesis (EEH) in which systems generally have exploitation-based regulation wherein organism abundance at a trophic level is largely determined by exploitation by organisms at levels above (Fretwell 1977, 1987, Oksanen et al. 1981). This model was refined further using productivity gradients to better differentiate structure in different types of systems, e.g. terrestrial versus aquatic (Oksanen 1983, 1988, 1991, Oksanen and Oksanen 2000). Low productivity systems tended to have two or three levels and high productivity systems had four or more. Under the EEH, a level must derive its energy in a regulatory manner from the level below it (Oksanen et al. 1981). This paradigm featured predators as system-structuring agents that determined the diversity and abundance of species at lower trophic levels.

Critics of the EEH questioned whether the producer trophic level could be regulated by herbivory when a significant portion of production is often inedible

(Murdoch 1966). Plants have evolved secondary compounds and other defenses that deter herbivory (Coley et al. 1985), which limits the ability of the upper trophic level to determine its abundance and diversity. Models that included inedible prey demonstrated that under these conditions, productivity transfer to higher trophic levels was limited by inability to be consumed (Phillips 1974). Another model tested empirically in a freshwater lake did not support the predictions of Phillips (1974), or the EEH, suggesting yet another level of complexity in community structure (Leibold 1989). This model for multiple freshwater system studies indicated the major determinant of biomass at each trophic level within these systems was the breadth of diet for the consumers, i.e. generalists versus specialists (Leibold 1989). Subsequent advancement in the predictive powers of models of trophic control would make similar discoveries, the pattern of which was that some aspect of the system (e.g., breadth of diet) mediated the flow of trophic interactions through the food web. The characteristics of different food webs therefore conferred varying degrees of interaction strength based on the species present and the structural components of their environment. Ecologists now recognize that a wide array of influences on interactions in a food web can alter predictions for the outcomes of top-down perturbation (e.g., Strong 1992, Power 1992, Hunter and Price 1992, Menge 1992, Polis and Strong 1996). Progress toward this conclusion first became apparent in studies of aquatic food webs.

THE AQUATIC STUDIES

Interaction strength and thus transmission of top-down effects was deemed strong after early descriptions of aquatic food webs appeared (Paine 1966, Estes and Palmisano 1974). Examples of a trophic cascade were documented in various types of aquatic systems (*e.g.*, Paine 1966, Fairweather 1985, Dungan 1986, Menge et al. 1986a, 1986b, Menge and Farrell 1989). These systems tended to be characterized by a set of species organized in a trophic system predisposed to cascade. Likelihood of cascades were higher in webs with a few strong, consecutive food chains (Estes and Palmisano 1974, Strong 1992). These strong links were prone to cascade often when herbivory defenses were lacking, e.g., algae that support most aquatic system webs are nutritious and readily consumable biomass (Strong 1992, Chase 2000). There are exceptions (Hanski 1987, Agrawal 1998), but algae generally are regulated by upper level consumers (Chase 2000). As a result, herbivory rates are about three times higher in aquatic systems relative to terrestrial systems (Cyr and Pace 1993, Chase 2000).

Nevertheless, not all aquatic systems have been characterized as having top-down control (Neill and Peacock 1980, Menge and Olson 1990), but rather, a combination of bottom-up and top-down controls (Hall et al. 1970, Hurd et al. 1971, Carpenter and Kitchell 1988, McQueen et al. 1989). Meta-analysis of 54 enclosure and pond studies found approximately one third of freshwater pelagic cases showed evidence for strong top-down trophic control, while about two thirds of the cases showed only weak responses (Brett and Goldman 1996). Productivity in a freshwater lake is a function of multiple properties including nutrient availability, turnover time, and degree of mixing (Schindler 1978, Carpenter and Kitchell 1988), but trophic interactions in which top predators alter energy pathways may account for up to half of the variation (Carpenter et al. 1985, Carpenter and Kitchell 1988). Synthesis in non-aquatic systems is less well-developed (Strong 1992), though recent work has indicated high variability in trophic regulation is found in many system types (Shurin et al. 2002).

The perception that aquatic systems are more prone to trophic cascades than other types of systems (Strong 1992) has led to productive debate over the nature of systems and their likelihood to cascade effects. Many types of systems have been found to exhibit strong cascades (Shurin et al. 2002), but the case for a greater prevalence of top-down regulation in wet systems on the whole has been suggested (Strong 1992, Brett and Goldman 1996, 1997) and challenged (Shurin et al. 2002). Again, a very diverse set of potential determining factors among systems influences these outcomes (Power 1990, 1992, Menge 1992, Polis and Strong 1996). Thus, prevailing thought is that ecosystems of all types are structured by energy flow that occurs both from the top and the bottom in complex, multi-directional interactions.

CASCADES IN DIVERSE SYSTEMS

Trophic cascades are not relegated to certain system types. Many new systems were subjected to testing of EEH predictions and examples accumulated for most types of systems and with respect to many climate regimes (*e.g.,* arctic, temperate, tropical). Reviews or meta-analyses have made reference to the relevant articles in aquatic systems (Strong 1992), terrestrial systems (Schmitz et al. 2000, Halaj and Wise 2001), and diverse systems (Pace et al. 1999). The relative strength of effects across systems was assessed by Shurin et al. (2002) with no system clearly having significantly more evidence than others. Quantified effects across six types of systems, lentic benthos, marine benthos, stream benthos, lentic plankton, marine plankton, and terrestrial, showed predators reduced herbivores in every system, but the magnitude of predator effects on plants varied considerably and were generally smaller than the direct effects on herbivores (Shurin et al. 2002). This indicated that in general, predator effects attenuate in transmission to lower levels.

ATTENUATION OF EFFECTS

The presence of trophic cascades has been linked to a suitable structure for transmitting effects that is found in diverse systems (Strong 1992, Shurin et al. 2002). Some systems, e.g., some freshwater aquatic (Brett and Goldman 1996) and intertidal (Paine 1980) had prominent food chains prone to cascade, while others, e.g., some terrestrial systems, tended not to have these food chains (Strong 1992). In the latter case, food web dynamics had been extolled as too complex to describe and predict well (Peters 1977, Yodzis 1988, Pimm and Kitchell 1988, Hastings and Powell 1991).

In complex systems, alternate interaction pathways will act to attenuate top-down responses in food webs (Polis and Strong 1996). Prevalence of attenuating factors in systems was used as a collective argument to dismiss the plausibility of unifying theories of trophic regulation like the EEH. Under the weight of complexity that governs most ecological systems, any generalized approach to describing regulation in ecological systems and predicting trophic processes has been of limited utility (Power 1992). A new paradigm, the donor-controlled, multi-channel omnivory theory (DCMO), was premised on the notion that complexity is important to community and web dynamics, and cannot be dismissed with overly simplistic descriptions (Polis and Strong 1996). The DCMO moved away from describing food webs with energy flow toward describing species interactions that better accounted for community dynamics (Polis 1991). Competing trophic governing theories (*e.g.,* Power 1992: Figure 4) including variations of the GWH and EEH that had found resurgence (Hairston and Hairston 1993, 1997; Oksanen and Oksanen 2000) and alternates like the DCMO continue to compete for favor among ecologists.

Under the DCMO, phenomena that attenuated transmission of trophic effects in food webs, and thus prevented regulation from either end, included omnivory, subsidies, shunts, pathogens, nutrient availability, symbiosis, and consumption resistance. Omnivory, or organisms that eat from different trophic levels, weaken consistent directional flow in the web. A process of outside nutrient input or energy flow, subsidies, can significantly alter structure and regulation within a system. An example is deciduous leaves falling into cold water streams provides nutrients to nutrient-poor systems. Similar to subsidies, shunts, or trophic pathways that are not well linked to the other pathways, might channel a significant portion of the energy flow in the system. Detritus shunts are exemplary—in some systems detritivores can provide food for predators that when abundant suppress other predators and herbivores, but when absent, impose no regulatory control on lower levels (Polis 1991). Another shunt occurred, for example, when prey scarcity in an open marine system led to killer whales (*Orcinus orca*) preying on sea otters (*Enhydra lutris*), which were the top predators in adjacent intertidal marine systems. This intermittent imposition of a higher trophic level can have cascading effects, but is not innately part of the system (Estes et al. 1998). The presence of pathogens and parasites with the potential to regulate host populations at numerous levels have defied conventional trophic classification, so do not fit well in trophic structure models or theories. The availability of nutrients is critical to productivity in all webs, but often cannot be traced to well-defined levels or pathways. The non-consumption process, symbiosis (either mutualistic or antagonistic), affects distribution, abundance, and richness throughout webs, and can give rise to entire systems such as the reef-building corals that support rich marine tidal systems (Polis and Strong 1996), but does not fit well in trophic classifications. Finally, the earlier identified example of consumption resistance (Coley et al. 1985) or differential edibility (Phillips 1974, Leibold 1989) often prevents regulation of vegetation species, particularly in terrestrial plant communities that have adaptations for discouraging herbivores.

The identification of many factors and conditions that limit the ability of consumers to regulate species in lower trophic levels has challenged the formulation of trophic regulation theory. Trophic cascade responses are rare in complex food webs due to these alternate pathways that attenuate transmission of effects in food webs (Polis and Strong 1996, Schmitz 1998, Polis 1999, Chase 2000).

TROPHIC REGULATION THEORY

An evolving set of trophic regulation theories, i.e., the GWH, the EEH, and the DCMO, have provided a context for understanding, describing, and predicting the effects of species and processes on the resulting structure of ecological systems. Ecologists have embraced the challenging issues of complexity in systems which now emphasize the identification of critical influences in food webs without excessive abstraction or generalization. Yet, ecologists have the directive to recognize patterns over multiple system types and how variation in the transmission of effects is mediated by the properties of systems. When identified and understood, these factors contribute to an enhanced ability to describe and predict the potential for a system to absorb or cascade trophic interactions.

Studies of the trophic effects of wolves must consider the broad context within which ecologists have been describing food web dynamics. Wolves can have direct and indirect effects in terrestrial systems throughout the world, but these effects are prefaced on conditions conducive to transmitting these effects. Thus, effects can vary widely within and among systems given variation in the conditions and components of the food web. The following chapters delve into specific case studies of wolf direct effects on prey species and the factors that lead to stable coexistence, as well as, the indirect effects of predation that, under specific conditions, will be transmitted through food webs to producers.

REFERENCES

Agrawal, A. A. 1998. Algal defense, grazers, and their interactions in aquatic trophic cascades. Acta Oecologica **19**:331–337.

Brett, M. T., and C. R. Goldman. 1996. A meta-analysis of the freshwater trophic cascade. Proceedings of the National Academy of Sciences of the USA **93**:7723–7726.

Brett, M. T., and C. R. Goldman. 1997. Consumer versus resource control in freshwater pelagic food webs. Science **275**:384–386.

Carpenter, S. R., J. M. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience **35**:634–639.

Carpenter, S. R., and J. F. Kitchell. 1988. Consumer control of lake productivity, Bioscience **38**:764–769.

Coley, P. D., J. P. Bryant, and E. S. Chapin. 1985. Resource availability and plant antiherbivore defense. Science **230**:895–899.

Chase, J. M. 1996. Abiotic controls of trophic cascades in a simple grassland food chain. Oikos **77**:495–506.

Chase, J. M. 2000. Are there real differences between aquatic and terrestrial food webs? Trends in Ecology and Evolution **15**:408–412.

Cyr, H., and M. L. Pace. 1993. Magnitude and patterns of herbivory in aquatic and terrestrial ecosystems. Nature **361**:148–150.

Dungan, M. L. 1986. Three-way interactions: barnacles, limpets, and algae in a Sonoran Desert rocky intertidal zone. American Naturalist **127**:292–316.

Ehrlich, P. R., and L. C. Birch. 1966. The ‘balance of nature’ and ‘population control’. American Naturalist **101**:97–107

Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science **185**:1058–1060.

Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science **282**:473–476.

Fairweather, P. G. 1985. Differential predation on alternative prey, and the survival of rocky intertidal organisms. Journal of Experimental Biology and Ecology **89**:135–156.

Flecker, A. S., and C. R. Townsend. 1994. Community-wide consequences of trout introduction in New Zealand streams. Ecological Applications **4**:798–807.

Fretwell, S. D. 1977. The regulation of plant communities by food chains exploiting them. Perspectives in Biology and Medicine **20**:169–185.

Fretwell, S. D. 1987. Food chain dynamics: the central theory of ecology? Oikos **50**:291–301.

Gastreich, K. R. 1999. Trait-mediated indirect effects of a theridid spider on an ant–plant mutualism. Ecology **80**:1066–1070.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist **94**:421–425.

Hairston, Jr., N. G., and N. G. Hairston, Sr. 1993. Cause-effect relationships in energy flow, trophic structure and interspecific interactions. American Naturalist **142**:379–411.

Hairston, Jr., N. G., and N. G. Hairston, Sr. 1997. Does food web complexity eliminate trophic-level dynamics? American Naturalist **149**:1001–1007.

Halaj, J., and D. H. Wise. 2001. Terrestrial trophic cascades: how much do they trickle? American Naturalist **157**:262–281.

Hall, D. J., W. E. Cooper, and E. E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnology and Oceanography **15**:839–928.

Hanski, I. 1987. Plankton that don't obey the rules. Trends in Ecology and Evolution **2**:350–351.

Hastings, A., and T. Powell. 1991. Chaos in a three-species food chain. Ecology **72**:896–903.

Hunter, M. D., and P. Price. 1992. Playing chutes and ladders. Heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology **73**:24–732.

Hurd, L. E., M. V. Mellinger, L. L. Wolf, and S. J. McNaughton. 1971. Stability and diversity at three trophic levels in terrestrial successional ecosystems. Science **173**:1134–1136.

Leopold, A. 1949. A Sand County Almanac and Sketches from Here and There. Oxford University Press, U. K.

Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. American Naturalist **134**:922–949.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology **23**:399–417.

McQueen, D. J., M. R. S. Johannes, J. R. Post, T. J. Stewart, and D. R. S. Lean. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecological Monographs **59**:289–309.

Menge, B. A. 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores. Ecology **73**:755–765.

Menge, B. A., J. Lubchenco, L. R. Ashkenas, and F. Ramsey. 1986a. Experimental separation of effects of consumers on sessile prey on a rocky shore in the Bay of Panama: direct and indirect consequences of food web complexity. Journal of Experimental Marine Biology and Ecology **100**:225–269.

Menge, B. A., J. Lubchenco, S. D. Gaines, and L. R. Ashkenas. 1986b. A test of the Menge-Sutherland model of community organization in a tropical rocky intertidal food web. Oecologia **71**:75–89.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist **130**:730–757.

Menge, B. A., and T. M. Farrell. 1989. Community structure and interaction webs in shallow marine hard-bottom communities: test of an environmental stress model. Advances in Ecological Research **19**:189–262.

Menge, B. A., and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. Trends in Ecology and Evolution 5:52–57.

Murdoch, W.W. 1966. Community structure, population control, and competition: a critique. American Naturalist **100**:219–226.

Neill, W. E., and A. Peacock. 1980. Breaking the bottleneck: interactions of invertebrate predators and nutrients in oligotrophic lakes. Pages 715–724 *in* W. C. Kerfoot, editor. Ecology and Evolution of Zooplankton Communities. New England University Press, Hanover, New Hampshire, USA.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemalä. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist **118**:240–261.

Oksanen, L. 1983. Trophic exploitation and arctic phytomass patterns. American Naturalist **118**:240–261.

Oksanen, L. 1988. Ecosystem organization: mutualism and cybernetics or plain Darwinian struggle for existence? American Naturlist **131**:424–444.

Oksanen, L. 1991. Trophic levels and trophic dynamics: a consensus emerging. Trends in Ecology and Evolution **6**:58–60.

Oksanen, L., and Oksanen, T. 2000. The logic and realism of the hypothesis of exploitation ecosystems. American Naturalist **155**:703–723.

Pace, M. L., J. J. Cole, and S. R. Carpenter. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution **14**:483–488.

Paine, R.T. 1966. Food web complexity and species diversity. American Naturalist **100**:65–73.

Paine, R.T. 1980. Food webs: linkage, interaction strength, and community infrastructure. Journal of Animal Ecology **49**:667–685.

Peters, R. H. 1977. The unpredictable problems of trophodynamics. Environmental Biology of Fishes **2**:97–101.

Phillips, O. M. 1974. The equilibrium and stability of simple marine systems. II. Herbivores. Archives of Hydrobiology **73**:310–333.

Pimm, S. L., and J. H. Lawton. 1977. The number of trophic levels in ecological communities. Nature **268**:329–331.

Pimm, S. L., and R. L. Kitching. 1988. Food web patterns: trivial flaws or the basis of an active research program? Ecology **69**:1669–1672.

Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation. Annual Review of Ecology and Systematics **20**:297–330.

Polis, G. A. 1991. Complex trophic interactions in deserts: empirical critique of food web theory. American Naturalist **138**:123–155.

Polis, G. A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. Oikos **86**:3–15.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist **147**:813–846.

Polis, G. A., S. D. Hurd, C. T. Jackson, and F. Sanchez-Piñero. 1998. Multifactor population limitation: variable spatial and temporal control of spiders on Gulf of California islands. Ecology **79**:490–502.

Polis, G. A., A. L. W. Sears, G. R. Huxel, D. R. Strong, and J. Maron. 2000. When is a trophic cascade a trophic cascade? Trends in Ecology and Evolution **15**:473–475.

Power, M. E. 1990. Effects of fish in river food webs. Science **250**:811–814.

Power, M. E. 1992. Top-down and bottom-up forces in food webs: Do plants have primacy? Ecology **73**:733–746.

Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. Science **171**:385–387.

Rosenzweig, M. L. 1973. Exploitation in three trophic levels. American Naturalist **107**:275–294.

Schindler, D. W. 1978. Factors regulating phytoplankton production and standing crop in the world's freshwaters. Limnology and Oceanography **23**:478–486.

Schmitz, O. J. 1998. Direct and indirect effects of predation and predation risk in old–field interaction webs. American Naturalist **151:**327–342.

Schmitz, O. J., P. A. Hambäck, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of top carnivore removals on plants. American Naturalist **155**:141–153.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters **5**:785–791.

Slobodkin, L. C. 1967. Regulation in terrestrial ecosystems and the implied balance of nature. American Naturalist **101**:109–124.

Smith, F. 1969. Effects of enrichment in mathematical models. Pages 631–645 in Eutrophication: causes, consequences and correctives. National Academy of Sciences, Washington, D. C., USA.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology **73**:747–754.

Wiegert, R. G. 1977. Population models: experimental tools for the analysis of ecosystems. Pages 233–277 *in* D. J. Horn, G. R. Stairs, and R. D. Mitchell, editors. Analysis of ecological systems. Ohio State University Press, Columbus, Ohio, USA.

Wolkind, D. J. 1976. Exploitation in three trophic levels: an extension allowing intraspecies carnivore interaction. American Naturalist **110**:431–447.

Yodzis, P. 1988. The indeterminacy of ecological interactions, as perceived by perturbation experiments. Ecology **69**:508–515.

CHAPTER 2

ADAPTIVE MANAGEMENT FOR REINTRODUCTIONS: UPDATING A WOLF RECOVERY MODEL FOR YELLOWSTONE NATIONAL PARK[1]

Adaptive management has been advocated for species reintroductions (Sarrazin and Barbault 1996, Bearlin et al. 2002, Hirzel et al. 2004) and translocations (Brook et al. 2002, Stockwell and Leberg 2002), but adaptive management has failed in the majority of attempted applications (Walters 1997). Adaptive management often fails to advance from simulation modeling to subsequent evaluation of the models after field experimentation, and quite often detailed modelling is substituted for empirical evaluation of models, particularly when the cost of acquiring data for model validation can be prohibitive (Walters 1997). Thus, few cases exist in which models were evaluated and refined using data from field experimentation to guide future management. Simulation models figured prominently in a plan to restore gray wolves (*Canis lupus*) to Yellowstone National Park, USA. Several models were developed to predict the recovery of wolves and their anticipated numerical effects on prey (see Boyce 1990, 1992, 1993, 1995, Garton et al. 1990, Singer 1990a, Vales and Peek 1990, Boyce and Gaillard 1992, Mack and Singer 1993). Wolves were reintroduced to YNP in 1995 providing ten years of data for examining the predictions made prior to recovery.

I have evaluated model assumptions and predictions for YNP's Northern Range (NR) from the WOLF5 model (Boyce and Gaillard 1992) based on data compiled since wolves were released in the park. The WOLF5 model predicted prey abundance well,

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underestimated wolf numbers, and made assumptions that need adjustment now that new data have become available. I have updated the simulation model, WOLF6, which better characterizes the YNP wolf-prey system. Elk (*Cervus canadensis*) were preferred over alternate prey in WOLF5, but the preference was underestimated relative to current data; about 90% of the estimated species composition of winter wolf kills has been elk (Smith 2005). Wolf functional and numerical responses in WOLF5 were estimated from data with different assemblages of prey, but parameters for WOLF6 were based on data directly from the NR. New data also revealed age/sex-specificity of wolf predation substantially different from that of hunter harvest that was not modelled in WOLF5. Quotas for elk harvest during the Gardiner (Montana) late hunt, a harvest of NR elk outside the park, were changed about the time of wolf recovery, requiring refinement in the simulation of harvests. Finally, I have evaluated the alternative of potential wolf culls in WOLF6. The objective for WOLF6, as with previous versions of the model, is to forecast the consequences of wolf predation on elk, other ungulate prey, and human harvests. With a narrowed focus on the NR, the projections of the WOLF6 model will be useful for adaptive management of the Yellowstone ecosystem.

METHODS

WOLF6 is based on the WOLF5 model developed and described by Boyce and Gaillard (1992) and validated by Boyce (1995). Both versions include stochastic variation simulating year-to-year variation in climate and forage production (Merrill and

Boyce 1991). In contrast to WOLF5, version WOLF6 includes age and sex structure for elk.

Elk population dynamics

The NR elk herd has fluctuated considerably since the beginning of record keeping in YNP (Houston 1982, Barmore 2002), and since 1972 counts have fluctuated around a mean of 13,716 (Lemke 2003, Figure 2.1). These counts are considered a minimum population size and have not been corrected for consistent detection bias of approximately 15% (Singer et al. 1997). Background data for the NR elk herd were based upon unpublished park records and published literature (Fowler and Barmore 1979, Houston 1982, Merrill and Boyce 1991, Singer 1990b, Mack and Singer 1993, Coughenour and Singer 1996, Taper and Gogan 2002).

Counts of the NR herd were typically collected at or near the end of the calendar year. Therefore, the five age/sex classes were defined to reflect herd composition at that time: calves (~6 months old), spikes (males ~18 months), cows (females ~18 months to 9 years), old-cows (females 10 years or older), and bulls (males ~30 months or older).

Transition matrix

A Lefkovitch projection matrix (Caswell 2001) was constructed for the 5 age/sex classes such that at the end of any given year, *t*, the total population size was:

$$N_{elk}(t) = \sum_{i}^{5} N_i(t) \tag{1}$$

where N_i is the number of elk in the i = calf, spike, cow, old-cow, and bull classes. The square projection matrix, $\mathbf{A}(t)$, which when postmultiplied by a column vector of the number of individuals in each stage class, **N**(*t*), yields a column vector for the population the following year:

$$\begin{bmatrix} N_{calf} \\ N_{spike} \\ N_{cow} \\ N_{oldcow} \\ N_{bull} \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & R_{calf.c} & R_{calf.oc} & 0 \\ P_{calf.m} & 0 & 0 & 0 & 0 \\ P_{calf.f} & 0 & S_{cow} & 0 & 0 \\ 0 & 0 & P_{cow} & S_{old} & 0 \\ 0 & P_{spike} & 0 & 0 & S_{bull} \end{bmatrix}_{t} \times \begin{bmatrix} N_{calf} \\ N_{spike} \\ N_{cow} \\ N_{oldcow} \\ N_{bull} \end{bmatrix}_{t} \qquad (2)$$

The population growth rate, λ, can be obtained from the dominant eigenvalue of the projection matrix such that $N_{elk}(t + 1) = N_{elk}(t)\cdot\lambda$, when the population is in a stable age distribution (Caswell 2001). I have modified the projection matrix to make it time varying, with an annual time step.

I define $R_i(t)$ to be the recruitment of calves from classes *i* at time *t*, $S_i(t)$ is the probability of surviving to remain in the same class *i* at time *t*+1, and $P_i(t)$ is the probability of surviving and advancing from the current class into the next class at time *t* +1 (e.g., P_{cow} is the probability of a cow surviving and advancing into the old-cow class). The $R_{calf.c}$ and $R_{calf.oc}$ terms are identical except for the effect of differential pregnancy rates (P.J. White, National Park Service, unpublished data), so $R_{calf.oc}$ was reduced to 90.85% of $R_{calf.c}$ to reflect lower pregnancy rates in old-cows. Differences between $P_{calf.f}$ and $P_{calf.m}$ reflect the effect of sex ratio and differential survival of male and female calves. On average, 47% of yearlings at 18 months are males (Houston 1982), thus $P_{calf.m}$ is the probability of survival for a calf multiplied by $\rho = 0.47$, and $P_{calf.f}$ is the probability of survival of a calf multiplied by $(1 - \rho)$.

While the projection interval of the matrix is one year, individuals in the cow class stay in that class for more than one year before advancing to the next class, old-cows. In this case, annual survival was partitioned into the probability of surviving and staying in the stage (S_{cow}) and the probability of surviving and advancing to the next stage (P_{cow}). I used the method of Crouse et al. (1987; see also Caswell 2001) to estimate S_{cow} and P_{cow} as follows

$$S_{cow} = \left(\frac{1 - p_{cow}{}^{dcow-1}}{1 - p_{cow}{}^{dcow}} \right) p_{cow} \qquad (3)$$

and

$$P_{cow} = \frac{p_{cow}{}^{d_{cow}} (1 - p_{cow})}{1 - p_{cow}{}^{d_{cow}}} \qquad (4)$$

where p_{cow} is annual survival for cows and d_{cow} is the duration in years of the cow class, d_{cow}= 9. Summing S_{cow} and P_{cow} gives p_{cow}, the annual probability of survival for cows. The probabilities of transition, reproduction, and survival in the transition matrix were time-varying functions of population density and climate described below.

Density dependence

Survival and fecundity of NR elk have been shown to be strongly density dependent (Fowler and Barmore 1979, Merrill and Boyce 1991, Singer et al. 1997, Taper and Gogan 2002, Garrott et al. 2003, National Research Council 2002), and nonlinear (Taper and Gogan 2002). I adopted a nonlinear equation reported by Clutton-Brock et al. (2002) to model density dependence for all classes,

$$\mathrm{S_i(t)} = 1/\{Q_i(\mathrm{t}) + \exp[X_i + Y_i N_{elk}(t)]\} \qquad (5)$$

where $S_i(t)$ is the probability of surviving and remaining in class i to time t+1. The constants Q_i, X_i, and Y_i scale density dependence for each class, i (Table 2.1). Density-dependent transition functions, $P_i(N_{elk})$ and the recruitment functions, $R_i(N_{elk})$, were modelled similarly to survival functions, $S_i(N_{elk})$, but with coefficients fit accordingly. All vital rates were density dependent with the exception of P_{spike}, the probability of spikes surviving to become bulls, which was 0.98, a constant reported in life tables by Houston (1982). Response to population density in all other elk classes was variable (Figure 2.2), and coefficients were estimated to be consistent with observed class composition as a function of population density. The sequence of density dependence in vital rates follows that suggested by Eberhardt (2002). The coefficients, Q_i, X_i, and Y_i were estimated for each class by iterative adjustment until herd composition predicted by the model matched that of the data. Reference data for cow:calf, cow:spike, and cow:bull ratios were taken from Houston (1982) for 19 years when data was available between 1930-1979 and Taper and Gogan (2002) for 7 years between 1987-1995, up to the period of wolf recovery. For density dependence of bulls, I chose to simulate the demographics observed for the period beginning five years after the implementation of "natural regulation" management (Boyce 1998, Singer et al. 1998), or 1973-1995. Data previous to this period included effects of artificial reductions by the National Park Service (Houston 1982, Barmore 2003), so a five-year buffer was chosen to allow culling-induced skewed sex ratios to normalize (Mack and Singer 1993).

Climatic variation

Summer forage production (Boyce and Merrill 1991, Merrill and Boyce 1991) and severe winter weather (Fowler and Barmore 1979, Houston 1982, Picton 1984, Clutton-Brock et al. 1987, Merrill and Boyce 1991, Garrott et al. 2003) significantly influence elk population dynamics. Survival of elk calves and yearlings is often a function of both winter severity and population density (Sauer and Boyce 1983, Merrill and Boyce 1991, Garton et al. 1990, Garrott et al. 2003). High-quality summer forage can enhance the condition of reproducing females and improve survival and growth of calves and yearlings (Merrill and Boyce 1991). As winter severity increases, less of the NR is available for foraging by elk, resulting in a higher fraction of the herd dispersing north of the park where they are subject to human harvest in the late-season hunt. This process links stochastic variation in climate to the density-dependent process.

Like WOLF5, WOLF6 simulates variation in winter severity and summer plant growth variables using random number generation (see Boyce 1992, 1995). Winter severity was represented by Lamb's Index, *L(t)*, which was calculated from winter temperature and precipitation measurements for the past 50 years on the NR. For each standard deviation from the average temperature and precipitation, integer additions or subtractions were made. Increased temperature negatively affects Lamb's Index whereas increased precipitation positively affects it. Lamb's Index in WOLF6 was modeled as an independent random variable, normally distributed, with mean zero and standard deviation of 6.5. Mean and variance of green herbaceous phytomass (kg/ha) was estimated from LANDSAT imagery (Merrill et al. 1993) and related to per capita elk population growth rates by Merrill and Boyce (1991). The phytomass term, *P(t)*, also was an independent random variable, normally distributed, with mean zero and standard deviation of 309 kg/ha.

Winter severity and summer phytomass were incorporated into the density-dependent functions of survival, recruitment, and transition in a way that essentially perturbed the carrying capacity. For example, the probability of survival for stage class *i* at time *t* was

$$S_i(t) = 1/(Q_i + \exp\{X_i + [Y_i N_{elk}(t)] - [Z_i P(t)] - [W_i L(t)]\} \qquad (6)$$

for class *i* in which $L(t)$ is Lamb's Index of winter severity at time *t,* and $P(t)$ is the summer green herbaceous phytomass at time *t*. The terms Z_i and W_i scale the response to variability in phytomass and winter severity, respectively, for each stage class (Table 1). The method for obtaining deterministic estimates of Q_i, X_i, and Y_i is described above with the functions illustrated in Figure 2.2. The range of values for the approximately linear middle portion of the curve for each class was estimated from the linear relationships reported by Merrill and Boyce (1991). Intercepts were anchored at values reported in life tables by Houston (1982) for the population when it was at low density, and at high density, decreasing, non-linear survival was used to reflect the relationships described by Taper and Gogan (2002). Small, iterative changes in the coefficients were made until model output converged with the relationships in the data for both herd composition and population mean and C.V. from 1973-1995.

Elk harvest

Harvest by humans has a significant influence on the NR elk herd (Houston 1982, Taper and Gogan 2002, Barmore 2003, Eberhardt et al. 2003), and wolf recovery may impact elk harvests (White and Garrott 2005). The simulations included a column vector of harvests, $\mathbf{H}(t)$, of the number of individuals harvested from each sex/age class subtracted after the projection matrix, $\mathbf{A}(\mathrm{t})$, was postmultiplied by the population vector, $\mathbf{N}(t)$, specifically,

$$\mathbf{N}(t + 1) = \mathbf{A}(t)\mathbf{N}(t) - \mathbf{H}(t). \tag{7}$$

The Montana Department of Fish, Wildlife and Parks manages winter elk hunts on the NR immediately north of the park. Hunter harvest of elk in the Gardiner late hunt (Unit 313) during January and February was modelled using the harvest objectives outlined by Montana Fish, Wildlife, and Parks in Table 2.2. The number of permits issued is based on the estimated number of elk in the NR herd (i.e., density dependent), and simulated harvest was based on past estimates of hunter participation and success (Lemke 2003).

Permits for the “Gardiner Late Hunt,” a hunt in January and February that targets mostly (>75%) adult females for population reduction each year, numbered between 2,310-2,660 antlerless elk annually between 1991 and 1996. The available permits were increased to 2,870 in 1996, the year after wolves were reintroduced, then beginning in 2001, permits issued gradually declined to 1,400 by 2004.

Severe winter conditions force elk to migrate out of YNP into areas of the NR where harvest can occur (National Research Council 2002). Harvest in WOLF6 was modeled as a density-dependent function of winter severity to have higher harvests coincide with severe winters, calculated as

$$h(t) = 30 \cdot L(t) \qquad (8)$$

in which $h(t)$ is the harvest adjustor at time t, $L(t)$ is Lamb's Index of winter severity at time t, and the constant, 30, was chosen so harvest would vary with a normal distribution around the mean harvest from 1976-1995, 965 elk (Lemke 2003). To attain total yearly harvest, $H(t)$, in WOLF6, the harvest adjustor, $h(t)$, was added to constants, 630, 310 or 0, depending upon the population estimate, $N_{elk}(t)$, as indicated in Table 2.2. In the absence of a harvest, $H(t) = -965 + h(t)$.

The column vector of harvests, $\mathbf{H}(t)$, is the total yearly harvest $H(t)$ distributed among the five elk age/sex classes based on the composition of the harvest (see Lemke, 2003; Wright et al. 2006): harvest of spikes was 9% of total, cows, 57%; old-cows, 19%; and bulls, 15%. While 18% of total harvest has been reported as "calf," these calves were >6 months of age; therefore, harvest of these individuals was deducted from spike (6-18 month males) and cow classes (includes 6-18 month females) in the model. Harvest of calves 0 to 6 months of age was negligible. I examined variation in composition of the harvest for the Gardiner Late Hunt to suggest approaches to optimization, particularly after wolf recovery (Nilsen et al. 2005).

Alternative prey

Currently elk constitute about 90% of the wolf diet for NR packs in YNP (Smith 2005) even though alternate prey for wolves also are abundant (Smith et al. 2002b).

Wolves have preyed upon seven other ungulate species on the NR: bison (*Bison bison*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), pronghorn (*Antilocapra americana*), white-tailed deer (*Odocoileus virginianus*), and mountain goat (*Oreamnos americana*). As in WOLF5, bison, moose, and mule deer were included in the model as alternate prey for wolves, because populations of these three species might be able to individually support a wolf population (*sensu* Dale et al. 1994). Population projections for bison, moose and mule deer were done as in previous versions of the WOLF model (see Boyce and Gaillard 1992, Boyce 1995). Per capita growth rates, density-dependent coefficients, and climatic-influence coefficients for moose and mule deer were retained from WOLF5 (Table 2.3), whereas for bison the per capita growth rate was retained but the density-dependent coefficient was reduced so K_{bison} = 800, because my focus is on the NR, rather than the entire park (National Park Service, unpublished data, 2004). Harvest was not modelled separately for alternative prey, but rather, was accounted for in the potential population growth rates used for these species. Initial populations of alternate prey were assumed to be at carrying capacity: K_{bison} = 800, K_{moose} = 800, and K_{deer} = 3,000.

Predators

Predation by cougars (*Felis concolor*), coyotes (*Canis latrans*), black bears (*Ursus americanus*), and grizzly bears (*Ursus arctos*), while probably significant to prey populations, were assumed to be intrinsic to the underlying population dynamics modeled for elk and alternate prey prior to wolf reintroduction. The possible effects of wolves on predation rates of these other predators, or the predation rate of wolves influenced by carrion loss to scavengers (see Wilmers et al. 2003, Wilmers and Getz 2004), and carcass-usurping behaviour of bears (see MacNulty et al. 2001) was not incorporated into WOLF6.

Functional response

Predation by wolves was modeled as a functional response, or the per capita rate at which prey is killed as a function of prey availability (Taylor 1984). Model simulations with predation included a predation column vector, $\mathbf{F}(t)$, containing the five functional response terms (one for each class) multiplied times the number of wolves, $N_{wolf}(t)$. The predation column vector $\mathbf{F}(t)$ was subtracted from the population composition vector after the projection matrix had been postmultiplied by $\mathbf{N}(t)$ and reduced by hunter harvest, $\mathbf{H}(t)$. So simulations that included both harvest and predation included reductions by both $\mathbf{H}(t)$ and $\mathbf{F}(t)$:

$$\mathbf{N}(t+1) = \mathbf{A}(t)\cdot\mathbf{N}(t) - \mathbf{H}(t) - \mathbf{F}(t). \tag{9}$$

I employed a multi-species prey-dependent functional response (Crawley 1992, Abrams 1993, 1994, Abrams and Ginzburg 2000). I note that Vucetich et al. (2002) and Eberhardt et al. (2003) found reasonable fits of data to ratio-dependent predator-prey models, but I could not reconcile the peculiar dynamics and implausible assumptions of ratio-dependent models (Hanski 1991, Oksanen et al. 1992, Abrams 1994, 1997). Although ratio-dependent models might be interpreted to accommodate group hunting by the predator (Cosner et al. 1991), variation in vulnerability among individual prey (Abrams and Walters 1996), and aggressive encounters between predators while searching for prey (Beddington 1975), alternative methods exist for modelling these phenomena that do not require such unreasonable assumptions (Abrams and Ginzburg 2000). My approach was to use a prey-dependent functional response while accounting for the effects of wolf density in the numerical response. As suggested by Abrams (1994), this works well when the reproductive period of the predator and prey matches the time scale of the model ($t = 1$ year for both predator and prey).

There is clear evidence that wolf density is related to prey abundance through a complex interaction between vulnerable prey availability and intraspecific limitation mechanisms (Fuller 1989, Messier 1994, Fuller et al. 2003). For mammals, functional response is often a Type III response, or logistic (S-shaped) curve; however, Walters et al. (1981) used a Type II disc equation for a similar wolf-prey model. Messier (1995) suggests that Type II is the correct version to use, but it is not possible to distinguish between a Type II or Type III with limited existing data on prey at low densities (Marshal and Boutin 1999). Eberhardt et al. (2003) advocate a constant predation rate as better supported by available data over a wide range of prey densities in multiple systems, and observed per capita predation rates have not decreased with decreasing elk density in YNP thus far (White and Garrott 2005). However, the moderate variation around the mean that has been observed in elk density since wolf recovery may not represent enough variation to measure long-term functional response over the wide range of primary and alternate prey densities that might be expected during the next century.

There is no agreement on how predation rate changes with prey or predator density (Eberhardt 1997, 2000; Vucetich et al. 2002), so I chose the logistic form of the Type III functional response justified by Boyce (1992) on the basis that predators confronting alternate prey species will switch prey as a function of the abundance of various prey

(Murdoch 1969). Increased stability in prey numbers are expected under Type III functional and numerical responses for predators, while Type II functional and numerical responses decrease stability, i.e., they are antiregulatory (Dale et al. 1994). In multiple ungulate systems, wolves can switch to alternate prey in response to availability, which is influenced by abundance, vulnerability (Scheel 1993, Abrams and Walters 1996), migration (Fryxell et al. 1988), use of refugia (Fryxell and Lundberg 1998), and anti-predator behaviour (Mech and Peterson 2003). These factors may be present in YNP. Increased use of bison by wolves where elk are scarce in YNP (Smith et al. 2000b) is an example of a response to differing abundance, and increased use of migratory mule deer during summer found by analysis of scat (Smith 2005) demonstrates wolf use of seasonally available prey. Use of low wolf-use areas by vulnerable elk classes (White and Garrott 2005) suggests that elk seek to minimize predation risk on the NR; the use by prey of refugia between wolf pack territories has been found in other systems (Mech 1977, Lewis and Murray 1995). Some forms of anti-predator behaviour by YNP elk have been documented (e.g., Fortin et al. 2005). Individually and in sum, these phenomena lead to the prediction of density-dependent predation as characterized by a Type III functional response. The form I used was:

$$F_i = \frac{A_i N_i \sum N_j}{1 + T_{hi} A_i \sum N_j^{\,2}} \tag{10}$$

where F_i is the functional response for the ith prey available, A_i is the attack rate by wolves on the ith prey, ΣN_j is the sum of all available prey, and T_{hi} is the handling time for the i-th prey (Table 2.3). Kill rates previously estimated for other populations were used to estimate functional response terms in WOLF5 (see Boyce, 1990, for review); however, kill rate estimates for wolves in YNP (Smith et al. 2004) were available to parameterize WOLF6. Predation rates on the NR vary by season and year, but the highest rate was recorded for a 30-day sampling period in March 1997 under conditions of severe winter and high prey density (Smith1998, Mech et al. 2001). If extrapolated to the entire year, this represents a theoretical maximum (F_{max}= 32 elk/wolf/year) for wolf predation on elk in YNP, 30% higher than in WOLF5 where F_{max}= 25 (Boyce 1990, 1995). However, the yearly rate would be significantly lower than F_{max}= 32, because yearly predation rates will be affected by variation in prey density, predator density, and prey vulnerability as influenced by seasonality (Messier 1994, 1995; Eberhardt 1997, 2000; Smith et al. 2004). Messier (1994) estimated summer wolf predation rates were 70% of winter rates.

Attack rates on each elk class were estimated based on the composition of wolf kills reported from YNP for 1995-2003 (Phillips and Smith 1997; Smith 1998; Smith et al. 1999; 2000, 2001, 2003; Mech et al. 2001; Smith and Guernsey 2002). Wolf kills on the NR during mid-November to mid-December and March study periods included 41% calves, 11% cows, 27% old-cows, and 21% bulls. These values characterize selection for winter months only (Mech et al. 2001, Smith et al. 2004) and few data were available for other seasons of the year. Needing to extrapolate these proportions for an entire year, I chose to reduce the proportion of bulls to 10% due to high incidence of bulls in winter kills collected during periods that coincide with high bull elk vulnerability following the rut, but normally low mortality during other seasons (Houston 1982, Barmore 2003). Attack rates in the functional response term of the WOLF6 model were iteratively adjusted until the following observed proportion of prey classes taken by wolves were predicted: 44% calves, 6% spikes, 11% cows (includes yearling females), 29% old-cows, and 10% bulls. While estimating attack rates, the available elk used in the functional response was 12,215 elk, the mean elk population during 1995-2003 when wolf kill data were collected (Figure 2.1).

Handling times were scaled relative to mean body size of the prey. Functional response curves derived from these attack rates and handling times were generated for each elk class (Figure 2.3) and alternate prey species (Figure 2.4). The F_{max} for each of the prey classes (Table 3) was derived from the asymptotic maximum of the curves in Figures 2.2 and 2.3. For elk, an F_{max} of 26.2 resulted when all elk age/sex classes were summed. Attack rates for alternate prey were adjusted to reflect the low levels of predation observed since wolf reintroduction (Table 2.4). Current consumption is estimated to be between 0.1 and 0.35 individuals per wolf per year for all three species of alternative prey as estimated from the data in Table 2.4.

Surplus killing, when excessive prey are killed by wolves and left unconsumed, has been observed in YNP (Smith 1998). In late winter, wolves may kill in excess of their food requirements particularly if the winter is severe with deep, crusted snow pack, and abundant prey in poor condition; however, this kind of predation tends to be rare and tends not to be additive due to the poor condition of prey and the tendency to succumb or migrate during severe winters (Eide and Ballard 1982, Miller et al. 1985), so surplus killing was not specifically modeled in WOLF6.

Numerical response

The numerical response is the rate at which prey consumed influences predator population growth. A multiple-species numerical response was used for wolf population growth. The form of the numerical response was

$$N_{wolf}(t+1) = N_{wolf}(t) \cdot \exp(T_r - T_{dd}) \qquad (11)$$

where $N_{wolf}(t)$ was the wolf population at time t, T_r was the reward term, and T_{dd} was a density-dependent term for wolves. The reward term was the rate at which prey were converted to predator population growth based on the size and number of prey taken, such that

$$T_r = \Sigma(B_i \cdot F_i(t)) \qquad (12)$$

for the i-th elk sex/age class and alternative ungulate prey, where F_i is the functional response (yearly per capita rate at which respective prey was taken) for each of the five classes of elk, and species of alternate prey, and B_i is the reward coefficient scaled to the body mass of each i-th prey item (Table 2.3).

Recent demographic data indicate that wolf population growth in YNP has subsided: adult mortality is high, inter-pack and intra-pack aggression has increased, mean pack size has increased, and dispersal has decreased (Smith 2005). These observations indicate that the population is experiencing social and spatial constraints (Fuller et al. 2003); hence the population appears to be approaching carrying capacity.

The density-dependence term for wolves described the numerical limitation of wolf populations imposed by social and spatial constraints, given by

$$T_{dd} = \frac{r_{wolf}}{K_{wolf}} \cdot N_{wolf}(t) \qquad (13)$$

where the constant, $r_{wolf} = 0.77$, was the maximum observed growth rate for the YNP wolf population (Smith 2005). The carrying capacity for wolves, K_{wolf}, was estimated by plotting the density-dependent relationship between the yearly population growth rates for wolves on the NR and population size, for which the linear relationship intersects zero per-capita growth rate at $K_{wolf} = 131$ (Smith 2005:Figure 6). The initial release of $N_{wolf}(t)$ in 1995 was 14, with 17 and 10 wolves added the two successive years, respectively, to reflect the total of 41 wolves released in the park (Phillips and Smith 1997, Smith 1998).

Wolf culling

About half of wolf mortality in the YNP ecosystem has been human-caused due to depredation control, vehicle collisions, and poaching (Smith 2005). Eventually the state of Montana may implement controlled harvest through hunting and trapping of wolves on the NR outside of the national park. To model the removal of wolves from all human sources, a quota of wolves removed per year was implemented. The "quota" should be interpreted as the number of wolves removed from the population each year by humans, irrespective of the source. I assumed density dependence in the quota-based removal, so that when $N_{wolf} > 90$, the full quota would be removed, when $50 < N_{wolf} < 90$, 67% of the quota would be removed, and when $N_{wolf} < 50$, 33% of the quota would be removed from the wolf population. Quota-based density dependent culls account for wolves using the refuge provided by the park portion of the NR less when density is high and more when density is low due to intraspecific limitations (e.g., territoriality, dispersal) interacting with the availability of vulnerable prey (Fuller et al. 2003).

RESULTS

Initial evaluation of WOLF5 performance suggests earlier efforts were reasonable. WOLF5 predictions for elk population trajectories subsequent to wolf reintroduction have closely matched those observed when taking climatic fluctuations into account (Figure 2.5). Wolf numbers on the other hand, were underestimated by 20-30% (Figure 2.6) because wolf carrying capacity was underestimated. In general, agreement between ecological simulation models and their real-life counterparts is poor (Eberhardt and Thomas 1991); however, given the data subsequent to wolf restoration, a comparison between past models and the updated version finds striking agreement (Table 2.5). Projections of WOLF5 (Boyce and Gaillard 1992, Boyce 1995) appear to have simulated well the dynamics of wolf recovery effects on elk herd size, variation in herd size, and predation rate (Table 2.5).

The first phase of my analysis of the current model, WOLF6, entailed studying the basic framework as a deterministic model without climate, elk harvest, or wolves. I then incorporated stochastic perturbations, beginning with climate (phase 2), then hunter harvest (phase 3) simulating conditions prior to wolf recovery, and finally wolves (phase 4), which included variations (with/with out elk harvest, with/with out wolf culling). The addition of each component to the model (phases 1-4) reduced average elk population size.

Elk population dynamics

The deterministic version of the model predicted an equilibrium population for the NR elk herd of 16,243 elk (Table 2.6), resulting from density-dependent vital rates alone. Although counts in the late 1980's and early 1990's of elk numbers were in excess of 18,000 (Figure 2.1), these large counts likely occurred because of mild climatic conditions (Taper and Gogan 2002). Predicted herd composition, as reflected in low calf:cow, spike:cow, and bull:cow ratios (Table 2.6), was dominated by adult females more so than other phases. Also, the percentage of old-cows in the herd was highest in phase 1 projections (55%); this estimate was higher than the 45% estimated by Houston (1982) for the herd in the 1970's.

Climatic influences (i.e. stochastic variation in winter severity and summer forage quality) were added in phase 2 causing a decrease of 9% in the mean population to 14,729 (*n*=25; Figure 2.7). The decrease is due to the inability of a population to match climate-influenced mortality in bad years with growth in good years (Boyce and Daley 1980). The addition of climate-caused stochastic variation resulted in substantial ungulate population fluctuations over time, as has been observed throughout the recorded history of the NR herd (Houston 1982, Singer et al. 1989, Boyce and Merrill 1991). Winter severity and summer forage production influenced both survival and recruitment. Without other sources of mortality in the model (i.e. harvest and wolves), the interaction between density dependence and climate caused high variability in population (C.V. = 0.20). The interaction between climate and density has been reported for this elk herd

(Merrill and Boyce 1991, Singer et al. 1997, Taper and Gogan 2002) and other ungulate herds (Picton 1984, Clutton-Brock et al. 1987, Choquenot 1991). For a non-harvested elk herd in a different region of YNP, calf recruitment was inversely correlated with snowpack (Garrott et al. 2003). Combined with high adult survival, variable recruitment caused this herd to be maintained in a dynamic equilibrium (Garrott et al. 2003). Taper and Gogan (2002) estimated population equilibrium for the NR herd in the absence of harvest to be 20,000 to 25,000 elk. Density dependence as modeled in WOLF6 predicts a lower long-term average population under these conditions. In Figure 2.7, the WOLF6 projection of population size surpassed 18,000 in 15 of 100 years, but large fluctuation in population resulted in a 100-year mean of 14,729.

In phase 3, hunter harvest of elk was added to the WOLF6 model; with mean annual harvest of 1,228 elk the projected 100-year population mean decreased 17% to 12,254. The observed minimum population from counts between 1973 and 2003 (Figure 2.1) averaged 13,716, but this was with a mean harvest of 1,092 elk. The WOLF6 projection gave a lower population size indicating that current harvest patterns will result in lower elk populations on average relative to the past 30 years. Because harvest rate was density-dependent (i.e. high populations coincided with higher harvests while low populations were subjected to lower harvests), harvest reduced the among-years variation in elk numbers (C.V. = 0.19). Current hunting regulations cause harvest to increase calf:cow, bull:cow, and spike:cow ratios (Table 2.6) and reduced the proportion of old cows in the herd as a result of selection for cows in the harvest.

Composition of the elk herd was compared with existing data to assess model performance. Phase 3 output for calf:cow (Figure 2.8), bull:cow (Figure 2.9), and spike:cow (Figure 2.10) ratios relative to density were compared with the same relationships from available empirical data for 1930-2003 from Houston (1982) and Taper and Gogan (2002). Some data from this period were missing or excluded purposefully (e.g. bull:cow ratios during years in which artificial herd reduction might have biased composition), but despite having fewer data relative to model output, these herd composition relationships for the model were nearly identical to the empirical relationships (Figures 2.8-2.10).

During Phase 4, I examined scenarios under wolf recovery. Wolves decreased long-term mean elk population 21% from 12,254 to 9,713; this level of predation supported a 100-year mean population of 109 wolves that consumed an average total of 1,035 elk per year (Figure 2.11, Table 2.6). Variance in elk numbers was reduced, C.V. = 0.17, indicating that an effect of wolf predation was to stabilize elk numbers. Wolves decreased the proportion of old-cows in the herd to 41%, but had little other effects on herd composition.

Harvest implications

Wolves decreased mean annual harvest by ~12% from 1,228 to 1,089 elk, while the combination of the two caused the greatest reduction in variability in elk numbers (C.V. = 0.17) with a combined mean annual removal of 2,107 elk (Figure 2.12). Previous WOLF model projections also showed that wolf recovery decreased hunter harvest—WOLF5 projected up to 10% decline in hunter harvests in the greater YNP area (Boyce and Gaillard 1992). The option to discontinue elk harvest was simulated in phase 4, and the effect of wolves was lessened, a reduction of 13% (versus 21%) in mean elk numbers from 14,729 to 12,727. Wolves took 19% more elk without hunter harvest of elk than with it, 1,277 versus 1,035 per year, due to increased prey availability. Variability in elk herd size increased slightly without harvest (C.V. = 0.18), and removing hunter harvest of elk resulted in more wolves, with $\overline{N}_{wolf}$ = 122. Composition of the herd (Table 2.7) and alternative prey taken (Table 2.8) changed suggesting that hunter harvest alters proportional prey availability causing wolves to alter selection. With no hunter harvests of elk, wolves took fewer bulls and calves and more old-cows compared to simulations that included elk harvests.

Due to the steep density dependence of bulls relative to cows in Figure 2.2, culling cows affected the number of bulls in the herd (Figure 2.13). Cow culling of 8-12% combined with varying levels of bull harvest maximized harvest at 1,200-1,500 elk (Figure 2.14). Although wolf recovery decreased projected hunter harvest, changing regulations to permit harvest of more bulls could allow overall harvest to increase. Bull harvest was modeled as 15% of herd total in all phases of model projections, but when cow harvest is decreased and bull harvest increased to 20%, a higher overall yield of nearly 1,600 elk annually could be achieved (Figure 2.14).

Phase 4 results include a harvest of the NR elk herd with wolves present in the system. Wolf predation will lower the long-term mean number of elk, and more so in combination with current harvest regimes. However, extinction of the NR herd was not predicted by any model projection as it was for a harvest model by Eberhardt et al. (2003: Figure 5) with removal of 1,500 elk per year. The difference that led to this disparity is that I modelled and documented a density-dependent harvest requiring that managers reduce elk harvest when populations are low, thereby ensuring the population will recover from low densities. Qualitatively, my predictions are similar to those of

Eberhardt et al. (2003) in that high harvests can cause elk numbers to drop to low levels; however, the ability of managers to monitor the population and change harvest levels accordingly ensures that elk numbers can be maintained even with a moderate harvest. The model projected a harvest of 1,089 elk per year with wolf predation, and reduced variation in elk population size allowing reasonably consistent numbers of hunting permits to be issued year-to-year.

Actual harvests during 1976 to 2003 averaged 1,081 elk (Lemke 2003). The population was relatively high during this period and above average harvests (>2,800) coincided with severe winters, e.g. 1988-1989, 1991-1992, and 1996-1997 when large numbers of elk moved out of the park where they were exposed to hunter harvests. Mean harvest from 1976-1988 was lower, 743 elk per year; but since 1989 a 75% increase occurred with 1,302 elk taken per year (Lemke 2003). The largest harvest occurred in the winter of 1991-1992 with 4,515 elk removed. With wolves, projection of mean harvest in WOLF6 was intermediate between the means for the periods before and after 1989. Elk harvest goals set by the Montana Department of Fish, Wildlife and Parks and used to simulate harvest in WOLF6 (Table 2.2) are sustainable but with mean harvest decreasing significantly relative to the recent past. Seasons fell within the "standard" or "conservative" types as few yearly elk counts exceeded 15,000 in WOLF6 projections (Figure 2.11), resulting in less than one in five hunting seasons considered "liberal" in which harvest exceeded 1,230 elk.

Alternative prey

Thus far, wolves have focused on elk as the primary prey, and little predation has occurred on other species (Table 2.4). Using these data to calibrate the WOLF6 model resulted in little to no effect of wolves on alternate prey species: bison, moose, and mule deer (Table 2.8). However, climate, wolves, and harvest combined to cause elk numbers to decrease, resulting in wolves preying relatively more often on alternate prey species than has been observed during the first ten years since wolf reintroduction. Elk harvest had little effect on the alternate prey species in the model, and coupled with wolves, had little effect on predation levels on alternate prey.

Wolf population dynamics

At the end of 2004, the YNP wolf population was estimated to number 169, with approximately 85 wolves on the NR (Smith 2005: Figure 5). The WOLF6 model projected a mean of 109 wolves on the NR. Wolf numbers tracked elk numbers over time (Figure 2.11), with periods of low wolf population preceded by periods of decline in the elk population and high wolf population preceded by growth in elk numbers. Wolf numbers were affected by the factors that influenced elk numbers, namely, density dependence, climate-induced stochastic variation, and hunter harvest of elk. This suggests that WOLF6 simulations of wolf population projections were influenced at least in part by bottom-up trophic level perturbations (Boyce and Anderson 1999, Vucetich and Peterson 2004).

Culling of wolves was predicted by the WOLF6 model to reduce wolf population size (Table 2.9). Populations persisted at yearly quotas of up to 28 wolves. Wolf culling quotas in excess of 30, or about 23% of K_{wolf}, caused extinction in some projections, and when quotas exceeded 50, extinction of the wolf population became likely. Wolf harvests of >40% have been found to cause declines in wolf populations (Keith 1983, Ballard et al. 1987), and in previous versions of the WOLF model (Boyce 1990, 1993).

Most of the NR lies within YNP so wolf packs may not be subject to high culling levels with the presence of this refuge. For each increase of five wolves in the quota, a mean increase of about 1% in the elk population and elk harvest was projected.

DISCUSSION

Experimental wolf restoration in YNP was suggested decades ago as one way to restore an ecological process (Leopold 1944; Despain et al. 1986), with far-reaching effects on prey population regulation and multi-level trophic dynamics. The National Research Council (2002) and others (Despain et al. 1986, Sarrazin and Barbault 1996; Singer et al. 1997, Fieberg and Jenkins 2005) have encouraged taking advantage of the opportunities of wolf recovery in YNP to learn about predator-prey dynamics and to evaluate the ramifications of ecological-process management as practiced in YNP (Boyce 1998, Huff and Varley 1999). Updating the WOLF model has been a fundamental contribution to this adaptive management process, and combined with future field studies, should remain a tool for anticipating wolf-elk dynamics and the implications of these dynamics on hunter harvest of elk.

Despite many differences in model structure and parameter estimates, the updated WOLF6 model gave predictions similar to its predecessors. The WOLF models consistently have predicted neither an insignificant effect of wolves on elk numbers as some had once believed (Houston 1971, Cole 1971), or enormous effects that are tantamount to ecological collapse as has been popularized outside the scientific community (Fritts et al. 2003). Rather, the predictions are of moderate reductions in elk numbers with a sustainable, moderate hunter harvest. The changes in WOLF6 ultimately failed to produce qualitatively different results from other WOLF models, which implied that the predictions of earlier versions of the model were generally robust.

Contrary to unsubstantiated claims by Boitani (2003: p. 333) and Fuller et al. (2003: p. 187) that the WOLF models were "problematic," previous versions performed reasonably at predicting the most current data. Wolf numbers had been slightly underestimated and elk harvest and the use of alternate prey by wolves had been overestimated. Several reasons may account for these discrepancies. Increases in harvest quotas occurred during the 1990's that were unforeseen in earlier versions of the WOLF models, and land acquisition beyond YNP made winter range available thereby expanding the carrying capacity of the NR herd (Lemke et al. 1998, Taper and Gogan 2002). Age structure in the elk population had been dropped from the WOLF5 version of the model due to lack of data and to make the model run fast on early vintage personal computers (Boyce 1995). Comparisons with current data acquired subsequent to wolf reintroduction may be confounded by transient dynamics coinciding with irruptive population growth (White and Garrott 2005); a WOLF6 projection of a 20% increase over the long-term mean in the first 10 years was noted (see Figure 2.12), and could account for a skewed perspective of long-term dynamics resulting from current data. In fact, the system may adjust for many years subsequent to wolf restoration (Klein 1995). The National Research Council (2002) suggested that achieving stable dynamics might take longer than the period during which wolves were absent, or about 70 years. Continued monitoring of elk demographic parameters and wolf predation will be necessary to evaluate the degree to which initial data on elk vital rates represent transient dynamics.

Disparity among predictions from WOLF6 and other recent YNP wolf recovery models (e.g., Eberhardt et al. 2003, Wilmers and Getz 2004, Vucetich et al. 2005) might be seen to cast doubt on the effectiveness of simulation modelling for management. If different models yield contrary results, how can managers assess which is reliable? Rather than presenting a dilemma, however, I argue that the differences in predictions among models are useful in helping to resolve key features of the system, exactly as prescribed by the adaptive management paradigm (Walters 1986). Some of the differences among models have been discussed elsewhere (White and Garrott 2005), but differences in the structure and intent of these models are fundamental to the differences among model predictions. The strength of density dependence operating through elk survival, reproduction, hunter harvest, and wolf predation is the most influential factor determining the population dynamics and resilience of the WOLF6 predator-prey system (Fieberg and Jenkins 2005). Density dependence in vital rates and hunter harvests is well documented for the NR elk herd (Fowler and Barmore 1979, Houston 1982, Merrill and Boyce 1991, Taper and Gogan 2002), giving me confidence in the model predictions. The ability to document density dependence for this elk herd was facilitated by the elk herd reductions of the 1960’s (Houston 1982) that provided a broad range of densities over which vital rates were then monitored (Merrill and Boyce 1991, Taper and Gogan 2002). While little density-dependent response has been seen in elk vital rates since wolf recovery (White and Garrott 2005), the range of elk population densities has been insufficient to detect these effects (Figures 2.8-2.10 present comparative composition data). Density dependence also may appear in ways that are not reflected in these vital rates, such as an improved individual elk condition at lower density that decreases vulnerability to wolf predation (Dale et al. 1994, Wilmers and Getz 2004) and the strong link between density and harvest (National Research Council 2002).

During the nearly 30 years between the implementation of the “natural regulation” policy for elk management (Huff and Varley 1999) and wolf reintroduction, the major drivers in elk population dynamics have been density and climate (Singer et al. 1998, Taper and Gogan 2002). Severe winters resulted in compression of the ecological carrying capacity (Houston 1979), and particularly at high densities, subsequent migration placed elk outside the park in areas of harvest (Houston 1982; Singer et al. 1997, 1998; National Research Council 2002). Thus, climate enforced a density-dependent source of mortality by hunting. Predation and harvest both work to decrease the magnitude of population fluctuation, but the stochastic effects of climate still alter carrying capacity from year-to-year. By implementing density-dependent harvest guidelines for elk, wildlife managers have implemented a policy that fosters the resilience and sustainability of the system, as has been recognized recently in an exploited marine system (Hughes et al. 2005).

Eberhardt et al. (2003) suggested the data do not support climate-driven population fluctuation, but they apparently failed to recognize the effect of climate on hunter harvest. The inextricability of density dependence, climate, and harvest in the data used to construct Figure 2.2 was confounding—I was unable to fully isolate these effects even though they were presented separately in phases 1-3 of the model. Specifically, the density-dependent vital rates in phase 1 are ultimately enforced by an interaction with hunter harvests. In phase 3 I injected the numerical effects of the hunter kill, but part of the dynamical consequences are already present in the density-dependent structure formed at phase 1. Harvest is density-dependent (Table 2.2), but climate dictates years when movements of elk outside the park allow for a harvest. I predict that climate-induced perturbations will continue but with wolf predation reducing the magnitude of fluctuations. In fact, the stabilizing effect of wolf predation on the NR may facilitate some consistency in permits offered and subsequent harvest. Altering the proportion of bulls in the harvest (Figure 2.14) also may help to mitigate the reduced elk harvests resulting from fewer "liberal" season types (Table 2.2) after wolf recovery.

Two mechanisms enforce the stabilizing influence of wolf predation in WOLF6: the Type III functional response and density dependence of wolves caused by territorial behaviour and social interactions. Wolves primarily removed elk calves and old-cows, which is consistent with many studies that have documented wolves taking mostly the non-productive segment of prey populations elsewhere (Peterson et al. 1998) and in YNP (Mech et al. 2001, Smith et al. 2004). The addition of age structure in the elk population contributed to dampened fluctuations in elk numbers caused by climate and amplified the consequences of harvest. Harvest and wolf predation often removed similar mean numbers of elk in the model (Figure 2.12), but differential selection of classes caused hunter harvest to reduce elk numbers more than predation (Table 2.6). Other recent models (Eberhardt et al. 2003, Vucetich et al. 2005) advocate lower elk harvest targets to avoid accelerated population decline due to both harvest and predation mortality, but these authors did not model harvest as self-correcting with changes in abundance.

Low use of alternate prey in WOLF6 projections (Table 2.8) suggests a moderately dense elk population can occur with little prey switching by wolves. The wolf numerical response stabilized with elk still constituting over 90% of the individual prey taken by wolves. Dale et al. (1994, 1995) found wolves in Gates of the Arctic National Park, Alaska, did not switch prey over a wide range of caribou (*Rangifer tarandus*) densities and at times high moose densities. Vulnerability of preferred prey and risks associated with attacking moose have been suggested as factors responsible for lack of prey switching in such multi-prey systems (Dale et al. 1994, Mech et al., 1995). The caribou population remained stable at low density, albeit a density sufficient to absorb high wolf predation rates without serious decline. Similarly, the NR elk were projected to sustain moderate densities with wolves relying substantially on them as the primary prey. Wolf density is thought to be ultimately limited by vulnerable prey density (Mech et al. 1995) with some of the proximate causes of limitation being social mechanisms, such as territoriality (Fuller et al. 2003). A significant proportion of the elk population in adult stages is consistently invulnerable, which leaves self-limiting mechanisms to cap wolf population growth.

Future updating of WOLF6 parameters should include refined estimates of seasonal predation rates and of alternate prey use with changing prey density and vulnerability. Average climate conditions were used to simulate future climate; however, climate change on the millennia scale has had a large effect on NR dynamics (Bartlein et al. 1997). Climate deviations from average in the next century would call for adjustment of parameters in the model. Similarly, the potential for disease and parasitic outbreaks with both wolves and elk could change predictions. While not much has been quantified, canine parvovirus and sarcoptic mange (*Sarcoptes scabiei*) are noted potential factors in wolf population limitation; however, examples to draw upon are few (e.g. Peterson 1995) suggesting population effects are rare (Fuller et al. 2003). Relatively few viral and parasitic infections affect North American elk populations (Worley 1991). While rare, bovine brucellosis (*Brucella abortus*) in elk and bison places the herd on a collision course with intensive efforts to eradicate this disease from domestic and wild sources in the region (Thorne et al. 1991). On its own, brucellosis imposes no threat to the elk population (Krebs 2002). Chronic wasting disease has not yet been found in the YNP region but occurs at very low prevalence in southeastern Wyoming (Miller et al. 2000).

The success of adaptive resource management for species reintroductions has had few examples upon which to draw (Sarrazin and Barbault 1996), in part because empirical testing of predictive models seldom occurs (Walters 1997). The models that have successfully undergone empirical testing and updating have been useful and insightful (e.g., Mills et al. 1997; Lindenmayer et al. 2001, 2003). After six revisions of WOLF models over 15 years and continued data gathering by the National Park Service, the WOLF models have been an integral part of adaptive management (sometimes referred to as experimental management, see Walters, 1986, 1997) for wolf recovery in the Yellowstone ecosystem. Models were built to predict the results of experimental wolf recovery, management actions were carried out based in part on the reassurance of these predictions (i.e., wolves were released in YNP), and then performance of the model was evaluated and the model revised based on subsequent monitoring of the response to wolf recovery.

Adaptive management for wildlife recovery has many potential applications. Recent recovery projects for golden eagles (*Aquila chrysaetos*) in Ireland (O'Toole et al. 2002) and beavers (*Castor fiber*) in Scotland (South et al. 2000) can now evaluate original models and refine them. These evaluations can improve the success of recovery programs, examples of which have included: curbing human development for reintroduced northern Florida panthers (*Puma concolor coryi*; Cramer and Portier 2001), altering fishery management for Australian trout cod (*Maccullochella macquariensis*; Todd et al. 2004), altering the age composition of Asiatic wild ass translocations (*Equus hemionus*) in Israel (Saltz and Rubenstein 1995), and creation and maintenance of patch corridors for samango monkeys (*Cercopithecus mitis*) in South Africa (Swart and Lawes 1996). Species recovery efforts in some cases require further empirical work to be able to evaluate model predictions. For example, competition and possible hybridization with domestic *Equus* spp. may challenge takhi (*Equus ferus przewalskii*) recovery in Mongolia (King and Gurnell 2005). Reintroduced white storks (*Ciconia ciconia*) in Switzerland suffered low juvenile survival (Schaub et al. 2004) leading to the suggestion that conservation or creation of additional brood-rearing habitat may help. Occasionally, updated models can affirm the recovery effort is proceeding without major needs or impediments (e.g., Bar-David et al. 2005), while others have indicated the opposite. In the Netherlands, a beaver population was evaluated after reintroduction and deemed only marginally viable due to high mortality of adults (Nolet and Baveco 1996). The translocation of lynx (*Lynx canadensis*) to southern portions of their USA range was later predicted to be unsuccessful on the basis that habitat lacked minimum prey densities (Steury and Murray 2004). The latter cases underscore the need for models at the planning stage to predict its outcome, but unfortunately, ecological modellers have been involved in few reintroduction efforts (Sarrazin and Barbault 1996). Direction for further lynx (*Lynx lynx*) recovery efforts in Germany hinge in part on current modelling assessments of habitat patch viability (Kramer-Schadt et al. 2005). Modeling of bearded vulture (*Gypaetus barbatus*) dynamics prior to reintroduction to isolated mountains in Spain indicated captive populations were insufficient to support the translocations that were required (Bustamante 1998). In sum, these examples illustrate the need for and value of modelling in an adaptive manner.

The translocation of wolves to YNP has been successful (*sensu* Griffith et al. 1989) with a self-sustaining population well established within 10 years (Smith 2005, White and Garrott 2005). During the planning phase, after reintroduction, and through to population recovery, the WOLF models have been used to simulate probable dynamics of a multi-species system to inform management alternatives. Building models that predict the outcomes of species recovery test our understanding of the ecology of the system, and iterative revisions of models gradually improve our ability to predict system dynamics. Reintroduction and translocation is likely to increase to meet future conservation demands (Griffith et al. 1989), in particular, wolves continue to expand their distribution through conservation efforts worldwide (Boitani 2003) including, but not limited to, 14 European countries, 4 Canadian provinces, and 11 US states where populations are increasing (Boitani 2003). Predictive modelling as a framework for adaptive management promises to assist with the evaluation of management alternative for future population recovery efforts.

Table 2.1. Density-dependent, summer phytomass and winter severity scaling coefficients for the five classes of elk.

Probability Function	Scaling Coefficients:				
	Density Dependence			Green Summer Phytomass	Winter Severity
	Q	X	Y	Z	W
R_{calf}	2.30	-6.0	0.0004320	0.0003	0.070
P_{calf}	1.20	-7.5	0.0005500	0.0001	0.050
p_{cow}	1.00	-8.5	0.0003000	0.0025	0.200
S_{oldcow}	1.00	-7.5	0.0003300	0.0045	0.095
S_{bull}	1.15	-6.2	0.0003025	0.0080	0.160

Table 2.2. Harvest goals for northern Yellowstone elk herd in Gardiner late hunt (unit 313) as set by Montana Department of Fish, Wildlife, and Parks (abbreviated, see Lemke, 2003), and the corresponding numerical adjustments for the WOLF6 model.

Season Type	Total Elk Count	Permits Issued	Estimated Elk Harvest	Annual harvest in the WOLF6 model
Liberal	15,000+	2,700+	1,230+	$630 + 30 \cdot L(t)$ *
Standard	10,000 – 15,000	2,000 – 2,700	910 – 1,230	$310 + 30 \cdot L(t)$
Conservative	< 10,000	< 2,000	< 910	$30 \cdot L(t)$
* $L(t)$ is the Lamb's Index of Winter Severity				

Table 2.3. Population, functional response, and numerical response coefficients for each of four ungulate prey species and five elk classes used in WOLF6.

Prey	K	F_{max}*	Attack Rate	Handling Time	Body Size coef. R	Density Dep. coef. β_1	Winter Severity coef. β_2	Summer Phytomass coef. β_3	Growth Rate, r_0
Elk:									
Calf		8.5	0.000002	0.02	0.05	**	**	**	n/a
Spike		2.3	0.0000001	0.035	0.06	**	**	**	n/a
Cow		7.5	0.00000003	0.04	0.075	**	**	**	n/a
Old Cow		6.3	0.0000004	0.04	0.075	**	**	**	n/a
Bull		1.8	0.000003	0.0425	0.082	**	**	**	n/a
Bison	800	2.9	0.000000005	0.1	0.13	0.0002	0.0079	0.0002	0.23
Moose	800	2.6	0.00000006	0.045	0.09	0.0001	0.01	0.0001	0.2
Deer	3000	57	0.000000006	0.009	0.015	0.0003	0.009	0.0003	0.4

* Maximum functional response, greatest number of prey taken per wolf per year

** See Table 1 for scaling coefficients of elk classes

Table 2.4. Proportion of elk, bison, deer and moose taken by the number of estimated wolves during winter sampling periods since reintroduction in 1995, data summarized in Smith (2005).

Year	Elk	Bison	Deer	Moose	Wolf
	Proportion of known kills, n	Proportion of known kills, n	Proportion of known kills, n	Proportion of known kills, n	Estimated population**
2003	84%, 291*	6%, 21	1%, 4	0%, 0	174
2002	87%, 311	2%, 6	2%, 6	0.5%, 1	148
2001	87%, 281	3%, 10	1.5%, 5	1%, 4	132
2000	87%, 276	4%, 14	1%, 2	2%, 7	119
1999	86%, 197	2%, 5	3%, 6	1%, 3	72
1998	98%, 46	1%, 1	1%, 1	1%, 1	83
1997	98%, 50	0%, 0	0%, 0	1%, 1	80
Mean Proportion	89.6%	2.6%	1.4%	0.9%	

* proportion of prey species in sample of wolf kills from March, late-November, and early December; number of kills.

** estimates of population in Yellowstone National Park from Smith (2005).

Table 2.5. Projections from various versions of the WOLF model since 1990.

Reference	Model Version	Area	N_{wolf}	Reduction in elk herd size	Reduction in elk C. V.
Boyce 1990, 1993	WOLF	YNP*	50-120	15-25%	30%
Boyce 1992	WOLF	YNP*	90-140	15-25%	30%
Boyce 1992, 1995; Boyce & Gaillard 1992	WOLF5	GYA*	114; 50-170	5-20%	10%
Current article	WOLF6	NR*	110-122	21%	10%
GYA = Greater Yellowstone Area, YNP = Yellowstone National Park, NR = Yellowstone's Northern Range					

Table 2.6. Projections of elk population and composition for four simulation phases of the WOLF6 model.

Simulation Phase	N_{Elk}	S.D.	C.V.	Percent old cows*	Calves: 100 cows	Bulls: 100 cows	Spikes: 100 cows
1. Deterministic	16,243	-	-	55	18	11	2
2. Climate n=25	14,728	2,913	0.20	43	22	12	4
3. Harvest n=25	12,254	2,304	0.19	50	29	34	9
4a. Wolves, with Harvest n=25	9,713	1,696	0.17	41	29	21	8
4b. Wolves, with No Harvest n=25	12,727	2,274	0.18	40	24	16	5

*Percent of all adult females (18+ months) that are in the old cow class (10+ years).

Table 2.7. Functional response for elk age/sex classes from 100-year projections of the WOLF6 model.

	F_{calf}	**Calves taken per year**	F_{spike}	**Spikes taken per year**	F_{cow}	**Cows taken per year**	$F_{old\ cow}$	**Old Cows taken per year**	F_{bull}	**Bulls taken per year**	F_{elk}	**Total elk taken per year**
Phase 4 simulations of the WOLF6 model, with wolves and elk harvest, n = 25												
Mean	4.07	450	0.39	42	1.18	128	2.49	275	1.24	138	9.38	1035
% total		**42%**		**4%**		**16%**		**26%**		**12%**		**100%**
Phase 4 simulations of the WOLF6 with wolves and no elk harvest, n = 25												
Mean	4.05	494	0.35	42	1.83	225	3.04	378	1.09	136	10.37	1277
% total		**39%**		**3%**		**18%**		**30%**		**10%**		**100%**
*Reference proportions estimated from data**												
1995-2002*		**43%**		**5%**		**13%**		**28%**		**11%**		**100%**

*data from Phillips and Smith 1997, Smith 1998, Smith et al. 1999, 2000, 2001, Smith and Guernsey 2002, Smith et al. 2003.

Table 2.8. The 100-year population mean, functional response (prey per wolf per year), and total removal by wolves of alternate prey species.

Stochastic Model Version, n = 25	N_{Bison}	F_{Bison}	Bison taken per year	N_{Moose}	F_{Moose}	Moose taken per year	N_{Deer}	F_{Deer}	Deer taken per year
Phase 4a: wolves, harvest	811	0.05	5.53	974	0.40	43.55	3048	0.26	28.70
Phase 4b: wolves, no harvest	811	0.06	6.97	974	0.39	47.22	3048	0.31	38.46

Table 2.9. Wolf quota, quota percent of K_{wolf}, N_{wolf} / K_{wolf}, wolves culled per year, C.V. of N_{wolf}, elk population, elk taken by wolves per year, and elk harvest per year from 25 runs of phase 4a of the WOLF6 model.

Wolf quota	Quota % of K_{wolf}	N_{wolf} / K_{wolf}	N_{wolf}	Wolves culled per year	C.V. N_{wolf}	N elk	Elk taken by wolves	Elk harvest per year
0	0	0.83	109	0.00	0.16	9702	1033	1074
5	4	0.79	103	5	0.16	9857	988	1093
10	8	0.74	97	9	0.17	10005	940	1113
15	11	0.70	91	13	0.17	10168	895	1127
20	15	0.66	86	16	0.18	10327	853	1136
25	19	0.62	81	19	0.19	10457	813	1144
28	21	0.60	78	20	0.20	10530	785	1151
30	23	Extinction occurred in 1 of 25 simulations of the stochastic model						
35	27	Extinction occurred in 2 of 25 simulations of the stochastic model						
40	31	Extinction occurred in 6 of 25 simulations of the stochastic model						
50	38	Extinction occurred in 23 of 25 simulations of the stochastic model						

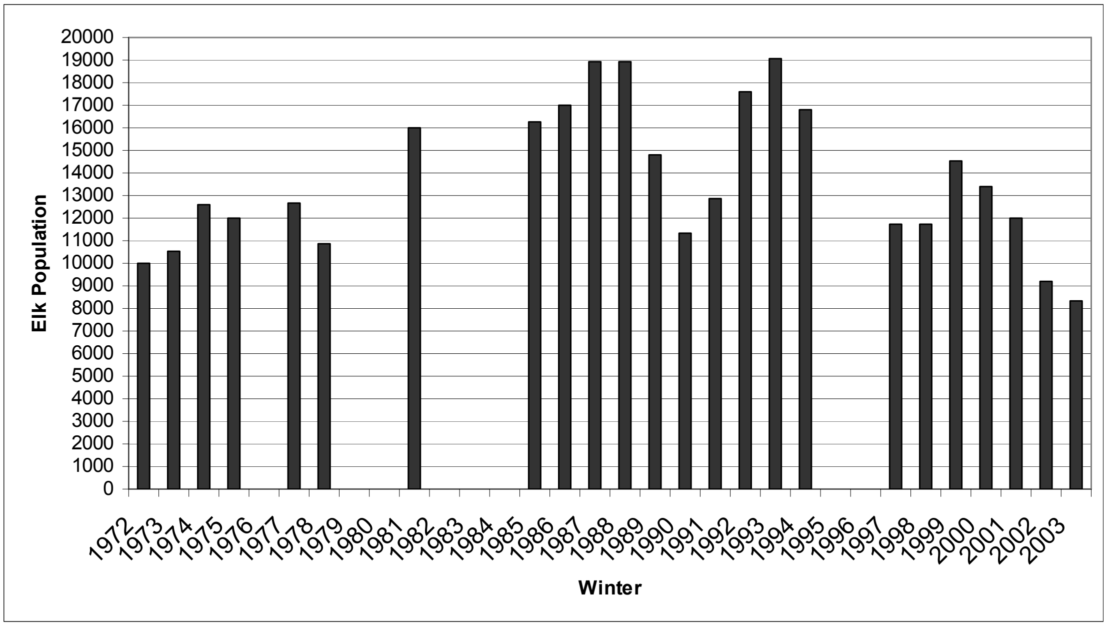

Figure 2.1. Counts of the Northern Yellowstone elk herd, 1972-2003, data from Lemke et al. (1998) and Taper and Gogan (2002); counts in 1988-89 and 1990-91 were adjusted for poor count conditions.

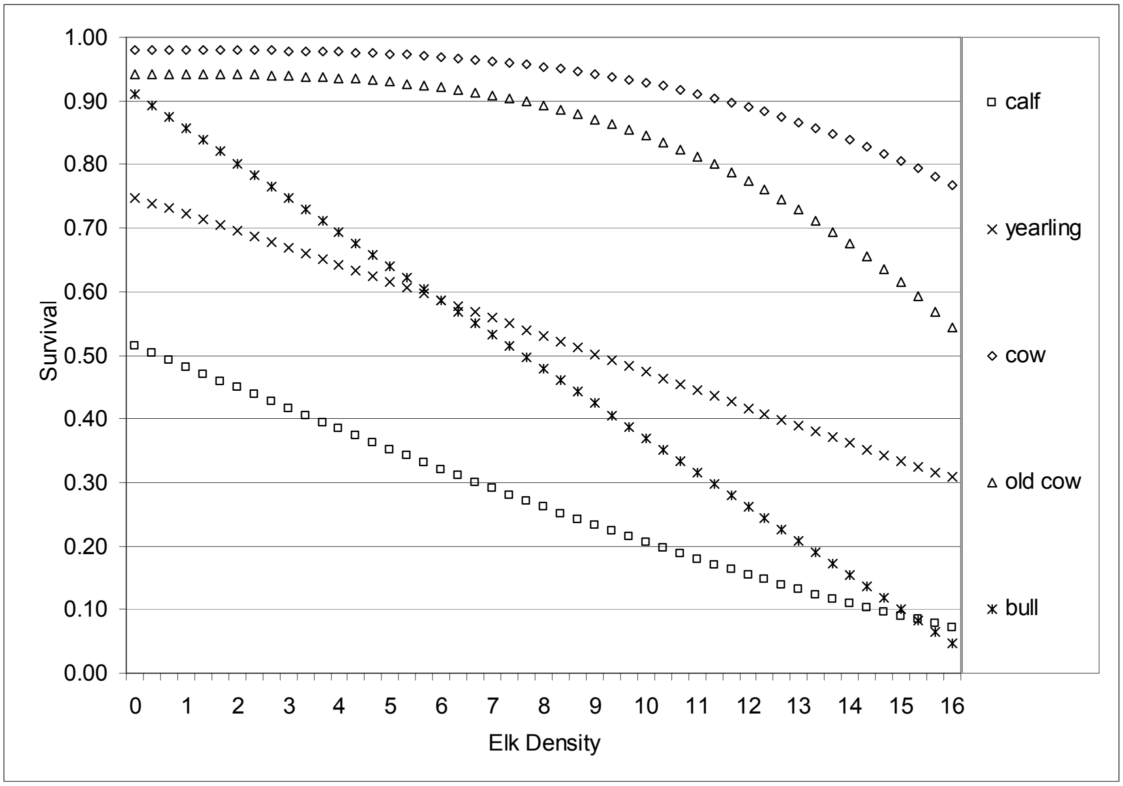

Figure 2.2. Density dependence for five classes of Northern Range elk, cows, old cows, bulls, calves (0 to 6 months), and yearlings (6 to 18 months).

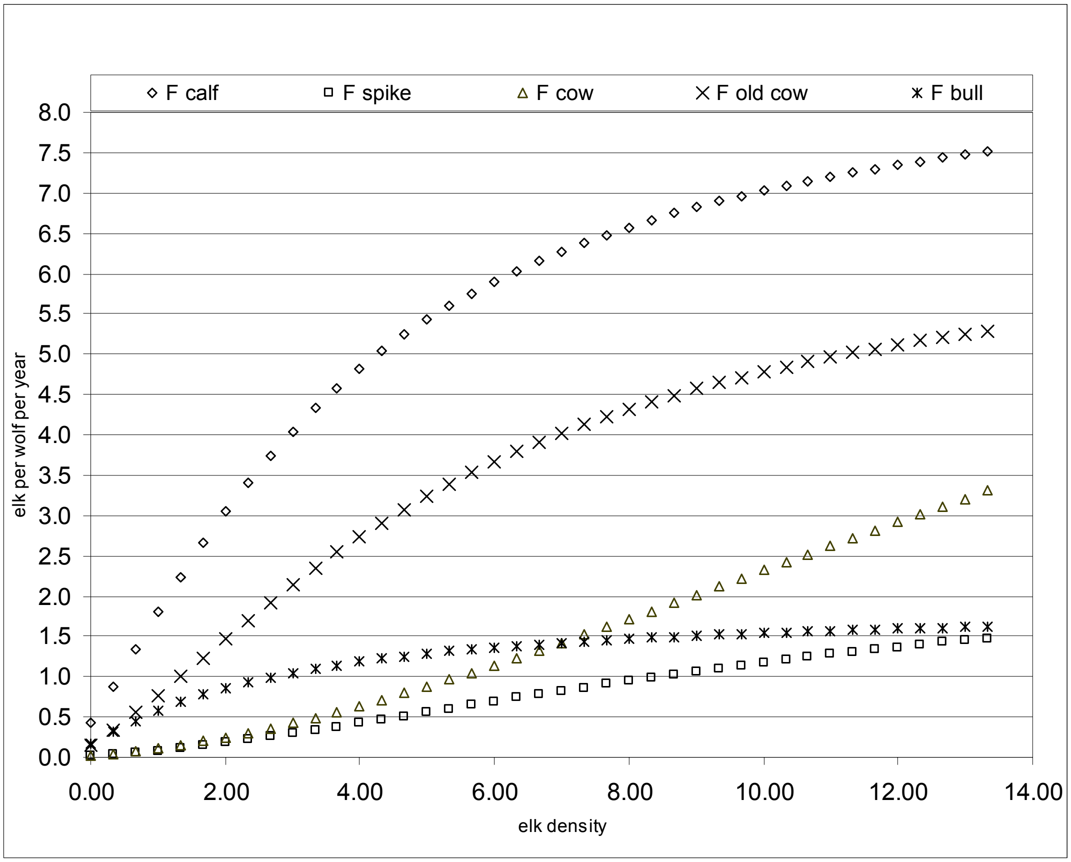

Figure 2.3. Functional response, or rate of elk consumption per wolf per year, for five classes of elk: calf, spike, cow, old-cow, and bull. Elk density is the number of elk per km^2.

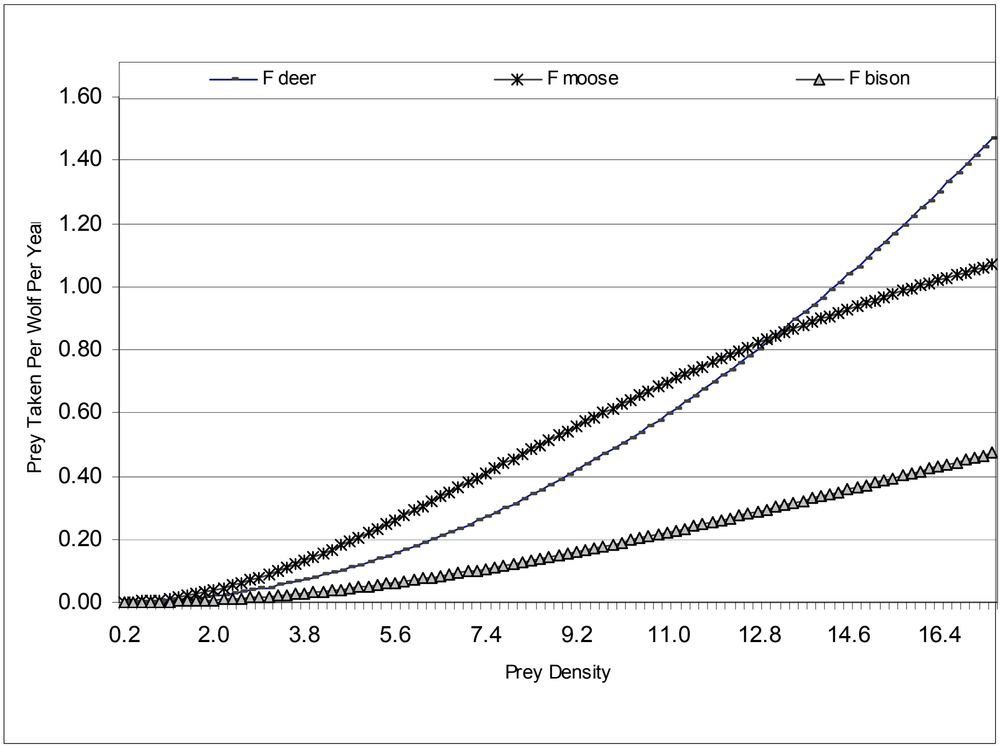

Figure 2.4. Functional response curves for bison, moose, and deer where F_{max} = 10, 20, and 110 individuals taken per wolf per year, respectively. Prey density is number of prey per km^2.

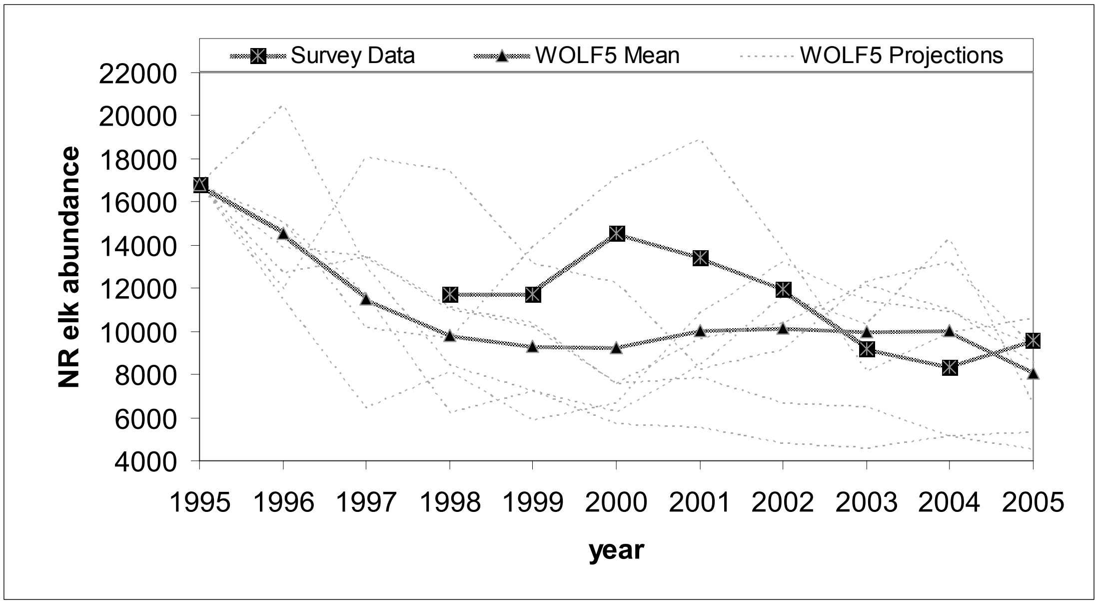

Figure 2.5. Time series projections from the WOLF5 model (Boyce and Gaillard 1992, Boyce 1995) compared with survey data for the Northern Range elk population (Lemke 2003), 1995-2004.

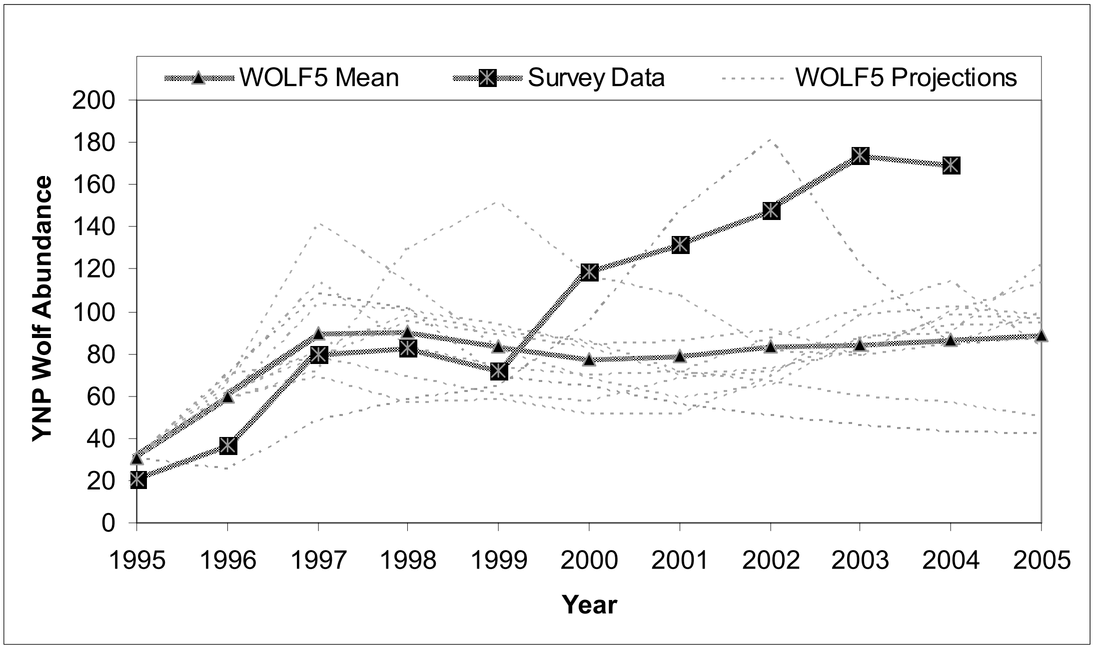

Figure 2.6. Time series of five projections of the WOLF5 model (Boyce and Gaillard 1992, Boyce 1995) compared with survey data of the Yellowstone National Park wolf population (Smith 2005), 1995-2005.

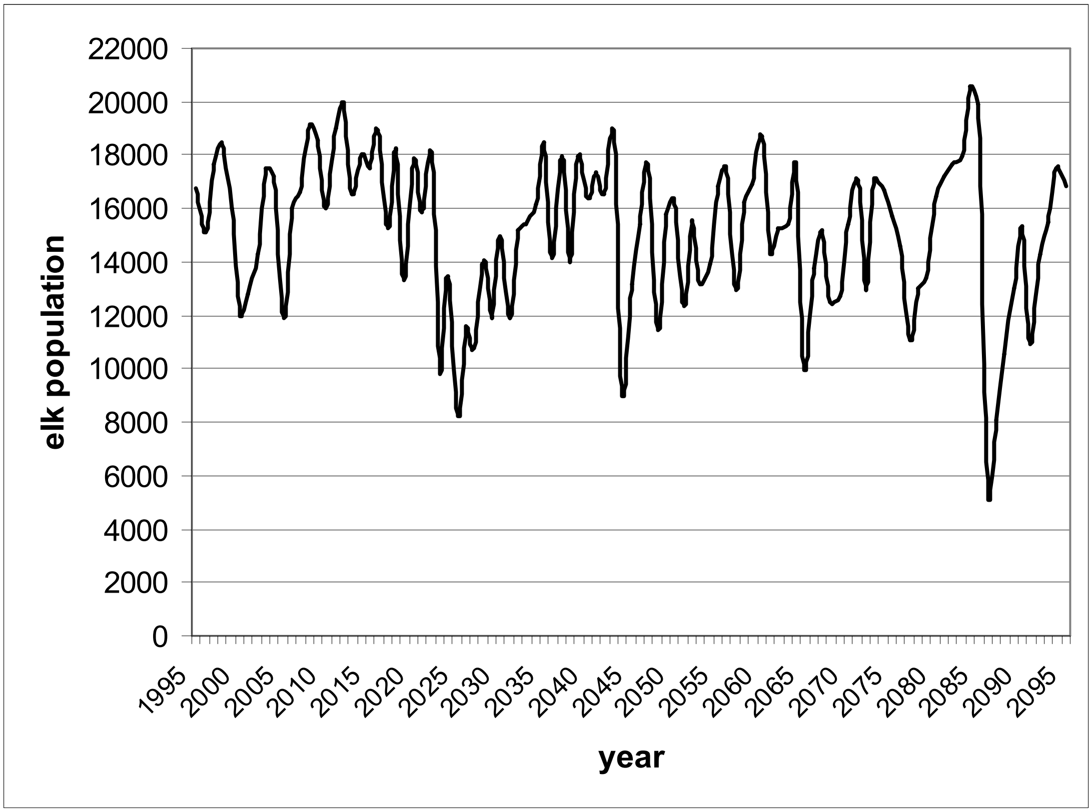

Figure 2.7. A phase 2 projection of the Northern Range elk herd with wide population fluctuation due to density dependence and variation in climate.

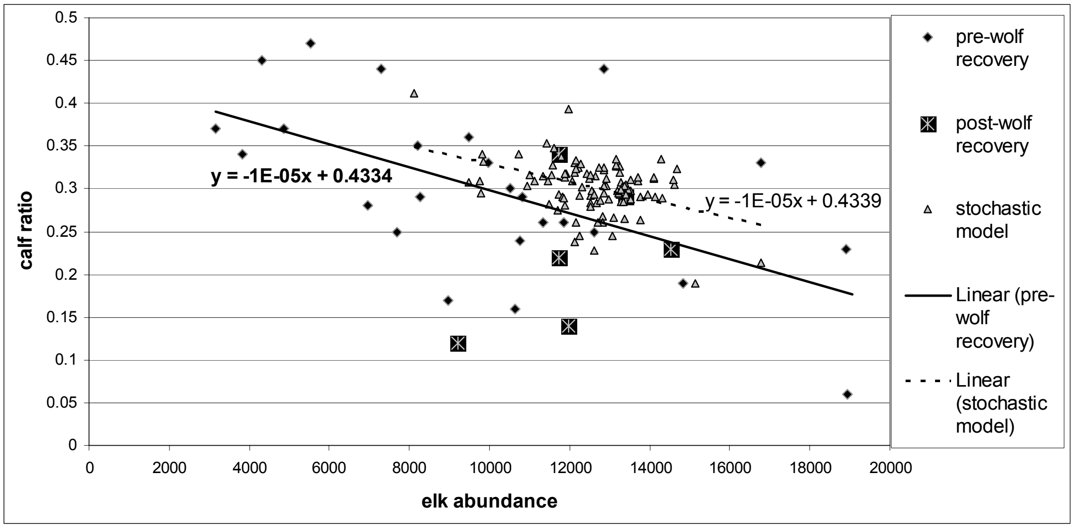

Figure 2.8. Comparison of the density-dependent relationship between calves per cow (female yearling, cow and old cow) and elk population from phase 3 simulation of WOLF6 versus data from 1973-1994 from Houston (1982) and Taper and Gogan (2002).

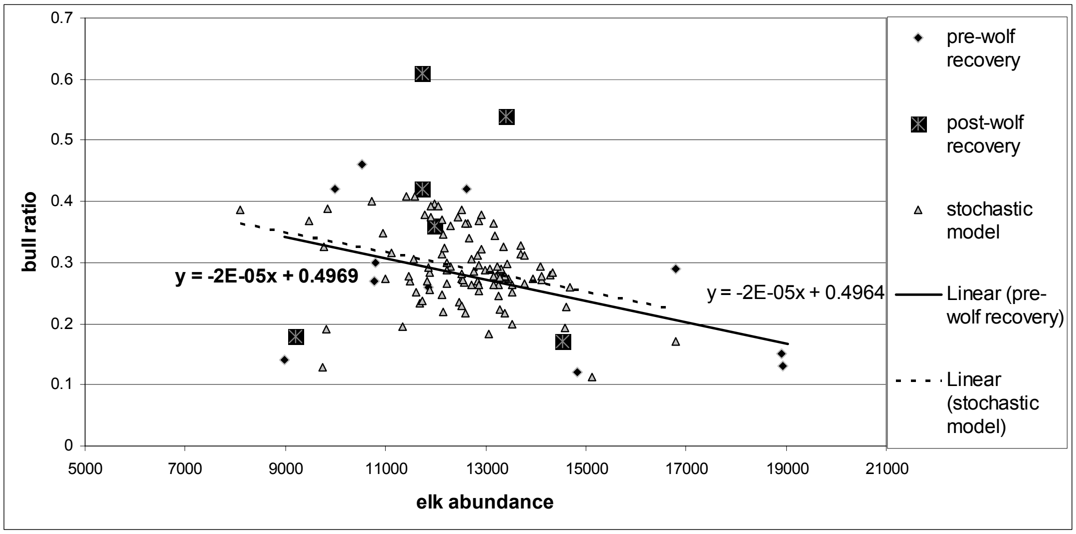

Figure 2.9. Comparison of the density-dependent relationship between bulls per cow (female yearling, cow and old cow) and elk population from the phase 3 simulation of WOLF6 versus data from 1973-1994 from Houston (1982) and Taper and Gogan (2002).

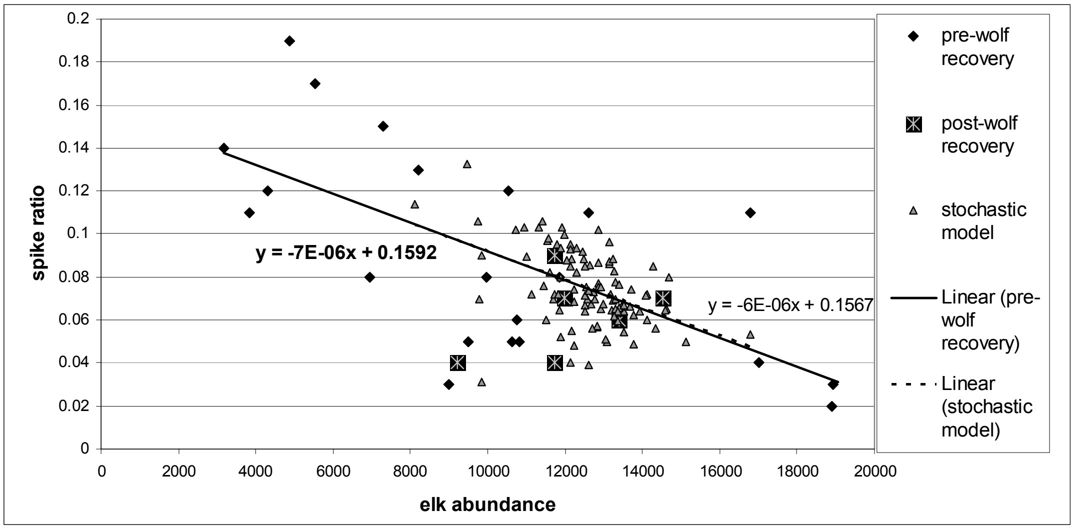

Figure 2.10. Comparison of the density-dependent relationship between spikes per cow (female yearling, cow and old cow) and elk population from phase 3 simulation of WOLF6 versus data from 1973-1994 from Houston (1982) and Taper and Gogan (2002).

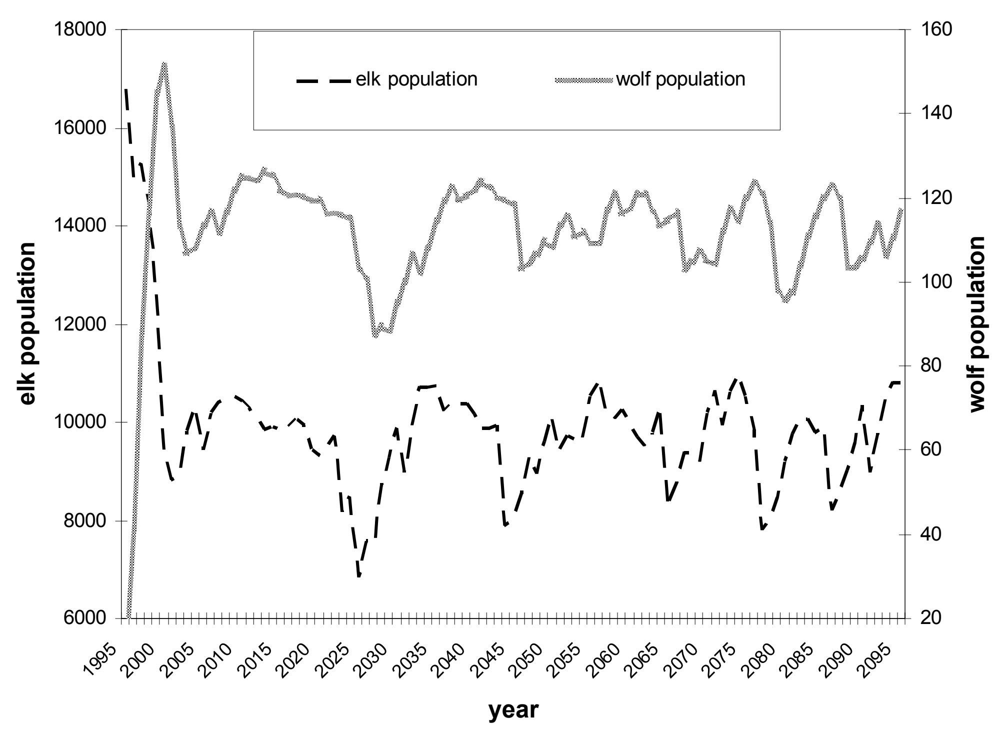

Figure 2.11. A 100-year projection of the Northern Range elk herd with climatic variation, harvest, and wolves.

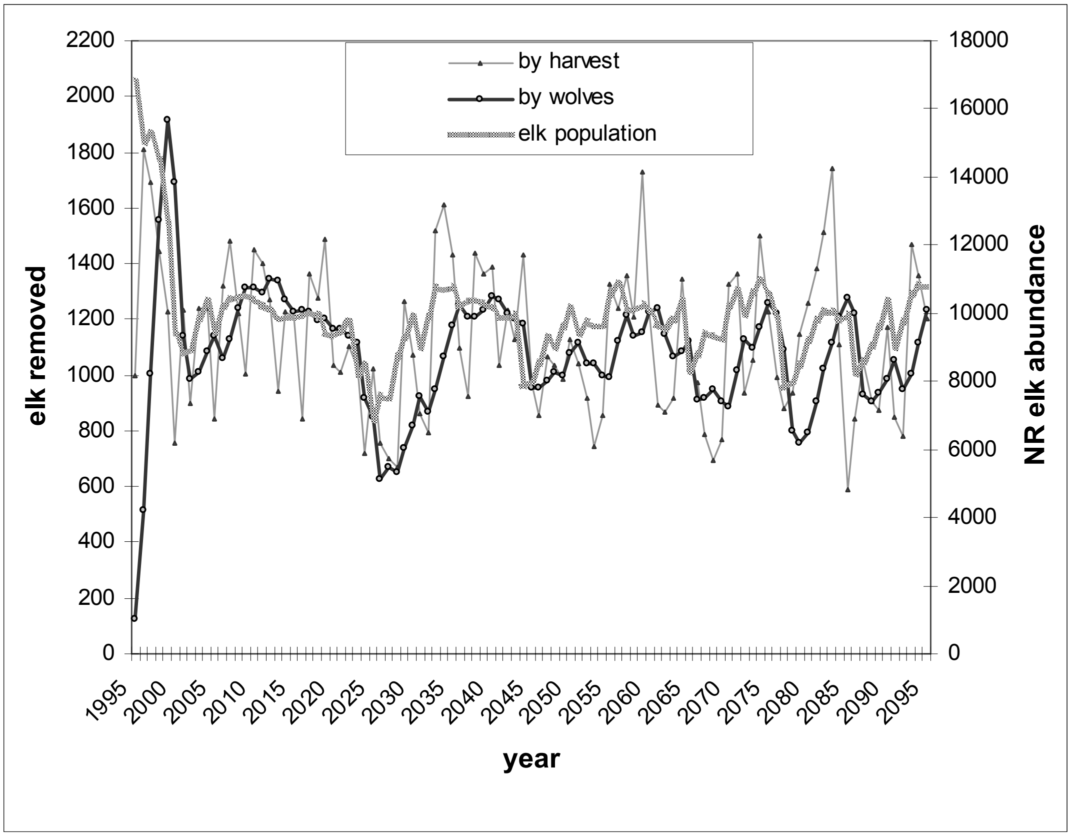

Figure 2.12. WOLF6 100-year projections of yearly removal of elk of the Northern Range by wolves and harvest.

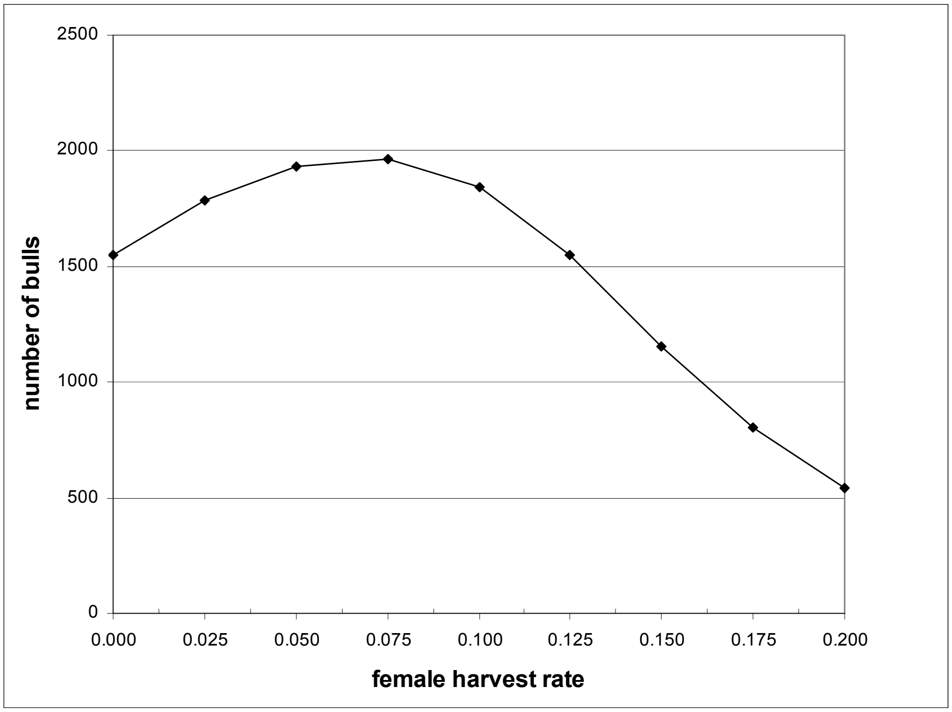

Figure 2.13. Number of bulls (males, 18+ months) as a function of proportion of females culled from harvest projections in the WOLF6 model.

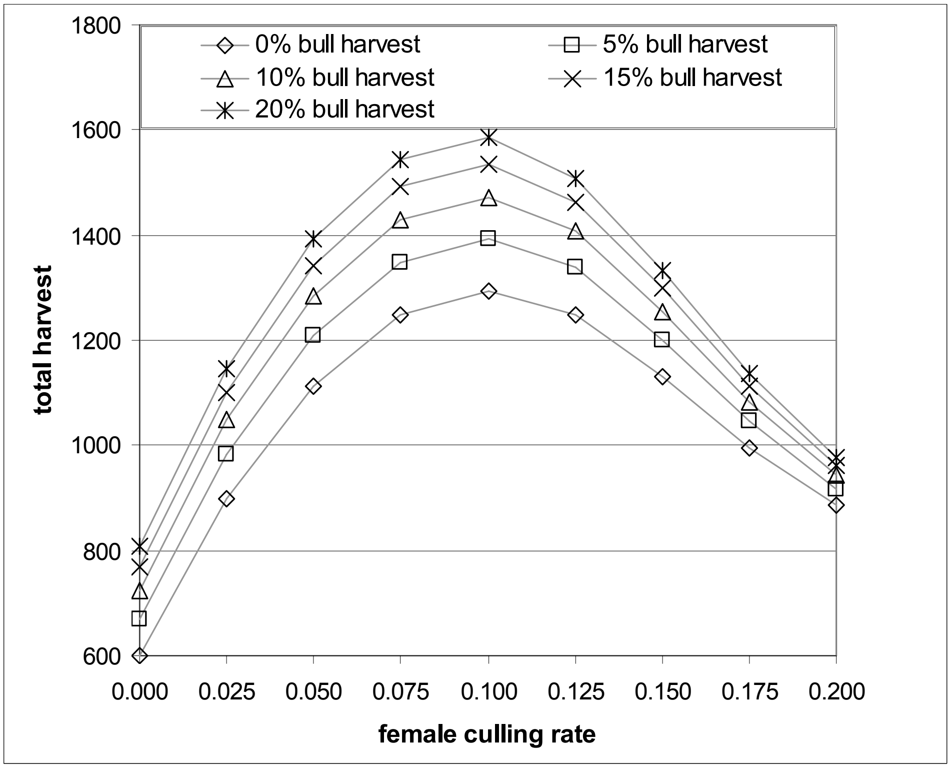

Figure 2.14. Total elk harvest as a function of the proportion of bulls and proportion of cows removed from projections of the WOLF6 model.

REFERENCES

Abrams, P. A. 1993. Why predation rate should not be proportional to predator density. Ecology **74**:726–733.

Abrams, P. A. 1994. The fallacies of ratio-dependent predation. Ecology **75**:1842–1850.

Abrams, P. A. 1997. Anomalous predictions of ratio-dependent models of predation. Oikos **80:**163–171.

Abrams, P. A., and L. R. Ginzburg. 2000. The nature of predation: prey dependent, ratio-dependent or neither? Trends in Ecology and Evolution **15**:337–341.

Abrams, P. A., and C. J. Walters. 1996. Invulnerable prey and the paradox of enrichment. Ecology **77**:1125–1133.

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife Monographs **98**:1–54.

Bar-David, S., D. Slatz, T. Dayan, A. Perelberg, and A. Dolev. 2005. Demographic models and reality in reintroductions: Persian fallow deer in Israel. Conservation Biology **19**:131–138.

Barmore, Jr., W. J. 2003. Ecology of Ungulates and their Winter Range in Northern Yellowstone National Park: Research and Synthesis, 1962-1970. National Park Service, Mammoth Hot Springs, Wyoming, USA.

Bartlein, P. J., C. Whitlock, and S. L. Shafer. 1997. Future climate in the Yellowstone National Park region and its potential impact on vegetation. Conservation Biology **11**:782–792.

Bearlin, A. R., E. S. G. Schreiber, S. J. Nicol, A. M. Starfield, and C. R. Todd. 2002. Identifying the weakest link: simulating adaptive management of the reintroduction of a threatened fish. Canadian Journal of Fisheries and Aquatic Sciences **59**:1709−1716.

Beddington, J. R. 1975. Mutual interference between parasites of predators and its effect on searching efficiency. Journal of Animal Ecology **44**:331−340.

Boitani, L. 2003. Wolf conservation and recovery. Pages 317−340 *in* L. D. Mech and L. Boitani, editors. Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, Illinois, USA.

Boyce, M. S. 1990. Wolf recovery for Yellowstone National Park: a simulation model. Pages 3-3 to 3-58 *in* Yellowstone National Park, U. S. Fish and Wildlife Service, University of Wyoming, University of Idaho, Interagency Grizzly Bear Study Team, and the University of Minnesota Cooperative Parks Study Unit, Editors. Wolves for Yellowstone? A report to the United States Congress, Volume 2, Research and Analysis, National Park Service, Yellowstone National Park, Mammoth, Wyoming, USA.

Boyce, M. S. 1992. Wolf recovery for Yellowstone National Park: A simulation model. Pages 123–138 *in* D. R. McCullough and R. H. Barrett, editors. Wildlife 2001: Populations, Elsevier Applied Science, London, U.K.

Boyce, M. S. 1993. Predicting the consequences of wolf recovery to ungulates in Yellowstone National Park. Pages 234–269 *in* R. S. Cook, editor. Ecological Issues on Reintroducing Wolves into Yellowstone National Park, Scientific Monographics. NPS/NRYELL/NRSM-93/22, U.S. Dep. Interior, National Park Service, U.S. Govt. Printing Office, Washington, D. C., USA.

Boyce, M. S. 1995. Anticipating consequences of wolves in Yellowstone: model validation. Pages 199–210 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and Conservation of Wolves in a Changing World, Canadian Circumpolar Institute. Publication. No. 35, Edmonton, Alberta, Canada.

Boyce, M. S. 1998. Ecological-process management and ungulates: Yellowstone's conservation paradigm. Wildlife Society Bulletin **26**:391–398.

Boyce, M. S., and E. M. Anderson. 1999. Evaluating the role of carnivores in the Greater Yellowstone Ecosystem. Pages 265–284 *in* T. K. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva, editors. Carnivores in Ecosystems: the Yellowstone Experience, Yale University Press, New Haven, Connecticut, USA.

Boyce, M. S., and D. J. Daley. 1980. Population tracking of fluctuating environments and natural selection for tracking ability. American Naturalist **115**:480–491.

Boyce, M. S., and J.-M. Gaillard. 1992. Wolves in Yellowstone, Jackson Hole, and the North Fork of the Shoshone River: Simulating ungulate consequences of wolf recovery. Pages 4/71–4/111 *in* Varley, J. D., and W. G. Brewster, editors. Wolves for Yellowstone? A report to the United States Congress, Volume 4 Research and Analysis, National Park Service, Yellowstone National Park, Wyoming, USA.

Boyce, M. S., and E. H. Merrill. 1991. Effects of the 1988 fires on ungulates in Yellowstone National Park. Proceedings of the Tall Timbers Fire Ecology Conference **17**:121–132.

Brook, B. W., A. D. Griffiths, and H. L. Puckey. 2002. Modelling strategies for the management of the critically endangered Carpentarian rock-rat (*Zyzomys palatalis*) of northern Australia. Journal of Environmental Management **65**:355–368.

Bustamante, J. 1998. Use of simulation models to plan species reintroductions: the case of the bearded vulture of Spain. Animal Conservation **1**:229–238.

Caswell, H. 2001. Matrix Population models: Construction, Analysis, and Interpretation. Second edition, Sinauer Associates, Sunderland, Massachusetts, USA.

Choquenot, D. 1991. Density-dependent growth, body condition, and demography in feral donkeys: testing the food hypothesis. Ecology **72**:805–813.

Clutton-Brock, T. H., M. Major, S. D. Albon, and F. E. Guiness. 1987. Early development and population dynamics in red deer. I. Density dependent effects on juvenile survival. Journal of Animal Ecology **56**:53–67.

Clutton-Brock, T. H., T. N. Coulson, E. J. Milner-Gulland, D. Thomson, H. M. Armstrong. 2002. Sex differences in emigration and mortality affect optimal management of deer populations. Nature **415**:633–637.

Cole, G. C. 1971. An ecological rationale for the natural and artificial regulation of native ungulates in parks. Transactions of North American Wildlife Conference **36**:417–425.

Cosner, C., D. L. DeAngelis, J. A. Ault, and D. B. Olson. 1999. Effects of spatial grouping on the functional response of predators. Theoretical Population Biology **56**:65–75.

Coughenour, M. B., and F. J. Singer. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. Ecological Applications **6**:573–583.

Cramer, P. C., and K. M. Portier. 2001. Modeling Florida panther movements in response to human attributes of the landscape and ecological settings. Ecological Modelling **140**:51–80.

Crawley, M. J. 1992. Population dynamics of natural enemies and their prey. Pages 40–89 *in* M .J. Crawley, editor. Natural Enemies: The Population Biology of Predators, Parasites and Diseases. Blackwell Scientific Publishing, Oxford, U.K.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. Stage-based population model for loggerhead sea turtles and implications for conservation. Ecology **68**:1412-1423.

Dale, B. W., L. G. Adams, and R. T. Bowyer. 1994. Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. Journal of Animal Ecology **63**:644–652.

Dale, B. W., L. G. Adams, and R. T. Bowyer. 1995. Winter wolf predation in a multiple prey system, Gates of the Arctic National Park, Alaska. Pages 223–230 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and Conservation of Wolves in a Changing World, Canadian Circumpolar Inst., No. 35, Edmonton, Alberta, Canada.

Despain, D., D. B. Houston, M. M. Meagher, and P. Schullery. 1986. Wildlife in Transition: Man and Nature on Yellowstone's Northern Range. Roberts Rinehart, Inc. Boulder, Colorado, USA.

Eberhardt, L. L. 1997. Is wolf predation ratio dependent? Canadian Journal of Zoology **75**:1940–1944.

Eberhardt, L. L. 2000. Reply: predator-prey ratio dependence and regulation of moose populations. Canadian Journal of Zoology **78**:511–513.

Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology **83**: 2841–2854.

Eberhardt, L. L., R. A. Garrott, D. W. Smith, and P. J. White. 2003. Assessing the impact of wolves on ungulate prey. Ecological Applications **13**:776–783.

Eberhardt, L. L., and J. M. Thomas. 1991. Designing environmental field studies. Ecological Monographs **61**:53–73.

Eide, S. H., and W. B. Ballard. 1982. Apparent case of surplus killing of caribou by gray wolves. Canadian Field-Naturalist **96**:87–88.

Fieberg, J., and K. J. Jenkins. 2005. Assessing uncertainty in ecological systems using global sensitivity analyses: a case example of simulated wolf reintroduction effects on elk. Ecological Modelling In press.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesné, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology **86**:1320–1331.

Fowler, C. W., and W. J. Barmore, Jr. 1979. A population model of the northern Yellowstone elk herd. Pages 427–434 *in* R. M. Linn, editor. Proceedings of the First Conference on Science and Resources in the National Parks, Vol. 1, Service. No. 5.

Fritts, S. H., R. O. Stephenson, R. D. Hayes, and L. Boitani. 2003. Wolves and humans. Pages 289–340 *in* L. D. Mech, and L. Boitani, editor. Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, Illinois, USA.

Fryxell, J. F., J. Greever, and A. R. E. Sinclair. 1988. Why are migratory ungulates so abundant? American Naturalist **131**:781–798.

Fryxell, J. M., and P. Lundberg. 1998. Individual Behaviour and Community Dynamics. Chapman & Hall, London, U. K.

Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. Wildlife Monographs **105**:1–41.

Fuller, T. K., L. D. Mech, and J. F. Cochrane. 2003. Wolf population dynamics. Pages 161−191 *in* L. D. Mech, and L. Boitani, editors. Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, Illinois, USA.

Garrott, R. A., L. L. Eberhardt, P. J. White, and J. Rotella. 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. Canadian Journal of Zoology **81**:33–45.

Garton, E. O., R. L. Crabtree, B. B. Ackerman, and G. Wright. 1990. The potential impact of a reintroduced wolf population on the northern Yellowstone elk herd. Pages 3-59–3-91 *in* Yellowstone National Park, U. S. Fish and Wildlife Service, University of Wyoming, University of Idaho, Interagency Grizzly Bear Study Team, and the University of Minnesota Cooperative Parks Study Unit, editors. Wolves for

Yellowstone? A report to the United States Congress, Volume 2 Research and Analysis, National Park Service, Yellowstone National Park, Mammoth, Wyoming, USA.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Reintroduction as a species conservation tool: status and strategy. Science **245**:477–480.

Hanski, I. 1991. The functional response of predators: worries about scale. Trends In Ecology and Evolution **6**:141–142.

Hirzel, A. H., B. Posse, P. A. Oggier, Y. Crettenand, C. Glenz, R. Arlettaz. 2002. Ecological requirements of reintroduced species and the implications for release policy: the case of the bearded vulture. Journal of Applied Ecology **4**:1103–1116.

Houston, D. B. 1971. Ecosystems in national parks. Science **172**:648–651.

Houston, D. B. 1979. The Northern Yellowstone elk—winter distribution and management. Pages 263–272 *in* M. S. Boyce and L. D. Hayden-Wing, editors. North American Elk: Ecology, Behavior and Management. University of Wyoming, Laramie, USA.

Houston, D. B. 1982. The Northern Yellowstone Elk: Ecology and Management. Macmillan, New York, New York, USA.

Huff, D. E., and J. D. Varley. 1999. Natural regulation in Yellowstone National Park's northern range. Ecological Applications **9**:17–29.

Hughes, T. P., D. R. Bellwood, C. Folke, R. S. Steneck, and J. Wilson. 2005. New paradigms for supporting the resilience of marine ecosystems. Trends In Ecology and Evolution **20**:380–386.

Keith, L. B. 1983. Population dynamics of wolves. Pages 66–77 *in* L. N. Carbyn, editor. Wolves in Canada and Alaska: Their Status, Biology, and Management. Canadian Wildlife Service Report Service No. 45.

King, S. R. B., and J. Gurnell. 2005. Habitat use and spatial dynamics of takhi introduced to Hustai National Park, Mongolia. Biological Conservation **124**:277–290.

Klein, D. R., 1995. The introduction, increase, and demise of wolves on Coronation Island, Alaska. Pages 275–280 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors.

Ecology and Conservation of Wolves in a Changing World, Canadian Circumpolar Institute. Occasional Publication No. 35, Edmonton, Alberta, Canada.

Kramer-Schadt, S., E. Revilla, and T. Wiegand. 2005. Lynx reintroductions in fragmented landscapes of Germany: Projects with a future or misunderstood wildlife conservation? Biological Conservation, In press.

Krebs, C. J. 2002. Two complementary paradigms for analyzing population dynamics. Philanthropic Transactions of the Royal Society of London B **357**:1211–1219.

Lemke, T. O., J. A. Mack, and D. B. Houston. 1998. Winter range expansion by the northern Yellowstone elk herd. Intermountain Journal of Science **4**:1–9.

Lemke, T. O. 2003. 2003 Gardiner Late Annual Hunt Report. Montana Fish, Wildlife and Parks, Helena, Montana, USA.

Leopold, A. 1944. Review of The Wolves of North America by S.P. Young and E.H. Goldman. Journal of Forestry **42**:928–929.

Lewis, M. A., and J. D. Murray. 1993. Modeling territoriality and wolf deer interactions. Nature **366**:738–740.

Lindenmayer, D. B., I. Ball, H. P. Possingham, M. A. McCarthy, M. L. 2001. A landscape-scale test of the predictive ability of a spatially explicit model for population viability analysis. Journal of Applied Ecology **38**:36–48.

Lindenmayer, D. B., H. P. Possingham, R. C. Lacy, M. A. McCarthy, and M. L. Pope. 2003. How accurate are population models? Lessons from landscape-scale population tests in a fragmented system. Ecology Letters **6**:41–47.

Mack, J. A., and F. J. Singer. 1993. Using POP-II models to predict effects of wolf predation and hunter harvest on elk, mule deer, and moose on the northern range. Pages 49–74 *in* R. S. Cook, editor. Ecological Issues on Reintroducing Wolves into Yellowstone National Park. U.S. Department of the Interior, National Park Service Monograph NPS/NRYELUNRSM-93/22.

MacNulty, D. R., N. Varley, and D. W. Smith. 2001. Grizzly bear, *Ursus arctos*, usurps bison calf, *Bison bison*, captured by wolves, *Canis lupus*, in Yellowstone National Park, Wyoming. Canadian Field-Naturalist **115**:495–498.

Marshal, J. P., and S. Boutin. 1999. Power analysis of wolf-moose functional responses. Journal of Wildlife Management **63**:396–402.

Mech, L. D. 1977. Wolf-pack buffer zones as prey reservoirs. Science **198**:320–321.

Mech, L. D., T. J. Meier, J. W. Burch, L. G. Adams. 1995. Patterns of prey selection by wolves in Denali National Park, Alaska. Pages 231–243 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and Conservation of Wolves in a Changing World, Canadian Circumpolar Institute. Occasional Publication No. 35, Edmonton, Alberta, Canada.

Mech, L. D., D. W. Smith, K. M. Murphy, and D. R. MacNulty. 2001. Winter severity and wolf predation on a formerly wolf-free elk herd. Journal of Wildlife Management **65**:998–1003.

Mech, L. D., and R. O. Peterson. 2003. Wolf-prey relations. Pages 131–160 *in* Mech, L. D., and L. Boitani, editors. Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago, Illinois, USA.

Merrill, E. H., and M. S. Boyce. 1991. Summer range and elk population dynamics in Yellowstone National Park. Pages 263–273 *in* R. B. Keiter, and M. S. Boyce, editors. The Greater Yellowstone Ecosystem: Redefining America's Wilderness Heritage. Yale University Press. New Haven, Connecticut, USA.

Merrill, E. H., M. K. Bramble-Brodahl, R. W. Marrs, and M. S. Boyce. 1993. Estimation of green herbaceous phytomass from Landsat MSS data in Yellowstone National Park. Journal of Range Management **46**:151–156.

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology **75**:478–488.

Messier, F. 1995. On the functional and numerical responses of wolves to changing prey density. Pages 187–197 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and Conservation of Wolves in a Changing World, Canadian Circumpolar Institute. Occasional Publication No. 35, Edmonton, Alberta, Canada.

Miller, F. L., A. Gunn, and E. Broughton. 1985. Surplus killing as exemplified by wolf predation on newborn caribou. Canadian Journal of Zoology **63**:295–300.

Miller, M. W., E. S. Williams, C. W. McCarty, T. R. Spraker, T. J. Kreeger, C. T. Larsen, and E. T. Thorne. 2000. Epizootiology of chronic wasting disease in free-ranging cervids in Colorado and Wyoming. Journal of Wildlife Diseases **36**:676–690.

Mills, L. S., C. Baldwin, M. J. Wisdom, J. Citta, D. J. Mattson, and K. Murphy. 1997. Factors leading to different viability predictors for a Grizzly Bear data set. Conservation Biology **10**:863–873.

Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecological Monographs **39**:335–354.

National Research Council. 2002. Ecological Dynamics on Yellowstone's Northern Range. National Academy Press, Washington, D. C., USA.

Nilsen, E. B., T. Pettersen, H. Gundersen, J. M. Milner, A. Mysterud, E. J. Solberg, H. P. Andreassen, and N. C. Stenseth. 2005. Moose harvesting strategies in the presence of wolves. Journal of Applied Ecology **42**:389–399.

Nolet, B. A., and J. M. Baveco. 1996. Development and viability of a translocated beaver *Castor fiber* population in The Netherlands. Biological Conservation **75**:125–137.

Oksanen, L., J. Moen, and P. A. Lundberg. 1992. The time-scale problem in exploiter–victim models: does the solution lie in ratio-dependent exploitation? American Naturalist **140**:938–960.

O'Toole, L., A. H. Fielding, and P. F. Haworth. 2002. Re-introduction of the golden eagle into the Republic of Ireland. Biological Conservation **103**:303–312.

Peterson, R. O. 1995. The Wolves of Isle Royale: A Broken Balance. Willow Creek Press, Wisconsin, USA.

Peterson, R. O., N. J. Thomas, J. M. Thurber, J. A. Vucetich, T. A. Waite. 1998. Population limitation and the wolves of Isle Royale. Journal of Mammalogy **79**:828–841.

Phillips, M. K., and D. W. Smith. 1997. Yellowstone Wolf Project Biennial Report 1995 and 1996. YCR-NR-97-4, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA.

Picton, H. D. 1984. Climate and the prediction of reproduction of three ungulate species. Journal of Applied Ecology **21**:869–879.

Saltz, D. 1998. A long-term systematic approach to planning reintroductions: the Persian fallow deer and the Arabian oryx in Israel. Animal Conservation **1**:245–252.

Saltz, D., and D. I. Rubenstein. 1995. Population dynamics of a reintroduced Asiatic wild-ass (*Equus hemionus*) herd. Ecological Applications **5**:327-335.

Sarrazin, F., and R. Barbault. 1996. Reintroduction: challenges and lessons for basic ecology. Trends in Ecology and Evolution **11**:474–478.

Sauer, J. R., and M. S. Boyce. 1983. Density dependence and survival of elk in northwestern Wyoming. Journal of Wildlife Management **47**:31–37.

Schaub, M., R. Pradel, and J. Lebreton. 2004. Is the reintroduced white stork (*Ciconia ciconia*) population in Switzerland self-sustainable? Biological Conservation **119**:105–114.

Scheel, D. 1993. Profitability, encounter rates, and prey choice of African lions. Behavioral Ecology **4**:90–97.

Singer, F. J. 1990a. Some predictions concerning a wolf recovery into Yellowstone National Park: how wolf recovery may affect park visitors, ungulates, and other predators. Pages 4/4–4/34 *in* Yellowstone National Park, U. S. Fish and Wildlife Service, University of Wyoming, University of Idaho, Interagency Grizzly Bear Study Team, and the University of Minnesota Cooperative Parks Study Unit, editors. Wolves for Yellowstone? A report to the United States Congress, Volume 2, Research and Analysis, National Park Service, Yellowstone National Park, Mammoth, Wyoming, USA.

Singer, F. J. 1990b. The ungulate prey base for wolves in Yellowstone National Park. Pages 323–348 *in* R. B. Keiter and M. S. Boyce, editors. The Greater Yellowstone Ecosystem: Redefining America's Wilderness Heritage. Yale University Press, New Haven, Connecticut, USA.

Singer, F. J., W. Schreier, J. Oppenheim, E. O. Garton. 1989. Drought, fires, and large mammals. BioScience **39**:716–722.

Singer, F. J., A. Harting, K. S. Symonds, and M. B. Coughenour. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. Journal of Wildlife Management **61**:12–25.

Singer, F. J., D. M. Swift, M. B. Coughenour, and J. D. Varley. 1998. Thunder on the Yellowstone revisited: an assessment of management of native ungulates by natural regulation, 1968-1993. Wildlife Society Bulletin **26**:375–390.

Smith, D. W. 1998. Yellowstone Wolf Project Annual Report 1997. YCR-NR-98-2. Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA.

Smith, D. W. 2005. Ten Years of Yellowstone Wolves 1995-2005. Yellowstone Science **13**:7–33.

Smith, D. W., K. M. Murphy, and D. S. Guernsey. 1999. Yellowstone Wolf Project Annual Report 1998. YCR-NR-99-1. Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA.

Smith, D. W., K. M. Murphy, and D. S. Guernsey. 2000a. Yellowstone Wolf Project Annual Report 1999. YCR-NR-2000-01. Yellowstone Center for Resources, Yellowstone National. Park, Wyoming, USA.

Smith, D. W., L. D. Mech, M. Meagher, W. E. Clark, R. Jaffe, M. K. Phillips, and J. A. Mack. 2000b. Wolf–bison interactions in Yellowstone National Park. Journal of Mammalogy **81**:1128–1135.

Smith, D. W., K. M. Murphy, and D. S. Guernsey. 2001. Yellowstone Wolf Project Annual Report 2000. YCR-NR-2001-02. Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA.

Smith, D.W., and D. S. Guernsey. 2002. Yellowstone Wolf Project Annual Report 2001. YCR-NR-2002-04. Yellowstone Center for Resources, Yellowstone Natl. Park, Wyoming, USA.

Smith, D. W., D. R. Stahler, and D. S. Guernsey. 2003. Yellowstone Wolf Project Annual Report 2002. YCR-NR-2003-04. Yellowstone Center for Resources, Yellowstone National. Park, Wyoming, USA.

Smith, D. W., T. D. Drummer, K. M. Murphy, D. S. Guernsey, and S. B. Evans. 2004. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995-2000. Journal of Wildlife Management **68**:153–166.

South, A., S. Rushton, and D. Macdonald. 2000. Simulating the proposed reintroduction of the European beaver (*Castor fiber*) to Scotland. Biological Conservation **93**:103–116.

Steury, T. D., and D. L. Murray. 2004. Modeling the reintroduction of lynx to the southern portion of its range. Biological Conservation **117**:127–141.

Stockwell, C. A., and P. L. Leberg. 2002. Ecological genetics and the translocation of native fishes: emerging experimental approaches. Western North American Naturalist **62**:32–38.

Swart, J., and M. J. Lawes. 1996. The effect of habitat patch connectivity on samango monkey (*Cercopithecus mitis*) metapopulation persistence. Ecological Modelling **93**:57–74.

Taper, M. L., and P. J. P. Gogan. 2002. The Northern Yellowstone elk: Density dependence and climatic conditions. Journal of Wildlife Management **66**:106–122.

Taylor, R. J. 1984. Predation. Chapman and Hall, New York, New York, USA.

Thorne, E. T., J. D. Herriges, Jr., and A. D. Reese. 1991. Bovine brucellosis in elk: conflicts in the greater Yellowstone area. Pages 296–302 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of the Elk Vulnerability Symposium, Bozeman, Montana, USA.

Todd, C. R., S. J. Nicol, and J. D. Koehn. 2004. Density-dependence uncertainty in population models for the conservation management of trout cod, *Maccullochella macquariensis*. Ecological Modelling **171**:359–380.

Vales, D. J., and J. M. Peek. 1990. Estimates of the potential interactions between hunter harvest and wolf predation on the Sand Creek, Idaho, and Gallatin, Montana elk populations. Pages 3-93–3-167 *in* Yellowstone National Park, U. S. Fish and Wildlife Service, University of Wyoming, University of Idaho, Interagency Grizzly Bear Study Team, and the University of Minnesota Cooperative Parks Study Unit, editors. Wolves for Yellowstone? A report to the United States Congress, Volume 2, Research and Analysis, National Park Service, Yellowstone National Park, Mammoth, Wyoming, USA.

Vucetich, J. A., and R. O. Peterson. 2004. The influence of top-down, bottom-up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. Proceedings of the Royal Society of London B **271**:183–189.

Vucetich, J. A., R. O. Peterson, and C. L. Schaeffer. 2002. The effect of prey and predator densities on wolf predation. Ecology **83**:3003–3013.

Vucetich, J. A., D. W. Smith, and D. R. Stahler. 2005. Influence of harvest, climate, and wolf predation on Yellowstone elk, 1961-2004. Oikos **111**:259–270.

Walters, C. J. 1986. Adaptive Management of Renewable Resources. Macmillan, New York, New York, USA.

Walters, C. J. 1997. Challenges in adaptive management of riparian and coastal ecosystems. Conservation Ecology **1**:1-1.

Walters, C. J., M. Stocker, and G. C. Haber. 1981. Simulation and optimization models for a wolf–ungulate system. Pages 317–337 *in* C. W. Fowler, and T. D. Smith, editors. Dynamics of Large Mammal Populations. John Wiley and Sons, New York, New York, USA.

White, P. J., and R. A. Garrott. 2005. Yellowstone's ungulates after wolves - expectations, realizations, and predictions. Biological Conservation **125**:141–152.

Wilmers, C. C., and W. M. Getz. 2004. Simulating the effects of wolf-elk population dynamics on resource flow to scavengers. Ecological Modelling **177**:193–208.

Wilmers, C. C., R. L. Crabtree, D.W. Smith, K. M. Murphy, and W. M. Getz. 2003. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. Journal of Animal Ecology **72**:909–916.

Worley, D. E. 1991. The role of internal parasites in management of free-ranging and captive North American elk (*Cervus elaphus nelsoni*). Pages 304–307 *in* A. G. Christensen, L. J. Lyon, and T. N. Lonner, editors. Proceedings of the Elk Vulnerability Symposium, Bozeman, Montana, USA.

Wright, G. J., R. O. Peterson, D. W. Smith, and T. O. Lemke. 2006. Selection of northern Yellowstone elk by gray wolves and hunters. Journal of Wildlife Management **70**:1070–1078.

CHAPTER 3

LANDSCAPE HETEROGENEITY INFLUENCES GRAY WOLF PREDATION AND TERRITORIAL PATTERNS [2]

Global efforts are underway to restore and conserve remnant populations of apex predators including lions (*Panthera leo*), grizzly bears (*Ursus arctos*), and wolves (*Canis lupus*) (Treves and Karanth 2003). Restoring predators to the large landscapes of their historic range has the potential to maintain biodiversity by recovering the strong, indirect species interactions inherent to these systems (Crooks and Soule 1999, Terborgh et al. 2001). However, such community-level benefits of carnivore restoration may come at a cost to their native ungulate prey, which form the basis of recreational and subsistence hunting by humans (Orians et al. 1997, Eberhardt et al. 2003, Nilsen et al. 2004). The perception that reintroduced predators will devastate native prey is a primary concern for some stakeholders, and successful carnivore restoration efforts often hinge on resolving these and other human-carnivore conflicts (Orians et al. 1997, Treves and Karanth 2003).

Native ungulates that have lived without predators are expected to become naïve and less vigilant, increasing their vulnerability to predation (Berger 1999, Berger et al. 2001, Sand et al. 2006). For example, in only 4 years at least ten adult moose (*Alces alces*) fell prey to grizzly bears at the frontier of bear recolonization in the greater Yellowstone area as compared with no records of predation where both had existed for 100+ years (Berger et al. 2001). The history of introductions of exotic predators to predator-free islands illustrates that novel predators can markedly reduce populations of

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[2] *A version of this chapter has been published: Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Ecology Letters 10:690-700.*

native prey and cause local extinctions (Fritts and Rodda 1998, Knapp et al. 2001, Blackburn et al. 2004). If native ungulate prey are naïve and thus highly susceptible to predation wherever they encounter recolonizing native predators, then similar reductions in prey numbers might be expected (Berger et al. 2001, Sand et al. 2006). Although native prey are likely to be vulnerable to predation from both exotic and newly restored predators, little is known about how the rates and spatial patterns of predation differ between exotic and restored predators.

A striking difference between exotic and native predators is that native predators typically confer greater stability and rarely instigate prey extinctions. Theory suggests that native predator-prey systems persist over the long term due to heterogeneity in predation rates caused by prey refugia in space or time (Fryxell et al. 1988, Kareiva and Wennegren 1995, Ellner et al. 2001). Presumably, such forms of refugia are lacking in systems where exotic predators cause extinction of native prey. Do the rates and patterns of predation by newly restored predators exhibit this type of heterogeneity? Quantifying the spatial structure of predation by recolonizing carnivores would enhance our understanding of apex predator effects on native prey populations (Sinclair and Arcese 1995).

In this study, I quantified the spatial structure of wolf predation on elk (*Cervus elaphus*) during winter on the Northern Range (NR) of Yellowstone National Park (YNP), USA. Wolves were reintroduced to YNP in 1995 after being extirpated from this ecosystem in the 1930's (Bangs and Fritts 1996). During the 10 years since reintroduction, the NR wolf population increased from 14 wolves in 3 packs to 84 wolves in 6 packs (Figure 3.1a). Over this time period, 92% of the ungulate prey taken by wolves during winter have been elk (Smith et al. 2004). I evaluated landscape-level variability in wolf predation on elk and found that spatial patterns of predation are more strongly influenced by landscape features than by wolf distribution.

METHODS

I quantified spatial patterns of wolf predation on NR elk by analyzing the factors controlling the spatial distribution of elk that were killed by wolves in winter during the first 10 years of wolf recovery. I estimated the extent to which variation in kill locations (Figure 3.1b) was determined by the annual distribution of wolf territories (Figure 3.1a) or physical features of the landscape where elk and wolves interact. I also evaluated whether the strength of landscape variables changed through time as wolves expanded their distribution and wolf predation on elk became less novel. The primary data for these analyses is a GIS dataset of the spatial locations of elk that were killed by wolves from 1996-2005.

Surveys for Wolf-killed Elk

During each winter, ground and aerial surveys for wolf-killed prey were conducted by crews tracking the wolf packs with radiotelemetry. All of the kills used in the analysis came from two 30-day periods in early (mid-Nov to mid-Dec) and late (March) winter, when wolf packs were intensively monitored by ground and air crews. These efforts resulted in 774 locations of wolf-killed elk across the NR (Figure 1b). While an estimated 27% of total kills went undiscovered, the two survey efforts combined resulted in minimal detection bias with respect to the landscape features used in the analysis (Smith et al. 2004). Using a double-count method, Smith et al. (2004) found that ground crews are biased towards detecting wolf-killed elk in close proximity to the road system, with no kills found further than 7.23 km from the road. However, aerial surveys were found to not be biased with respect to vegetation type (conifer forest vs. open sage/grasslands) or roads.

Wolf kills are distinguished readily from kills made by other carnivores. Kills were classified as wolf-caused when wolves were observed making the kill, or evidence supported wolves as the cause (e.g., wolves were observed feeding on a fresh carcass). Necropsies were performed on the vast majority of kills (≥ 90%), and evidence from the carcass site such as chase tracks and signs of struggle also were used to evaluate cause. In rare cases, cougar (*Puma concolor*) kills were usurped by wolves, but these tended to be discernible by evidence that cougars had hidden or cached a carcass. Grizzly bears occasionally kill elk, but only rarely in the winter when, for the most part, bears are hibernating.

Kill Site Model

I used logistic regression to estimate a model of the relative probability of a kill by analyzing the spatial attributes of known kill locations versus random available locations in the NR study area (Manly et al. 2002). I employed a matched case-control design with strata consisting of 774 kills matched to 20 random control points each (Hosmer and Lemeshow 2000). Case-control logistic regression fits the following likelihood for each stratum (k = 774):

$$l_k(\beta) = \frac{e^{\boldsymbol{\beta}'\mathbf{x}_{k,1}}}{e^{\boldsymbol{\beta}'\mathbf{x}_{k,1}} + e^{\boldsymbol{\beta}'\mathbf{x}_{k,2}} \ldots + e^{\boldsymbol{\beta}'\mathbf{x}_{k,21}}} \tag{1}$$

where $\boldsymbol{\beta}$ is a vector of fitted coefficients, $\mathbf{x}_{k,n}$ are the explanatory variables for observation n (1= the kill location, 2-21 = the random locations) in stratum k. This equation is not interpretable as the probability that a predation event will occur at a given location. Rather, it is the probability that the location with data $\mathbf{x}_{k,1}$ is in fact the kill site relative to the 20 control locations. However, the set of fitted coefficients are interpretable as the odds ratio as in standard logistic regression (Hosmer and Lemeshow 2000). Relative probability of kill occurrence was calculated with respect to a reference vector ($\mathbf{x}_r$), defined as the set of mean values for each variable within the domain of availability. The resulting odds ratio expression for a given landscape location ($\mathbf{x}$) was calculated following Keating and Cherry (2004) as:

$$\Psi(\mathbf{x}|\mathbf{x}_R) = \exp[\beta_1(x_1 - x_{1,R}) + \ldots + \beta_n(x_n - x_{n,R})] \qquad (2)$$

Because the true probability of a predation event for any individual location (30×30 m grid cell) on the NR is close to zero, I assume the odds ratio to be interpretable as relative probability of kill (Keating and Cherry 2004). Thus, a $\Psi(\mathbf{x}|\mathbf{x}_R) = 1$ denotes no difference between location i and the reference (mean probability on the landscape), whereas a $\Psi(\mathbf{x}|\mathbf{x}_R) = 10$ would indicate a kill probability 10× greater than the average.

Accounting for Elk Distribution

One obvious driver of the spatial distribution of wolf-killed elk is the spatial distribution of elk themselves. During winter elk select south-facing grassland habitats, where the snow level is not deep or crusted enough to impede their ability to forage (Houston 1982, Skovlin et al. 2002). On the NR, it is well known that snow accumulation throughout winter (if deep enough) pushes elk to lower-elevation winter range; thus, elk distribution on the landscape changes within and among annual winter seasons. I sought to account for this by estimating the spatial distribution of elk with an existing NR habitat model derived from radio-collared elk that includes – among other habitat variables – the influence of recorded annual variability in snow accumulation (Mao et al. 2005).

Although the NR elk population has declined since wolf reintroduction (Smith et al. 2004, White and Garrott 2005), the habitat model assumed (aside from the influence of snow) that the relative distribution of elk within each year was constant. As in the original elk habitat model of Mao et al. (2005), I used the daily snow water equivalent (SWE) estimated from an existing snow model that interpolates SWE across Yellowstone National Park from 28 fixed snow measurement sites (Wockner et al. 2006). I averaged the daily SWE estimates within the 4 2-week periods from which the kills were collected each winter. I used a natural log transformation of the Mao et al. (2005) RSF as the estimate of elk use in the kill site analysis. Within the case-control design of the kill site model, the elk variable assigned to each of the 20 random control locations came from the same 2-week period of the winter in which the kill occurred.

Wolf Distribution

I estimated the annual spatial distribution of wolves on the basis of individual packs. To characterize pack territories in a GIS, I constructed a utilization distribution (UD) using a 95% kernel estimation (Seaman and Powell 1996) for each pack from aerial locations of radiocollared wolves using a Home Range extension for ArcView 3.2 (Hooge and Eichenlaub 1997). A smoothing factor of 1500 m was chosen because it appeared to best approximate the extent of territory boundaries known from field observations. Aerial relocations of wolf packs known to be on a kill were excluded from the UD estimation to reduce the spatial dependence of kill sites on pack territories. Kernel percentile values were divided by the number of cells within each percentile category to approximate a probability distribution such that all 30 × 30 m cells within a pack UD summed to one. To account for variation in wolf pack size (range 2-37), I multiplied each pack UD by the number of wolves observed within each pack during winter. All individual pack UDs for a given year were summed across the NR resulting in an annual composite measure of wolf use.

Landscape Variables

Explanatory landscape variables were derived from a GIS of the study area and included: slope, openness, proximity-to-roads, proximity-to-streams, and SWE. Slope was derived from a 30 m digital elevation model of YNP (range 0 – 70°). Openness was calculated as per Boyce et al. (2003) using the sum of non-forested cells within a 500 × 500 m moving window centered on each grid cell (range 0 [deep forest] – 289 [open grassland]). The proximity-to-roads measure (range 0 – 13,435 m) was calculated as the shortest distance between each grid cell and the nearest road. Trails and roads that were not maintained were not included in the analysis. Proximity-to-streams (range 0 – 2,352 m) was calculated as the shortest distance to the nearest major stream or river. Snow was calculated as the average SWE for each of the 4 2-week periods during each winter (40 snow layers total) and matched to kills as described for the elk variable above.

RESULTS

I began the analysis of the kill site data by first building a set of "encounter" models in which elk and wolf distributions alone describe the spatial distribution of kills. A model including both elk and wolf distributions fit the kill data much better than did single-term models that included the distribution of only predator or prey (Likelihood Ratio $\chi^2 = 88.57$, d.f. = 1, $P < 0.0001$; Table 3.2). This indicates that wolves were not simply making kills on the landscape in strict proportion to the distribution of elk, or their own spatial patterns of winter territory use.

To characterize the influence of landscape features on predation risk, I constructed a set of "landscape effects" models that retained the effects of wolves and elk in addition to landscape features including: proximity to roads, proximity to streams, openness, slope, and snow. The best-fit landscape model included all landscape variables and vastly outperformed the elk + wolf encounter model (Likelihood Ratio $\chi^2 = 270.11$, d.f. = 6, $P < 0.0001$; Table 3.1; Table 3.2). Because these models take into account the spatial distribution of elk and wolves, they indicate that landscape factors strongly shape where wolves kill elk in this newly restored predator-prey system.

To determine whether the factors controlling the distribution of kills have changed over time, I built a third set of "time-varying" models that allowed the influence of wolves and landscape factors to vary linearly through time. Such temporal changes might result from learned hunting patterns by wolves in new habitats, learned antipredator behaviour by elk, or intraspecific predator interference as the number of wolf packs increased. The best-supported time-varying models included a negative wolf × time interaction (Likelihood Ratio $\chi^2 = 23.66$, d.f. = 1, $P < 0.0001$; Table 3.1; Table 3.2), indicating that the influence of wolf distribution on kills has diminished over time. There was negligible support for temporal interactions with landscape variables, indicating that the type of habitats where wolves have killed elk have changed little over the 10 years of wolf recolonization. Likelihood Ratio χ^2 values and associated P values (from nested model comparisons) were non-significant for temporal interactions with all landscape variable except for distance-to-stream (slope × time: $\chi^2 = 0.43$, $P < 0.51$; open × time: $\chi^2 = 3.42$, $P < 0.06$; road × time: $\chi^2 = 1.35$, $P < 0.25$; stream × time: $\chi^2 = 4.40$, $P < 0.04$). I do not believe that the significant stream × time interaction is indicative of a temporal change in wolf or elk behaviour with respect to streams. Rather, I believe this results from the formation of the Slough Creek Pack in 2002, which has been making kills (n=23) in close proximity to the banks of lower Slough Creek (Figure 3.1).

I used k-fold cross validation (Boyce et al. 2002) to evaluate the fit of the kill occurrence models to the kill site data. The kill data set was partitioned into five equal sets, and models were fit to each 80% partition of the data, while the remaining 20% of the data were held out for model evaluation. In each cross validation, the estimated probabilities were binned into 10 equal bins and correlated with the observed proportion of kills within the evaluation set. The average Spearman-rank correlations across the five partitions of the data were 0.90, 0.96, and 0.95 for the best-fit encounter, landscape effects, and time-varying models, respectively. Correlations of this magnitude indicate a very good fit of models to data (Boyce et al. 2002).

To illustrate the patterns of predation revealed by the analysis, I used the best-fitting (time-varying) model to map relative annual probability of kill occurrence onto the NR landscape for the 2005 winter (Figure 3.2a). I modified these model predictions at each landscape location to approximate per capita predation risk by scaling each probability of kill occurrence by the relative probability (log transformed) of elk occurrence from the Mao et al. (2005) elk habitat model. In rescaling the probabilities in this manner, I assume that elk group sizes across the study area are proportional to habitat use as estimated by Mao et al. (2005). In 2005, the influence of landscape features created a predation-risk landscape that was highly variable, with areas of low and high risk varying by nearly two orders of magnitude (Figure 3.2a). In the early years after wolf reintroduction, wolf distribution also created considerable spatial variation in risk. For example, comparing a risky area with a refuge area, I found that an increase in wolf density that caused a 10-fold increase in risk (relative to mean annual risk) in 1996 caused only a 1.25-fold increase in risk in 2005 (Figure 3.2b). Thus, during the first 10 years of wolf population expansion in Yellowstone, wolf distribution became less important in determining variation in predation risk relative to landscape features.

Logistic regression models such as the one I used are sensitive to spatial variation in explanatory variables. If the variability of a spatial attribute decreases through time, so too will the strength of its influence (Garshelis 2000). Therefore, I assessed whether the wolf distribution had become less variable over the 10-year study period and found that no temporal decline in the variance of the wolf density index was evident (see Figure 3.4). Rather, an increase in overall variance was observed, in part because of the emergence of areas of high wolf use where several packs overlapped (Figure 3.1a). Thus, the finding that kill locations became decoupled from the wolf distribution over time does not appear to be an artefact of a changing wolf distribution.

Wolf Influence on Kill Distribution

To further examine the decoupling of kill sites from predator distribution, I conducted post-hoc analyses to explore a potential mechanism for this phenomenon. I hypothesized that as the wolf population increased, wolves shifted their territories away from the areas where they were most successful at hunting elk (to dark blue patches in Figure 3.2) to reduce inter-pack conflict and mortality.

Pack Conflict

There is ample evidence that inter-pack conflict has increased as the density of NR wolf packs has increased. Long-term monitoring in this system has recorded 2.8 (± 0.8 SE) aggressive inter-pack interactions (i.e., intraspecific chase/flee, attack, or kill) per year during the first half of the study period (1996-2000) and 11.8 (± 2.6 SE) such interactions per year during the latter half of the study (2001-2005). Confirmed intraspecific killing by wolves increased over the same period, from 0.8 (± 0.3 SE) per year to 2.5 (± 1.0 SE) per year (D.W. Smith, National Park Service, unpublished). The per-capita kill rate for wolves on the NR has not declined sharply over the study period (D.W. Smith, National Park Service, unpublished), suggesting that wolf packs made behavioural adjustments to maintain a relatively constant annual kill rate. Given this, it seems unlikely that a predator-dependent functional response is responsible for the decoupling of predation from predator distribution.

Catchability

To evaluate whether wolves have established their territories in poorer hunting habitats through time, I estimated the “catchability” of the landscape occupied by each wolf pack in each year. I defined catchability as the relative probability of kill occurrence that was due to elk density and habitat features. I estimated catchability by fitting kill occurrence models without wolf distribution as an explanatory variable. I first fit a new model analogous to the best-fit landscape effects model including elk distribution and all landscape variables (but not presence of wolves). The catchability model is thus a composite measure of prey availability and the landscape attributes that influence wolf hunting success. Annual catchability maps were derived from the odds ratio of the catchability model coefficients (Table 3.1) using Equation 2. Mean values across the NR were used as the reference for each static variable, while the annual means were used for the time-varying terms (elk and snow). I assumed that annual catchability maps roughly approximate the relative quality of wolf habitat as it relates to their likelihood of successfully finding and killing elk.

I then sought to estimate the average catchability of each pack’s winter territory as an index of territory quality. I estimated mean catchability for each pack territory as the sum of all catchability scores within the area of the pack UD weighted by the UD values. The UDs of a few wolf packs extended beyond the study area in some years, so in these cases I rescaled the pack UD so that it summed to one within the study area.

After controlling for pack size, a decline through time in the average catchability of elk within each pack’s winter territory area was evident (Multiple regression; Pack size: $t = -2.48$, $P = 0.0166$; Year: $t = -3.47$, $P = 0.0011$; Figure 3.3), with a significant pack size × time interaction ($t = 2.33$, $P = 0.0238$) whereby large packs had access to high-quality hunting grounds and small packs were relegated to poor hunting grounds over time (Figure 3.3). A few large, competitively dominant packs retained access to the best hunting grounds over the ten years, but the majority of pack territories shifted away from the best hunting grounds as wolf density increased. These results are consistent with the hypothesis that individual wolf packs shifted their winter territories away from but adjacent to the best hunting grounds, thus decoupling kill locations from wolf distribution.

DISCUSSION

In this newly restored wolf-ungulate system, I found a striking degree of spatial variability in predation at the landscape level. Most of this variability appears to be caused by physical features of the landscape where prey and predator interact. Because I found a strong influence of landscape variables on kill site occurrence after accounting for the distribution of predator and prey, I believe that habitat mediates predation by controlling the occurrence or outcome of wolf-elk encounters. Although the precise mechanisms for strong landscape control of predation in this system are unclear, I believe such spatially heterogeneous rates of predation to be a general feature of native (or restored) predator-prey systems. Further, the decoupling of kill occurrence from predator distribution in the NR system calls into question the common assumption that predator distribution drives predation risk. The study suggests that hunting grounds – habitat patches with physical features that benefit wolf hunting success – exist on the NR, and that their distribution on the landscape influences both territorial space use by wolves and spatial variation in predation risk for elk.

Hunting grounds on the NR were flat, snow-covered grasslands close to streams and roads. The risky influence of these habitat features for elk is consistent with the cursorial (as opposed to stalking) hunting strategy of wolves. Streams and roads provide convenient travel corridors that likely increase prey encounter rates (Kunkel and Pletscher 2000), while open habitats likely facilitate prey detection (Kunkel and Pletscher 2000, Creel et al. 2005). With few visual barriers, open habitats could also enhance the wolves' ability to sort through an elk group and scan its members for vulnerable individuals to attack (Mech et al. 1998, MacNulty et al., 2007) (mean chase distance for a subset of kills was 978.20, SE ±141.73 m). Deep snow also favours wolves after encounters because it can hinder ungulate locomotion (Huggard 1993, Post et al. 1999). Similarly, streams and associated channels and ravines provide physical obstacles that may impede elk escape (Bergman et al. 2006). Overall, the physical attributes of the hunting grounds identified in this study are consistent with the natural history of wolf hunting behaviour. This work suggests that the well documented pattern of wolf selection of prey made vulnerable due to sex, age, or body condition (Mech and Peterson 2003) is likely to be mediated also by the type of habitats where wolves encounter and target vulnerable prey.

Predator distribution has been commonly used as a surrogate for predation risk in ecological studies (e.g., Ripple et al. 2001, Creel et al. 2005, Fortin et al. 2005), however, the findings suggests that this approach may not accurately represent predation risk. Instead, I found predation risk to be a function of both predator distribution and habitat features, with habitat playing the larger role. Hopcraft et al. (2005) found similar patterns for Serengeti lions (*Panthera leo*), whereby lion kills were more closely associated with good hunting habitat (in this case, stalking cover) than areas of high prey abundance. In a study similar to ours, Hebblewhite et al. (2005) found that topographic features appeared to determine patterns of wolf-elk encounters, while habitat (i.e., vegetation) mediated post-encounter outcomes. Wolves are inefficient predators with generally low rates of hunting success (≈20%, D.W. Smith, National Park Service, unpublished) due, in part, to the large size and defensive capabilities of their prey. In wolf-ungulate systems, as in other large mammal systems (Sinclair and Arcese 1995), prime-age adult prey are largely invulnerable to predation, and predators are highly selective, targeting the young, old, or weak (Mech and Peterson 2003). The finding of strong landscape control over predation in the NR system suggests that landscape features may often "tip the balance" in predator-prey encounters, thus controlling the post-encounter outcomes when predators are inefficient at subduing their prey. By contrast, it seems reasonable to expect that landscape features play a diminished role in outcomes when predators are fierce and prey have few antipredator defences after encountered (Caro 2005).

Hunting grounds of the NR are used by multiple wolf packs, a situation that does not conform to the widely held conceptual model of distinct territorial boundaries with interstitial prey refuges that has been suggested on an empirical (Mech 1977) and theoretical (Lewis and Murray 1993) basis. In Minnesota, boundaries between wolf pack territories appear to function as buffers where most inter-pack killings occur (Mech 1994) and where ungulate prey densities are elevated (Hoskinson and Mech 1976). By contrast, wolf territory overlap is high in the NR system, and territory buffers do not appear to reduce the likelihood of kill occurrence. Instead, the relative high density of wolf and elk populations on the NR and the strong landscape controls on predation success interact to create a pattern of high territorial overlap where the best hunting opportunities exist. In this system, it appears necessary that multiple packs maintain access to the some of the same hunting grounds.

Visualizing the kill site model as a map of relative predation risk (Figure 3.1a) provides some insights into how the spatial scale of safe and risky patches influences the ability of prey to manage the risk of predation – from new and current predators – while foraging, moving, and selecting habitats (Brown and Kotler 2004). The mosaic of risky and safe habitat patches available to NR elk suggests that elk can reduce their risk of wolf predation by making movements on the order of 1-2 km, easily achieved within daily movements (Fortin et al. 2005). This notion is supported by recent findings showing that elk move out of open areas when wolves are near (Creel et al. 2005) or in high density (Fortin et al. 2005), and aggregate in increasingly larger groups in open areas the longer wolves are absent (Creel and Winnie 2005). The ability of elk to mediate predation risk in such a dynamic way may explain why elk do not avoid the riskiest habitat patches. Indeed, elk have increased their use of open (i.e., risky) areas following wolf reintroduction (Mao et al. 2005). Unlike the highly vulnerable native prey of introduced predators, the heterogeneity of the landscape that elk historically shared with wolves allows them to mediate their risk of predation from this newly restored predator.

The map of relative kill occurrence indicates that refugia for elk of considerable size exist on the NR. The availability of these refugia for elk, and their ease of accessing them, should buffer the population from extreme levels of predation. The existence of prey refugia also is likely to influence long-term wolf and elk dynamics by reducing predator-caused fluctuations in elk numbers, as found in theoretical studies (Kareiva and Wennegren 1995). Since wolf reintroduction, the NR elk population has declined by an average of 8% annually (White and Garrott 2005), resulting in much debate about the long-term equilibrium size of the elk herd (Eberhardt et al. 2003, Vucetich et al. 2005, Varley and Boyce 2006). The highly heterogeneous pattern of predation found in this system offers a measure of assurance that economically and socially valuable ungulate populations will not suffer runaway predation as occurs with most exotic predator invasions (Fritts and Rodda 1998, Knapp et al. 2001).

These results have implications for the potential of restored predators to initiate trophic cascades by changing the habitat-selection patterns or foraging behaviour of their prey (i.e., behaviourally mediated trophic cascades, Schmitz et al. 2004). Several studies on Yellowstone's NR have suggested that wolves are affecting willow (*Salix* spp.), cottonwood (*Populus* spp.), and aspen (*P. tremuloides*) communities by changing the behaviour of elk that heavily browse these woody plants during winter (Ripple et al. 2001, Ripple and Beschta 2004, Beyer et al. 2007). However, a rigorous test has been thus far hindered by the lack of an empirical assessment of landscape-level predation risk. The strength of such behaviourally mediated cascades will depend on the cost and benefits of antipredator behaviour (i.e., avoiding or foraging less efficiently in risky areas, Schmitz et al. 2004). This study makes clear that NR elk in winter face a trade-off between forage quality and predation risk: most of these browse communities are found in open, flat areas near rivers and roads, which are risky places for elk. However, it unlikely to be optimal for elk to simply avoid these resources, because many of them provide forage during the critical winter months (Creel et al. 2005, Mao et al. 2005) when NR elk (and other northern ungulates) experience diminishing fat reserves (Cook et al. 2001). This need for winter forage most likely explains why broad-scale changes in winter habitat selection by elk with respect to wolves have not occurred (Mao et al. 2005, Fortin et al. 2005). How elk perceive and manage the trade-off between food and safety will ultimately determine the existence and strength of a behaviourally mediated trophic cascade in the NR system.

Table 3.1. Estimated coefficients for models used to estimate the probability of occurrence of wolf-killed elk on Yellowstone's Northern Range, 1996-2005.

	Landscape effects		Time-varying		Catchability	
Effect	β	SE	β	SE	β	SE
elk	1.238	0.131	1.238	0.132	1.331	0.131
wolf	1682.00	197.24	4988.00	706.44		
road	-0.00013	2.14E-05	-0.00013	2.15E-05	-0.00012	2.06E-05
stream	-0.00078	0.00014	-0.00017	0.00032	-0.00080	0.00014
openness	0.0026	0.0005	0.0046	0.0010	0.0028	0.0005
slope	-0.0749	0.0175	-0.0761	0.0176	-0.0795	0.0174
slope^2	0.0028	0.0007	0.0028	0.0007	0.0030	0.0007
snow	0.0112	0.0018	0.0115	0.0018	0.0120	0.0018
wolf × time			-462.95	97.01		
openness × time			-0.00032	0.00015		
stream × time			-0.00011	4.94E-05		

Table 3.2. Model selection results from kill occurence model describing the distribution of wolf-killed elk on Yellowstone's Northern Range, 1996-2005. ΔAIC values and AIC weights (ω_i) were calculated across all models within a set (i.e., encounter, landscape effects, and time-varying, $_T$) and across all models in all sets.

Model Sets			Within set[a]		All models[a]	
Encounter models	Log Likelihood	AIC	ΔAIC	ω_i	ΔAIC	ω_i
elk, wolf	-2076.0	4156.1	0.0	1.00	285.9	0.00
elk	-2120.3	4242.6	86.6	0.00	372.4	0.00
wolf	-2272.5	4546.9	390.9	0.00	676.7	0.00
Landscape effects models						
elk, wolf, roads, streams, open, slope, snow	-1941.0	3898.0	0.0	1.00	27.8	0.00
elk, wolf, roads, streams, open, snow	-1949.7	3911.3	13.4	0.00	41.1	0.00
elk, wolf, roads, open, slope, snow	-1957.6	3929.2	31.2	0.00	59.0	0.00
elk, wolf, roads, streams, slope, snow	-1957.9	3929.7	31.7	0.00	59.5	0.00
elk, wolf, streams, open, slope, snow	-1960.2	3934.5	36.5	0.00	64.3	0.00
elk, wolf, roads, streams, open, slope	-1961.9	3937.8	39.8	0.00	67.6	0.00
elk, wolf, roads, streams, open	-1967.0	3944.0	46.0	0.00	73.8	0.00
elk, wolf, roads, open, snow	-1969.0	3948.0	50.0	0.00	77.8	0.00
elk, wolf, streams, open, snow	-1970.0	3949.9	52.0	0.00	79.7	0.00
elk, wolf, roads, streams, snow	-1975.6	3961.2	63.2	0.00	91.0	0.00
elk, wolf, roads, open, slope	-1975.4	3962.8	64.9	0.00	92.6	0.00
elk, wolf, open, slope, snow	-1975.4	3962.9	64.9	0.00	92.7	0.00
elk, wolf, streams, open, slope	-1976.5	3965.0	67.1	0.00	94.8	0.00

elk, wolf, roads, slope, snow	-1978.5	3969.0	71.0	0.00	98.8	0.00
elk, wolf, streams, open	-1982.5	3973.0	75.1	0.00	102.8	0.00
elk, wolf, roads, open	-1983.4	3974.7	76.8	0.00	104.5	0.00
elk, wolf, open, snow	-1988.6	3985.1	87.1	0.00	114.9	0.00
elk, wolf, open, slope	-1989.3	3988.6	90.6	0.00	118.4	0.00
elk, wolf, streams, slope, snow	-1991.6	3995.2	97.3	0.00	125.0	0.00
elk, wolf, roads, streams, slope	-1993.3	3998.6	100.6	0.00	128.3	0.00
elk, wolf, open	-1998.8	4003.6	105.6	0.00	133.4	0.00
elk, wolf, roads, snow	-2002.3	4012.5	114.6	0.00	142.3	0.00
elk, wolf, roads, streams	-2011.0	4030.0	132.0	0.00	159.7	0.00
elk, wolf, roads, slope	-2010.5	4030.9	132.9	0.00	160.7	0.00
elk, wolf, slope, snow	-2011.3	4032.6	134.6	0.00	162.4	0.00
elk, wolf, streams, snow	-2018.1	4044.1	146.1	0.00	173.9	0.00
elk, wolf, streams, slope	-2023.6	4057.2	159.2	0.00	187.0	0.00
elk, wolf, roads	-2034.7	4075.3	177.4	0.00	205.1	0.00
elk, wolf, slope	-2040.1	4088.3	190.3	0.00	218.1	0.00
elk, wolf, snow	-2046.5	4099.1	201.1	0.00	228.9	0.00
elk, wolf, streams	-2050.1	4106.2	208.3	0.00	236.0	0.00
Time-varying models						
elk, wolf, road, stream, open, slope, snow, wolf$_T$, open$_T$, stream$_T$	-1924.1	3870.2	0.0	0.22	0.0	0.22
elk, wolf, road, stream, open, slope, snow, wolf$_T$, open$_T$, road$_T$, stream$_T$	-1923.5	3870.9	0.7	0.16	0.7	0.16
elk, wolf, road, stream, open, slope, snow, wolf$_T$, open$_T$, slope$_T$, stream$_T$	-1923.9	3871.8	1.6	0.10	1.6	0.10

elk, wolf, road, stream, open, slope, snow, wolf$_T$, road$_T$, stream$_T$	-1925.0	3871.9	1.7	0.10	1.7	0.10
elk, wolf, road, stream, open, slope, snow, wolf$_T$, open$_T$, slope$_T$, road$_T$, stream$_T$	-1923.2	3872.5	2.3	0.07	2.3	0.07
elk, wolf, road, stream, open, slope, snow, wolf$_T$, stream$_T$	-1926.4	3872.9	2.7	0.06	2.7	0.06
elk, wolf, road, stream, open, slope, snow, wolf$_T$, open$_T$	-1926.5	3873.0	2.8	0.06	2.8	0.06
elk, wolf, road, stream, open, slope, snow, wolf$_T$, open$_T$, road$_T$	-1925.9	3873.8	3.5	0.04	3.5	0.04
elk, wolf, road, stream, open, slope, snow, wolf$_T$, road$_T$	-1926.9	3873.8	3.6	0.04	3.6	0.04
elk, wolf, road, stream, open, slope, snow, wolf$_T$, slope$_T$, road$_T$, stream$_T$	-1925.0	3873.9	3.7	0.04	3.7	0.04
elk, wolf, road, stream, open, slope, snow, wolf$_T$, open$_T$, slope$_T$	-1926.1	3874.2	4.0	0.03	4.0	0.03
elk, wolf, road, stream, open, slope, snow, wolf$_T$	-1928.2	3874.4	4.2	0.03	4.2	0.03
elk, wolf, road, stream, open, slope, snow, wolf$_T$, slope$_T$, stream$_T$	-1926.4	3874.9	4.7	0.02	4.7	0.02
elk, wolf, road, stream, open, slope, snow, wolf$_T$, open$_T$, slope$_T$, road$_T$	-1925.4	3874.9	4.7	0.02	4.7	0.02
elk, wolf, road, stream, open, slope, snow, wolf$_T$, slope$_T$, road$_T$	-1926.8	3875.6	5.4	0.01	5.4	0.01
elk, wolf, road, stream, open, slope, snow, wolf$_T$, slope$_T$	-1928.2	3876.4	6.2	0.01	6.2	0.01
elk, wolf, road, stream, open, slope, snow, open$_T$, stream$_T$	-1936.0	3891.9	21.7	0.00	21.7	0.00
elk, wolf, road, stream, open, slope, snow, open$_T$, road$_T$, stream$_T$	-1935.2	3892.5	22.3	0.00	22.3	0.00
elk, wolf, road, stream, open, slope, snow, open$_T$, slope$_T$, stream$_T$	-1935.8	3893.6	23.4	0.00	23.4	0.00
elk, wolf, road, stream, open, slope, snow, open$_T$, slope$_T$, road$_T$, stream$_T$	-1935.1	3894.1	23.9	0.00	23.9	0.00
elk, wolf, road, stream, open, slope, snow, open$_T$	-1938.4	3894.8	24.6	0.00	24.6	0.00
elk, wolf, road, stream, open, slope, snow, road$_T$, stream$_T$	-1937.5	3894.9	24.7	0.00	24.7	0.00
elk, wolf, road, stream, open, slope, snow, open$_T$, road$_T$	-1937.7	3895.4	25.2	0.00	25.2	0.00
elk, wolf, road, stream, open, slope, snow, open$_T$, slope$_T$	-1938.0	3896.1	25.9	0.00	25.9	0.00
elk, wolf, road, stream, open, slope, snow, stream$_T$	-1939.3	3896.6	26.4	0.00	26.4	0.00

elk, wolf, road, stream, open, slope, snow, open$_T$, slope$_T$, road$_T$	-1937.3	3896.6	26.4	0.00	26.4	0.00
elk, wolf, road, stream, open, slope, snow, road$_T$	-1939.3	3896.7	26.5	0.00	26.5	0.00
elk, wolf, road, stream, open, slope, snow, slope$_T$, road$_T$, stream$_T$	-1937.5	3896.9	26.7	0.00	26.7	0.00
elk, wolf, road, stream, open, slope, snow, slope$_T$, stream$_T$	-1939.2	3898.5	28.3	0.00	28.3	0.00
elk, wolf, road, stream, open, slope, snow, slope$_T$, road$_T$	-1939.3	3898.6	28.4	0.00	28.4	0.00
elk, wolf, road, stream, open, slope, snow, slope$_T$	-1941.0	3900.0	29.8	0.00	29.8	0.00

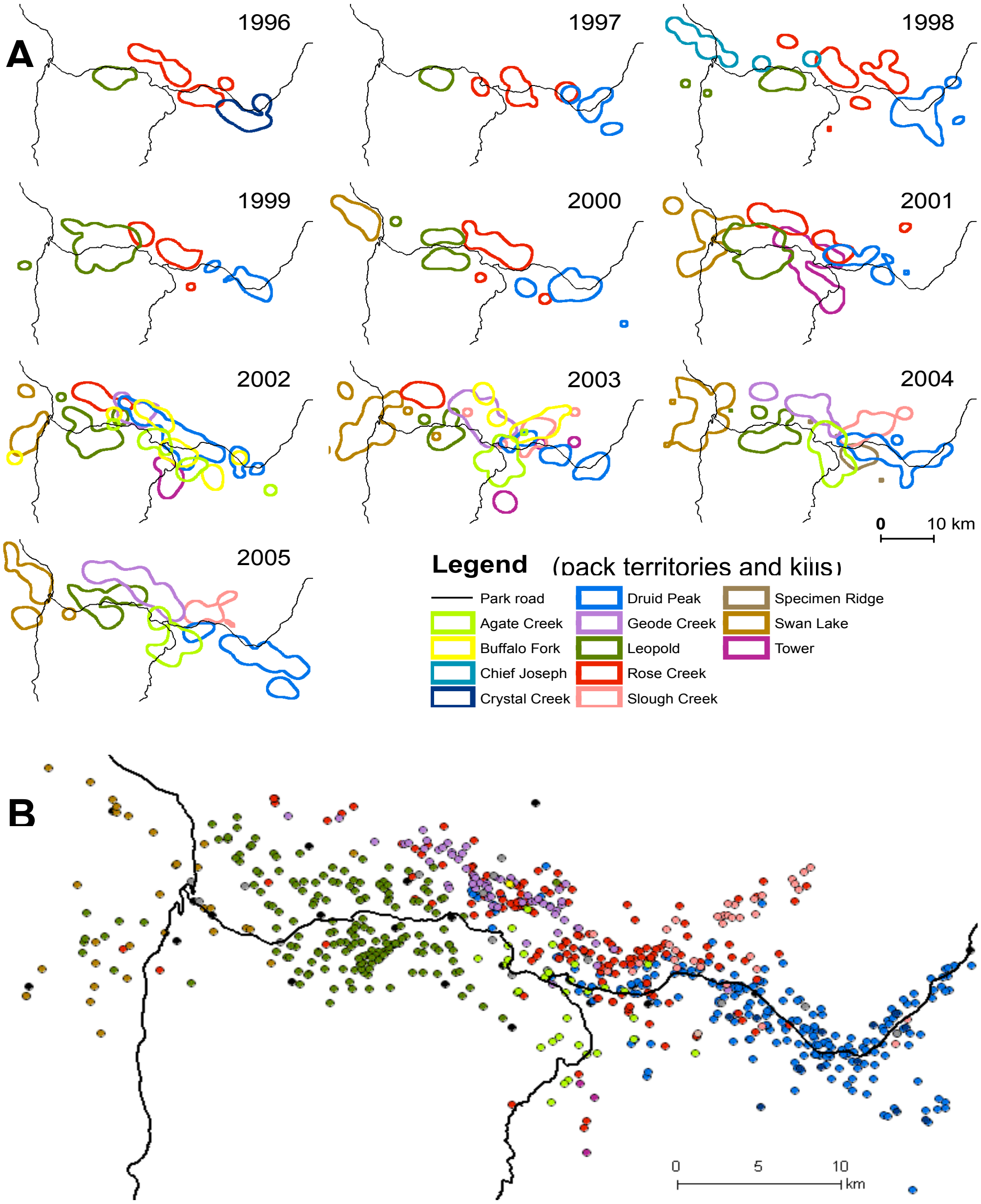

Figure 3.1. The spatial distribution of wolf pack territories and wolf-killed elk on Yellowstone's Northern Range, 1996-2005. Wolf pack territory boundaries (panel A) represent an 80% kernel home range. Wolf-killed elk (panel B) are color-coded according to the pack that made the kill. The legend in panel A) gives the colour codes for both pack territories and kills (in B, grey circles = dispersers or unformed pack).

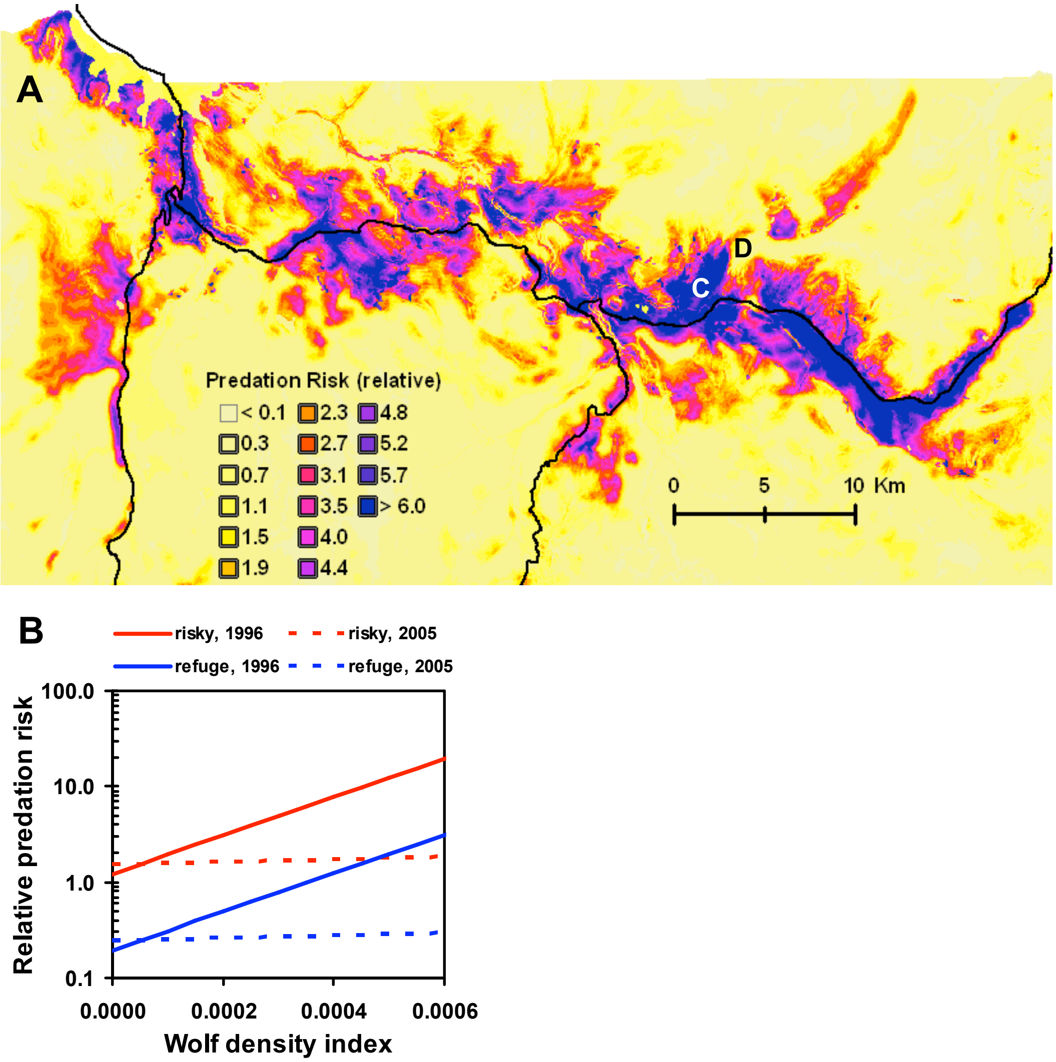

Figure 3.2. Relative risk of wolf predation for elk on Yellowstone's Northern Range, 2005 (Panel A). Spatial variation in predation risk is largely driven by landscape features, which create a limited number of hunting grounds where predation risk is often 10 times higher than the landscape average (a map value of 1 denotes average risk). When first reintroduced, wolf pack distribution also strongly influenced predation risk (Panel B), but this influence has largely diminished after 10 years of wolf recolonization. By 2005, variation in predation risk is largely determined by landscape features that create risky (location C in risk map) and refuge (location D in risk map) habitats.

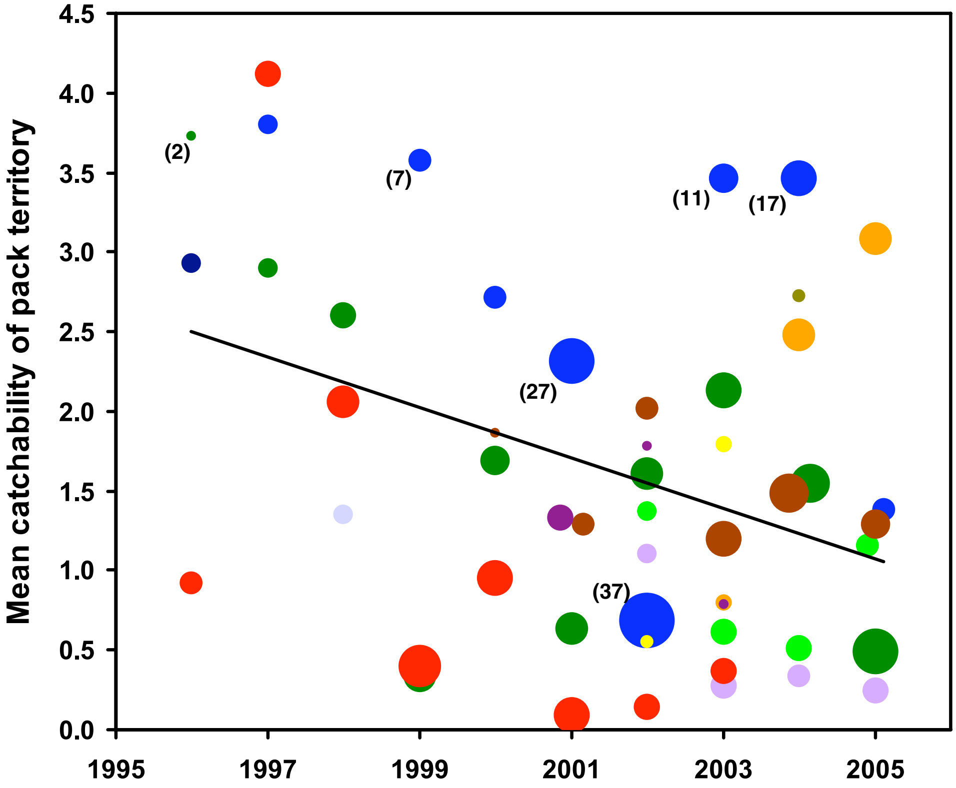

Figure 3.3. The distribution of wolf packs on the Northern Range of Yellowstone National Park in relation to elk catchability (≈ wolf territory quality), 1996-2005. Wolf packs have responded to the increase in the number of neighbouring packs by selecting habitat that minimizes interpack conflict, resulting in pack territories with significantly poorer catchability over time. Catchability scores were standardized within years to account for the dependency of elk distribution on observed snow levels (in all years, average catchability = 1). Bubble size scales with winter wolf pack size (representative sizes shown in parentheses), and bubbles are color coded by pack according to the legend in Figure 3.1.

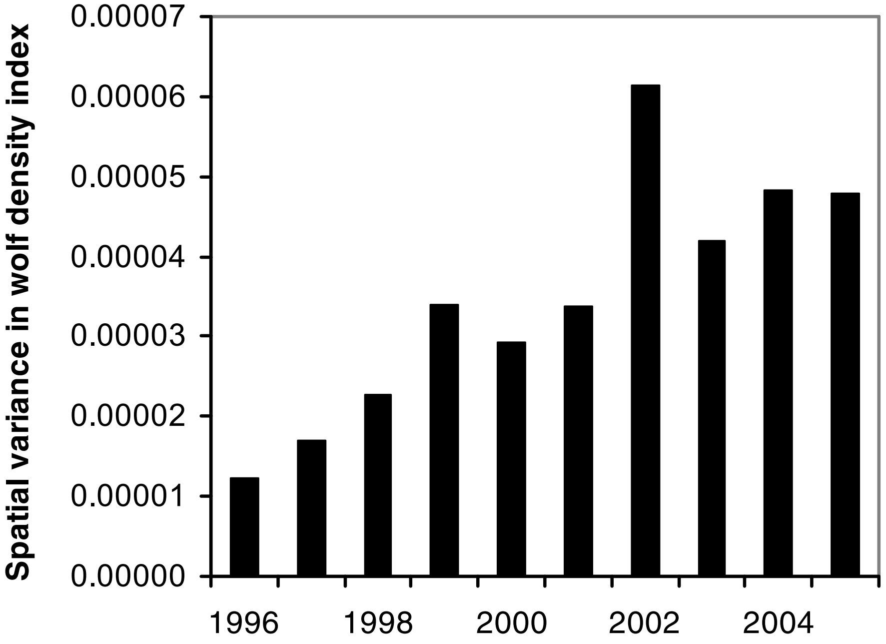

Figure 3.4. Spatial variance in wolf density index on the Northern Range of Yellowstone National Park, 1996-2005. The spatial variance in wolf distribution has increased in part because of the development of high density areas where several packs territories overlap.

REFERENCES

Bangs, E. E., and S. H. Fritts. 1996. Reintroducing the gray wolf to central Idaho and Yellowstone National Park. Wildlife Society Bulletin **24**:402–413.

Berger, J. 1999. Anthropogenic extinction of top carnivores and interspecific animal behaviour: implications of the rapid decoupling of a web involving wolves, bears, moose and ravens. Proceedings of the Royal Society B **266**:2261–2267.

Berger, J., J. E. Swenson, and I.-L. Persson. 2001. Recolonizing carnivores and naïve prey: conservation lessons from Pleistocene extinctions. Science **291**:1036–1039.

Bergman, E. J., R. A. Garrott, S. Creel, J. J. Borkowski, R. Jaffe, and F. G. R. Watson. 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. Ecological Applications **16**:273–284.

Blackburn, T.M., P. Cassey, R. P. Duncan, K. L. Evans, and K. J. Gaston. 2004. Avian extinction and mammalian introductions on oceanic islands. Science **305**:1955–1958

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling **157**:281–300.

Boyce, M.S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Écoscience **10**:421–431.

Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters **7**:999–1014.

Beyer, H. L., E. H. Merrill, N. Varley, and M. S. Boyce. 2007. Willow on Yellowstone's northern range: evidence for a trophic cascade in a large mammalian predator-prey system? Ecological Applications **17**:1561–1573.

Caro, T. 2005. Antipredator Defenses in Birds and Mammals. The University of Chicago Press, Chicago, USA.

Cook, R. C., J. G. Cook, D. L. Murray, P. Zager, B. K. Johnson, and M. W. Gratson. 2001. Development of predictive models of nutritional condition for Rocky Mountain elk. Journal of Wildlife Management **65**:973–987.

Creel, S., and J. A. Winnie, Jr. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. Animal Behaviour **69**:1181–1189.

Creel S., J. A. Winnie, Jr., B. Maxwell, K. Hamlin, and M. Creel M. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology **86**:3387–3397.

Crooks, K. R. and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature **400**:563–566.

Eberhardt, L. L., R. A. Garrott, D. W. Smith, and P. J. White. 2003. Assessing the impact of wolves on ungulate prey. Ecological Applications **13**:776–783.

Ellner, S. P., E. McCauley, B. E. Kendall, C. J. Briggs, P. R. Hosseini, S. N. Wood, A. Janssen, M. W. Sabelis, P. Turchin, R. M. Nisbet, W. W. Murdoch. 2001. Habitat structure and population persistence in an experimental community. Nature **412**:538–542.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesné, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology **86**:1320–1331.

Fritts, T. H., and G. H. Rodda. 1998. The role of introduced species in the degradation of island ecosystems: a case history of Guam. Annual Review of Ecological Systems **29**:113–140.

Fryxell, J. F., J. Greever, and A. R. E. Sinclair. 1988. Why are migratory ungulates so abundant? American Naturalist **131**:781–798.

Garshelis, D. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pages 111–153 *in* L. Boitani, and T. K. Fuller, editors. Research Techniques in Animal Ecology. Columbian University Press, New York, NewYork, USA.

Hebblewhite, M., E. H. Merrill, and T. L. McDonald. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system. Oikos **111**:101–111.

Hooge, P. N., and B. Eichenlaub. Animal Movement Extension to Arcview 3.2, Version 2.0 1997. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, Alaska; http://www.absc.usgs.gov/glba/gistools/animalmovementdoca.pdf.

Hopcraft, J. G. C., A. R. E. Sinclair, and C. Packer. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology **74**:559–566.

Hoskinson, R. L., and L. D. Mech. 1976. White-tailed deer migration and its role in wolf predation. Journal of Wildlife Management **40**:429–441.

Hosmer, D. W., and S. Lemeshow. 2000. Applied Logistic Regression. Wiley, New York, New York, USA.

Houston, D. B. 1982. The Northern Yellowstone Elk: Ecology and Management. Macmillan, New York, New York, USA.

Huggard, D. J. 1993. Effect of snow depth on predation and scavenging by gray wolves. Journal of Wildlife Management **57**:382–388.

Kareiva, P., and U. Wennegren. 1995. Connecting landscape patterns to ecosystem and population processes. Nature **373**:299–302.

Keating, K. A., and S. Cherry. 2004. Use and interpretation of logistic regression in habitat-selection studies. Journal of Wildlife Management **68**:774–789.

Knapp, R. A., K. R. Matthews, and O. Sarnelle. 2001. Resistance and resilience of alpine lake fauna to fish introductions. Ecological Monographs **71**:401–421.

Kunkel, K. E., and D. H. Pletscher. 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. Canadian Journal of Zoology **78**:150 –157.

Lewis, M. A., and J. D. Murray. 1993. Modeling territoriality and wolf-deer interactions. Nature **366**:738–740.

MacNulty, D. R., L. D. Mech, and D.W. Smith. 2007. A proposed ethogram of large carnivore predatory behaviour, exemplified by the wolf. Journal of Mammalogy In press.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource Selection by Animals: Statistical Analysis and Design for Field Studies. Kluwer, Dordrecht, The Netherlands.

Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. Journal of Wildlife Management **69**:1691–1707.

Mech, L. D. 1977. Wolf-pack buffer zones as prey reservoirs. Science **198**:320–321.

Mech, L. D. 1994. Buffer zones of territories of gray wolves as regions of intraspecific strife. Journal of Mammalogy **75**:199–202.

Mech, L. D., L. G. Adams, T. J. Meier, J. W. Burch, and B. W. Dale. 1998. The Wolves of Denali. University of Minnesota Press, Minneapolis, USA.

Mech, L. D., and R. O. Peterson. 2003. Wolf-prey relations. Pages 131–160 *in* L. D. Mech, and L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois, USA.

Nilsen, E. B., T. Pettersen, H. Gundersen, J. M. Milner, A. Mysterud, E. J. Solberg, H. P. Andeassen, and N. C. Stenseth. 2004. Moose harvesting strategies in the presence of wolves. Journal of Applied Ecology **41**:1021–1031.

Orians, G. H., J. Cochran, J. W. Duffield, T. K. Fuller, R. J. Gutierrez, W. M. Hanemann. 1997. Wolves, Bears, and their Prey in Alaska: Biological and Social Challenges in Wildlife Management. National Academy Press, Washington D.C.

Post, E. S., R. O. Peterson, N. C. Stenseth, and B. E. McLaren. 1999. Ecosystem consequences of wolf behavioural response to climate. Nature **401**: 905–907.

Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. Biological Conservation **102**:227–234.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience **54**:755–766.

Sand, H., C. Wikenros, P. Wabakken, and O. Liberg. 2006. Cross-continental differences in patterns of predation: will naïve moose in Scandinavia ever learn? Proceedings of the Royal Society B **273**:1421–1427.

Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. Ecology Letters **7**:153–163.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology **77**:2075–2085.

Sinclair, A. R. E. and P. Arcese. 1995. Population consequences of predation-sensitive foraging: the Serengeti wildebeest. Ecology **76**:882–891.

Skovlin J. M., P. Zager, and B. K. Johnson. 2002. Elk habitat selection and evaluation. Pages 531–555 *in* D. E. Toweill, and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D. C., USA.

Smith, D. W., T. D. Drummer, K. M. Murphy, D. S. Guernsey, and S. B. Evans. 2004. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. Journal of Wildlife Management **68**:153–166.

Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. Science **294**:1924–1926.

Treves, A., and K. U. Karanth. 2003. Human-carnivore conflict and perspectives on a carnivore management worldwide. Conservation Biology **17**:1491–1499.

Varley, N., and M. S. Boyce. 2006. Adaptive management for reintroductions: Updating a wolf recovery model for Yellowstone National Park. Ecological Modelling **193**:315–339.

Vucetich, J. A., D. W. Smith, and D. R. Stahler. 2005. Influence of harvest, climate, and wolf predation on Yellowstone elk, 1961–2004. Oikos **111**:259–270.

White, P. J., and R. A. Garrott. 2005. Yellowstone's ungulates after wolves – expectations, realizations, and predictions. Biological Conservation **125**:141–152.

Wockner, G., F. J. Singer, M. Coughenour, and P. Farnes. 2006. Yellowstone Snow Model. Natural Resources Ecology Lab, Colorado State University, Fort Collins, Colorado. http://www.nrel.colostate.edu/projects/yellowstone/.

CHAPTER 4

YELLOWSTONE'S TROPHIC CASCADE A TRICKLE? ELK, WOLF, AND HUMAN INFLUENCES ON WILLOW BROWSE

Studies following gray wolf (*Canis lupus*) recovery in Yellowstone National Park (YNP), Wyoming, USA, (e.g., Beschta 2005; Fortin et al. 2005; Ripple and Beschta 2004, 2006; Beyer et al. 2007) have suggested that a trophic cascade is underway, similar to that reported for Banff National Park, Alberta, Canada (Hebblewhite et al. 2005). In YNP, deciduous woody vegetation has been browsed intensively, mainly by elk (*Cervus elaphus*), for >5 decades (Singer et al. 1994, 2002; Wagner et al. 1995; Singer 1996; White et al. 1998). As a result, woody plants persist largely in an on-going state of "arrest" characterized by low growing forms (<1 m) unable to become tall trees (>3 m) (Singer et al. 1994, YNP 1997, Wagner 2006). A late 1980's survey of willow (*Salix* spp.) on YNP's elk winter range prior to wolf recovery indicated >80% of willow were height-suppressed as a result of >50% annual off-take due to herbivore browsing (Singer et al. 1994).

After wolf reintroduction in 1995, increased growth in some local populations of willow (*Salix* spp.), aspen (*Populus tremuloides*), and cottonwood (*P. angustifolia, P. trichocarpa*) appeared due to reduced elk density and/or altered foraging patterns attributed to wolves (Ripple and Beschta 2006, Beyer et al. 2007). Despite these indications, aspen, cottonwood, and most willow in YNP's northern elk winter range are still experiencing substantial herbivory (Ripple et al. 2001, Beschta 2005, Beyer et al.

2007) suggesting the trophic cascade may be manifesting only weakly, and that suppression by elk herbivory may not have been substantially alleviated.

In YNP, wolves have had a large influence on habitat selection by elk during spring and summer when wolf distribution is constrained by pup-rearing (Mao et al. 2005). As much as 25% of total browsing was estimated to occur during summer (Singer et al. 1994), and so vegetation measurements taken in the summer (e.g., Ripple and Beschta 2006, Beyer et al. 2007) possibly reflect only an ephemeral release from herbivory. Elk habitat selection has undergone less overall change in the winter relative to the summer (Mao et al. 2005), and if winter browsing remains intense, growth gained in summer use still may be consumed during winter. Thus far, no studies after wolf recovery have directly quantified willow use by elk during winter.

In this study, I estimated the extent of elk browsing of willow during winter. To estimate recent browse history of willow, I characterized growth form of individual plants at 23 sites on YNP's northern elk winter range (NR). To estimate winter off-take by browsing, I measured available willow stems before and after winter 2003-2004. The influences of (1) changes in elk habitat selection (pre- and post-wolf re-introduction), (2) human-mediated effects, (3) landscape effects, and (4) wolf predation risk on willow browsing by elk were modeled to explain the relative contribution of each factor to willow growth. The interaction of these various factors will likely determine the long-term prospects for woody browse recovery in YNP.

STUDY AREA

The NR is a low elevation (1,500–2,000 m) grassland that receives ~25 cm of precipitation in the west to ~45 cm of precipitation in the east. I sampled willow within a portion of the NR that lies inside YNP of approximately 884 km^2 (Figure 4.1). The area is dominated (55%), by sagebrush (*Artemisia tridentata*), grasses (*Festuca idahoensis, Elymus canadensis*, *Agropyron spicatum*) and sedges (*Carex* spp.), patchy conifer stands (41%, mainly *Pseudotsuga menzeseii*), and widely dispersed aspen stands (4%). Willow (<1%) exist in small patches along riparian corridors and some upland seeps (YNP 1997, National Research Council (NRC) 2002). Common willow species included *S. geyeriana, S. boothii, S. drummondiana, S. bebbiana, S. exigua,* and *S. planifolia*, which if unbrowsed can grow to heights >3 m. Hybridization occurs among some species of willow on the NR (J. Whipple, National Park Service botanist, personal communication) making identification of some species challenging.

Wolves were reintroduced to YNP in 1995 (Bangs and Fritts 1996) and the population expanded exponentially to occupy the entire NR by 1998 (Smith et al. 2004). The wolf population estimate for the NR for the winter 2003-2004 was 89 in 8 packs, close to an estimate of carrying capacity for wolves on the NR (Varley and Boyce 2006). Elk are the principal prey for wolves, making up the majority (80-90%) of the winter diet (Smith et al. 2004, White and Garrott 2005). Approximately 8,000 elk wintered on the NR in 2003-2004 (White and Garrott 2005), a moderate to low density compared with the 30 prior years of elk population estimates for the NR (Varley and Boyce 2006). NR elk demographics have received much attention and are described in detail elsewhere (Houston 1982, Taper and Gogan 2002, White and Garrott 2005, Varley and Boyce 2006, Eberhardt et al. 2007). Willow is highly preferred by elk during winter (Singer et al. 1994, 2002), but browsing of NR willow by ungulates other than elk appears to be minor in winter (YNP 1997, Barmore 2003). Moose (*Alces alces*) are rare on the NR and were not seen during field work because they migrate during winter to old-growth spruce-fir forests at elevations higher than the NR (Tyers and Irby 1995). Mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*) and most bighorn sheep (*Ovis canadensis*) migrate to lower elevations (Barmore 2003). Only bison (*Bison bison*) share upper NR winter range with elk, but no winter observations of bison browsing willow occurred during this study.

METHODS

I selected sample sites where *Salix geyeriana,* a common willow across the NR, were abundant in a 30 × 30 m area, where sites were >500 m from other sites, and where elk would have access to the sites based on typical elk distribution in winter (Houston 1982, Barmore 2003, Mao et al. 2005). I distributed sites throughout the NR study area (Figure 4.1), but were constrained to sites where access by hiking was <10 km from NR roads. The areal extent of sites sampled matched as closely as possible the 30 × 30 m size of geographic information system (GIS) grid cells used for the analysis. To locate the site in GIS, a UTM coordinate was taken in the approximate center of the cluster of stems using a Trimble© Global Positioning System (GPS) device that specified accuracy to within 1 m.

For the seasonal estimates of willow browsing pressure, I used the percent difference in length of individually tagged willow stems measured during fall (November 11 – December 4) and early spring (April 3 – 16), because this approach provides unbiased estimates of browse removal under high levels of browsing (Bilyeu et al. 2007). Twenty stems (rooted individual stem and its shoots) were selected >2 m apart at the periphery of willow clumps but within an approximate 30 × 30 m area, marked with a small, drab basal collar, and mapped by hand to facilitate relocation after winter. At most sites, the overall height of stems was <1 m, and these were considered equally accessible to elk. At some sites where tall (> 2 m), thick clumps of willow stems occurred, I avoided sampling stems on the interior of clumps because the structure created physical refuge for interior stems from elk (Ripple and Beschta 2005). The intent was to standardize the availability of willow stems within and between sites by selecting accessible stems.

Browse history of an individual willow is reflected in its architecture, so I first characterized predominate architectural types found at each site. Four classifications based on Keigley et al. (2003)'s description refer to architecture with an associated browse history as follows: (1) uninterrupted/light browsing, (2) arrested/intense browsing, (3) retrogressed/change from light to intense browsing, and (4) released/change from intense to light browsing. Each of the 20 stems sampled was associated with distinct clumps of multiple stems that had generally the same architecture. The overall architecture of the willow clump associated with each of the 20 stems was recorded as 1 of these 4 forms. Characterization of the overall site was made from summary statistics for the individual stem architecture of a clump.

On each of the 20 rooted stems, the length of all shoots (portion of plant branching from the stem) and the basal stem diameter were recorded to the nearest centimeter and millimeter, respectively. I measured both current annual growth and previous year's growth. Because *S. geyeriana* was sometimes difficult to distinguish from other species after leaf drop, other species might have been inadvertently sampled, but only to a limited extent.

The marked willow stems were located and measured again in late April and early May 2004 to acquire post-winter estimates of willow removal. In instances where a marked stem could not be located after the winter, or it had been completely pulled from the ground, a mean was calculated from the remaining stems ($N_{i\ min}$=17) to maintain equal sample sizes in the pre- and post winter sampling period. The difference between the sum of pre-winter and sum of post-winter stem lengths at sites was taken as the percent estimate of browse removal for each stem, x_{stem}. To scale willow removal from the stem to the site, I used a biomass comparison method equation (Bilyeu et al. (2007: Equation 7):

$$x_{site} = [1- (\sum x_{\text{stem\_length}}\ after\ /\ \sum x_{\text{stem\_length}} before)]\ \text{x}\ 100 \qquad \text{Eq. 1}$$

then transformed the variable to render a normal distribution to the sample,

$$y_{site} = \text{Arcsin}(\text{sqrt}(x_{site})) \qquad \text{Eq. 2}$$

Additionally, I repeatedly examined willow on 7 plots to estimate the rate and timing of browse removal during the winter. For this, separate plots were established <100 m adjacent to 7 of the 23 willow sites. Sites were selected where *Salix* spp. were abundant and could be assessed easily from viewpoints <10 m from the site. Observers minimized their presence at the site and did not disturb elk when elk were present at sampling sites. A visual estimate of the initial willow stem lengths available at the site was made in late November. The sites were then monitored bimonthly from December through March. The percent of willow stem length removed was estimated with each observation. The same observers were used throughout the winter to minimize observer bias.

Site variables

All independent variables used to model relationships with the response variables, y_{site}, were values derived from GIS databases and matched to the 30 × 30 m pixel that contained the location of the willow site. Variables were screened for distribution, outliers, and collinearity.

Elk habitat: As indices to the overall attractiveness of the willow sites to elk, I used Mao et al. (2005: Table 6)'s winter resource selection functions (RSF), which predicted the relative probability of elk use based on elevation, slope, vegetation types, and snow water equivalents. Two variants of the model were used—the pre-wolf RSF model ($ELK_{prewolf}$) that characterized elk habitat selection prior to wolf restoration and the post-wolf RSF model ($ELK_{postwolf}$) that characterized selection after wolf restoration. Use of the former avoided the issue of elk site selection biased by wolf presence, while the latter allowed me to examine shifts in site selection that occurred after wolf restoration to the NR system.

Because the probability of elk use of areas varies across spatial scales (Boyce et al. 2003, Boyce 2006), I first explored the influence of spatial extent for measuring elk habitat selection (RSF values from Mao et al. 2005) and its influence on the relationship between willow browsed and site use by elk. I examined model fit at 11 scales of measurement ranging from the value of the RSF for the 30 × 30 m cell containing the willow site location to summing all RSF values in cells adjacent to the willow site with incremental radii from 100 m to 1 km. The RSF value at the scale with the highest log likelihood in the *a priori* univariate model set was used as the measure of elk attraction to a willow site in the multiple-variable model set.

Wolf predation: I used two approaches to characterize predation risk. I first directly compared the fit of both RSF values, $ELK_{prewolf}$ and $ELK_{postwolf}$, to verify if $ELK_{postwolf}$ provided a better fit because it reflected resource selection with wolves present. Secondly, I introduced the difference between the predictions of the two RSF's as a separate variable, $RISK_{site}$, which at the 30 × 30 m cell containing the willow site this variable, $RISK_{site}$, was calculated as

$$RISK_{site} = (ELK_{prewolf} - ELK_{postwolf}) \qquad \text{Eq. 3}$$

where high $RISK_{site}$ values indicated locations that were selected less after wolf reintroduction, i.e., where greater risk of predation was presumed. As described for the *ELK* variable, I examined the fit of the *RISK* variable at multiple scales by summing the values at incremental radii around the willow site, and chose the scale that maximized the log-likelihood of the fit to the y_{site} data.

Second, elk do not altogether avoid areas of wolf use, but their use of these sites appears to be mediated by the frequency of wolf presence (Fortin et al. 2005). I characterized wolf presence using utilization distributions (UDs) built from a 95% kernel estimator (Seaman and Powell 1996). Each of the 8 packs that occupied the NR during winter 2003-2004 was periodically located from the air using radiotelemetry and the location recorded using a GPS device (described by Smith et al. 2004). Location coordinates for each pack from December 2003 to April 2004 were used to construct separate pack UDs. A minimum number of 13 locations per pack were used with a mean of 26. A smoothing factor of 1500 m was selected to account for the wolf's wide-ranging movement patterns (Mech and Peterson 2003) and to approximate the boundaries of wolf pack territories on the NR identical to the approach of Kauffman et al. (2007). The individual pack UDs were multiplied by individual pack size (mean = 9.5) and then individual pack UDs were summed across the NR to produce a cumulative wolf-density estimate (Figure 4.2). The summed UD values at the 30 × 30 m cell at the willow locations were indicated as the variable vector, *WOLF*.

Snow: Snow depth is an important variable that affects both resource use by elk (Boyce et al. 2003) and vulnerability to an attack by wolves (Huggard 1993, Bergman et al. 2006). To reflect the importance of both snow depth and density, snow within the 30 × 30 m cell at willow sites was estimated in snow water equivalents (SWE). An existing snow model that interpolated SWE from 28 snow measurement stations in and around YNP (Wockner et al. 2006) provided daily SWE estimates for all locations on the NR from December 2003 to March 2004. Daily estimates were averaged for a composite snow map of the study area for the winter, November 1, 2003 to April 30, 2004. The value at each of the 30 × 30 m cells containing a willow site served as the *SNOW* variable.

Geographic variables: Many topographic features, e.g., slope, cover, and stream corridors, as well as, human activities are known to influence elk distribution and movements (Skovlin et al. 2003, Fortin et al. 2005, Gude et al. 2006). Willow sites were near streams and rivers and occupied flat areas; therefore, the low variation in the distribution of values for these topographic variables was inadequate to draw meaningful conclusions and dropped from consideration. Because an elk's ability to see approaching wolves and escape may be an important factor in its willingness to use a location (Ripple and Beschta 2004, 2006), I calculated a measure of habitat openness (*OPEN*) by totalling the number of non-forested cells within a 500 × 500 m buffer around a willow site (Boyce et al. 2003). Forested versus non-forested cells were determined using forest-cover type GIS maps for YNP. To quantify human activity, I used the shortest straight line distance (m) measured in a GIS between willow sites and the nearest road for the variable vector, *ROAD*.

Statistical Analyses

A set of generalized linear models was constructed from combinations of the independent variables and fit to the set of response variables, y_{site}. Multiple linear regression was used to estimate the coefficients and standard errors of the independent variables (Hosmer and Lemeshow 2000), and models were ranked using AIC_c, Akaike's Information Criterion corrected for small sample size. The best model minimized AIC_c and $\Delta AIC_c > 4$ was considered a poorer model when comparing among models (Burnham and Anderson 2002). Akaike weights, w_i, were used to evaluate the relative likelihood of each model given the data. To illustrate the relative effect of each variable on the response variable, the best model containing the variable in question was used to predict browse removal incrementally across the range of values for that variable. To graphically display the results of the influence of individual variables on the response variable, I plotted the predicted values of each variable from their best model across 10 equal increments of the response variable within the range measured while keeping all other variables constant using their mean.

RESULTS

Willow architectural types found at the sites were predominately (>50% of clumps) of the arrested form (19 of 23 sites) in which a history of intense browsing has resulted in low-growing forms (Figure 4.3). Of 391 individual willow clumps classified in the study area, 76% were arrested. All willow sampled at 10 sites (43%) were arrested. Four of the 23 sites had tall willow (*sensu* Chadde and Kay 1991) where stems >2 m in height were found. Three of the 4 sites were predominately of the released form in which browse intensity was alleviated allowing arrested willow to escape and grow tall. Thus, these 3 sites were the only sites that appeared to have experienced improved growth since wolf recovery, and as such, have been used as photographic evidence for wolf effects, e.g., Ripple and Beschta (2004: Figure 6; 2006: Figure 2). Only one site was found with predominately uninterrupted architectural type in which a history of light browsing allowed willow to grow unabated. The site was at the fringe of elk range and had the lowest elk RSF value of the 23 sites, because it was too high in elevation (2120 m) for winter use by elk under the snow conditions of 2003-2004.

Elk consumed an average of 49% (median: 57%; maximum: 72%) of the lengths of willow leaders at the 23 NR sites with moderate variability (SD = 16.8; CV = 0.4) among sites (Figure 4.5). Over half of the sites (56%) experienced removal of over half of the measured stem lengths. The mean sum of fall leader lengths within sites was 461 cm (SD = 213) and spring shoot lengths was 208 cm (SD = 141), a difference of 248 cm (SD = 151). Among all sites, the mean basal diameter of leaders was 0.88 cm with low variation (SD = 0.09, CV = 0.1) and the mean diameter of leaders at point of branching was 4 mm with low variation (SD = 0.06, CV = 0.01). Very low variation in shoot diameters across sites indicated measured leaders were generally about the same thickness at the base, which warranted the use of summed shoot lengths as the index of willow available for elk.

Biweekly willow removal

Biweekly estimates of willow removal at 7 adjacent sites indicated that on average the most rapid browse removal in 2003 occurred between the beginning and middle of January, but that three patterns of browse removal were evident (Figure 4.6). The rate of removal in early January at 3 sites where >80% of the biomass was removed within a 2-week period. Two sites showed more gradual use that resulted in <80% off-take and had the lowest *WOLF* and *SNOW* values and the highest *ELK* (RSF) values. Three with abrupt increases in use in January leading to >80% off-take had the highest *WOLF*, lowest *ELK* (RSF), and intermediate *SNOW* values. The final two experienced early winter use resulting in 90% consumption prior to mid-January were intermediate in *WOLF, SNOW,* and *ELK* (RSF) values (Figure 4.6).

Univariate model set

In univariate modeling of the proportion of browse removed, $ELK_{prewolf}$ and $ELK_{postwolf}$ minimized the log likelihoods when measured at the 600-m and 500-m scales, respectively. Further, $ELK_{postwolf}$ provided a better fit to the browse removal data than the $ELK_{prewolf}$ by a considerable margin ($\Delta AIC_c = 6.78$) indicating elk habitat selection after wolf recovery was the better predictor of browse removal, as expected. I used the variable with the best fit, $ELK_{postwolf}$ at the 500-m scale, for the *ELK* variable in the multivariate model set. Also, because I found a stronger quadratic than linear relationship between $ELK_{postwolf}$ and browse removed, I included a squared term for

$ELK_{postwolf}$ in the multivariate model set. Because $ELK_{postwolf}$ and *SNOW* were highly correlated ($R^2 > 0.70$) these variables were not entered into the same models.

Values of $RISK_{site}$ (the difference between $ELK_{prewolf}$ and $ELK_{postwolf}$) summed at a 6-km radius around willow sites provided a good fit relative to the $ELK_{postwolf}$ ($\Delta AIC_c = 1.02$); however, while exploring the fit of differing scales of $RISK_{site}$ to the willow browse data, I noted correlation with *SNOW* and $ELK_{postwolf}$ increased as scale increased (Table 1). From predictions of the single-term model, the effect of $RISK_{site}$ was highly variable (Figure 4.7). For example, two sites predicted to have the greatest decreased selection since wolf recovery also had 2 of the 5 highest browse estimates (Figure 4.7). Due to its correlation with $ELK_{postwolf}$ and *SNOW*, *RISK* at scales >2 km was not incorporated in the same models with these variables to avoid colinearity.

Multivariate model set

The three multivariable, explanatory models with the highest AIC_c accounted for >70% of the variation in total willow stem length removed (Table 2), and were equally supported ($\Delta AIC_c < 4$). $ELK_{postwolf}$, or attractiveness of the site as predicted by the Mao et al. (2005) RSF models after wolf recovery, and *ROAD* were in all 3 models. The term *WOLF* occurred in one top model ($\Delta AIC_c = 0.73$), and had a negative coefficient (Table 3) indicating elk browsed willow less where wolf presence was high in 2003-2004. Seventy-one percent of the variance was explained by the best model, and adding *WOLF* increased this by only 3.5%. The model without *WOLF* had 1.4 times more weight of evidence than the one with *WOLF* as determined by Akaike weights (Table 2). *OPEN* appeared in one top model ($\Delta AIC_c = 2.93$), and had a negative coefficient indicating as sites became more open (less forested) browsing decreased. However, the Akaike weights indicate the weight of evidence for the model without *OPEN* was 4.4 times greater than with *OPEN* (Table 2). Quadratic forms of both *WOLF* and *OPEN* were examined, but these did not improve the fit ($\Delta AIC_c = 10.9$, $\Delta AIC_c = 11.4$, respectively). *SNOW* did not appear in any of the top models, but as noted, *SNOW* was correlated ($R^2 = 0.86$) with the $ELK_{postwolf}$ variable (Table 1). Model predictions for the influence of each variable indicate variation in $ELK_{postwolf}$ caused large variation in browsing, while the effect of *WOLF* and *OPEN* were moderate, and *ROAD* was small in multivariate models (Figure 4.8).

DISCUSSION

Heavy use of willow was documented for 3 decades prior to wolf recovery in YNP (Chadde and Kay 1991, Singer et al. 1994, Singer 1996, Wagner 2006, Wolf et al. 2007), and in other areas where elk density is high (Brookshire et al. 2002, Singer et al. 2002, Thorne et al. 2003). With few exceptions among the willow sites, this trend appears to have continued through 2004 where arrested growth with short, dense forms having many small shoots in the intercanopy space (Figure 4.3) predominated (>49% of clumps) at 19 of 23 willow sites sampled (Figure 4.4).

A decade after wolf recovery, some data (e.g., Ripple and Beschta 2004, 2006; Beyer et al. 2007) indicate wolves are triggering a top-down trophic cascade on woody browse species, e.g., willow, on the NR. While an effect of wolves on the rates of willow browse was found in this study, this effect may be of limited consequence under current browsing levels. Across the NR, 76% of willow classified was arrested after a history of browsing that has been intense (>50% of annual growth) and consistent in recent years (Singer et al. 1994, Thorne et al. 2003, Keigley et al. 2003). This browse level may not have significantly changed since Singer et al. (1994)'s survey 16 years earlier. In the late 1980's, an estimated 80% of willow was height-suppressed with a mean of 59% of shoot length removed in the winter (Singer et al. 1994) compared with 76% and 49% in this study. Continued use by elk caused even the site of highest wolf use to experience 40% willow removal.

Winter measurements revealed a strongly seasonal component in YNP's trophic cascade. Release of browse species during the summer growing season (e.g., Beyer et al. 2007) may be due to wolf-avoidance strategies by elk (Mao et al. 2005), and might have contributed to the released architectural types found at 3 sites (Figure 4.3). Yet, even within these stands some willow had a retrogressed appearance (Figure 4.4). Having experienced a release from browse, likely in the late 1990's or early 2000's, some (18% of the released willow clumps) again experienced heavy browsing, particularly around the perimeter (Figure 4.4). The reliance of elk on willow in the winter may be one of the strongest determining factors for the long-term state of willow and could negate seasonal release from herbivory experienced in summer.

Willow is preferred winter forage (Singer et al. 1994) and rapid removal, >80% of estimated biomass in a 2-week period at 5 of 7 sites (Figure 4.6), also suggests little willow biomass may be available relative to the elk density on the NR in 2003-2004. While measurements were coarse, they were adequate for describing the temporal pattern of elk browsing willow at sites. Temporal patterns of willow browse (Figure 4.6) may be related to a dynamic, fine-scale temporal pattern of elk use described by

Creel et al. (2005), Fortin et al. (2005), and Gude et al. (2006). Interactions with wolves may cause elk to temporarily avoid an area, but the response is short-term and occurs on a small scale (Kunkel and Pletscher 2001, Creel et al. 2005) allowing elk access, albeit occasionally interrupted, to the small amount of willow that is available to them.

Other trophic cascade cases involving wolves (McLaren and Peterson 1994, Klein 1995, Hebblewhite et al. 2005) have hinged largely on changes in prey density, i.e., a density-mediated indirect interaction (Schmitz et al. 2004). In YNP, elk density has decreased >40% since wolf reintroduction (White and Garrott 2005), and the growth response in willow that has been detected (Ripple and Beschta 2006, Beyer et al. 2007) may be, in part, interpretable as a response to this decline in winter density along with changes in summer use patterns. Even with this wolf effect, NR winter elk density in 2003-2004 is still relatively high (4-6 elk/km^2) for what may be necessary for significant alleviation of browse. Less than 1 elk/km^2 was necessary for release of aspen in some Rocky Mountain regions (see White et al. 1998). Trophic cascades may be in an early stage in YNP (Ripple and Beschta 2004, 2006), but a greater response hinges on further declines in elk density. Only moderate (14-21%) long-term declines in NR elk density were predicted with simulation models that did not predict densities <1 elk/km^2 (Varley and Boyce 2006). Hence, wolf predation may not be sufficient on its own to hold elk at low density long enough for a substantial willow response because wolf predation is highly selective for non-productive herd members (Wright and Peterson 2006, Eberhardt et al. 2007) and might be compensatory with climate-driven mortality sources (Vucetich et al. 2005). Additionally, wolf density on the NR is limited by intraspecific competition and territoriality (Kauffman et al. 2007) which has caused the population growth rate to stabilize (Smith et al. 2006).

If the 14% of released willow clumps classified in this study (Figure 4.4) were due to a wolf effect, can this be viewed as a trophic cascade? A change in the overall community that includes a redistribution of biomass affecting a diverse group of species has been favoured as the definition of the trophic cascade (*sensu* Polis et al. 2000). Indeed, around wolf den sites and during periods of low-density elk, wolf-mediated browse may lead to the community-wide effects that occurred in Banff National Park (Hebblewhite et al. 2005). In the context of the Banff study, YNP's trophic cascade currently lacks the songbird, beaver (*Castor canadensis*), and microtine community that returned in accord with widespread released willow stands. Trophic effects due to wolves may be inconsistent and outcomes difficult to predict across the wide range of ecological conditions under which they occur (Garrott et al. 2005). They may be strongest when low-density prey populations result (e.g., Klein 1995, Hebblewhite et al. 2005), which has not occurred thus far in YNP. The effect of wolves on browse may accumulate locally over longer periods, perhaps many decades as the NRC (2002) noted. But the future of willow and other woody browse species on the NR appears to most directly relate to high herbivore densities and marginal growth conditions that have determined growth patterns for >1,600 years (Whitlock et al. 1991). The effect of variation in growth conditions and herbivore density (mediated by predation) will likely continue to lead to episodic recruitment of these browse species for many centuries.

For example, in the late 1800's, willow, aspen and cottonwood were recruited to tree height on the NR (Romme et al. 1995, Beschta 2005, Wagner 2006). At that time, elk were at low density due to human exploitation (Schullery and Whittlesey 1995), climate was wetter than at present (Whitlock et al. 1991, YNP 1997), and the effects of beavers and wolves had not been lost functionally from the landscape (Schullery and Whittlesey 1995). In contrast, at the onset of wolf recovery in 1995, elk density was high (>8 km^2, White and Garrott 2005), willow was in a state of on-going suppression (Singer et al. 1994, YNP 1997, Wagner 2006), and beaver were rare on the NR. The lack of beaver activity throughout much of the NR has increased the severity of conditions for willow on many streams (Singer et al. 1994, Bilyeu 2006) causing willow to be kept more easily in a state of suppression. Whether elk density is the proximate or ultimate cause of browse species decline on the NR (see Singer et al. 1994, Wagner et al. 1995, YNP 1997, Wagner 2006) relates to variation in the diverse factors that mediate both herbivore density and growth conditions.

While the consequences of wolves in YNP have been highly anticipated (e.g., Smith et al. 2003, Ripple and Beschta 2004, Terborgh et al. 2006), the consequences of YNP's productive elk herd have been underappreciated. Past predictions for the outcomes of perturbations to YNP's dynamic ecosystem have fallen short when discounting the high herbivore density that YNP supports. In the 1960's large reductions in elk density were intended to address, among other perceived impacts, an over-browsed woody vegetation community (NRC 2002). The expected restoration of these communities failed to occur (Ripple et al. 2001, NRC 2002, Beschta 2005), perhaps because density (1-3 elk/km^2) had not been held low enough for long enough for effects to manifest (Wagner 2006). The extensive wildfires of 1988 were similarly predicted to aid in restoring aspen communities on the NR, but elk density (>10 km^2)

effectively prevented new stems from reaching heights capable of escaping browse (Romme et al. 1995). YNP hosts one of the greatest concentrations of native large mammalian herbivores on the continent (Frank and MacNaughton 1992), and conditions on the NR have become increasingly marginal for willow (YNP 1997, NRC 2002, Beyer et al. 2007). Perhaps not surprisingly, I found winter browsing by elk continues to be the leading proximate factor determining willow growth.

Table 4.1. Minimum, mean, median, maximum, and R^2 with associated P-values at the 95% confidence level for correlation between the independent variables for predicting willow removal by elk.

	$ELK_{postwolf}$	$ELK_{prewolf}$	$WOLF$ ($x\ 10^{-4}$)	$RISK$	$ROAD$, meters	$OPEN$	$SNOW$
Minimum	629	935	0.02	2727	134	105	95
Mean	686	1078	9.78	4659	540	269	138
Median	687	1082	3.29	4353	987	237	136
Maximum	726	1440	48.39	10728	3842	289	209
Correlation matrix:							
$ELK_{postwolf}$		0.92/ 0.000	0.28/ 0.010	0.36/ 0.003	0.04/ 0.234	0.03/ 0.455	0.86/ 0.000
$ELK_{prewolf}$	0.92/ 0.000		0.19/ 0.035	0.21/ 0.280	0.02/ 0.219	0.04/ 0.351	0.75/ 0.000
$WOLF$	0.28/ 0.010	0.19/ 0.035		0.06/ 0.253	0.00/ 0.453	0.04/ 0.350	0.31/ 0.006
$RISK$	0.36/ 0.003	0.21/ 0.280	0.06/ 0.253		0.02/ 0.498	0.04/ 0.372	0.37/ 0.002
$ROAD$	0.04/ 0.234	0.02/ 0.219	0.00/ 0.453	0.02/ 0.498		0.24/ .0160	0.00/ 0.914
$OPEN$	0.03/ 0.455	0.04/ 0.351	0.04/ 0.350	0.04/ 0.372	0.24/ 0.160		0.00/ 0.952
$SNOW$	0.86/ 0.000	0.75/ 0.000	0.31/ 0.006	0.37/ 0.002	0.00/ 0.914	0.00/ 0.952	

Table 4.2. Models for detecting factors related to willow removal by elk. Number of parameters (K), degrees of freedom (d.f.), residual deviance (Dev.), percent variation explained (% var.), log-likelihood (LL), AIC$_c$, change in AIC$_c$ compared with the best model (ΔAIC$_c$), and AIC$_c$ weight (w_i) are given for each model.

Model Description	K	d.f.	Dev.	% var.	LL	AIC$_c$	ΔAIC$_c$	(w_i)
ELK* ROADS*	5	18	0.36	70.84	15.17	-16.80	0.00	0.44
ELK* ROADS* WOLF	6	17	0.32	74.39	16.66	-16.07	0.73	0.31
ELK* ROADS* OPEN	6	17	0.35	71.83	15.56	-13.88	2.93	0.10
ELK*	3	20	0.57	54.20	9.97	-12.69	4.12	0.06
ELK* ROADS* WOLF OPEN	7	16	0.31	74.71	16.81	-12.14	4.66	0.04
ELK* WOLF	4	19	0.53	56.79	10.64	-11.07	5.74	0.03
ELK* OPEN	4	19	0.57	54.21	9.98	-9.73	7.07	0.01
SNOW ROAD* WOLF	5	18	0.49	60.14	11.57	-9.62	7.19	0.01
ELK* WOLF OPEN	5	18	0.53	57.09	10.72	-7.92	8.89	0.00
SNOW ROAD*	4	19	0.63	48.76	8.68	-7.15	9.66	0.00
NULL MODEL	1	22	1.24	0	0	2.19	19.03	0.00

* denotes a quadratic form, e.g., $ELK + ELK^2$ and $ROAD + ROAD^2$

Table 4.3. Coefficient, standard error, z-value, P value, and 95% confidence interval variables of the top 3 models explaining variation in willow removal by elk at 23 willow sites on the Northern Range of Yellowstone National Park, winter 2003-2004.

Term	Coefficient	Std. Error	z	P > |z|	[95% confidence interval]	
constant	-82.88431	18.034	-4.6	0.000	-118.2291	-47.53952
ELK	0.2410828	0.0533871	4.52	0.000	0.136446	0.3457195
ELK^2	-0.000174	0.000039	-4.40	0.000	0.0002512	-0.000096
ROAD	0.0003745	0.0001187	3.16	0.002	0.0001419	0.0006072
ROAD^2	-9.21E-08	3.15E-08	-2.93	0.003	-1.54E-07	-3.05E-08
constant	-57.71653	23.89213	-2.42	0.016	-104.5442	-10.88881
WOLF	-561.1947	365.3536	-1.54	0.125	-1277.275	154.8852
ELK	0.1647083	0.0715703	2.3	0.021	0.0244331	0.3049836
ELK^2	-0.000116	0.0000536	-2.16	0.03	-0.000221	-1.09E-05
ROAD	0.0003475	0.0001158	3	0.003	0.0001205	0.0005744
ROAD^2	-7.72E-08	3.19E-08	-2.42	0.015	-1.40E-07	-1.47E-08
constant	-91.494	21.374	-4.28	0.000	-133.3875	-49.60167
OPEN	-0.000534	0.0006913	-0.77	0.44	-0.0018891	0.00082
ELK	0.26678	0.06341	4.21	0.000	0.1425	0.3911
ELK^2	-0.00019	0.000047	-4.12	0.000	-0.00028	-0.0001
ROAD	0.00041	0.000128	3.20	0.001	0.000158	0.000658
ROAD^2	-1.06E-07	3.64E-08	-2.91	0.004	-1.77E-07	-3.44E-08

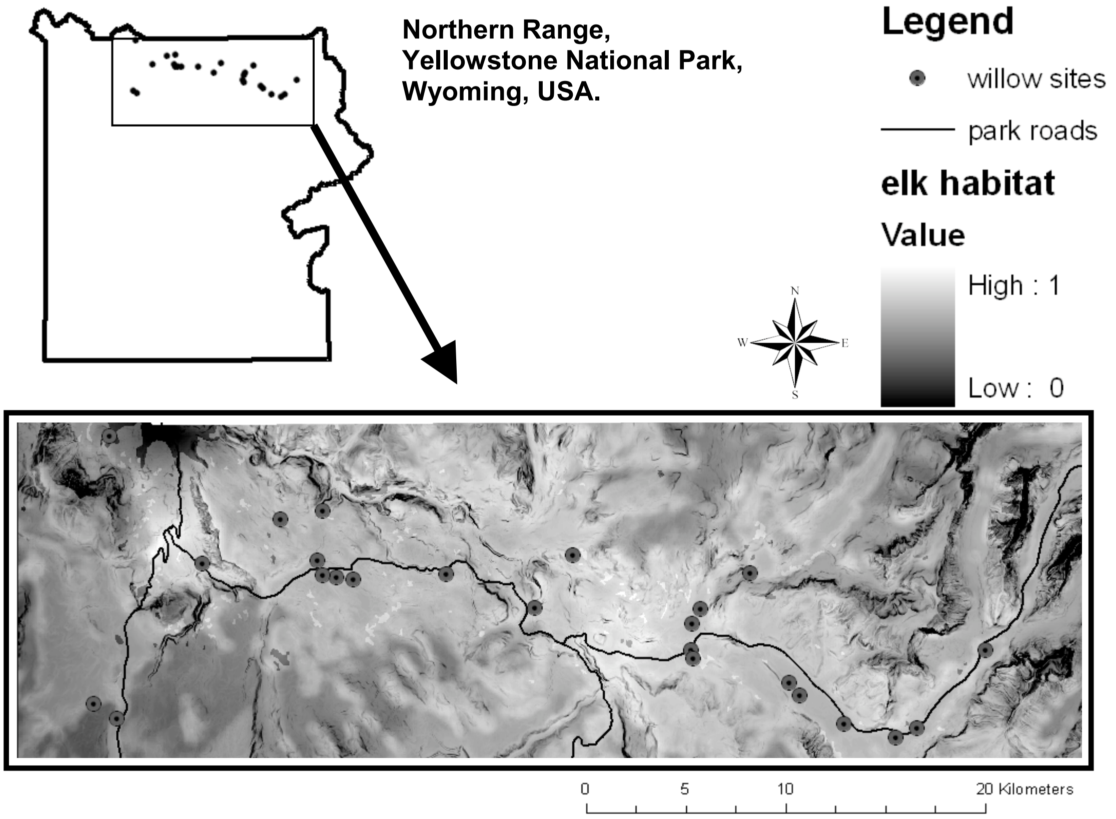

Figure 4.1. The Northern Range of Yellowstone National Park with locations of park roads and willow sampling sites in relation to elk resource selection for winter 2003-2004.

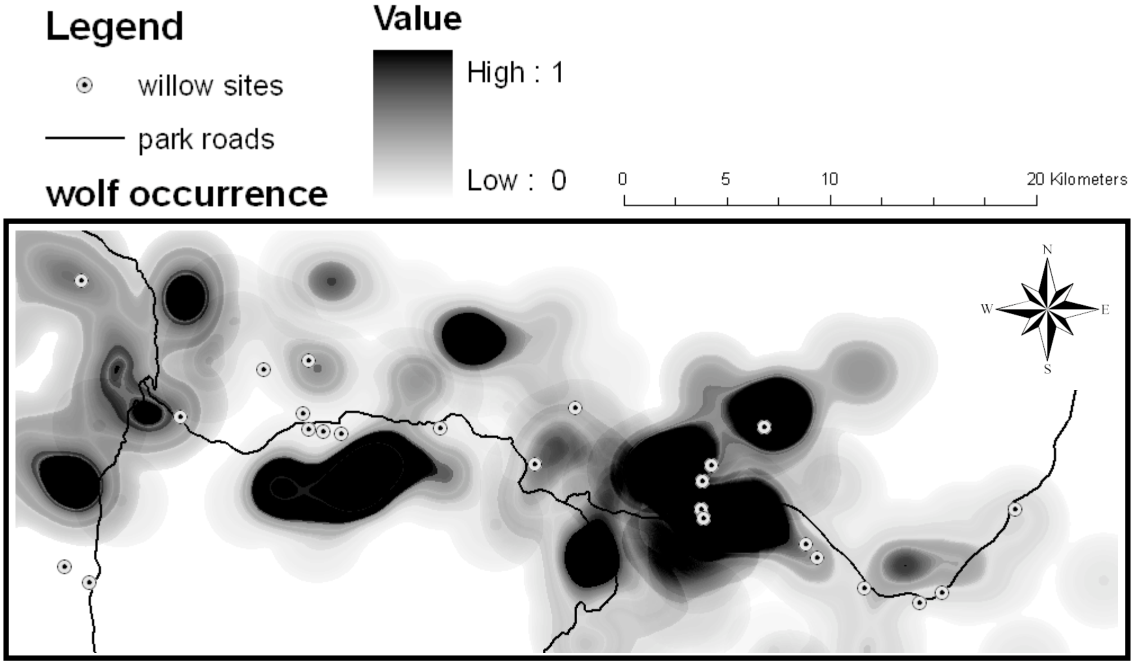

Figure 4.2. The Northern Range of Yellowstone National Park with locations of park roads and willow sampling sites in relation to wolf density for winter 2003-2004.

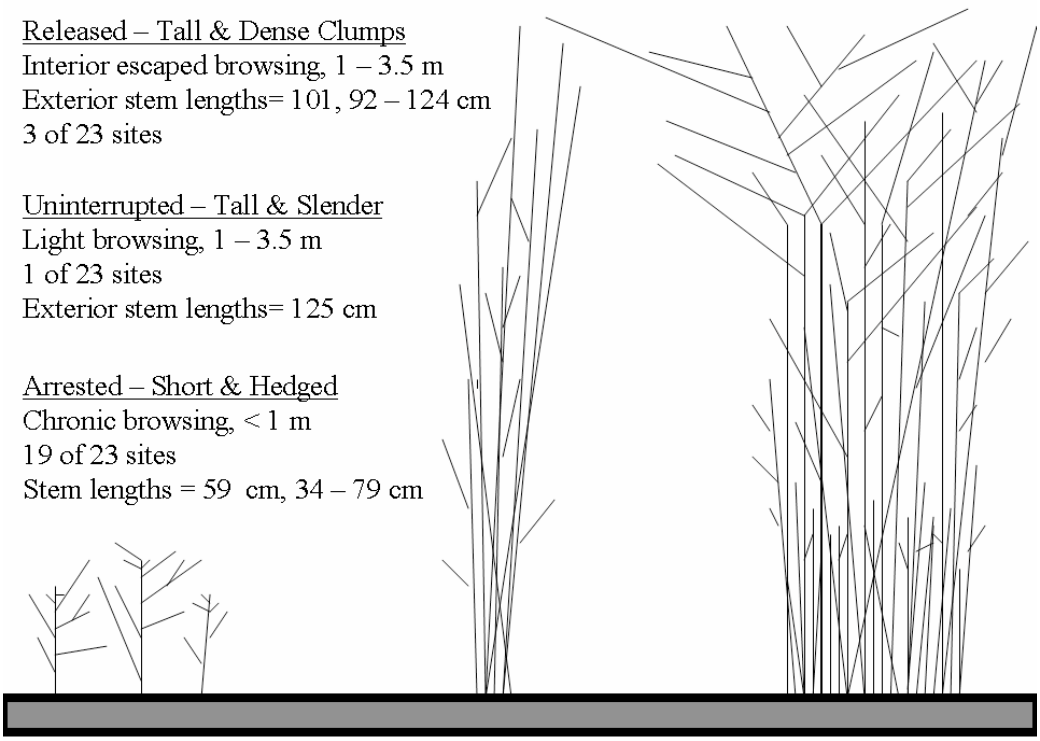

Figure 4.3. Willow architectural types found at 23 sites on the Northern Range of Yellowstone National Park in the fall of 2003.

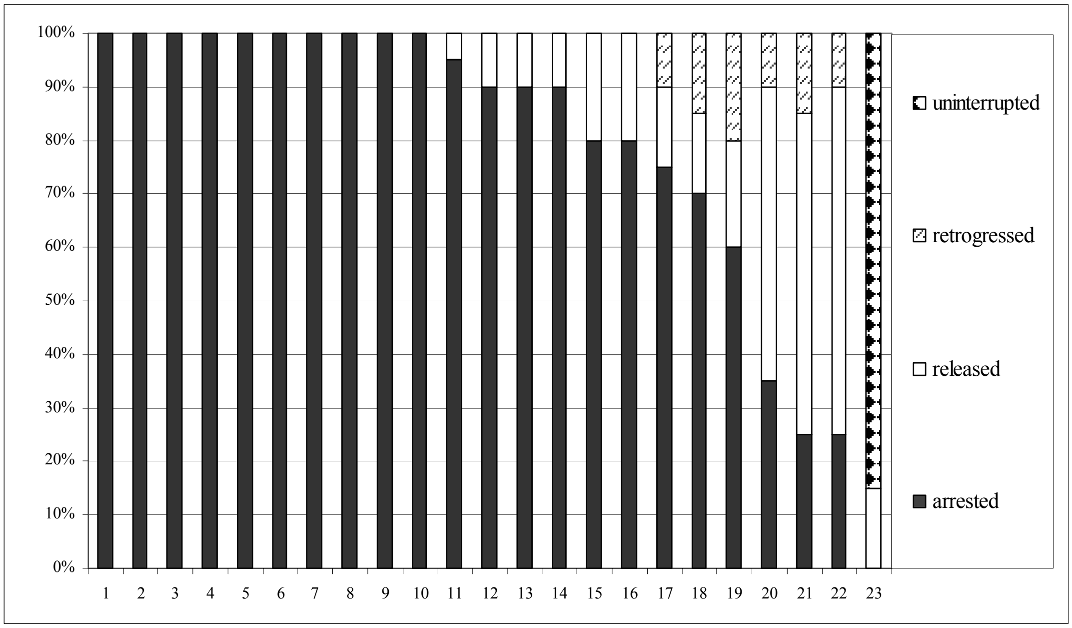

Figure 4.4. Proportion of willow architectural types found within the 23 sites on the Northern Range of Yellowstone National Park in the fall of 2003.

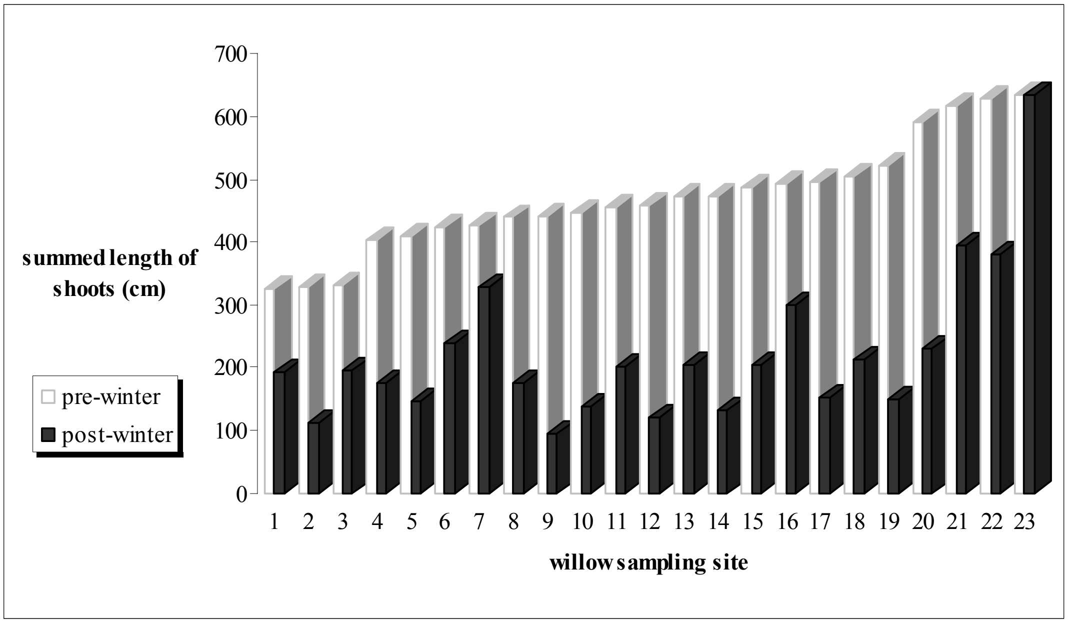

Figure 4.5. Pre-winter and post-winter measurement comparisons of the summed length of willow shoots at 23 sites on the Northern Range of Yellowstone National Park.

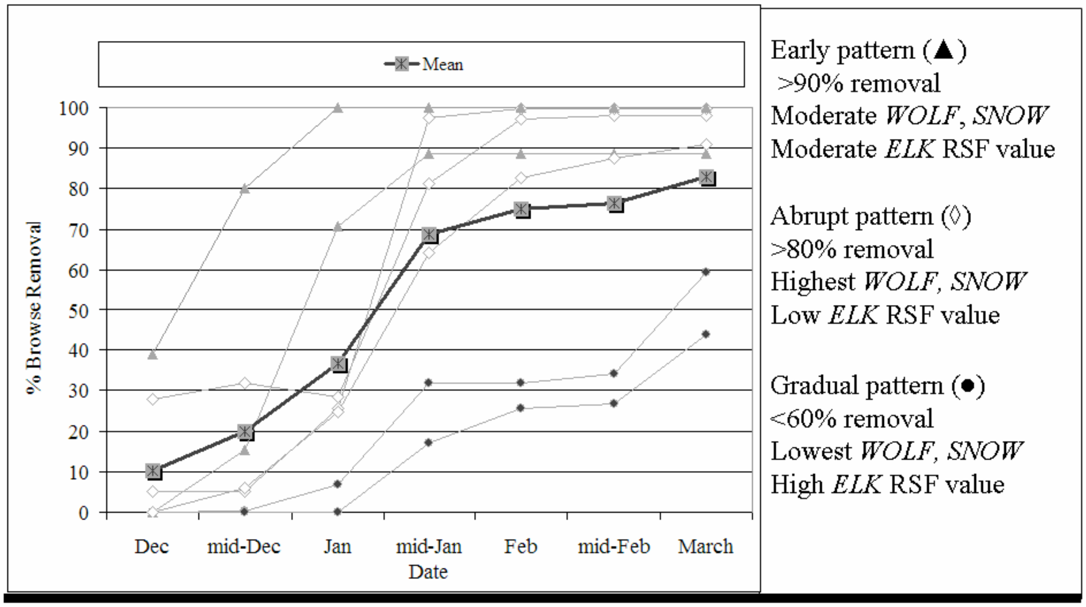

Figure 4.6. Estimates of willow removal for biweekly periods, December 2003 to March 2004, at 7 willow sampling sites on the Northern Range of Yellowstone National Park. Patterns are indicated by symbols as: early pattern (▲), abrupt pattern (◊), and gradual pattern (●).

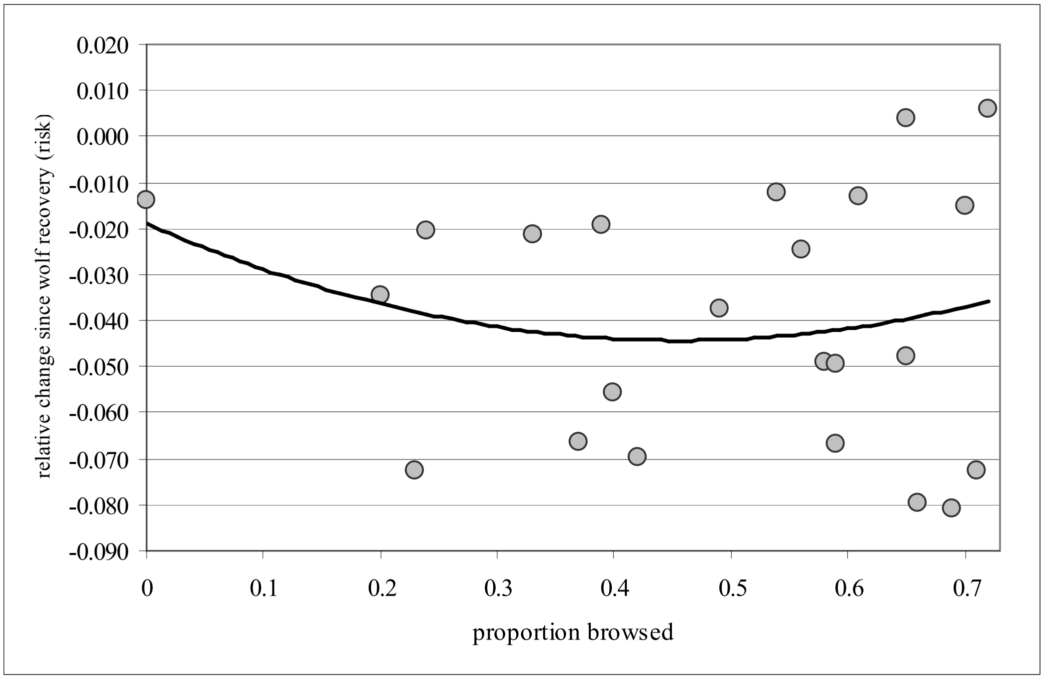

Figure 4.7. The effect of changes in elk resource selection since wolf restoration in Yellowstone National Park on proportion of willow browsed. Greater predation risk was assumed with increasing relative change since wolf recovery.

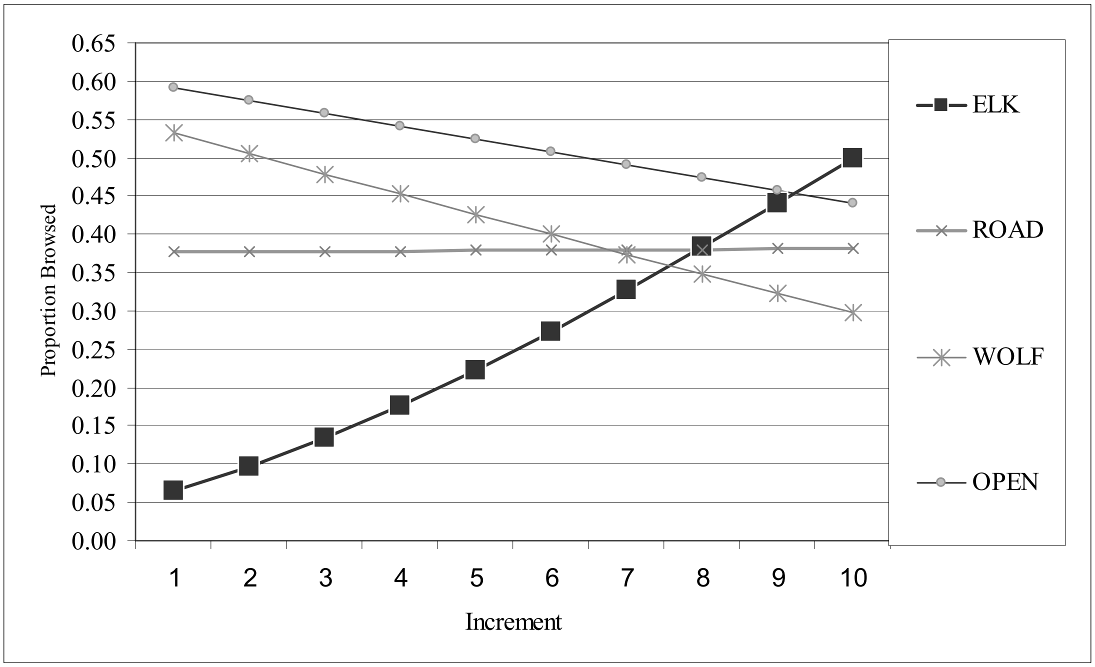

Figure 4.8. Model predictions for the relative effect of the *ELK, WOLF, OPEN,* and *ROAD* variables on the proportion of willow browsed at sampling sites. Each term was varied individually in 10 equal increments across the range measured while keeping all other terms constant using their mean value from the sample.

REFERENCES

Bangs, E. E., and S. H. Fritts. 1996. Reintroducing the gray wolf to central Idaho and Yellowstone National Park. Wildlife Society Bulletin **24**:402–413.

Barmore, W. J., Jr. 2003. Ecology of ungulates and their winter range in northern Yellowstone National Park: research and synthesis, 1962–1970. Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA.

Berger, J., P. B. Stacey, L. Bellis, and M. P. Johnson. 2001. A mammalian predator–prey imbalance: Grizzly bear and wolf extinction affect avian neotropical migrants. Ecological Applications **11**:967–980.

Bergman, E. J., R. A. Garrott, S. Creel, J. J. Borkowski, R. Jaffe, and F. G. R. Watson. 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. Ecological Applications **16**:273–284.

Beschta, R. L. 2005. Reduced cottonwood recruitment following extirpation of wolves in Yellowstone's Northern Range. Ecology **86**:391–403.

Beyer, H. L., E. H. Merrill, N. Varley, and M. S. Boyce. 2007. Willow on Yellowstone's northern range: evidence for a trophic cascade in a large mammalian predator-prey system? Ecological Applications **17**:1563–1571.Bilyeu, D. 2006. Effects of elk browsing and water table on willow growth and physiology: implications for willow restoration in Yellowstone National Park. Ph.D. dissertation, Fort Collins: Colorado State University, USA.

Bilyeu, D., D. J. Cooper, and N. T. Hobbs. 2007. Assessing impacts of large herbivores on shrubs: tests of scaling factors for utilization rates from shoot-level measurements. Journal of Applied Ecology **44**:168–175.

Boyce, M. S. 2006. Scale for resource selection functions. Diversity and Distributions **12**:269–276.

Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Écoscience **10**:421–431.

Brookshire, E. N. J., J. B. Kauffman, D. Lytjen, and N. Otten. 2002. Cumulative effects of wild ungulate and livestock herbivory on riparian willows. Oecologia **132**:559–566.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Chadde, S., and C. Kay. 1991. Tall-willow communities on Yellowstone's northern range: a test of the "natural regulation" paradigm. Pages 231–262 *in* Keiter, R. B., and M. S. Boyce, editors. The greater Yellowstone ecosystem: redefining America's wilderness heritage. Yale University Press, New Haven, Connecticut, USA.

Creel, S., J. Winnie, Jr., B. Maxwell, K. L. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology **86**:3387–3397.

Eberhardt, L. L., P. J. White, R. A. Garrott, and D. B. Houston. 2007. A seventy-year history of trends in Yellowstone's northern elk herd. Journal of Wildlife Management **71**:594–602.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology **86**:1320–1331.

Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology **73**:2043–2058.

Garrott, R. A., J. A. Gude, E. J. Bergman, C. Gower, P. J. White, and K. L. Hamlin. 2005. Generalizing wolf effects across the Greater Yellowstone Area: a cautionary note. Wildlife Society Bulletin **33**:1245–1255.

Gude, J. A., R. A. Garrott, J. J. Borkowski, and F. King. 2006. Prey risk allocation in a grazing ecosystem. Ecological Applications **16**: 285–298.

Hebblewhite, M., C. A. White, C. N. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. Ecology **86**:2135–2144.

Hosmer, D. W., and S. Lemeshow. 2000. Applied Logistic Regression. Wiley, New York, New York, USA.

Houston, D. B. 1982. The northern Yellowstone elk: ecology and management. Macmillan Publishing, New York, New York, USA.

Huggard, D. J. 1993. Effect of snow depth on predation and scavenging by gray wolves. Journal of Wildlife Management **57**:382–388.

Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. Ecology Letters **10**:690–700.

Keigley, R. B., M. R. Frisina, and C. Fager. 2003. A method for determining the onset year of intense browsing. Journal of Range Management **56**:33–38.

Klein, D. R. 1995. The introduction, increase, and demise of Wolves on Coronation Island, Alaska. Pages 275–280 *in* Carbyn, L. N., S. H. Fritts, D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Canada.

Kunkel, K. E., and D. H. Pletscher. 2001. Winter hunting patterns of wolves in and near Glacier National Park, Montana. Journal of Wildlife Management **65**:520–530.

Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. Journal of Wildlife Management **69**:1691–1707.

McLaren, B. E., and R. O. Peterson. 1994. Wolves, moose, and tree rings on Isle Royale. Science **266**:1555–1558.

Mech, L. D., and R. O. Peterson. 2003. Wolf-prey relations. Pages 131-160 *in* Mech, L. D., and L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois, USA.

National Research Council. 2002. Ecological dynamics on Yellowstone's northern range. National Academy Press, Washington, D.C., USA.

Polis, G. A., A. L. W. Sears, G. R. Huxel, D. R. Strong, and J. Maron. 2000. When is a trophic cascade a trophic cascade? Trends in Ecology & Evolution **15**:473–475.

Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. Biological Conservation **102**:227–234.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience **54**:755–766.

Ripple, W. J., and R. L. Beschta. 2005. Willow thickets protect young aspen from elk browsing after wolf reintroduction. Western North American Naturalist **65**:118–122.

Ripple, W. J., and R. L. Beschta. 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. Forest Ecology and Management **230**:96–106.

Romme, W. H., M. G. Turner, L. L. Wallace, and J. S. Walker. 1995. Aspen, elk and fire on the northern range of Yellowstone National Park. Ecology **76**:2097–2106.

Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. Ecology Letters **7**:153–163.

Schullery, P., and L. Whittlesey. 1995. A summary of the documentary record of wolves and other wildlife species in the Yellowstone National Park area prior to 1882. Pages 63–76 *in* Carbyn, L. N., S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Canada.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology **77**:2075–2085.

Singer, F. J. 1996. Differences between willow communities browsed by elk and communities protected for 32 years in Yellowstone National Park. Pages 270–290 *in* F. J. Singer, editor. Effects of grazing by wild ungulates in Yellowstone National Park. Technical Report NPS/NRYELL/NRTR/96-01, NPS, Natural Resource Information Division, Denver, USA.

Singer, F. J., L. C. Mark, and R. C. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern range. Journal of Range Management **43**:295–299.

Singer, F. J., L. C. Zeigenfuss, B. Lubow, and M. J. Rock. 2002. Ecological evaluation of ungulate overabundance in U.S. national parks: a case study. Pages 205–248 *in* Singer, F. J., and L. C. Zeigenfuss, editors. Ecological evaluation of the abundance and effects of elk herbivory in Rocky Mountain National Park, Colorado, 1994-1999. Open file report 02-208. U. S. Department of the Interior, U. S. Geological Survey, and Natural Resources Ecology Lab, Colorado State University, Fort Collins, Colorado, USA.

Smith, D. W., R. O. Peterson, and D. B. Houston. 2003. Yellowstone after wolves. BioScience **53**:330–340.

Smith, D. W., T. D. Drummer, K. M. Murphy, D. S. Guernsey, and S. B. Evans. 2004. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995-2000. Journal of Wildlife Management **68**:153–166.

Smith, D. W., D. R. Stahler, and D. S. Guernsey. 2006. Yellowstone wolf project annual report 2005. Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA.

Taper, M. L., and P. J. P. Gogan. 2002. The northern Yellowstone elk: density dependence and climatic conditions. Journal of Wildlife Management **66**:106–122.

Terborgh, J., K. Feeley, M. Silman, P. Nunez, and B. Balukjian. 2006. Vegetation dynamics of predator-free land-bridge islands. Journal of Ecology **94**:253–263.

Tyers, D. B., and L. R. Irby. 1995. Shiras moose winter habitat use in the upper Yellowstone River Valley prior to and after the 1988 fires. Alces **31**:35–43.

Varley, N., and M. S. Boyce. 2006. Adaptive management for reintroductions: Updating a wolf recovery model for Yellowstone National Park. Ecological Modelling **193**:315–339.

Vucetich, J. A., D. W. Smith, and D. R. Stahler. 2005. Influence of harvest, climate, and wolf predation on Yellowstone elk, 1961-2004. Oikos **111**:259–270.

Wagner, F. H. 2006. Yellowstone's destabilized ecosystem: elk effects, science, and policy conflict. Oxford University Press, New York, USA.

Wagner, F. H., R. B. Keigley, and C. L. Wamboldt. 1995. Comment: ungulate herbivory of willows on Yellowstone's northern winter range: Singer et al. (1994). Journal of Range Management **48**:475–477.

White, P. J., and R. A. Garrott. 2005. Yellowstone's ungulates after wolves - expectations, realizations, and predictions. Biological Conservation **125**:141–152.

White, C. A., C. E. Olmsted, and C. E. Kay. 1998. Aspen, elk and fire in the Rocky Mountain national parks of North America. Wildlife Society Bulletin **26**:449–462.

Whitlock, C. A., S. Fritz, and D. R. Engstrom. 1991. A prehistoric perspective on the northern range. Pages 289-308 in R. B. Keiter, and M. S. Boyce, editors. The greater Yellowstone ecosystem: redefining America's wilderness heritage. Yale University Press, New Haven, Connecticut, USA.

Wockner, G., F. J. Singer, M. Coughenour, and P. Farnes. 2006. Yellowstone Snow Model. Natural Resources Ecology Lab, Colorado State University, Fort Collins, Colorado. http://www.nrel.colostate.edu/projects/yellowstone/.

Wright, G. J., R. O. Peterson, D. W.Smith, and T. O. Lemke 2006. Selection of northern Yellowstone elk by gray wolves and hunters. Journal of Wildlife Management **70**:1070-1078.

Yellowstone National Park. 1997. Yellowstone's northern range: complexity and change in a wildland ecosystem. Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA.

CHAPTER 5

THE ROLE OF GRAY WOLVES IN ECOLOGICAL COMMUNITIES

Throughout the northern hemisphere, the gray wolf (*Canis lupus*) is the most widespread apex carnivore in terrestrial communities. In recent history wolves have been extirpated throughout much of their former range due largely to conflicts with human agrarian culture. Evolving attitudes and increased appreciation for the predator among cultures in mostly urban areas (Fritts et al. 2003, Mech and Boitani 2003a) has resulted in increased tolerance and protection for wolves, including reintroductions in the Rocky Mountains and desert southwest of the United States. Boitani (2003: Figure 13.1) lists increasing population trends in 16 of 46 countries, 8 of 8 U. S. states, and 4 of 10 Canadian provinces. With gray wolf recovery efforts in many parts of their former circumpolar range (e.g., Blancó et al. 1990, Bangs and Fritts 1996, Wabakken et al. 2001), the wolf's role in community ecology has emerged as a potential emphasis in how the species is managed.

Yet, recent reviews on wolf ecology (Carbyn et al. 1995, Mech and Boitani 2003b) focused mainly on natural history, predator-prey interactions, social behavior, and conflicts between wolves and humans without delving substantively into the indirect effects of wolf predation in community structure and function (but see Mech and Boitani 2003c). Gray wolves may be one of the most-studied vertebrate species (Mech and Boitani 2003b, Boyce 2005), but only recently has research investigated their role in community ecology. With their return as apex predators is the expectation for significant restructuring of their ecosystems via top-down pathways (Soulé et al. 2003, 2005, Smith et al. 2003, Terborgh et al. 2006).

Wolves fail to meet the ideal criteria for multiple single-species management designations including flagships, indicators, and umbrellas (Landres et al. 1988, Niemi et al. 1997, Linnell et al. 2000, Mech and Boitani 2003a). Mech and Boitani (2003a) claim wolves are not keystone species because they are not essential for many other species to exist (sensu Simberloff 1998); however, a keystone species according to some (e.g., Power et al. 1996, Halaj and Wise 2001, Soulé et al. 2005) need only have a disproportionate effect on system dynamics relative to its total biomass in the system. Often the loss of wolves in food webs leads to diminished community diversity and function, i.e., they may affect crucial processes in food webs (Estes 1996; Berger 1999, Berger et al. 2001, Soulé et al. 2005, Terborgh et al. 2006), and extirpation of keystone species often reveals these losses of top-down processes (Pace et al. 1999). Specifically, the loss of wolves may lead to overabundant large herbivores, suppression of vegetation, and impact to species that rely on these components of an ecosystem. When wolves are restored, this interaction may be reversed to influence biomass distribution and species diversity (Pace et al. 1999). Terborgh et al. (1999, 2001) have suggested that ecosystems are in decline globally while carnivore conservation and the role it plays in maintaining species diversity and evenness have not been acknowledged. Thus, a shift in management emphasis to acknowledge the systemic influences of wolves and other top predators requires strong advocacy (Terborgh et al. 1999, Soulé et al. 2005) and a clear understanding of the community effects associated with wolf extirpation/restoration.

Currently, management in many countries is at a crossroads while transitioning from recovery to long-term maintenance of populations. For example, wolves in the

Great Lakes and Rocky Mountain states of USA have reached biological recovery goals prompting state managers to adopt long-term management plans for wolf conservation (U. S. Department of Interior 2006, 2007). The course management will take will be influenced by the tendency for wolves to reduce herbivore abundance that invokes controversy when human harvest opportunities are lost (Boitani 2003, Fritts et al. 2003), as well as, livestock depredation conflicts that will limit wolf density and distribution (Fritts et al. 2003).

Managing wolves for keystone effects has at least two major impediments. First, the afore-mentioned conflicts with human interests have discouraged the growth and expansion of populations beyond minimum recovery goals (Mech and Boitani 2003a, Pyare and Berger 2003). Second, the keystone effects associated with wolves have been investigated only recently and require a rigorous review and synthesis of available evidence to build a strong case. Understanding how and when wolves increase biodiversity and evenness, as well as, influence the structure and energy flow in communities provides a context for a more compelling justification for managing wolves widely for these properties. Providing this motivation may be one of the best opportunities that ecologists have had in decades for encouraging the implementation of ecological management on large scales. To this end, I reviewed wolf studies to assess the case for wolves having keystone effects and what factors affect their magnitude.

REDUCING OVERABUNDANT HERBIVORES

The undesired effects of overabundant native herbivores receive little attention among ecologists relative to the impact they have on communities (Garrott et al. 1993). Wolf predation can reduce herbivore abundance and release vegetation from intense herbivory to influence entire communities. Wolves select individual prey made vulnerable by age (Wright et al. 2006, Eberhardt et al. 2007), health (Fuller and Keith 1980, Mech and Peterson 2003), and/or landscape conditions (Hebblewhite et al. 2005a, Kauffman et al. 2007). Diseased and parasitized individuals are taken disproportionately, which slows spread in populations (Mech and Peterson 2003). Wolves trim continuously from prey populations in accord with their vulnerability. In this manner, prey population growth is slowed and large density-dependent die-offs occurring due to forage depletion and/or extreme weather are less frequent (Varley and Boyce 2006, Eberhardt et al. 2007). Similarly, wolf predation buffers against the effects of climate change by the reduction in amplitude of population fluctuation that extreme weather conditions cause (Wilmers and Getz 2005). Selection for mostly the unproductive fringe of an herbivore population further reduces density without a proportional reduction in reproductive potential. This contributes to both maintaining stable coexistence of wolves and prey and prey and its forage (Mech and Peterson 2003, Kauffman et al. 2007). Mortality due to selective predation is less costly in terms of population growth relative to the less-selective human harvest regimes that cull more productive age classes (Wright et al. 2006, Eberhardt et al. 2007); therefore, human hunters do not perform the same function because the benefits to prey populations and to ecosystems from highly selective culling are not conferred (Berger 2005).

BENEFITING SCAVENGERS

Wolves support a diverse scavenger guild by providing a consistent supply of carrion. Greater than 30 species of vertebrates and an even greater number of invertebrates benefit from foraging at carcasses provided by wolves (Jedrejewski et al. 2002, Wilmers et al. 2003a, 2003b, Ballard et al. 2003, Wilmers and Getz 2004). Wolves consume prey incompletely and often leave carcasses in conspicuous locations thereby providing opportunities for scavengers (Jedrzejewski et al. 1992). Carrion made available from mortality by food limitation and winter severity tends to be highly aggregated in time, which limits the ability of scavengers to take advantage of the resource when made available by these other mortality sources (Wilmers et al. 2003b). In contrast, wolf predation occurs more predictably, year-round, making it a more consistently available resource that scavengers are better able to exploit.

Competition at carcasses may have contributed to group living among wolves in that larger groups could take better advantage of the food resource by minimizing losses to scavengers (Vucetich et al. 2004). Despite this, wolves still support more scavengers relative to other predators in their community. The caching and guarding behavior of predators such as bears (*Ursus* spp.) and cougars (*Puma concolor*) does not confer the same benefits to many scavengers, and offal and other remains left by human hunters is often highly aggregated in time and space (Wilmers et al. 2003b). Provisioning of scavengers by wolves supports a greater abundance and diversity of scavenger species, and dependent relationships between scavengers and carnivores, such as that described for ravens (*Corvus corax*) following wolves (Stahler et al. 2002), have evolved as a consequence.

TRIGGERING TROPHIC CASCADES

The effects of wolves on prey populations have received much attention while the effects these have on lower trophic levels have been investigated only recently (Schmitz et al. 2000, 2004). From these studies, it is evident that wolf restoration can have strong influences on community structure and dynamics through indirect pathways, i.e., a trophic cascade. When wolves are restored to a system, they tend to affect prey negatively and producers positively, while extirpation produces the opposite effect. But when is an indirect effect a trophic cascade? A disturbing trend in ecology has been to describe indirect effects, regardless of the magnitude of impact on the system, as a trophic cascade (Polis et al. 2000). Such use diminishes the context within which I understand, describe, and evaluate the community-level consequences of trophic interactions. But by differentiating a *species* from a *community* cascade, Polis et al. (2000) made an appeal for clarity. Interactions that fundamentally structure whole food webs, rather than within a linear food chain or small part of a food web, constitute a community cascade (Polis et al. 2000). While wolves are capable of many indirect effects (Smith et al. 2003, Soulé et al. 2003), when and how often do they fundamentally change the community around them? I emphasize this distinction in evaluating the indirect effects of wolves on vegetation. Few cases of wolf-induced indirect effects included interactions described beyond two trophic levels, but some that did described startling community-wide effects (e.g., Klein 1995, Hebblewhite et al. 2005b) in which species throughout the food web were affected as interactions cascaded to benefit producers in the system and many species that relied on the producers.

WOLVES IN COMMUNITIES

Here I discuss the specific cases of multi-trophic interactions associated with wolf predation. Wolves must reach effective population densities for their impact to be realized in communities, but throughout much of the wolf's range, conflicts with humans prevent wolves from achieving densities capable of adequately limiting herbivore populations (Soulé et al. 2003). For this reason, some of the best examples of community effects originate in parks and natural areas where sufficient protection is afforded so that predator density can alter community structure (Pyare and Berger 2003, Berger and Smith 2005).

North American Hardwood Forests

Despite much documentation of the impact of overabundant white-tailed deer (*Odocoileus virginianus*) populations, no studies have reported on the direct remediation of this impact through wolf restoration. However, North American deer distribution supports the conclusion that predators limit deer abundance and allow vegetation to accumulate (Crête 1999). In areas lacking wolves, deer biomass can be as much as 5 times higher than areas with wolves (Crête 1999). This high prey density has been linked to reducing growth and recruitment of forest herbs, shrubs, and tree species (Waller and Alverson 1997, Rooney and Waller 2003, Horseley et al. 2003). Foraging by deer modifies the competitive relationships among plants resulting in altered species abundance and evenness (Côté et al. 2004). These effects cascade to other species of insects, birds, and mammals. For example, overabundance of deer has been shown to decrease the diversity of arachnids (Miyashita et al. 2004) and songbirds (DeCalesta 1994, McShea and Rappole 2000) in forest ecosystems.

High density deer populations also may readily transmit disease and other infectious agents such as bovine tuberculosis, chronic wasting disease, and Lyme disease to other wildlife, livestock, and humans (Côté et al. 2004). The selective pattern of wolf predation may slow the transmission of these diseases by reducing density, redistributing deer, and culling the stricken individuals from populations as observed for wolves preying on bison (*Bison bison*) (Bradley and Wilmhurst 2005). More studies on this dynamic are needed, but the ability of wolves to detect and prey upon the infectious individuals appears to slow spread of infectious agents and limit out-breaks (Mech and Peterson 2003).

Côté et al. (2004) have advocated more work on the “landscape of fear” idea (sensu Brown et al. 1999) in which predators like wolves redistribute deer in landscapes, i.e., the risk of predation causing altered habitat use and foraging patterns that result in vegetation change. Avoidance of wolves by deer in the Superior National Forest, Minnesota, USA, created prey refugia between wolf territories (Mech 1977). While vegetation response was not reported, intense herbivory on vegetation in the reservoirs would be expected with less in the core of territories. The restoration of wolves and subsequent limitation of prey may impede or reverse impacts, but the overabundance of deer species has in many cases created new stable states that are not easily reversed without further facilitation (Beisner et al. 2003, Suding et al. 2004, Côté et al. 2004).

Coronation Island

Perhaps the most clear-cut case of wolf reduction of herbivores that resulted in recovery of plant species occurred on a small island of north temperate rain forest that apparently had no wolves originally (Klein 1965). Coronation Island (COR), a 73 km^2 island in southeast Alaska, USA, was populated by Sitka black-tailed deer (*O. hemionus sitkensis*) limited in number by forage and winter weather that mediated the availability of forage prior to wolf introduction to the island (Klein 1965). High abundance (5.8-7.8 km^2) on the island had led to nutritional deficiencies in deer resulting in decreased body size, increased parasite loads, and slowed maturation (Klein 1965). Competition for preferred forage species reduced and even eliminated some species from the island (Klein 1965). After wolves were brought to the island in 1960 they dramatically reduced deer density before dying off due to a lack of vulnerable prey after only 10 years (Klein 1995). The reduction of deer that wolves caused resulted in a 63% increase in forest forbs and a 34% increase in woody shrubs and tree seedlings (Klein 1995). Subsequent to wolf extinction, the deer population recovered and began again to limit forb density and shrub and tree recruitment on the island (Klein 1995).

Banff National Park

In Banff National Park (BNP), Canada, wolf-induced changes in elk distribution were tantamount to community transformation. Following the recovery of wolves to BNP in the late 1980's, riparian willow (*Salix* spp.) communities experienced greater biomass accumulation and structural complexity that then fostered a diverse avian and microtine assemblage relative to before wolf recovery (Hebblewhite et al. 2005b). Willow habitat change was concurrent with the return of beavers (*Castor canadensis*) whose ability to create flooding in riparian habitats alters productivity (Naimen et al. 1986, Baker et al. 2005). In BNP, beaver populations appear to have been limited by competition with elk (Baker et al. 2005, Hebblewhite et al. 2005b), which was subsequently alleviated by the return of wolves.

The interaction between wolves and human influences in BNP brings up a number of important points. The presence of a refuge can intensify predation risk effects, but also increase conflicts with humans. Human activity in BNP appeared to facilitate the trophic cascade by redistributing elk in and around the townsite of Banff, Alberta (Hebblewhite et al. 2005b). In low elk density areas outside the townsite, elk impact on riparian communities was minimized and led to the observed community effects. At the same time, an artificially high concentration of elk in Banff put them in close proximity to humans, an obvious safety and management issue. The removal of human-habituated elk from the townsite for translocations (Frair et al. 2007) removed elk that were aggressive toward humans, and increased the likelihood that the elk population as a whole would decrease. Further, where year-round human activity has deterred wolf predation, traditional migration patterns have been lost to the degree that some elk no longer leave some BNP winter ranges for high-elevation summer range (see Hebblewhite et al. 2006).

Isle Royale National Park

A 544 km^2 island in Lake Superior, USA, known as Isle Royale National Park (IRNP), hosts wolves that prey on moose (*Alces alces*) and indirectly affect balsam fir

(*Abies balsamea*) biomass (McLaren and Peterson 1994). The importance of this food chain to the diversity and function of the IRNP system relates to the impact forage selection and browse intensity by moose have on forest structure and diversity. Browsing suppresses primary production and nitrogen cycling in the soil and mediates competitive relationships between hardwoods and conifers (Pastor et al. 1992); therefore, changes in browsing regime can have large community-wide effects.

The IRNP food chain has been studied for nearly five decades (Vucetich and Peterson 2004a, Wilmers et al. 2006). It contains relatively few species and linkages (Smith et al. 2003), but the links between wolves, moose, and balsam fir are strong. IRNP has a low diversity of large alternate prey species for wolves—only moose and beaver, no other large predators of moose, and during winter moose rely largely on balsam fir (Peterson and Page 1988, Peterson 1999). Further, the island system has no significant emigration or immigration (Vucetich and Peterson 2004b) similar to the previous COR case. Characterized in this way, the IRNP food web is predisposed to cascade top-down effects (Strong 1992, Polis 1999), and yet, long-term research on this system's dynamics reveals complex interactions that vary in direction and strength, punctuated by major stochastic events (such as disease outbreaks and severe winters) that ultimately result in a dynamic system (Boyce and Anderson 1999).

The role of wolves as top-down regulators of moose and balsam fir is supported by correlative evidence for 2 of the 5 decades (Peterson et al. 1998, Vucetich and Peterson 2004a). Limitation was suggested between 1959 and 1980, but in 1981 an outbreak of canine parvovirus substantially reduced wolf density (Vucetich and Peterson 2004b). After the outbreak, variation in moose growth rates was best explained by balsam fir abundance, density dependence, and abiotic factors (climate)—with little influence from wolves (Vucetich and Peterson 2004a, Wilmers et al. 2006). Annual snow depth has intervened throughout the period to mediate the transmission of effects from wolves to balsam fir (Post et al. 1999).

After McLaren and Peterson (1994) suggested top-down effects were dominating in balsam fir growth, subsequent years of observation showed that food limitation caused by climate contradicted this (Post et al. 1999) and diseases in the wolf population caused variation in top-down strength of transmission (Wilmers et al. 2006). Thus, the IRNP case reinforces our notion that systems are dynamic and structured by interactions originating from the top and bottom simultaneously (Power 1992, Hunter and Price 1992). The apparent change in IRNP from largely biotic (wolves) to abiotic (climate) influence on balsam fir illustrates the interactive role these influences play. Moose vulnerability, and therefore wolf predation, is influenced by snow depth and density. Both wolves and snow interact to determine moose density and moose impact on balsam fir. The magnitude of perturbations from the top or from the bottom creates the perception that a system is driven by top-down versus bottom-up influences (Boyce and Anderson 1989), but in reality neither is appropriate because such interactions are invariably a dynamic interaction among trophic levels (Hunter and Price 1992).

Białowieża Primeval Forest

The Białowieża Primeval Forest (BPF) in eastern Poland and western Belarus is a productive forest ecosystem that supports multiple species of both predator and prey. Wolves and lynx (*Lynx lynx*) feed on European bison (*Bison bonasus*), moose, red deer (*C. elaphus*), roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*). Human hunting and poaching has been a strong influence on ungulate biomass intermittently in the past (Jedrzejewska and Jedrzejewski 2005). Predation provides a steady source of carrion for >30 bird and mammal scavenging species (Jedrzejewski et al. 2002). Ungulate biomass increases with percentage of deciduous trees and with maturity of trees in mixed conifer and deciduous forests (Jedrzejewska et al. 1994), though occasional overabundance of herbivores may impede recruitment and maturation of deciduous trees as in North American forests (Waller and Alverson 1997). Hence, herbivore-forest plant species interactions are important to the structure and function of BPF, but how wolves and other predators influence this dynamic is still being investigated (Jedrzejewska and Jedrzejewski 2005).

The long-term research in BPF provides a good case study for holarctic temperate and boreal forests. Strong associations with ungulate biomass were found with average temperature and predator abundance trends over 110 years in BPF (Jedrzejewska and Jedrzejewski 2005). Predators and the productivity of the system combine to determine herbivore biomass. When productivity is high (indexed by high temperatures), the limitation imposed by predators on ungulates was relatively low—10-20% below estimated carrying capacity; however, when productivity was low, predators could further limit ungulates to 40-50% below estimated carrying capacity. Similarly, more productive habitats support prey populations that appear to be better able to sustain wolf predation (Jedrzejewska and Jedrzejewski 2005). Territory size for wolves is in part determined by the productivity of herbivore habitats on a global scale (Jedrzejewska et al. 2007). Large predator-caused decreases in prey occurred mainly when prey were at low-density (Jedrzejewski et al. 2002), or in the least productive habitats. This may be due to prey growth rates having better capability to compensate for predator-caused mortality in richer habitats (Jedrzejewska, unpublished data).

Yellowstone National Park

Expectations for wolves to be highly interactive with many species (Berger et al. 2001, Soulé et al. 2003) accompanied their reintroduction to Yellowstone National Park (YNP), Wyoming, in 1995 (Bangs and Fritts 1996); however, similar to BPF, the trophic web of the YNP system is complex with many species and links among trophic levels (Smith et al. 2003: Figure 1). Diverse prey selection includes elk (Smith et al. 2004), mule deer (*O. hemionus*) (Smith 2005), and bison (Smith et al. 2000). Seasonal migrations diminish the year-round link between wolves and prey (Smith 2005) and between prey and their forage (Houston 1982, YNP 1997).

The dominant biome for elk in YNP is grasslands where large herbivores can enhance nutrient cycling and productivity (Frank and MacNaughton 1992). Conversely, the heavily browsed woody species communities on the northern winter elk range have elicited more controversy (see Romme et al. 1995, Huff and Varley 1999, Wagner 2006) due to an on-going state of browse suppression (Singer et al. 1994, Kay 1998, White et al. 1998, National Resource Council 2002, Wagner 2006). Coincident with wolf eradication in the 1920's, recruitment of willow, aspen (*Populus tremuloides*), and cottonwood (*Populus* spp.) to tall trees essentially ceased in the northern part of the park (Romme et al. 1995, Ripple and Larsen 2000, Beschta 2003). No fewer than 10 recent studies have offered evidence that recruitment of these species will be aided by wolf restoration (Ripple et al. 2001, Ripple and Beschta 2003, 2004, 2006, 2007, Beschta 2003, 2005, Fortin et al. 2005, Beyer et al. 2007, Wolf et al. 2007, Chapter 4).

Elk may be less likely to reside in aspen stands where wolf use is high (Fortin et al. 2005); however, this result has thus far failed to result in aspen ramets >0.8 m in 14 aspen stands across elk winter range predicted to have relief from browsing (Varley, unpublished data). A positive response in aspen ramet growth within wolf territories that was detected by Ripple et al. (2001) was a difference of <10 cm. While statistically significant, this height increase is <10% of the height ramets must achieve to escape browse and be recruited to the overstory (White et al. 1998, Ripple et al. 2001). Aspen in upland areas showed mostly continued suppression, but some in riparian areas thought to be higher predation risk, showed reduced browsing and increased heights (Ripple and Beschta 2007). Cottonwood recruitment has essentially failed for >8 decades in YNP—a state not due to lack of flooding or seedling establishment (Beschta 2003, 2005). Rather, elk browsing prevents seedlings from becoming tall trees; wolves are invoked in the case for recovery only as a factor that may contribute to a reversal of this trend in the future. The case for willow recovery is supported by a mean growth increase across winter range stands since wolf recovery (Beyer et al. 2007). Despite this growth increase, willow stands remain largely in a suppressed state (<1 m in height) that appears unchanged since Singer et al. (1994) surveyed willow prior to wolf restoration (Chapter 4). High elk density has been implicated in the competitive exclusion of beaver that, through lack of beaver-caused flooding, has left conditions generally poor for willow (Wolf et al. 2007). Thus, willow remains largely in a continued state of suppression (Chapter 4).

SYNTHESIS

These cases illustrate how wolves can have disproportionate effects on system dynamics (i.e., keystone function), but the magnitude of effects was highly variable. Like other keystone species, wolves may not have the same influence on all systems, at all times, or across the range of conditions that occur within one system (Power et al. 1996). To better predict these responses, the information from these cases were synthesized and presented within the context of the two primary mechanisms for transmission of predator effects to communities, (1) density-mediated interactions and (2) behavior-mediated interactions (described by Abrams 1995, Schmitz et al. 2004).

Density-mediated Interactions

Wolf trophic effects appeared to be driven by herbivore density declines in the COR (Klein 1995), BNP (Hebblewhite et al. 2005b), and IRNP (Peterson and McLaren 1994) cases. In YNP and BPF where community changes have been less perceptible, herbivore density remains often >10 individuals/km^2 (Jedrzejewski et al. 2002) and so may hinge on further decreases in prey density, similar to the other cases (White et al. 1998). With the degree of limitation on prey populations imposed by wolves varying widely (Seip 1995), so, too, will wolf effects on communities vary widely. This variation may be related to many factors including the density of predator and prey, prey diversity, predator diversity, and human harvest strategies for wolves and prey (Messier 1994, 1995, Mech and Peterson 2003, Jedrzejewska and Jedrzejewski 2005), all of which relate to the productivity of the ecosystem.

Hence, the productivity of ecosystems that in part determines the density and diversity of herbivores and predators will influence the strength of transmission of effects from wolves to producers. Fuller et al. (2003: Figure 6.2) assert that the relationship between prey biomass (in part determined by system productivity) and wolf biomass is a linear relationship, even at high prey density. The authors claim the relationship does not "level off" when prey densities are high because wolves are limited only by vulnerable prey. The evidence for the linear relationship (Fuller et al. 2003: Figure 6.2) is scarcely better than the log-linear relationship ($r^2 = 0.64$ vs. $r^2 = 0.62$; Figure 5.1), and the data do not include high productivity systems like YNP and BPF. Adding these data, the evidence for a log-linear relationship in which wolf biomass levels off with high prey biomass was stronger than for the linear relationship ($r^2 = 0.50$ vs. $r^2 = 0.30$; Figure 5.2).

The rate of trophic conversion from prey biomass to wolf biomass (Figure 5.3), also referred to as Lindeman efficiency (Lindeman 1942, Colinvaux and Barnett 1979), was examined in Figure 5.3. As a rule of thumb, ecologists have suggested this conversion rate is around 10%, but one empirical estimate of Lindeman efficiency available from IRNP data was only 1.3% (Colinvaux and Barnett 1979). This prompted the authors' conclusion that, in general, Lindeman efficiency for wolves and other large mammalian predators in ecosystems was much lower than 10% (Colinvaux and Barnett 1979). The mean conversion of prey to wolf biomass (Figure 5.3) from 33 study areas was 0.03%, less than the IRNP estimate, which the authors suggested may have been too high (Colinvaux and Barnett 1979). The apparent disparity between high and low biomass systems relative to the mean proportion in Figure 5.3 may be due to two factors related to wolf population limitation and prey population compensation. Evidence from YNP indicates social and spatial limitations on wolf populations occurred after only moderate reductions in prey density (Varley and Boyce 2006, Kauffman et al. 2007). For low productivity systems, prey may have less potential to compensate for predation losses, as reported for low productivity periods and habitats in BPF (Jedrzejewska and Jedrzejewski 2005).

System productivity and prey biomass also may factor into determining mean territory size of wolf packs (Figure 5.4). Data from Fuller et al. (2003:Table 6.3) was used to construct Figure 5.4 that indicates at low prey biomass, wolf territories are highly variable (100—1650 km^2), but generally large relative to higher prey biomass. When prey biomass reaches >500,000 kg per 1000 km^2, territories appear to remain between about 100 km^2 and 200 km^2. When wolf density increases it presumably forces smaller territories, but then aggression among packs increases adult mortality to again promote lower density and larger territories (Kauffman et al. 2007). Perhaps 100 km^2 is a reasonable estimate for minimum territory size beyond which interpack conflicts limit density and further territorial restrictions.

In ecosystems that support wolves as part of a diverse, native predator assemblage, limitation on prey populations may be greater (Messier 1994). Synergisms with sympatric predator populations may amplify predation effects on herbivore populations, e.g., when brown bears (*Ursus arctos*) benefit from wolf predation by usurping carcasses (MacNulty et al. 2001, Ballard et al. 2003). Further study on the interaction between these two large carnivores is needed (Boertje et al. 1988), but bear populations may benefit from wolf restoration, and if so, wolf predation rates may increase. In wolf-moose systems throughout North America, prey was limited to low density (0.2 – 0.4 moose/km^2) when wolves were sympatric with grizzly bears (Messier

1994). Where a diverse predator assemblage occurs, a greater degree of herbivore limitation by predators may result (Messier 1994).

Behavior-mediated Interactions

Non-lethal mechanisms have been shown as capable as lethal mechanisms of altering web pathways (Abrams 1995, Schmitz et al. 2004), and as such, the simple risk of predation can contribute to community-altering effects (Lima 1998, Peacor and Werner 2000, Werner and Peacor 2003). While I found many examples of prey responses to wolves, e.g., altered movements (Fortin et al. 2005, Gude et al. 2006), grouping patterns (Heard 1992, Hebblewhite and Pletscher 2002, Mao 2003), and heightened vigilance (Laundré et al. 2001, Wolff and Van Horne 2002, Lung and Childress 2007), these may not functionally alleviate the limitation on forage imposed by herbivores. That is, prey must respond in a manner that reduces their intake of forage that is suppressed by herbivory to affect the community that relies on the forage (Sih 1992, Werner and Peacor 2003). Behavior-mediated interactions have been detected in mostly aquatic and terrestrial arthropod case studies (Schmitz et al. 2004), while data from large, behaviorally complex mammalian systems are notably underrepresented.

The energy demands of some antipredator behavioral responses, e.g., increased vigilance, are purported to be consequential at the population or community level (Brown 1999, Laundré et al. 2001); however, vigilance may be only a modest energetic adjustment to foraging efficiency (Fortin et al. 2004a, 2004b), or a short-term adjustment to the presence of a new predator (Laundré et al. 2001). Many antipredator defenses employed by prey for wolves (Mech and Peterson 2003: Table 5.1) coupled with their multi-tasking abilities (Fortin et al. 2004a) may not be so energetically costly

(Fortin et al. 2004b) as to lead to patterns of substantial resource avoidance and subsequent community change (Sih 1992).

A predator's strategy can be used to predict the expected magnitude of behavior-mediated interactions. The wolf is generally smaller than its prey (Peterson and Cuicci 2003), which limits the vulnerability of many age classes to wolf predation. In general, this ratio of predator to prey body size has been used as a predictor for whether predators (rather than resources) will limit herbivore populations (e.g., Sinclair et al. 2003, Jedrzejewska and Jedrzejewski 2005). In BPF and YNP, large prey like bison and moose were limited far less by predation than red deer and roe deer (Smith et al. 2000, Jedrzejewska and Jedrzejewski 2005). These patterns relate to antipredator defenses of large prey that tend not to necessitate habitat or resource avoidance. These defenses include confrontation (MacNulty et al. 2007), early detection through vigilance (Lung and Childress 2007, Winnie and Creel 2007), and grouping (Heard 1992, Hebblewhite and Pletscher 2002). Large prey such as bison, elk, musk-oxen (*Ovibos moschatus*), and moose have greater degrees of reliance on these defenses than do smaller prey like deer (*Odocoileus* spp.). Deer tend to rely more on hiding and/or spacing, which entails giving up resources in conspicuous habitats or scattering resource use over large areas, respectively. The body size-antipredator defense dynamic may be variable among prey species, or within prey species, particularly for mid-size prey, e.g., elk and caribou (*Rangifer tarandus*). Adult male elk were less responsive to predation risk than adult females with calves despite a greater risk of predation (Lung and Childress 2007, Winnie and Creel 2007).

Schmitz et al. (2004) predict that prey facing highly mobile predators roaming over a large domain cannot predict where and when predators will be encountered, and so have high costs of predator avoidance. Wolves use larger home ranges relative to their prey (Table 5.1) because wolves must roam great expanses to get sufficient access to vulnerable individuals (Mech and Peterson 2003). Wolf territory size (Fuller et al. 2003: Table 6.3) combined with approximate home ranges for some prey species (Harestad and Bunnell 1979), indicates home ranges for wolves are larger by a factor >9 (Table 5.1). Thus, prey may alter their forage patterns only modestly in response to wolves (see Gude et al. 2006).

Relative to a wide array of species, wolves may be described as inefficient predators (Packer and Ruttan 1988: Appendix) in that most encounters do not result in captured prey. An estimate of the success rate for hunting wolves (per individual prey) for a variety of prey ranges between 1% and 56%, but averages about 14% (Mech and Peterson 2003: Table 5.3). Individual prey that encounter wolves therefore have a low likelihood of being captured that may influence the degree to which foraging patterns are affected. Given that prey balance predation risk and resource use (Sih 1992), cascading wolf effects may vary seasonally with the availability of resources and associated predation risk. Reported changes in habitat use in YNP indicate that elk may be altering resource use more in summer than in winter (Mao et al. 2005). The disparity was attributed to elk having abundant, well-dispersed resources on summer range, the selection for which could be readily modified to reduce predation risk through use of more dense cover and steep terrain (Mao et al. 2005). Being perhaps a more predictable part of the landscape, wolf den or rendezvous sites also are avoided (Mao et al. 2005).

Conversely, on winter range resources are relatively scarce and patchy, the access to which is critical despite an associated predation risk. Elk may be adjusting only the time spent in these risky areas because they do not altogether avoid them (Fortin et al. 2005, Creel et al. 2005, Gude et al. 2006, Kauffman et al. 2007). This pattern is reflected in YNP willow browse data that indicate an ephemeral release from browsing in summer appears to be negated by heavy winter use (Chapter 4).

Lastly, despite little support for behavior-mediated trophic cascades (relative to density-mediated) in wolf-prey systems, a recent study links behavioral interaction costs with a density-reducing mechanism. Antipredator behavior manifested physiologically in elk as reduced pregnancy and recruitment rates near YNP (Creel et al. 2007). Synergisms between altered behavior and reduced density in prey may lead to more pronounced trophic cascades as it did in BNP where distributional changes (due to refuge) coupled with predation (outside the refuge) reduced elk density that then affected community change.

CONCLUSIONS

Community diversity and species evenness are enhanced by the presence of wolves. The copious study of wolves has previously lacked clear contributions to a broader understanding of community dynamics and predator-prey interactions (Boyce 2005) that is now beginning to take form. Recent, compelling studies indicate wolves affect critical linkages and processes in food webs. Through predation on herbivores, wolves provision scavengers (Wilmers et al. 2003a, Wilmers and Getz 2004) and alleviate suppressed vegetation communities that are then able to support a wider variety of species at moderate abundances (Berger 1999, Berger et al. 2001, Hebblewhite et al. 2005b). Additionally, wolves may slow the infectious agents that readily spread in high herbivore concentrations affecting other wildlife, livestock, and humans (Côté et al. 2004, Bradley and Wilmhurst 2005). Wolves buffer against the effects of weather extremes and changing climate on prey populations (Wilmers and Getz 2005, Sala 2006).

Wolf influence on communities will vary widely in space, time, and magnitude. Due to the variability of trophic interactions in systems, wolf effects may range from a detectible but minor influence (e.g., Ripple et al. 2001, Chapter 4) to transforming whole communities (e.g., Klein 1995, Hebblewhite et al. 2005b). While this may make it difficult to predict the outcome of wolf restoration (Garrott et al. 2005), it restores a process that contributes to the heterogeneous patterns of ecosystems. The magnitude and variation of the response will be related to the particular food web—more complex, diverse, and productive communities like BPF and YNP appear to be less influenced by wolf predation than other systems (Figure 5.2, Smith et al. 2003, Jedrzejewski et al. 2007). This may be due to density-dependent constraints on wolf population growth that then limits the degree to which prey density is reduced (Figure 5.3).

Variation in the magnitude of response does not diminish the importance of wolves in any system. Rather, the influence will be present but in productive systems may be more diffused or absorbed in multiple, intricate food web pathways (Strong 1992, Polis and Strong 1996). Even in very diverse, highly productive systems, wolves will have subtle but important influences, e.g., mediating competitive relationships among herbivores and provisioning scavengers and other carnivores.

Sufficient evidence from diverse systems now exists to indicate wolves have keystone effects in food webs. The ecological benefits of wolves should be encouraged in management for community diversity and evenness with a greater emphasis. A fortified motivation for advancing community ecology ideals across the holarctic landscape now exists as land managers embark on ecological restoration efforts and the next century of wolf management.

Table 5.1. Prey species, mean home range size, wolf home range size, and wolf:prey home range size ratios for 4 prey species.

Prey	Home Range * (km^2)	Wolf Home Range (km^2)** Mean, Range	Ratio Mean, Range
Elk	13	293	1:22.5, --
White-tailed Deer	2	199, 143-344	1:99.5, 1:71.5–172
Moose	16	873, 145-1645	1:54.5, 1:9.1–102.8
Bighorn Sheep	14	754	1:53.9, --
Mean, range for all prey			1:57.6, 1:9.1–172

* Harestad and Bunnell (1979) compiled a mean from multiple studies

** Fuller et al. (2003) reported means from individual studies, the mean and range reported here are for when more than one study was available for a given prey species.

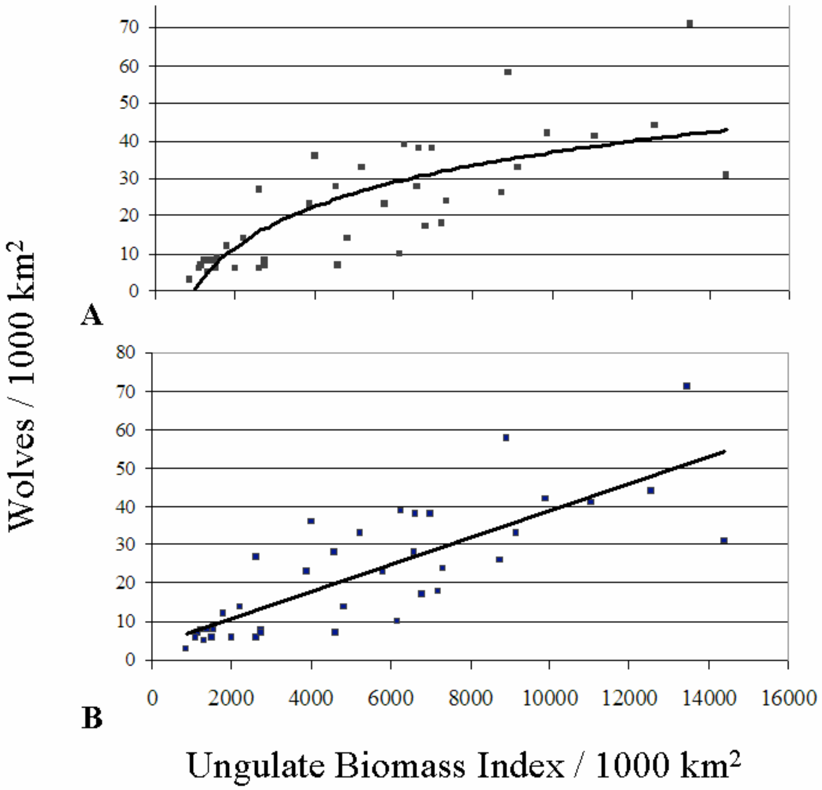

Figure 5.1. Relationship between ungulate biomass and wolf density adapted from Fuller et al. 2003: Figure 6.2, fit with (A) a log-linear relationship, $r^2 = 0.61$, and (B) with a linear relationship, $r^2 = 0.64$. The ungulate biomass index uses population estimates for prey species multiplied by values for prey type as follows: bison, 8; moose, 6; elk, 3; caribou, 2; bighorn sheep, 1; Dall sheep, 1; mountain goat, 1; mule deer, 1; white-tailed deer, 1.

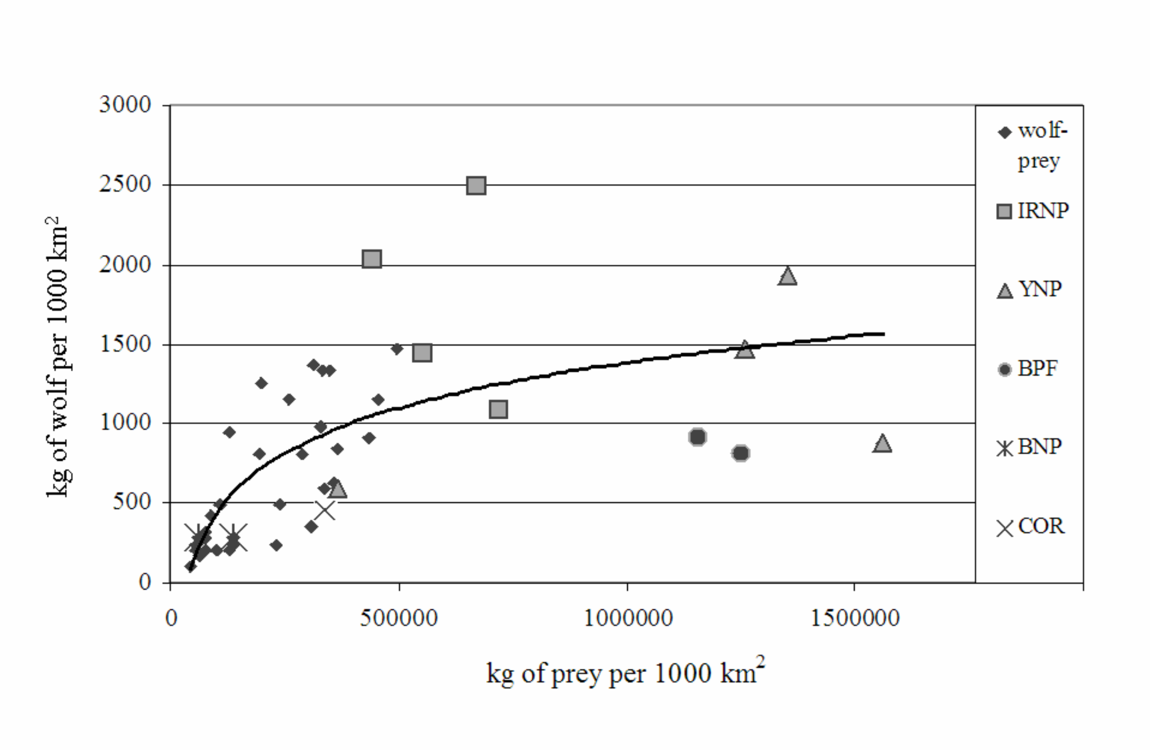

Figure 5.2. Relationship between prey density and wolf density adapted from Fuller et al. 2003 using data from wolf-prey systems. Prey biomass has been converted to kg per 1000 km^2 and data have been added from additional ecosystems as follows: IRNP, Isle Royale National Park; YNP, Yellowstone National Park; BPF, Białowieża Primeval Forest; BNP, Banff National Park; and COR, Coronation Island.

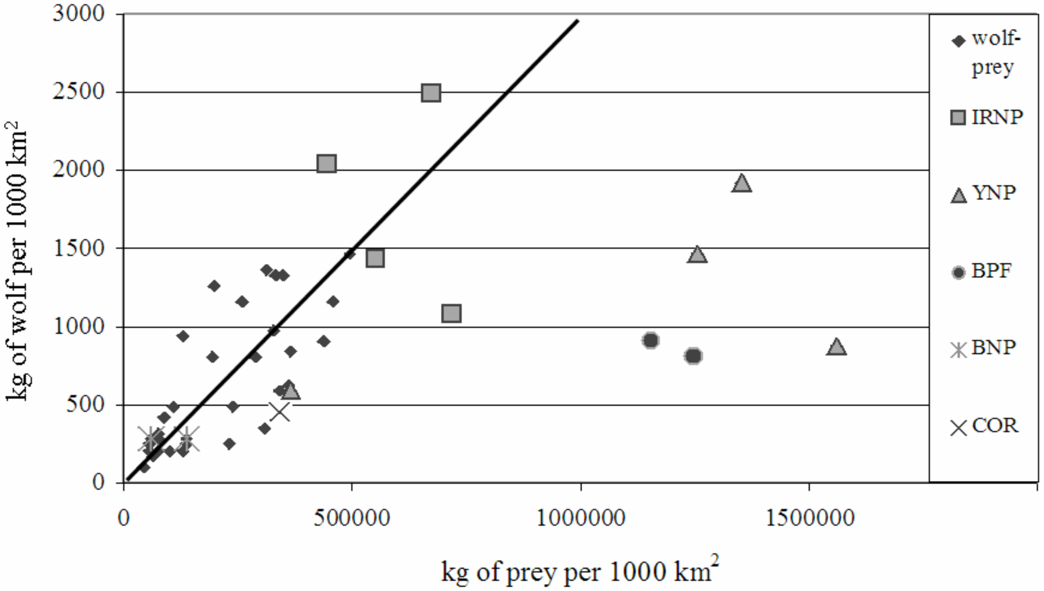

Figure 5.3. Relationship between prey density and wolf density adapted from Fuller et al. 2003 using data from wolf-prey systems. The line represents the Lindeman efficiency rate of prey biomass conversion to wolf biomass at 0.03%, the mean value from the sample of all wolf-prey systems used. Prey biomass has been converted to kg per 1000 km^2 and data have been added from additional ecosystems as follows: IRNP, Isle Royale National Park; YNP, Yellowstone National Park; BPF, Białowieża Primeval Forest; BNP, Banff National Park; and COR, Coronation Island.

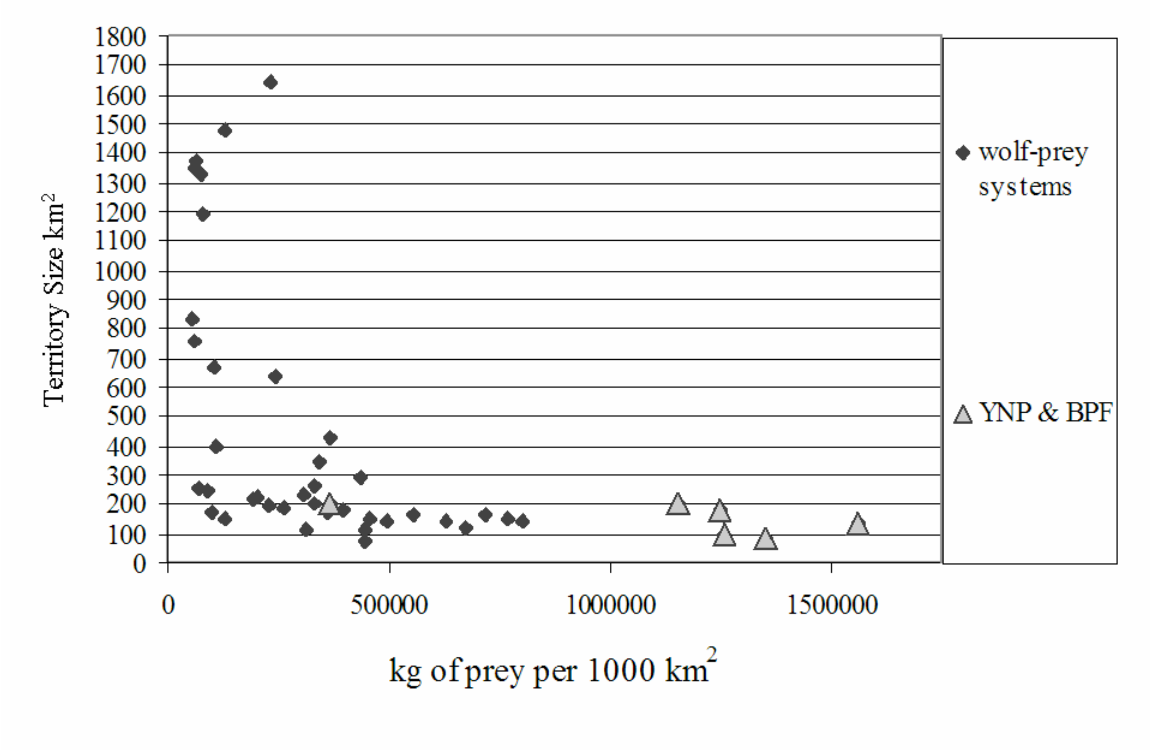

Figure 5.4. Relationship between prey density and wolf territory size using data from mostly deer and moose systems from Fuller et al. 2003: Table 6.3. Prey biomass has been converted to kg per 1000 km^2 and additional data have been added from YNP, Yellowstone National Park, and BPF, Białowieża Primeval Forest.

REFERENCES

Abrams, P. A. 1995. Implications of dynamically variable traits for identifying, classifying and measuring direct and indirect effects in ecological communities. American Naturalist **146**:112–134.

Baker, B. W., H. C. Ducharme, D. C. S. Mitchell, T. R. Stanley, and H. R. Peinetti. 2005. Interaction of beaver and elk herbivory reduces standing crop of willow. Ecological Applications **15**:110–118.

Ballard, W. B., L. A. Ayres, P. R. Krausman, D. J. Reed, and S. G. Fancy. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. Wildlife Monographs **135**:1–47.

Ballard, W. B., L. N. Carbyn, and D. W. Smith. 2003. Wolf interactions with non-prey. Pages 259–271 *in* Mech, L. D., and L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois, USA.

Bangs, E. E., and S. H. Fritts. 1996. Reintroducing the gray wolf to central Idaho and Yellowstone National Park. Wildlife Society Bulletin **24**:402–413.

Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment **1**:376–382.

Berger, J. 1999. Anthropogenic extinction of top carnivores and interspecific animal behaviour: implications of the rapid decoupling of a web involving wolves, bears, moose and ravens. Proceedings of the Royal Society of London B **266**:2261–2267.

Berger, J. 2005. Hunting by carnivores and humans: does functional redundancy occur and does it matter? Pages 315-340 *in* Ray, J. C., K. H. Redford, R. S. Steneck, and J. Berger, editors. Large carnivores and biodiversity conservation. Island Press, Washington, D. C., USA.

Berger, J., P. B. Stacey, L. Bellis, and M. P. Johnson. 2001. A mammalian predator-prey imbalance: grizzly bear and wolf extinction affect avian neotropical migrants. Ecological Applications **11**:947– 960.

Berger, J., and D. W. Smith. 2005. Restoring functionality in Yellowstone with recovering carnivores: gains and uncertainties. Pages 100–108 *in* Ray, J. C., K. H.

Redford, R. S. Steneck, and J. Berger, editors. Large carnivores and biodiversity conservation. Island Press, Washington, D. C., USA.

Beschta, R. L. 2003. Cottonwoods, elk, and wolves in the Lamar Valley of Yellowstone National Park. Ecological Applications **13**:1295–1309.

Beschta, R. L. 2005. Reduced cottonwood recruitment following extirpation of wolves in Yellowstone's Northern Range. Ecology **86**:391–403.

Beyer, H. L., E. H. Merrill, N. Varley, and M. S. Boyce. 2007. Willow on Yellowstone's Northern Range: evidence for a trophic cascade in a large mammalian predator-prey system? Ecological Applications **17**:1563–1571.

Bilyeu, D. 2006. Effects of elk browsing and water table on willow growth and physiology: implications for willow restoration in Yellowstone National Park. Ph.D. dissertation. Colorado State University, Fort Collins, Colorado, USA.

Blancó, J. C., L. Cuesta, and S. Reig. 1990. Distribution, status, and conservation problems of the wolf *Canis lupus* in Spain. Biological Conservation **60**:73–80.

Boertje, R. D., W. C. Gasaway, D. W. Grangaard, and D. Kellyhouse. 1988. Predation of moose and caribou by radio-collared grizzly bears in east central Alaska. Canadian Journal of Zoology **66**:2492–2499.

Boitani, L. 2003. Wolf conservation and recovery. Pages 317 –340 *in* Mech, L. D. and L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois, USA.

Boyce, M. S. 1998. Ecological-process management and ungulates: Yellowstone's conservation paradigm. Wildlife Society Bulletin **26**:391–398.

Boyce, M. S. 2005. Wolves are consummate predators. Quarterly Review of Biology **80**:87–92.

Boyce, M. S., and E. M. Anderson. 1999. Evaluating the role of carnivores in the Greater Yellowstone Ecosystem. Pages 265–284 *in* Clark, T. K., A. P. Curlee, S. C. Minta, and P. M. Kareiva, editors. Carnivores in ecosystems: the Yellowstone experience. Yale University Press, New Haven, Connecticut, USA.

Bradley, M., and J. Wilmhurst. 2005. The fall and rise of bison populations in Wood Buffalo National Park: 1971 to 2003. Canadian Journal of Zoology **83**:1195-1205.

Brown, J. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. Evolutionary Ecology Research **1**:49–71.

Brown, J. S., J. W. Laundré, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of Mammalogy **80**:385–399.

Carbyn, L. N., S. H. Fritts, and D. R. Seip, editors. 1995. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Canada.

Colinvaux, P. A., and B. D. Barnett. 1979. Lindeman and the ecological efficiency of wolves. The American Naturalist **114**:707–718.

Côté, S. D., T. P. Rooney, J. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics **35**:113–147.

Creel, S., D. Christianson, S. Liley, and J. A. Winnie, Jr. 2007. Predation risk affects reproductive physiology and demography of elk. Science **315**:960.

Creel, S., J. A. Winnie, Jr., B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology **86**:3387–3397.

Crête, M. 1999. The distribution of deer biomass in North America supports the hypothesis of exploitation ecosystems. Ecology Letters **2**:223–227.

DeCalesta, D. S. 1994. Effect of white-tail deer on songbirds within managed forests in Pennsylvania. Journal of Wildlife Management **58**:711–718.

Eberhardt, L. L., P. J. White, R. A. Garrott, and D. B. Houston. 2007. A seventy-year history of trends in Yellowstone's northern elk herd. Journal of Wildlife Management **71**:594–602.

Estes, J. A. 1996. Predators and ecosystem management. Wildlife Society Bulletin **24**:390–396.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesné, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology **86**:1320–1331.

Fortin, D., M. S. Boyce, and E. H. Merrill. 2004a. Multi-tasking by mammalian herbivores: overlapping processes during foraging. Ecology **85**:2312–2322.

Fortin, D., M. S. Boyce, E. H. Merrill, and J. M. Fryxell. 2004b. Foraging costs of vigilance in large mammalian herbivores. Oikos **107**:172–180.

Frair, J. L., E. H. Merrill, J. R. Allen, and M. S. Boyce. 2007. Know thy enemy: experience effects elk translocation success in risky landscapes. Journal of Wildlife Management **72**:541–554.

Frank, D. A., and S. J. MacNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology **73**:2043–2058.

Fritts, S. H., R. O. Stephenson, R. D. Hayes, and L. Boitani. 2003. Wolves and humans. Pages 289–316 *in* Mech, L. D., and L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois, USA.

Fuller, T. K., and L. B. Keith. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. Journal of Wildlife Management **44**:583–602.

Fuller, T. K., L. D. Mech, and J. F. Cochrane. 2003. Wolf population dynamics. Pages 161–191 *in* Mech, L. D., and L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois, USA.

Garrott, R. A., P. J. White, and C. A. Vanderbilt White. 1993. Overabundance: an issue for conservation biologists? Conservation Biology **7**:946–949.

Garrott, R. A., J. A. Gude, E. J. Bergman, C. Gower, P. J. White, and K. L. Hamlin. 2005. Generalizing wolf effects across the Greater Yellowstone Area: a cautionary note. Wildlife Society Bulletin **33**:1245–1255.

Gude, J. A., R. A. Garrott, J. J. Borkowski, and F. King. 2006. Prey risk allocation in a grazing ecosystem. Ecological Applications **16**:285–298.

Halaj, J., and D. H. Wise. 2001. Terrestrial trophic cascades: how much do they trickle? American Naturalist **157**:262-281.

Harestad, A. S., and F. L Bunnell. 1979. Home range and body weight—a reevaluation. Ecology **660**:389–402.

Heard, D. C. 1992. The effect of wolf predation and snow cover on musk-ox group size. American Naturalist **139**:193–204.

Hebblewhite, M, and D. H. Pletscher. 2002. Effects of elk group size on predation by wolves. Canadian Journal of Zoology **80**:800–809.

Hebblewhite, M., E. H. Merrill, and T. L. McDonald. 2005a. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator-prey system. Oikos **111**:101–111.

Hebblewhite, M., C. A. White, C. N. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. Bayley, and P. C. Paquet. 2005b. Human activity mediates a trophic cascade caused by wolves. Ecology **86**:2135–2144.

Hebblewhite, M., E. H. Merrill, L. E. Morgantini, C. A. White, J. R. Allen, E. Bruns, L. Thurston, and T. E. Hurd. 2006. Is the migratory behaviour of montane elk herds in peril? The case of Alberta's Ya Ha Tinda elk herd. Wildlife Society Bulletin **34**:1280– 1294.

Horseley, S. B., S. L. Stout, and D. S. DeCalesta. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecological Applications **13**:98–118.

Houston, D. B. 1982. The northern Yellowstone elk: ecology and management. Macmillan Publishing, New York, New York, USA.

Huff, D. E., and J. D. Varley. 1999. Natural regulation in Yellowstone National Park's Northern Range. Ecological Applications **9**:17–29.

Hunter, M. D., and P. Price. 1992. Playing chutes and ladders. Heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology **73**:724–732.

Jedrzejewska, B., H. Okarma, W. Jedrzejewski, and L. Milkowski. 1994. Effects of exploitation and protection on forest structure, ungulate density and wolf predation in Białowieża Primeval Forest, Poland. Journal of Applied Ecology **31**:664–676.

Jedzrejewska, B., and W. Jedrzejewski. 2005. Large carnivores and ungulates in European temperate ecosystems: bottom-up and top-down control. Pages 230–246 *in* Ray, J. C., K. H. Redford, R. S. Steneck, and J. Berger. Large Carnivores and Biodiversity Conservation. Island Press, Washington, D. C., USA.

Jedrzejewsk, W., B. Jedrzejewska, H. Okarma, and A. L. Ruprecht. 1992. Wolf predation and snow cover as mortality factors in the ungulate community of the Białowieża National Park, Poland. Oecologia **90**:27–36.

Jedrzrzejewski, W., K. Schmidt, J. Theuerkauf, B. Jedrzejewska, N. Selva, K. Zub, and L. Szymura. 2002. Kill rates and predation by wolves in ungulate populations in Białowieża Primeval Forest, Poland. Ecology **83**:1341–1356.

Jedzrzejewski, W., K. Schmidt, J. Theuerkauf, B. Jedrzejewska, and R. Kowalczyk. 2007. Territory size of wolves *Canis lupus*: linking local (Bialowieza Primeval Forest, Poland) and Holarctic-scale patterns. Ecography **30**:66–76.

Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. Ecology Letters **10**:690–700.

Kay, C. E. 1998. Are ecosystems structured from the top-down or bottom-up: a new look at an old debate. Wildlife Society Bulletin **26**:484–498.

Klein, D. R. 1965. Ecology of deer range in Alaska. Ecological Monographs **35**:259–284.

Klein, D. R. 1995. The introduction, increase, and demise of Wolves on Coronation Island, Alaska. Pages 275–280 *in* Carbyn, L. N., S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Canada.

Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. Conservation Biology **2**:316–328.

Laundré, J. W., L. Hernandez, and K. B. Altendorf. 2001. Wolves, elk, and bison: re-establishing the "landscape of fear" in Yellowstone National Park, U.S.A. Canadian Journal of Zoology **79**:1401–1409.

Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. What are the ecological effects of anti-predator decision-making? BioScience **48**:25–34.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology **23**:399–417.

Linnell, J. D. C., J. E. Swenson, and R. Andersen. 2000. Conservation of biodiversity in Scandinavian boreal forests: large carnivores as flagships, umbrellas, indicators, or keystones? Biodiversity & Conservation **9**:857–868.

Lung, M. A., and M. J. Childress. 2007. The influence of conspecifics and predation risk on the vigilance of elk (*Cervus elaphus*) in Yellowstone National Park. Behavioral Ecology **18**:12–20.

MacNulty, D. R., L. D. Mech, and D. W. Smith. 2007. A proposed ethogram of large carnivore predatory behavior, exemplified by the wolf. Journal of Mammalogy **88**:595–605.

MacNulty, D. R., N. Varley, and D. W. Smith. 2001. Grizzly bear, *Ursus arctos*, usurps bison calf, *Bison bison*, captured by wolves, *Canis lupus*, in Yellowstone National Park, Wyoming. Canadian Field–Naturalist **115**:495–498.

Mao, J. S. 2003. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park, Wyoming. M.S. thesis. University of Alberta, Edmonton, Alberta, Canada.

Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. Journal of Wildlife Management **69**:1691–1707.

McLaren, B. E., and R. O. Peterson. 1994. Wolves, moose, and tree rings on Isle Royale. Science **266**:1555–1558.

McShea, W. J., and J. H. Rappole. 2000. Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. Conservation Biology **14**:1161–1170.

Mech, L. D. 1977. Wolf-pack buffer zones as prey reservoirs. Science **198**:320–321.

Mech, L. D., and L. Boitani. 2003a. Conclusion. Pages 341–344 *in* Mech, L. D., and L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois, USA.

Mech, L. D., and L. Boitani. 2003b. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois, USA.

Mech, L. D., and L. Boitani. 2003c. Ecosystem effects of wolves. Pages 158–160 *in* Mech, L. D., and L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois, USA.

Mech, L. D., and R. O. Peterson. 2003. Wolf-prey relations. Pages 131–157 *in* Mech, L. D., and L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois, USA.

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology **75**:478–488.

Messier, F. 1995. On the functional and numerical responses of wolves to changing prey density. Pages 187–197 *in* Carbyn, L. N., S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Canada.

Miyashita, T., M. Takada, and A. Shimazaki. 2004. Indirect effects of herbivory by deer reduce abundance and species richness of web spiders. Écoscience **11**:74–79.

Naiman, R. J., J. M. Melillo, and J. E. Hobbie. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology **67**:1254–1269.

National Research Council. 2002. Ecological Dynamics on Yellowstone's Northern Range. National Academy Press, Washington, D.C., USA.

Niemi, G. J., J. M. Hanowski, A. R. Lima, T. Nicholls, and N. Weiland. 1997. A critical analysis on the use of indicator species in management. Journal of Wildlife Management **61**:1240–1262.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution **14**:483–488.

Packer, C., and L. Ruttan. 1988. The evolution of cooperative hunting. American Naturalist **132**:159–198.

Pastor, J., B. Dewey, R. J. Naiman, P. F. McInnes, and Y. Cohen. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. Ecology **74**:467–480.

Peacor, S. D., and E. E. Werner. 2000. Predator effects on an assemblage of consumers through induced changes in consumer foraging behavior. Ecology **81**:1998–2010.

Peterson, R. O. 1999. Wolf-moose interaction on Isle Royale: the end of natural regulation? Ecological Applications **9**:10–16.

Peterson, R. O., and P. Cuicci. 2003. The wolf as a carnivore. Pages 105 –130 *in* Mech, L. D., and L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois, USA.

Peterson, R. O., and R. E. Page. 1988. The rise and fall of Isle Royale wolves, 1975–1986. Journal of Mammalogy **69**:89–99.

Polis, G. A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. Oikos **86**:3–15.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist **147**:813–846.

Polis, G. A., A. L. W. Sears, G. R. Huxel, D. R. Strong, and J. Maron. 2000. When is a trophic cascade a trophic cascade? Trends in Ecology & Evolution **15**:473–475.

Post, E. S., R. O. Peterson, N. C. Stenseth, and B. E. McLaren. 1999. Ecosystem consequences of wolf behavioural response to climate. Nature **401**:905–907.

Power, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? Ecology **73**:733–746.

Power, M. E, D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystone species. BioScience **46**:609–620.

Pyare, S., and J. Berger. 2003. Beyond demography and delisting: ecological recovery for Yellowstone's grizzly bears and wolves. Biological Conservation **113**:63–73.

Ripple, W. J., and R. L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. Forest Ecology and Management **184**:299–313.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience **54**:755–766.

Ripple, W. J., and R. L. Beschta. 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. Forest Ecology and Management **230**:96–106.

Ripple, W. J., and R. L. Beschta. 2007. Restoring Yellowstone's aspen with wolves. Biological Conservation **138**:514-519.

Ripple, W. J., and E. J. Larsen. 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. Biological Conservation **95**:361–370.

Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's Northern Range. Biological Conservation **102**:227–234.

Romme, W. H., M. G. Turner, L. L. Wallace, and J. S. Walker. 1995. Aspen, elk and fire on the Northern Range of Yellowstone National Park. Ecology **76**:2097–2106.

Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management **181**:165–176.

Sala, E. 2006. Top predators provide insurance against climate change. Trends in Ecology and Evolution **21**:479–480.

Schmitz,O. J., P. A. Hambäck, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of top carnivore removals on plants. American Naturalist **155**:141–153.

Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated indirect interactions. Ecology Letters **7**:153–163.

Seip, D. R. 1995. Introduction to wolf-prey interactions. Pages 275–280 *in* Carbyn, L. N., S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Canada.

Sih, A. 1992. Prey uncertainty and the balancing of antipredator and feeding needs. American Naturalist **139**:1052–1069.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Biological Conservation **83**:247–257.

Sinclair, A. R. E., S. Mduma, and J. S. Brashares. 2003. Patterns of predation in a diverse predator–prey system. Nature **425**:288–290.

Singer, F. J., L. C. Mark, and R. C. Cates. 1994. Ungulate herbivory of willows on Yellowstone's Northern Range. Journal of Range Management **43**:295–299.

Singer, F. J., L. C. Zeigenfuss, R. G. Cates, and D. T. Barnett. 1998. Elk, multiple factors, and persistence of willows in national parks. Wildlife Society Bulletin **26**:419–428.

Smith, D. W. 2005. Ten years of Yellowstone wolves 1995–2005. Yellowstone Science **13**:7–33.

Smith, D. W., T. D. Drummer, K. M. Murphy, D. S. Guernsey, and S. B. Evans. 2004. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. Journal of Wildlife Management **68**:153–166.

Smith, D. W., L. D. Mech, M. Meagher, W. E. Clark, R. Jaffe, M. K. Phillips, and J. A. Mack. 2000. Wolf–bison interactions in Yellowstone National Park. Journal of Mammalogy **81**:1128–1135.

Smith, D. W., R. O. Peterson, and D. B. Houston. 2003. Yellowstone after wolves. BioScience **53**:330–340.

Soulé, M. E., J. A. Estes, J. Berger, and C. Martinez Del Rio. 2003. Ecological effectiveness: conservation goals for interactive species. Conservation Biology **17**:1238–1250.

Soulé, M. E., J. A. Estes, B. Miller, and D. L. Honnold. 2005. Strongly interacting species: conservation policy, management, and ethics. BioScience **55**:168–176.

Stahler, D., B. Heinrich, and D. Smith. 2002. Common ravens, *Corvus corax*, preferentially associate with grey wolves, *Canis lupus*, as a foraging strategy in winter. Animal Behaviour **64**:283–290.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology **73**:747–754.

Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. Trends in Ecology & Evolution **19:**46–53.

Terborgh, J., J. A. Estes, P. Paquet, K. Ralls, D. Boyd-Heger, B. J. Miller, and R. F. Noss. 1999. The role of top carnivores in regulating terrestrial ecosystems. Pages 39–64 *in* M. E. Soulé and J. Terborgh, editors. Continental conservation: scientific foundations of regional reserve networks. Island Press, Covelo, California, USA.

Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. Science **294**:1924–1926.

Terborgh, J., K. Feeley, M. Silman, P. Nunez, and B. Balukjian. 2006. Vegetation dynamics of predator-free land-bridge islands. Journal of Ecology **94**:253–263.

U. S. Department of the Interior. 2006. Endangered and Threatened Wildlife and Plants; Designating the Western Great Lakes Population of Gray Wolves as a Distinct Population Segment; Removing the Western Great Lakes Distinct Population Segment of the Gray Wolf From the List of Endangered and Threatened Wildlife. Federal Register **71**:58.

U. S. Department of the Interior. 2007. Endangered and Threatened Wildlife and Plants; Designating the Northern Rocky Mountain Population of Gray Wolf as a Distinct Population Segment and Removing This Distinct Population. Federal Register **72**:26.

Varley, N., and M. S. Boyce. 2006. Adaptive management for reintroductions: updating a wolf recovery model for Yellowstone National Park. Ecological Modelling **193**:315–339.

Vucetich, J. A.**,** R. O. Peterson, and T. A. Waite. 2004. Raven scavenging favours group foraging in wolves. Animal Behaviour **67**:1117–1126.

Vucetich, J. A., and R. O. Peterson. 2004a. The influence of top-down, bottom-up and abiotic factors on the moose (*Alces alces*) population of Isle Royale. Proceedings of the Royal Society of London B **271**:183–189.

Vucetich, J. A., and R. O. Peterson. 2004b. The influence of prey consumption and demographic stochasticity on population growth rate of Isle Royale wolves *Canis lupus*. Oikos **107**:309–320.

Wabakken, P., H. Sand, O. Liberg, and A. Bjarvall. 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978–1998. Canadian Journal of Zoology **79**:710–725.

Wagner, F. H. 2006. Yellowstone's destabilized ecosystem: elk effects, science, and policy conflict. Oxford University Press, New York, USA.

Waller, D. M., and W. S. Alverson. 1997. The white-tailed deer: a keystone herbivore. Wildlife Society Bulletin **25**:217–226.

Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology **84**:1083–1100.

White, C. A., C. E. Olmsted, and C. E. Kay. 1998. Aspen, elk and fire in the Rocky Mountain national parks of North America. Wildlife Society Bulletin **26**:449–462.

Wilmers, C. C., R. L. Crabtree, D. W. Smith, K. M. Murphy, and W. M. Getz. 2003a. Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park. Journal of Animal Ecology **72**:909–916.

Wilmers, C. C., D. R. Stahler, R. L. Crabtree, D. W. Smith, and W. M. Getz. 2003b. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. Ecology Letters **6**:996–1003.

Wilmers, C. C., and W. M. Getz. 2004. Simulating the effects of wolf-elk population dynamics on resource flow to scavengers. Ecological Modelling **177**:193–208.

Wilmers, C. C., and W. M. Getz. 2005. Gray wolves as climate change buffers in Yellowstone. PLoS Biology **3**:92.

Wilmers, C. C., E. Post, R. O. Peterson, and J. A. Vucetich. 2006. Predator disease out-break modulates top-down, bottom-up and climatic effects on herbivore population dynamics. Ecology Letters **9**:383–389.

Winnie, J. Jr., and S. Creel. 2007. Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. Animal Behaviour **73**:215–225.

Wolf, E. C., D. J. Cooper, and N. T. Hobbs. 2007. Hydrologic regime and herbivory stabilize an alternative state in Yellowstone National Park. Ecological Applications **17**:1572–1587.

Wolff, J. O., and T. Van Horn. 2003. Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. Canadian Journal of Zoology **81**:266–271.

Wright, G. J., R. O. Peterson, D. W. Smith, and T. O. Lemke. 2006. Selection of northern Yellowstone elk by gray wolves and hunters. Journal of Wildlife Management **70**:1070–1078.

Yellowstone National Park. 1997. Yellowstone's Northern Range: complexity and change in a wildland ecosystem. Yellowstone Center for Resources, Yellowstone National Park, Wyoming, USA.

CHAPTER 6

GENERAL DISCUSSION AND CONCLUSIONS

Wolves may have keystone effects that are only beginning to be understood. Thus, continuing studies on the community effects of wolf restoration is imperative. The magnitude of wolf effects will vary with the system and set of current conditions to which wolves are restored (Chapter 5). Because wolf interactions vary in strength, consistency, and duration, both within and among systems, an understanding of system dynamics will be necessary for understanding and predicting the ecological impacts of wolves. Wolf predation effects may cascade to lower trophic levels, so regardless of the magnitude of these effects, the influence is important and must be understood in the context of interactive processes that structure food webs and maintain dynamic patterns in ecological communities.

Wolves can limit or regulate prey in systems which may diminish the effects of overabundant herbivores. In Chapter 2, I found that wolf predation reduced long-term mean abundance of a prey population with less extreme annual fluctuation. Accompanying moderate reductions in the long-term mean of a prey population is a reduction in the sometimes extreme effects that a combination of climate and density can have on prey populations. Wolf predation may reduce temporal population fluctuation (Chapter 2), but may increase spatial population fluctuation through prey responses to heterogeneous risk patterns (Chapter 3). Harvest by humans of prey populations may decline after wolf restoration, but only a moderate decline in the human harvest of the migratory herd in the YNP system is anticipated (Chapter 2).

While wolves may limit prey populations, prey selection for non-prime aged individuals (Chapter 2), as well as, competition among wolves for preferred hunting areas (Chapter 3), may reduce the proportional effect on prey population growth. These factors buffer against the possibility of a severe impact to prey populations due to wolf predation and contribute to a more stable coexistence among predator and prey (Chapter 3).

The degree to which prey are limited by wolves can influence the effect of wolves have on communities of organisms. Studies including the analysis of Chapter 4 have detected the top-down effect wolves can have on vegetation and the community that it supports; however, the magnitude of these effects may be variable. In YNP, effects were small relative to what might be necessary to affect large numbers of species and their abundances (Chapter 5). In some low productivity systems, wolves can have very large effects (Chapter 5) that may not occur in some high productivity systems. In YNP, for example, high productivity results in abundant herbivores that, despite a diverse predator assemblage, remain numerous enough to continue to suppress some low-abundance vegetation, e.g., willow (Chapter 4). In high productivity systems like YNP, density-dependent limitation of wolves may intercede prior to limiting prey populations at a level necessary to cascade effects to lower levels. Alternately, in low productivity systems prey may be less able to compensate for predation resulting in greater prey population limitation and indirect effects on other species.

Regardless of the magnitude of wolf effects, these interactions contribute to the maintenance of ecological patterns within systems. Ecologists must continue to study and understand the indirect effects of wolves in food webs, including when and to what extent trophic cascades will manifest. Conservation biologists are then encouraged to apply this information where wolf populations are recovering to affect management for ecological processes across large landscapes.