

# **Predator-Prey Management in the National Park Context: Lessons from a Transboundary Wolf, Elk, Moose and Caribou System**

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## **Introduction**

Wolves (*Canis lupus*) are recolonizing much of their former range within the lower 48 states through active recovery (Bangs and Fritts 1996) and natural dispersal (Boyd and Pletscher 1999). Wolf recovery is being touted as one of the great conservation successes of the 20<sup>th</sup> century (Mech 1995; Smith et al. 2003). In addition to being an important single-species conservation success, wolf recovery may also be one of the most important ecological restoration actions ever taken because of the pervasive ecosystem impacts of wolves (Hebblewhite et al. 2005). Wolf predation is now being restored to ecosystems that have been without the presence of major predators for 70 years or more. Whole generations of wildlife managers and biologists have come up through the ranks, trained in an ungulate- management paradigm developed in the absence of the world's most successful predator of ungulates—the wolf. Many questions are now facing wildlife managers and scientists about the role of wolf recovery in an ecosystem-management context. The effects wolves will have on economically important ungulate populations is emerging as a central issue for wildlife managers. But, questions about the important ecosystem effects of wolves are also emerging as a flurry of new studies reveals the dramatic ecosystem impacts of wolves and their implications for the conservation of biodiversity (Smith et al. 2003; Fortin et al. 2005; Hebblewhite et al. 2005; Ripple and Beschta 2006; Hebblewhite and Smith 2007).

In this paper, I provide for wildlife managers and scientists in areas in the lower 48 states (where wolves are recolonizing) a window to their future by reviewing the effects of wolves on montane ecosystems in Banff National Park (BNP), Alberta. Wolves were exterminated in much of southern Alberta, similar to the lower 48 states, but they recovered through natural dispersal populations

to the north in the early 1980s, between 10 and 20 years ahead of wolf recovery in the northwestern states (Gunson 1992; Paquet, et al. 1996). Through this review, I aim to answer the following questions: (1) what have the effects of wolves been on population dynamics of large-ungulate prey, including elk (*Cervus elaphus*), moose (*Alces alces*) and threatened woodland caribou (*Rangifer tarandus tarandus*), (2) what other ecosystem effects have wolves had on montane ecosystems, (3) how sensitive are wolf-prey systems to top-down and bottom-up management to achieve certain human objectives, and (4) how is this likely to be constrained in national park settings? Finally, I discuss the implications of this research in the context of ecosystem management and long-term ranges of variation in ungulate abundance.

## Study Area

I only briefly review details of the BNP ecosystem and refer readers to more detailed accounts in (Holroyd and Van Tighem 1983; Holland and Coen 1983; Hebblewhite et al. 2005, 2006). BNP itself is 2,564.10 square miles (6,641 km<sup>2</sup>) and is on the eastern slope of the continental divide in the Canadian Rocky Mountains (51° 15" latitude, 116° 30" longitude). The park has extreme, mountainous topography (1,531.06 to 3,718.29 yards [1,400–3,400 m]) and a climate characterized by long, cold winters and short, dry summers. Vegetation is described in detail by Holland and Coen (1983). Importantly, BNP has conducted an aggressive prescribed-fire restoration policy since the 1980s, burning approximately 77.22 square miles (200 km<sup>2</sup>) of predominantly forest communities (White et al. 2003), with expected benefits for ungulate foraging habitat (Sachro et al. 2005). Seven species of large ungulates exist in BNP; in approximate order of abundance they are: elk, bighorn sheep (*Ovis canadensis*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), moose, mountain goat (*Oreamnos americanus*) and a small, threatened population of woodland caribou. Elk were the most abundant ungulate in BNP, comprising 40 to 70 percent of the diet of wolves (Hebblewhite et al. 2004), and are partially migratory in BNP; some elk migrate and others are resident year round. Other predators included cougars (*Felis concolor*), coyotes (*Canis latrans*), grizzly bears (*Ursus arctos*) and black bears (*Ursus americanus*). However, wolves were the only species to recover from extirpation (Paquet et al. 1996).

I examine effects of wolves in two study areas in and adjacent to BNP: the Bow Valley of BNP, which lies almost completely within the protected areas of the national park, and the Ya Ha Tinda (YHT) area, which is a transboundary system spanning the national park's boundaries into adjacent provincial lands. The Bow Valley study area comprises the best winter range habitat for elk inside BNP, with low elevation valley bottoms between 1.24 to 3.11 miles (2–5 km) in width and 1,476.38 to 1,749.78 yards (1,350–1,600 m) elevation. The Bow Valley system has pervasive human impacts with the national railway and highway system, secondary roads, and human developments (ski resorts, golf courses) fragmenting the valley bottom. Wolves avoided human developments in the Bow Valley (Paquet et al. 1996). This led to very low wolf use in a large area surrounding the townsite of Banff, and high wolf use in the remaining area, providing a serendipitous experimental comparison of elk with and without wolf predation.

The YHT winter range lies outside of BNP and is considered much higher quality winter range for elk that migrate seasonally from summer ranges inside BNP. YHT means “mountain prairie” in the Stoney-Sioux language, aptly describing the azonal, high elevation, 7.72 square mile (20 km<sup>2</sup>) montane, rough, fescue grasslands along the north side of the Red Deer River. The YHT area represents one of the most pristine and largest rough fescue montane grasslands left in Alberta (Willoughby 2001), and has much lower levels of human use. Summer ranges of the Bow Valley and YHT elk populations have minimal overlap (Hebblewhite 2006). Migrant elk in the YHT population have been declining; in 2006, I used a comparative research design to compare migrant and resident elk to determine the causes of migratory changes.

## **Effects of Wolves on Ungulates**

### ***Elk***

In the Bow Valley, Hebblewhite et al. (2005) compared adult female elk survival and recruitment between the low and high wolf areas during 1997 to 2000. Differences in wolf-caused mortality were tested using chi-square tests. In the high wolf zone, adult survival equaled  $0.62 \pm 0.06$ ; *n* equaled 22, where *n* represents the number of adult female elk. And, calf recruitment equaled  $14.6 \pm 1.97$  percent. The combination of this survival and recruitment led to rapid population decline (Hebblewhite et al. 2005). But, in the low-wolf area, survival

equaled  $0.89 \pm 0.06$ ;  $n$  equaled 23. And, recruitment equaled  $27.4 \pm 1.58$  percent, which both are high and the same as before wolf recolonization; it led to a stable or increasing population (Woods 1991; Hebblewhite and Smith 2007). The main survival difference was wolf mortality increasing from about 16 percent to 56 percent; Hebblewhite and Smith 2007) between the low and high wolf area, which was consistent with an increase in wolf-kill rate of elk in the high-wolf area (Hebblewhite et al. 2004). These strong differences in mortality and demography led to elk densities in the high-wolf zone that were 10 percent of prewolf density (Hebblewhite et al. in press). The mechanism for elk declines was because kill-rates increased with winter climatic severity. Whereas, in the low-wolf areas, elk were regulated by their own density presumably through resource limitation (Hebblewhite 2005). Wolf recolonization was correlated with a decline in the ratio of migrant to resident elk in the population from about 0.75 before wolves to 0.15 following wolf recolonization (Woods 1991; McKenzie 2001). The exact mechanisms causing migratory changes were unknown in the Bow Valley but were the focus of research in the YHT area.

In the YHT study area, Hebblewhite et al. (2006) showed that the migratory behavior of elk changed since the 1970s in three ways. First, both the proportion and number of elk migrating into BNP declined. The ratio of migratory to resident elk declined from 13:1, in 1980, to 2.5:1, in 2004; the numbers of migrants declined from 980, in 1984, to 580, in 2004. Second, the spatial distribution of elk shifted to the winter range year round. Third, the duration of migration declined because fall migration occurred almost a month earlier. Of eight broad hypotheses proposed to explain these migratory changes, winter range enhancements, access to hay fed to wintering horses, recolonization by gray wolves and management relocations of elk were closely associated with observed elk population dynamics and migratory decline (Hebblewhite et al. 2006). Importantly, prescribed fires, competition with horses for winter forage, and human harvest were unrelated to changes in the ratios of migratory to resident elk.

To examine causes of migratory changes, Hebblewhite (2006) examined the forage and predation risk mechanisms generating these differences between migrant and resident elk between 2001 and 2005, 20 years after wolf recolonization. Migrants exploited phenological gradients by selecting intermediate forage biomass to maximize exposure to high forage quality (Fryxell et al. 1988). This resulted in a 6-percent higher average digestibility of forage for

migrants, which translated to higher fecal diet quality, pregnancy rates and calf weights (Hebblewhite et al., in press). Based on elk nutrition studies (Cook et al. 2004), these differences would be expected to result in higher migrant survival rates and population growth rates from just a bottom-up perspective. However, because wolves were avoiding human activities near the winter range (Hebblewhite and Merrill 2007), residents successfully reduced fine-scale risk to only 15 percent higher than migrants. And, by living in larger group sizes during summer, resident elk were able to reduce relative predation risk by 20 percent (Hebblewhite 2006). Thus, migrant elk failed to realize any predation risk reduction benefits of migrating. In fact, we found that risk of mortality was highest during actual spring and fall migrations when elk had to move through low elevation areas close to wolf dens (Hebblewhite and Merrill 2007).

These differences in resource selection translated to similar demographic differences. Despite the benefits from migration from a forage perspective, migratory elk populations were declining due to predation by wolves and grizzly bears, which were responsible for 47 percent and 29 percent of all migrant mortality, respectively. In comparison, resident elk died more from human hunting (35%) than from wolf predation (30%) and experienced almost no grizzly bear predation (Hebblewhite 2006). Treaty hunting by First Nations peoples is 60 percent of all mortality. These mortality differences translated to slight survival differences between strategies. Residents had higher adult ( $0.87 \pm 0.032$ ,  $n = 53$ ) and calf ( $0.19 \pm 0.067$ ,  $n = 46$ ) survival than migrant adults ( $0.84 \pm 0.035$ ,  $n = 68$ ) and calves ( $0.16 \pm 0.08$ ,  $n = 33$ ) (Hebblewhite 2006). When combined in Leslie-matrix population models, these low survival rates resulted in a stable or slightly declining resident elk herd, but a migrant segment was declining rapidly at about 12 percent per year. The ratio of migrant and resident population growth rates matched long-term trends in the decline in this system as determined from population surveys (Hebblewhite et al. 2006). Therefore, given the low survival caused by high wolf and grizzly bear predation, it is difficult to envision high elk densities as a long-term ecosystem state.

### ***Moose***

Hurd (1999) undertook a 4-year study (1993–1997) in BNP of competition between moose and elk to understand causes for moose declines following wolf recolonization. Hurd examined both exploitative competition for forage and apparent competition mediated by predation by wolves. The study

revealed, at fine-spatial scales, that elk were exploitatively outcompeting moose because of their greater diet breadth and higher abundance. Yet, at large spatial scales, apparent competition mediated by wolves seemed the most compelling reason for moose declines. Wolves were the leading cause of moose mortality, causing 56 percent. Adult moose (male and female were the same) survival rates were very low ( $0.71 \pm 0.03$ ,  $n = 45$ ) and were combined with low calf recruitment ( $23 \pm 7.5$  percent, most likely a result of predation but unknown). Moose populations were declining at about 8 percent per year because of wolf predation. Moose and elk in the high-wolf area had similar demography evidencing the strong top-down effect of wolf predation. In summary, Hurd found apparent competition mediated by wolves was occurring in combination with exploitative competition in a negatively additive fashion, which caused moose population declines.

### ***Caribou***

A similar example of conservation concern is apparent competition between elk and threatened woodland caribou, which have declined during wolf recolonization (Hebblewhite et al. 2007b) in the Canadian Rocky Mountains. Elk and caribou diets differ enough to make exploitative competition an unlikely explanation for caribou declines. Instead, similar to moose, the likely mechanism for caribou declines is competition between elk and caribou mediated by wolf predation, and this hypothesis was supported by modeling work by Hebblewhite et al. (2007b) and Lessard (2005). Because of the strong numeric response of wolves to elk density, even at low caribou densities and even with extremely low wolf-kill rates of caribou, wolves would continue to kill caribou in an inversely density-dependent fashion (Messier 1995, Hebblewhite et al. 2007b). Consequences of this for national park management in the Parks Canada system are dramatic; with current densities of wolves and elk in BNP, the Banff caribou subpopulation will almost certainly become extirpated. Even in Jasper, Wyoming, where caribou densities are higher, high elk densities could lead to enough wolf predation to cause caribou declines. The main management recommendations of Alberta's and British Columbia's woodland caribou recovery plans and modeling studies are to reduce high, primary, prey densities, followed, if necessary, by wolf population reductions (Alberta Woodland Caribou Recovery Team 2005). Within the national park context, caribou viability may well depend on low density elk populations (Hebblewhite et al. 2007b).

## Ecosystem Effects of Wolves

The effects of wolves on ecosystems will manifest in terrestrial ecosystems through direct and indirect effects. Direct effects include predation, competition between wolves and other carnivores, and trophic cascades caused by wolf predation. Indirect effects occur when the effects of wolves are mediated by intermediate species, such as apparent competition between elk and caribou mediated by wolf predation, but they can also include behaviorally mediated effects. Hebblewhite and Smith (2007) provide a comprehensive review of the ecosystem effects of wolves, as do other authors (Smith et al. 2003, Berger and Smith 2005), and here we briefly summarize recent studies in BNP.

The strong top-down effects of wolves on elk density was felt on lower trophic levels including the important forage plant species of willow (*Salix* spp.) and aspen (*Populus tremuloides*). In low-wolf areas, willow and aspen regeneration was essentially zero. Whereas, in high-wolf areas, willow productivity was seven times higher, and aspen sapling densities were significantly higher than in low-wolf areas (Hebblewhite et al. 2005, Hebblewhite and Smith 2007). These differences translated down trophic levels to result in double the riparian songbird abundance and diversity in areas with high wolf predation (Hebblewhite et al. 2005), similar to studies in the Greater Yellowstone Ecosystem (Berger et al. 2001). This link between wolves and willow extended to perhaps the ultimate keystone species, beavers (*Castor canadensis*), because, as elk densities declined with wolf recolonization, the number of active beaver lodges in the Bow Valley of BNP increased (Hebblewhite et al. 2005). Wolves also outcompeted cougars through exploitative competition for ungulate prey (elk) and intraspecific mortality (Kortello et al. 2007). Wolves also successfully stole 57 percent of kills from adult grizzly bears (Hebblewhite and Smith 2007). But perhaps the most pervasive ecosystem effects of wolves will be felt through the scavenger community. In BNP, we detected a minimum of 20 species of vertebrates scavenging on wolf-killed prey, including ravens (*Corvus corax*), coyotes, wolverines (*Gulo gulo*), marten (*Martes americana*), golden eagles (*Aquila chrysaetos*) and grizzly bears. In Yellowstone National Park (Yellowstone), wolves provided a supply of carrion in a much more consistent and spatially dispersed fashion when compared to carrion produced by human hunters (Wilmers et al. 2003). Field studies confirmed the importance of scavenging to literally hundreds of species in Yellowstone. Sikes (1994) documented 445

species of beetles using wolf-killed carcasses during just 2 field seasons. Clearly, the ecosystem effects of wolves will be broad and, likely, beneficial for the conservation of biodiversity.

## **Evaluating Potential Management Scenarios**

Given the strong effects of wolves on ungulates and other important ecosystem components, a natural question for achieving other management objectives will be how sensitive are wolf-prey systems to manipulation. For example, managers may want to maintain levels of ungulate harvest management from before wolf recolonization in the postwolf era. I now review the relative sensitivity of ungulate populations to bottom-up changes in forage and top-down control of wolves in BNP. Based on experiences in BNP, I show that wildlife managers face tough choices ahead and must come to terms with the truth that maintaining prewolf ungulate harvest regimes may be a fantasy in postwolf landscapes and, moreover, may be incompatible with ecosystem management.

### ***Relative Sensitivity to Management Changes in Forage***

There was essentially no evidence that the extensive prescribed fires (more than 77.22 square miles [200 km<sup>2</sup>] of burns) actually translated to increased elk populations in BNP. This was despite the higher forage biomass in burns (Sachro et al. 2005) and the higher forage quality for migrants in general (Hebblewhite et al. in press); migrants still declined due to wolf and grizzly predation. Furthermore, time-series modeling in both the Bow Valley and YHT area suggested that burning in areas with high-wolf density can actually reduce elk population growth rates (White et al. 2005, Hebblewhite et al. 2006). Although speculative, these studies suggest a bottom-up effect of fire on wolf numbers instead of elk mediated by rapid numeric responses of wolves. In essence, any increased elk productivity from fires translated to increased wolf productivity through a rapid numeric response. One caveat is that prescribed fires had high overlap with areas of high predation risk, which may have attracted elk to low-elevation fires where they were killed by wolves. This suggests that prescribed burns in low wolf-predation risk areas might maximize benefits to migratory elk. The success of this hypothesis will depend, however, on the strength of the wolf numeric response to increases in elk (Messier 1994). Because migration decouples predator numeric responses (Fryxell et al. 1988), burning in low-



predation-risk areas inhabited seasonally by elk would be expected to generate the largest increases in elk following fires. Within an ecosystem management context, this management prescription to burn low-predation-risk areas is likely incompatible with long-term ranges of variation in forest-fire frequency. This is because both wolf-predation risk and fire frequency will decline at high elevations in most montane systems (White et al. 2003, Hebblewhite and Merrill 2007), and the approach of burning low-predation-risk habitat to maximize benefits to migratory elk would require burning habitats that burn only infrequently. Thus, the best management recommendation to increase elk in this transboundary system is counter to the principles of ecosystem management that are based on long-term range of variation in montane fire frequencies, and it provides indirect evidence that the stable state for montane systems was low elk densities.

In contrast, nonmigratory, resident elk may be more sensitive to changes in forage biomass for two reasons. First, winter range enhancements outside parks increased resident elk numbers (Hebblewhite et al. 2006). Second, because human use of areas outside parks was higher and because wolf harvest in Canada is quite liberal, wolf avoidance of resident winter ranges (whether because wolves avoided them or were shot) allowed residents to benefit from habitat enhancements (Hebblewhite et al. 2006, Hebblewhite and Merrill 2007). Management implications of the increased sensitivity of resident elk to forage are clear. Any further enhancements to forage within elk ranges that are outside the parks but still are inside areas of high human activity will further contribute to migratory changes. This situation seems to be occurring near the townsites of Gardiner, in Montana, and Estes Park, in Colorado, both areas of high human activity.

### ***Relative Sensitivity of and Management Constraints to Changing Wolf Predation***

The typical conclusion of previous studies where wolves limited prey densities to low numbers was usually a recommendation to reduce predation via large-scale wolf control (Hayes et al. 2003). While there is some controversy over the success of wolf controls (Orians et al. 1997), there is some experimental evidence that wolf control—when applied consistently to reduce wolf populations by greater than 80 percent over huge areas (more than 3,861.02 square miles [10,000 km<sup>2</sup>]) for long terms (5-years) at great financial costs can be partially successful at enhancing ungulate populations (Boertje et al. 1996; Bergerud and

Elliot 1998; Hayes et al. 2003; Valkenburg et al. 2004) for short periods of time. I feel compelled to reiterate, however, that the main conclusions of the authors of perhaps, to date, the best executed wolf-control study in the Yukon (Hayes et al. 2003) pointed out the seeming futility of their wolf-control program as a long-term solution to ungulate population declines. Within 2 years of the end of wolf control, wolf densities and ungulate vital rates returned to precontrol levels. To be successful, wolf control needs to be conducted for long periods of time with greater than 70 percent of the wolf population removed from huge areas (Hayes et al. 2003). While future harvest plans for wolves once delisting occurs will undoubtedly include some wolf harvest, it remains difficult to conceive of states being able to conduct wolf control at the spatial and temporal scales required to even obtain short-term increases in ungulate populations.

Within transboundary park systems, the spatial structure of land management will make the necessarily large-scale and sustained wolf-control measures very unlikely. For example, migrant elk, which suffer the highest mortality from wolves and grizzly bears, migrate into BNP, where wolves and grizzly bears are protected from hunting. Similar transboundary migrations often occur in U.S. national parks (e.g., Yellowstone). There is no precedent within the Canadian National Parks Act or the U.S. National Parks Act to permit wolf control within park boundaries. Moreover, in the successful Yukon wolf controls cited above (Hayes et al. 2003), Parks Canada and the Yukon Territorial Government came to an agreement to not kill any wolves within a set buffer of Kluane National Park because of the controversies surrounding wolf control in the public arena (Parks Canada 1995). Given that the viability of both wolves and grizzly bear populations has become a regional concern (Herrero et al. 2000, Callaghan 2002) in many montane systems, such as the Canadian Rocky Mountains, it seems very unlikely that large-scale wolf controls in or even adjacent to BNP would be implemented.

A second option of reducing wolves only outside of national parks (notwithstanding buffer management, such as in the Yukon) may only exacerbate the problem of growing resident elk outside parks because: (1) mortality of both migrants and residents was lowest during winter when migrant elk would benefit from any provincial wolf reductions, thus benefits of provincial wolf control would accrue more to residents, and (2) resident elk already have slightly lower wolf mortality than migrants which contributed to their increase. Therefore, despite the potential for elk populations to change in response to changes in wolf

predation, the jurisdictional structure of transboundary park systems makes it unlikely that wolf control would result in increased densities of migratory elk and could potentially contribute to migratory declines.

## **Implications for Transboundary Management in the National Park Context**

### ***Long-term Stable States for Elk Population Dynamics and Management***

Given the high mortality rates, elk density and the proportion of migratory elk will likely decline following wolf recolonization in transboundary systems. Reviews of the wolf-bear-moose literature support the interpretation that bear and wolf predation will regulate elk to a low-density equilibrium (Messier 1994; Orians et al. 1997; Testa 2004). This suggests that the long-term stable state under wolf recovery will be low migrant elk density in western montane ecosystems. Indeed, wolf predation was required to achieve aspen regeneration, riparian willow regeneration, and an associated doubling of riparian songbird diversity (Hebblewhite et al. 2005). The case of woodland caribou persistence in the Canadian Rocky Mountains suggests that low-density elk is a prerequisite for caribou persistence (Alberta Woodland Caribou Recovery Team 2005, Hebblewhite et al. 2007b). Evidence from alternate methods of scientific inquiry also supports this interpretation of the long-term state for low elk densities. Archaeological studies and historical accounts conclude the long-term range of variation for the Canadian Rocky Mountains may have been characterized by low elk density (White et al. 1998, Magne 1999). Early historical explorer accounts indicates that elk were observed with one third the frequency of bison, less than one fifth the frequency of bighorn sheep, and less than one half the frequency of moose and mountain goats (Kay et al. 2000), roughly opposite to present day densities. A large-scale experimental test of herbivore optimization with grassland dynamics indicates that many western rangeland systems may also be adapted to between low and moderate ungulate densities (Stewart et al. 2006). Similar findings have also been reported throughout many other western transboundary park ecosystems (Smith 2001, Hessel 2002, White et al. 2003). These convergent lines of inquiry across disciplines suggest that long-term ecosystem dynamics in the Canadian Rocky Mountains were characterized by low elk densities.

Wolves may, therefore, be a keystone species (Power et al. 1996) capable of moving terrestrial ecosystems between two stable states, as predicted by theory and data (Messier 1994) for moose-wolf-bear systems. Like other keystone species, such as sea otters (*Enhydra lutris*), that prey on sea urchins (Estes and Duggins 1995), these effects manifested through large population declines in herbivores following wolf recolonization. Without wolves, ungulate densities increase, vegetation communities become overbrowsed, specialist herbivores (e.g., moose and beaver) decline through competitive exclusion by the generalist elk, and biodiversity is reduced (e.g., loss of riparian songbirds). As wolf populations recover, wolf numbers rapidly increase, causing alternate prey species (e.g., woodland caribou and moose) to decline through competition. But, declines in species (e.g., elk) bring about slow changes to the vegetation community that lead to enhanced aspen and willow regeneration and to increased biodiversity. In this context, wolf predation should be viewed as a critical component of an ecosystem management approach across jurisdictions.

## **A Proposed Approach to Reconcile Conflicting Paradigms**

Within national parks, where management objectives are often ecosystem based, low- density elk populations may be consistent with long-term management objectives. However, in the managed lands surrounding national parks, management objectives include both consumptive and nonconsumptive wildlife use. In this context then, low-density population of elk may not meet historical agency management objectives. This contradiction will become a common management problem in ecosystems with recovering wolf populations.

First, it should be recognized that objectives that call for high densities of large ungulates for human consumption have little basis in the principles of ecosystem management for montane systems. The evidence presented here, along with growing body of literature (White et al. 1998, Magne 1999, Stewart et al. 2006) strongly suggests, especially with wolf predation, the long-term ecosystem state was characterized by low elk density. Thus, wolf recolonization provides an opportunity for agencies to implement for broader ecosystem management, such as managing for riparian biodiversity.

I recognize, however, that cultural and social systems are slow to change. Some areas outside national parks will still include management for high densities of large ungulates despite the conflict with an ecosystem management

approach. In transboundary settings, the difficulty with these objectives will be in defining common management goals despite different management paradigms (Clark 1999, Pedynowski 2003). In the similarly complex transboundary Jackson Hole elk population, Clark et al. (2000) concluded exactly that the lack of an effective, common framework for problem definition and for management objectives had contributed to management conflicts. I believe jointly defining common management objectives for transboundary predator-prey systems will be a crucial step to build a consensus approach to managing these important areas. The lack of a common definition between management agencies itself may be the biggest obstacle to overcome (Clark et al. 2000, Clark 2001).

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