Chapter 11

Potential for and Implications of Wolf Restoration in the Southern Rockies

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INTRODUCTION

A healthy ecosystem requires its full complement of native species, as well as the ecological functions and processes linking those species to their environment, such as fire and predator-prey relationships. An environment able to support a full array of native carnivores for an extended time is likely healthier than one that cannot. We believe the presence of self-sustaining populations of gray wolves (*Canis lupus*) within their native range indicates the healthiest ecosystems. The extirpation of gray wolves distorted ecological and evolutionary relationships well beyond the changes in numbers and behavior of ungulates, because wolves perform several important functions, such as changing pathways of energy flow through an ecosystem, influencing the adaptations with other organisms that evolved with wolves (e.g., prey species, smaller predators, parasites), and affecting the amount (or biomass) and production of plants in the system.

Ecologists have been interested in how wolves affect the broader ecosystem for decades. From 1939 to 1941, Adolph Murie (1944) conducted field studies in Mount McKinley (now Denali) National Park, Alaska, to determine how wolves contributed to the ecology of the park. Murie entertained questions that delved into the relationships between park wolves and other wolves, between wolves and their prey, and between wolves and other predators. During that time, other ecologists, such as S. Charles Kendeigh, Aldo Leopold, Ernest Thompson Seton, and Victor Shelford, began questioning the ecological wisdom of killing wolves.

Recent research suggests that the impact wolves and other large carnivores have on an ecosystem may be more profound than previously expected (see chap. 3). In this chapter, we examine the probability that wolves could live in the Southern Rockies and the implications of that restoration by exploring wolf population dynamics, the interactions of wolves and other carnivores, the potential impact of wolves on native ungulates and livestock in the Southern Rockies, and how wolves might affect land use and human safety in the region.

POTENTIAL FOR WOLVES IN THE SOUTHERN ROCKIES

The wolf has long been gone from the Southern Rockies. When livestock arrived at Jamestown, Virginia, in 1609, the fate of North America's wolves seemed sealed (see chap. 2). By the 1930s, the wolf was nearly extirpated from the Lower 48; in 1945, the last wolf was shot in Colorado (Bennett 1994; Boitani 2003). Yet evidence of the important role wolves play in their ecosystems is mounting rapidly (see chap. 3 and Soulé et al. 2003a, 2005). Important ecological drivers such as wolves must exist at sufficient distribution and density to exert that role. Far more wolves are necessary for the species to play its ecological role than are needed for simple viability of a taxon. While a viable population of wolves may exist in the

Greater Yellowstone Ecosystem, that population does not contribute to the ecological functioning of the Southern Rockies.

Substantial interest has developed in restoring wolves to the Southern Rockies (see chap. 6). This has spurred questions about whether the Southern Rockies can support wolves. Bennett (1994), working with the US Fish and Wildlife Service and the University of Wyoming Cooperative Fish and Wildlife Research Unit, estimated that western Colorado could support around 500 to 1,000 wolves. Martin et al. (1999) and Carroll et al. (2003) identified areas in northwestern, west-central, and southwestern Colorado where wolves could thrive (figures 11.1 and 11.3). In addition, they noted good wolf habitat at the Colorado-Wyoming border and in northern New Mexico (Carroll et al. 2003). Carroll et al. (2003) predicted that perhaps 1,300 wolves could eventually live in the Southern Rockies, with nearly 90 percent of those wolves using public land. The Southern Rockies Ecosystem Project's Southern Rockies Wildlands Network Vision (Miller et al. 2003) outlined a plan to retain and enhance connectivity for wolves among these areas, largely using least-cost path analysis (Fink et al. 2003).

Carroll et al. (2003) further estimated the success of reintroducing wolves to four core areas of 2,500 sq. km (965 sq. mi.) of high-quality habitat (figures 11.2). They predicted that ninety-seven wolves could inhabit a northern New Mexico–south-central Colorado core area (the Carson National Forest, Santa Fe National Forest, Vermejo Park Ranch); seventy-five wolves could live in a southwestern Colorado core area that is probably the wildest area in the Southern Rockies (the San Juan National Forest, Rio Grande National Forest, and the Grand Mesa, Uncompahgre, and Gunnison national forests); 102 wolves could exist in a west-central Colorado core area (northern portions of the Grand Mesa, Uncompahgre, and Gunnison national forests and the southern portion of the White River National Forest); and 155 wolves could reside in a northwestern Colorado core area (the Flattops, encompassing portions of the White River National Forest and Routt National Forest). Eventually some wolves would disperse from these core areas and promote growth of the population throughout the ecoregion and beyond.

Carroll et al. (2003) also considered the likelihood of wolves inhabiting the Southern Rockies Ecoregion as a result of dispersers arriving from Wyoming, concluding that such movements would produce less than one pack in the Southern Rockies over 200 years. Since Carroll et al.'s analyses, it has become clear that the state of Wyoming will manage wolves aggressively to minimize the size of the population there, including the number of dispersing wolves. While it seems appropriate for the Colorado Division of Wildlife to adopt a management plan that promotes the survival of wolves dispersing from Wyoming, it further seems certain that reintroducing wolves to core areas of high-quality habitat is the most certain and cost-effective way to restore the species to the Southern Rockies Ecoregion.

The message from the models of Martin et al. (1999), Bennett (1994), Phillips et al. (2000), and Carroll et al. (2003) is that the Southern Rockies Ecoregion could support a viable population of around a thousand wolves under current landscape conditions. Those wolves would largely inhabit public lands, and genetic exchange would occur among populations. While the social structure of wolves hastened their decline a century ago, that same social structure can help wolves restore themselves quickly, as evidenced by the results in Yellowstone National Park (Smith and Ferguson 2005).

Wolves likely will leave protected areas such as Rocky Mountain National Park, but populations will remain dependent on those protected areas (Fritts and Carbyn 1995; Haight et al. 1998; Woodruffe and Ginsberg 1998). Even though elk (*Cervus elaphus*) numbers in the Southern Rockies rival prey availability in the Greater Yellowstone Ecosystem, the smaller size of protected areas in the Southern Rockies (figure 5.1) means humans may kill more wolves as wolves move throughout the region. That could slow the rate of wolf establishment in the Southern Rockies. While wolf recovery efforts in the Great Lakes region of the United States suggest that wolves can coexist with high levels of development, people there have lived with wolves for several decades. Wolf reintroduction to the Southern Rockies will likely face heavy initial resistance. Other factors such as states' rights, concerns over possible restrictions from implementing the Endangered Species Act, and fear of change undoubtedly will all come into play (see chap. 6 and 7). It may take years to alter such perceptions. After a decade, the Mexican wolf reintroduction still falters due to human resistance and lack of a core protected area (see chap. 2).

The small size and relative isolation of core areas in the Southern Rockies Ecoregion means connectivity among populations will remain important (Haight et al. 1998). The Southern Rockies Ecosystem Project's Southern Rockies Wildlands Network Vision outlines a plan to retain and enhance such connectivity (Miller et al. 2003). Combined with proposed reintroductions into the Grand Canyon area, a place that enjoys the largest potential for wolves in the southwestern United States (Carroll et al. 2004), reintroducing wolves into the Southern Rockies provides an outstanding opportunity to help recover the animal throughout a significant portion of its range, as mandated by the Endangered Species Act. These two proposed reintroductions would reconnect wolves along the spine of the continent—the Rocky Mountains and Sierra Madre—from Mexico through Canada and into Alaska. Noted wolf biologist L. D. Mech concluded the following when considering wolf restoration to the Southern Rockies Ecoregion:

> Ultimately then this restoration could connect the entire North American wolf population from Minnesota, Wisconsin, and Michigan through Canada and Alaska, down the Rocky Mountains into Mexico. It would be difficult to overestimate the biological and conservation value of this achievement.

Reintroduction to these two areas would also restore a linkage for wolves along the Colorado River, thus connecting two extremely popular national parks, Grand Canyon and Rocky Mountain (as well as Arches and Canyonlands national parks and the Glen Canyon National Recreation Area, all in Utah). Sufficient habitat and prey for wolves exist in these regions now, and we should not wait.

We have a rare opportunity to re-create the evolutionary potential of wolves, as well as reestablish the role of wolves as a keystone species with strong ecological interactions throughout the Rocky Mountains (see chap. 3). Evolutionary and ecological restoration will not occur if we limit wolf recovery to a few small and isolated populations in the Northern Rockies, north-central United States, and southwestern United States, all of which will come to more closely resemble museum pieces rather than functioning ecological and evolutionary processes (see Soulé et al. 2003a, 2005).

WOLF POPULATION DYNAMICS

In North America, wolf densities vary widely across regions, but they generally remain relatively stable within populations. Wolf populations and the population sizes of their ungulate prey are closely linked (Keith 1983; Fuller 1989). Generally, densities of wolves are highest where prey biomass is highest. Social factors including pack formation, territorial behavior, exclusive breeding, deferring reproduction to dominant individuals, aggression among wolves (i.e., intraspecific aggression), dispersal, and shifts in the primary prey that wolves target can alter how the amount of food affects wolf demography (Keith 1983). Packard and Mech (1980) concluded that social factors and the influence of food supply are interrelated in determining population levels of wolves. Changes in habitat composition and distribution can affect prey densities and distributions, and therefore wolf spatial distribution and abundance (Paquet et al. 1996).

Average annual densities of wolves are around one wolf per 23 sq. km (9 sq. mi.) (see Fuller 1989; Darimont and Paquet 2002). During periods of exceptionally high concentrations of prey, wolf densities may increase dramatically. Kuyt (1972) reported that in some parts of Canada's Northwest Territories (Mackenzie) winter wolf densities increased to about one wolf per 10 sq. km (3.8 sq. mi.) when concentrations of caribou (*Rangifer tarandus*) were high. When deer (*Odocoileus* spp.) reached densities of 64 per sq. km (24.7 sq. mi.) in Superior National Forest (Minnesota), wolves reached a density of one per 14 sq. km (5.4 sq. mi.) (Van Ballenberghe 1974). The highest density of wolves ever recorded was one per about 2 sq. km (0.77 sq. mi.) at a winter deeryard near Algonquin Provincial Park, Ontario (Forbes and Theberge 1995), reflecting a seasonal concentration of wolf packs. The lowest reported density in North America for a stable population occurred in the central Canadian Rocky Mountains, with a density of one wolf per 250 to 333 sq. km (96.5 to 128.6 sq. mi.) over ten years (Paquet et al. 1996).

The amount of prey per wolf, the prey's vulnerability to predation, and the degree of human exploitation of wolves may largely drive wolf population dynamics (Keith 1983; Fuller 1989). Building on work by Keith, Fuller reviewed twenty-five studies of North American wolf and prey populations and found that availability of ungulate biomass and human-caused mortality affected rates of increase for wolves the most. Ungulate biomass was particularly important for pup survival during the first six months of life (Fuller 1989). Fuller (1989) found the index of ungulate biomass per wolf is highest for heavily exploited (Ballard et al. 1987) or newly protected (Fritts and Mech 1981) wolf populations and lowest for unexploited wolf populations (Oosenbrug and Carbyn 1982; Mech 1986) or those where ungulates are heavily harvested (Kolenosky 1972).

The rates at which wolves consume prey explain the importance of ungulate biomass as a factor limiting wolf populations. Mech (1977a) determined that 3.2 kg (7 lb.) per wolf per day is the minimum rate of consumption required for all wolves of a pack to survive and rear pups successfully. In southwestern Quebec (Messier 1985) and in Minnesota (Mech 1977b), researchers noted that low ungulate biomass increased starvation rates and intraspecific aggression among wolves.

Overall, quantifying the importance of food to population growth is difficult, and results vary among studies. Some researchers have accepted this variability and decided any sign of starvation among adult wolves means food is limiting population growth (Fritts and Mech 1981; Ballard et al. 1997). This assumption is reasonable given that adults typically are the last members of the population affected by food shortages.

Many studies have reported no disease-related mortality (Van Ballenberghe et al. 1975; Mech 1977b; Fritts and Mech 1981; Messier 1985; Hayes et al. 1991; Pletscher et al. 1997). In other studies, disease accounts for 2 to 21 percent of wolf mortality (Carbyn 1982; Peterson et al. 1984; Fuller 1989; Ballard et al. 1997). The link between disease and low availability of food is uncertain, but intuitively the relationship makes sense. A population of wolves lacking food should be more vulnerable to disease than one with food easily available. Furthermore, a food shortage could combine with disease to increase the significance of otherwise innocuous or sublethal disease conditions (Brand et al. 1995).

Human-caused mortality can also be a primary limiting factor for wolf populations (Peterson et al. 1984; Ballard et al. 1997). Large carnivores typically did not need to evolve any response to high levels of mortality from predation. Human-related causes of mortality include legal harvest (Fuller and Keith 1980; Keith 1983; Gasaway et al. 1983; Messier 1985; Ballard et al. 1987, 1997; Peterson et al. 1984; Bjorge and Gunson 1989; Fuller 1989; Hayes et al. 1991; Pletscher et al. 1997), illegal harvest (Fritts and Mech 1981; Fuller 1989; Pletscher et al. 1997), collisions with vehicles on highways (Fuller 1989; Paquet 1993; Forbes and Theberge 1995; Paquet and Hackman 1995; Thiel and Valen 1995; Bangs and Fritts 1996) or collisions with trains (Paquet 1993; Paquet and Hackman 1995; Paquet et al. 1996), and introduced diseases (see chap. 10).

The annual rate of mortality that causes a population decline in wolves remains uncertain. To complicate matters, many researchers consider only harvests (i.e., hunting or trapping) when they calculate mortality rates. Keith (1983) reviewed studies of thirteen exploited populations and determined that populations declined when harvests exceeded 30 percent in autumn. Similarly, Fuller (1989) found that the annual rates at which wolf population increase varies in direct response to rates of mortality; where wolves are killed by humans, harvests exceeding 28 percent of autumn or early winter populations might result in a population decline. He concluded that a population would stabilize with an overall rate of annual mortality of 35 percent or a human-caused mortality rate of 28 percent. Gasaway et al. (1983), Keith (1983), Peterson et al. (1984), Ballard et al. (1987), and Fuller (1989) found that harvest levels of 20 to 40 percent can limit wolf populations but that lower rates have a more significant effect in areas with low ungulate biomass (Gasaway et al. 1983). Indeed, the effects of mortality also vary over time and with different population structures (Peterson et al. 1984; Fuller 1989). If wolf productivity is high, and consequently the ratio of pups to adults is high, the population can withstand a higher overall mortality because pups (nonreproducers) make up a disproportionate amount of deaths (Fuller 1989). Lastly, net immigration into or emigration out of a wolf population may mitigate the effects of harvest (Fuller 1989).

INTERACTIONS BETWEEN WOLVES AND OTHER CARNIVORES

Wolves profoundly influence other carnivores and scavengers (secondary consumers), and in turn, these species affect ungulates and other prey. Yet researchers have yet to adequately address the extent and full implications of these interactions (Smith et al. 1999). Wolves may change the distribution and abundance of competitors such as coyotes (*Canis latrans*) (Paquet 1989, 1991, 1992; Crabtree and Sheldon 1999). In addition to these competitive interactions, wolves also provide a regular supply of carrion, which is exploited by smaller carnivores. For coyotes, the benefits from scavenging wolf kills can compensate for the associated risk of conflict with wolves (Paquet 1992); Paquet demonstrated that, although wolves occasionally killed coyotes, coyotes nonetheless followed wolves and scavenged at their kills.

Following wolf reintroduction into the northern range of Yellowstone National Park, the ecosystem entered a period of adjustment. During this period, competition among carnivores that exploit similar prey was amplified and thus more easily detected. Such adjustment may occur more slowly during natural recolonization than during reintroductions. During reintroduction, the naiveté of newly coexisting predators probably affects the intensity of interaction (Berger et al. 2001b). Educated coyotes (i.e., those that have learned how to survive in the presence of wolves), for example, have done well in the presence of educated gray wolves, but naive coyotes have fared poorly in Yellowstone, suffering heavy mortality during the early stages of the reintroduction (Crabtree and Sheldon 1999). In some regions, wolves and coyotes have reduced the level of competition between them by focusing on different, nonlimiting (i.e., relatively abundant) prey species (Paquet 1992).

Kunkel et al. (1999) compared patterns of prey selection between wolves and pumas (*Puma concolor*). Their results suggest that wolves and pumas might exhibit the two classic types of competition: exploitation, in which species exploit the same resource, and interference, in which species physically interfere with each other. Both types of competition affect the behavior and population dynamics of each species and of its prey. Wolves in Yellowstone killed several pumas (Kunkel, pers. obs.; Ruth, pers. comm.) and also pushed pumas off their kills, resulting in pumas consuming their prey at lower rates and being forced to kill their prey at higher rates (Kunkel, pers. obs.; Ruth, pers. comm.).

In Yellowstone, grizzly bears (*Ursus arctos*; usually large individual animals that were presumably males) discovered a reliable source of food in wolf kills, and that could happen with black bears (*Ursus americanus*) if wolves are restored to the Southern Rockies. Alternatively, researchers have also observed wolves harassing black bears and grizzly bears, and even killing a grizzly cub and a black bear (Paquet, pers. obs.).

POTENTIAL EFFECTS OF WOLVES ON NATIVE UNGULATES IN THE SOUTHERN ROCKIES

Viable, well-distributed wolf populations depend on abundant, available, and stable ungulate populations. Researchers have heatedly debated the relationship between wolves and their prey (Gasaway et al. 1983; Boutin 1992; Boertje et al. 1996; Ballard and Gipson 2000). Differences notwithstanding, researchers agree that myriad biological and nonbiological factors affect wolf predation, including weather, time of year, habitat area and characteristics, disease, species of ungulate, sex and age structure of the herd, numbers and types of other prey, numbers and types of other carnivores including humans, and size and distribution of the wolf population. Due to complex interactions among factors, it will remain exceedingly difficult to understand the dynamics of wolf-prey numbers and the importance of contributing factors.

GENERAL PREDATOR-PREY INTERACTIONS

Ungulate density, snow depth, weather, and predation all affect the population dynamics of ungulates living in northern latitudes. Studies conducted in areas without predators emphasize density dependence and weather as drivers of ungulate population dynamics (Merrill and Boyce 1991; Singer et al. 1997; Post et al. 1999; Singer and Mack 1999). Increasing ungulate density and severe weather interact to decrease survival. Weather and population density affect adult survival less than juvenile survival, with the former often representing the prime determinant of population growth rate (Singer et al. 1997).

Overall, the lack of large carnivores in North America in recent decades has resulted in low deer mortality rates, likely leaving most populations close to carrying capacity of the vegetation (Crête and Daigle 1999). Consistent with the hypothesis of top-down pressures on ecosystems (Oksanen et al. 2001; see chap. 3), ungulate biomass in North America is much higher without wolves than with them (Crête 1999). Crête (1999) concluded that wherever wolves remained relatively free from human persecution for decades, ungulate densities were low.

Predation by wolves can limit and possibly regulate the growth rate and size of ungulate populations (Skogland 1991; Messier 1994). Anything causing mortality or affecting birthrates can function as a limiting factor (Caughley and Sinclair 1994). Ecologists refer to sources of mortality that occur regardless of the size of the population as density-independent factors. A limiting factor is density dependent if it causes increasing mortality with an increasing population size, such as density-induced starvation (Sinclair 1989). Density-independent sources of mortality are additive to density-dependent mortality. Density-dependent sources of mortality tend to move a population toward equilibrium and thus regulate it (Caughley and Sinclair 1994). If one type of mortality substitutes for another and leaves the overall mortality rate unchanged, ecologists refer to it as compensatory mortality. Sometimes predator populations lag behind prey population, causing a delay in density-dependent mortality. In some circumstances this can result in what ecologists refer to as depensatory mortality, which accentuates a population trend instead of regulating it (Caughley and Sinclair 1994). For example, if predators take an increasing proportion of a declining, secondary prey population as they decline (which might happen if the predators' primary prey population is increasing), they hasten that decline rather than allowing it to recover back toward equilibrium (Caughley and Sinclair 1994).

Despite difficulties in applying rigorous experimental design to predator-prey studies (Boutin 1992; Minta et al. 1999), many researchers report that wolf predation decreases survival or population growth rates of prey (Gauthier and Theberge 1986; Gasaway et al. 1992; Boertje et al. 1996; Jedrzejewska and Jedrzejewski 1998; Kunkel and Pletscher 1999; Hayes and Harestad 2000). The interactions of ungulates and their predators may overshadow the amount of forage as a controlling factor for ungulate populations. Researchers also found that wolf predation increased with snow depth (Nelson and Mech 1986; Huggard 1993; Post et al. 1999), indicating that predation can interact with weather to affect ungulates. In situations where other factors reduce prey populations (e.g., winter weather), predation by wolves may therefore inhibit the recovery of prey populations for long periods of time (Gasaway et al. 1983).

Many studies emphasize the direct effects (e.g., prey mortality) of wolves on the population dynamics of their ungulate prey (Mech and Karns 1977; Carbyn 1983; Gasaway et al. 1983; Messier 1994; Messier and Crete 1985; Peterson et al. 1984; Ballard et al. 1987; Boutin 1992). However, predation can affect prey populations indirectly by influencing their behavior, such as the types of habitat and times of habitat use, activity patterns, foraging mode, diets, mating systems, and life histories. Several studies describe the influence of wolves on the movements, distribution, and habitat selection of caribou, moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*) (Mech 1977b; Ballard et al. 1987; Nelson and Mech 1981; Messier and Barrette 1985; Messier 1994), and elk (Ripple and Larson 2000; Ripple and Betscha 2003, 2004; Fortin et al. 2005). Berger et al. (2001a) showed that naive moose improved their antipredator behavior after a single aversive experience with wolves.

Prey can lower their mortality rate by preferentially residing in areas with few or no wolves. Several studies suggest that ungulates seek out predator-free refugia to avoid predation by wolves (Mech 1977b; Paquet 1993). Research shows that wolf predation in the Superior National Forest of northern Minnesota affects deer distributions within wolf territories (Mech 1977b). For example, deer existed in higher densities along the edges of wolf territories, where predation was less likely.

Unusually mild or severe winter weather can temporarily increase or depress ungulate populations relative to that predicted by habitat potential (which reflects a long-term average). Wolf packs may react to changing conditions in varying ways, depending on the location of their territories in relation to other packs and on prey distribution. If packs encounter lower prey densities within their territories, they may exploit their territories more intensely. This may be achieved by (1) persevering in each attack; (2) using carcasses more thoroughly; (3) feeding on alternative, possibly less attractive food resources, such as beaver (*Castor canadensis*); and (4) patrolling their territory more intensely (Messier and Crête 1985).

WOLF-UNGULATE INTERACTIONS IN NORTH AMERICA

In western North America, wolves prey primarily on elk, deer, moose, and caribou. As opportunistic predators, wolves typically focus their predation on the most abundant species (Huggard 1993; Kunkel 1997; Smith et al. 2000). Thus, elk and deer would likely comprise the primary diet for wolves in the Southern Rockies. Kill rates by wolves vary greatly, from 2.0 to 7.8 kg (4.4 to 17.2 lb.) per wolf per day (Mech 1966; Fuller 1989; Thurber and Peterson 1993; Ballard and Gipson 2000; Hayes et al. 2000; Jedrzejewski et al. 2002), depending on numerous factors. Wolves generally kill animals most vulnerable to predation because of age, body condition, or habitat and weather conditions (Mech 1996; Kunkel et al. 1999; Kunkel and Pletscher 2001).

Through 1997, wolf packs in Yellowstone killed approximately 130 ungulates per year (Smith et al. 2000). Studies found that elk comprised 90 percent of wolf prey in Yellowstone (the Environmental Impact Statement predicted 53 percent) (US Fish and Wildlife Service 1994). Wolves killed about fifteen elk per wolf per year. Winter severity explained more of the variations in kill rates than did naiveté of prey (Mech et al. 2001). For example, wolves killed 6.1 kg (13.4 lb.) of prey per wolf per day in the mild winter of 1998 and 17.1 kg (37.7 lb.) of prey per wolf per day in the severe winter of 1997 (Mech et al. 2001). From 1995 to 2000, estimated wolf kill rates in Yellowstone National Park were higher in late winter (2.2 kills per wolf per month) compared to early winter (1.6 kills per wolf per month), with an overall estimated rate of 1.9 kills per wolf per month (Smith et al. 2004)

Where wolves and deer coexist in the northern United States and Canada, deer populations remained unstable for the duration of the monitoring period (twenty to forty years) (Potvin et al. 1988; Fuller 1990). The level of predation that affects ungulate populations depends on whether predation is additive or compensatory relative to other sources of mortality. In general, compensatory effects are most likely when prey numbers approach the carrying capacity of the habitat (Bartmann et al. 1992; Dusek et al. 1992; White and Bartmann 1998). In contrast, when prey populations lie well below carrying capacity, we hypothesize that wolf predation acts at least partially additive to other sources of mortality.

Dusek et al. (1992) reported that among heavily exploited deer populations in Montana, hunting mortality by humans was largely additive to other forms of mortality including predation, and there was little opportunity for compensatory mortality in the adult segment of the population. Kunkel and Pletscher (1999) reported similar findings for deer and elk populations in which predation represented the main source of mortality. For calves, however, the situation appears to be different. Singer et al. (1997) reported possible compensation in elk calf mortality for Yellowstone's northern range because predators primarily killed calves with lower birth weights and those born later in the year. These results were similar to those of Adams et al. (1995) for caribou in Denali National Park, Alaska. The significant difference in prey selection by wolves and humans provides a further argument for compensatory mortality (Kunkel et al. 1999). While wolves typically kill the youngest and oldest segment of the prey population, human hunters usually take animals in their prime. For example, since 1995, the average age of wolf-killed ungulates in and around Yellowstone has been fourteen, while the average age for hunter-killed ungulates is six (Smith et al. 2001).

In the Northern Rockies, wolves, pumas, bears, coyotes, and humans are important predators of native ungulates. There, wolf predation, one of many mortality factors affecting cervid (i.e., members of the deer family) survival, may negatively affect hunter harvests (Kunkel and Pletscher 1999). This issue remains a central concern to the public regarding wolf recovery in the region (US Fish and Wildlife Service 1987b, 1994). In northern Minnesota, wolf predation did not affect harvests of white-tailed deer bucks by humans in "good" habitat; however, adjustments to female harvest have been necessary (Mech and Nelson 2000). For more than twenty years at the end of the last century, wolf populations have increased in Minnesota while hunter harvests of deer have also increased, despite variable weather and deer deaths from vehicle collisions, other predators, and other sources (Minnesota Department of Natural Resources 2001). Alternatively, in some areas of Alaska and Canada where game managers or hunters did not reduce wolf numbers, human harvests of moose declined (Gasaway et al. 1992). Mean survival rate of moose calves at locations in Alaska, Canada, Norway, and Wyoming with wolves and grizzly bears were three times lower than at sites without these predators (Berger et al. 2001b).

Six years after wolf reintroduction, scientists estimated that the northern Yellowstone elk herd included 13,400 animals, a number nearly identical to the twenty-five-year average (1976 to 2001) of 13,890 (Lemke et al. 1998). Similarly, total ungulate numbers in Yellowstone had tripled from 1968 to 1988, with elk alone numbering about 52,000 in 1988 (Singer and Mack 1999). At such high numbers of elk, it makes sense that in the first years after wolf reintroduction, weather remained a dominant factor for ungulate numbers. Ten years after wolf reintroduction to the northern range, however, elk numbers there dropped to 8,335 (White and Garrott 2005). The population continued to drop until 2006 and then leveled off for the next three years, with a population of 6,279 in the northern range in early 2008 (US National Park Service 2008). Yet it remains unclear as to how much of that decline could be attributed to wolf predation (Vucetich et al. 2006). As such, data on elk survival do not provide an early indicator of whether wolves are exerting a top-down role. Yet a change in elk behavior should appear more rapidly than changes in survival. Ripple and Beschta (2004) propose that fear of predation in ungulates can restructure ecosystems because of behavioral changes. Fortin et al. (2005) documented changes in elk behavior following wolf restoration in Yellowstone. As a result of changes in numbers and behavior of prey, studies suggest that wolves are showing signs of ecological effectiveness in Yellowstone National Park already. In the absence of wolves over the last seventy-five years, cottonwoods and willows suffered lower recruitment (Beschta and Ripple 2006). Since the reintroduction of wolves, that recruitment has increased, permitting beavers to reestablish and create additional wetlands (Ripple and Beschta 2004).

ESTIMATED EFFECTS OF WOLVES ON UNGULATES IN THE SOUTHERN ROCKIES

The research being conducted in the Northern Rocky Mountains greatly influenced our assessment of the potential effects of wolf predation on ungulates in the Southern Rockies. We used data from the Yellowstone area to generate reasonable estimates of the effects of wolf predation on prey populations for the Southern Rockies. Although we report our estimates of effects of a possible wolf restoration as single figures (as opposed to ranges), we emphasize that they should be viewed in a relative sense to gain an appreciation of the potential magnitude of wolf predation.

Our hypothetical wolf population for the Southern Rockies includes 100 animals distributed in ten packs (each including ten animals: six adults and four pups). Each hypothetical pack occupies a territory of about 500 sq. km (or 193 sq. mi. or 123,520 acres) in size and kills the equivalent of 230 elk per year (i.e., each wolf would kill the equivalent of twenty-three elk per year). We further assumed that 95 percent of the wolf kills would involve elk and 5 percent would involve deer. We consider three deer to equal one elk (Fuller 1989). Finally, we assumed that of the elk killed, 43 percent would be calves, 28 percent adult females, 20 percent adult males, and 9 percent of unknown age and sex (Smith and Ferguson 2005; Smith et al. 2004). Therefore, the total population of 100 wolves in ten packs would inhabit a total area of about 5,000 sq. km (or 1,930 sq. mi. or 1.23 million acres) and annually kill about 2,185 elk and 345 deer. Of the elk killed, 940 would be calves, 612 would be cows, 437 would be bulls, and 196 would be of unknown age and sex.

Depending on a wide variety of circumstances, a population of more than 100 wolves could proportionately increase the effects on wild ungulates above the figures predicted above. Assuming a directly linear relationship between wolf population size and effects (which is probably overly simplistic), a population of 1,000 wolves (the approximate carrying capacity of wolves in the Southern Rockies as predicted by ecological factors alone; see above) would inhabit a total area of about 50,000 sq. km (19,305 sq. mi.) and annually kill about 22,000 elk and 3,500 deer.

Because of the high elk numbers throughout the Southern Rockies Ecoregion, a combination of factors working simultaneously may be required to reduce large populations of elk to a lower density and keep them there. The elk herds in both Colorado and New Mexico exceed state goals. Recent game management statistics for Colorado indicate that the state hosted approximately 291,960 elk and 538,770 deer in 2007 (Colorado Division of Wildlife 2008). For simplicity, this analysis utilizes the 2007 statewide game population numbers from Colorado, given that the majority of the Southern Rockies fall within the borders of Colorado. The hypothetical area occupied by 100 packs represents approximately 31 percent of the 41,721,141 acres in the Southern Rocky Mountains. We predict a level of wolf predation that takes roughly 7.5 percent of the 2007 elk population and 0.6 percent of the 2007 deer population in the Colorado portion of the Southern Rockies Ecoregion. This may overestimate the actual effect if wolves are restored to the ecoregion, because it seems unlikely that a restored wolf population in the Southern Rockies would reach 1,000 wolves. Social intolerance would likely constrain the size of the wolf population with a consequent reduction in effects on elk and deer.

Regional Deer Population

Generally, deer are doing well in the Southern Rockies as they recover from relatively low populations in the 1990s and early this century. Colorado's mule deer population has been expanding over the past decade, and in 2007 it reached 538,770 (Colorado Division of Wildlife 2008).

Historically, New Mexico's deer population fluctuated dramatically (New Mexico Game and Fish 1999). The deer population in the state reached a peak of about 301,000-plus animals in the mid-1960s, but declined to approximately 200,000 deer in 1999 (New Mexico Game and Fish 1999). Unfortunately, we could not obtain more recent deer population estimates because New Mexico recently moved away from statewide population estimates to regional projections. New Mexico Game and Fish believes that the period of peak numbers represented an anomalous irruption of deer numbers caused by several factors including: (1) abundant growth of high-quality forage due to widespread disturbances (caused by infrequent suppression of fire and extensive clear-cutting of forests); (2) widespread predator control programs; and (3) favorable climatic conditions (B. Hale, New Mexico Department of Game and Fish, pers. comm.). The decline in deer numbers likely resulted from many factors, not the least of which was habitat succession (resulting from more frequent fire suppression) that caused a reduction in shrub forage and an overall reduction in carrying capacity. Other factors included increases in human population and development of deer habitat, weather patterns, increased grass production for cattle, and increased predator densities.

The addition of wolves to the Southern Rockies Ecoregion could exacerbate the effects of other predators on mule deer unless interference competition between wolves and other large carnivores proves to be significant (Ballard et al. 1999, 2001; Crabtree and Sheldon 1999). This would help repress population growth in Colorado, where deer surpass current objectives, but might negatively impact deer recovery efforts in New Mexico.

Alternatively, the presence of wolves may benefit mule deer if wolves differentially prey on elk, which is likely (Smith et al. 2000). If wolf predation helps reduce the size of the elk population in the Southern Rockies, mule deer may benefit from reduced competition with elk for forage and space. This would help deer recovery in New Mexico, but add to the challenge of restraining mule deer population growth in Colorado.

Regional Elk Population

If wolves establish themselves in very high densities in parts of the Southern Rockies (e.g., one wolf per 25 sq. km or 10 sq. mi., though very few locations in the ecoregion could sustain such densities), they might exert enough predation pressure on small, isolated elk herds to prompt wildlife managers to stop or decrease hunting of cow elk in these herds. However, because the region hosts such significant elk numbers, we feel that the likelihood of this scenario is low.

Colorado has the largest elk population of any state. The Colorado Division of Wildlife estimated the total population as being 305,000 in 2002 (Colorado Division of Wildlife 2002). That number far exceeded the state's objective at the time of 188,580 elk (Colorado Division of Wildlife 2002; Burkhead 2006). Since that time, the state has successfully decreased the size of the elk herd through increased hunting pressure. The Division of Wildlife estimated a population of 291,960 elk in 2007 (Colorado Division of Wildlife 2008), which is still higher than the Division of Wildlife's recently revised population objective for elk of 228,000 animals (Kahn 2006).

New Mexico supports the sixth largest elk herd in North America, with an estimated population of 70,000 to 90,000 animals in 2007 (D. Weybright, New Mexico Department of Game and Fish, pers. comm.). The 2002 population exceeded the statewide goal of 62,000 elk by 13 to 45 percent.

Three ecoregions contain 80 percent of the population: north-central (Southern Rockies Ecoregion), with 51 percent; southwestern (Gila Ecoregion), with 23 percent; and south-central (Sacramento Mountain Ecoregion), with 6 percent.

Hunting represents the major source of elk mortality where it is allowed in North America, with predation being second (Ballard et al. 2000). And yet, Colorado and New Mexico have been forced to markedly increase hunting pressure in an attempt to decrease elk numbers toward population targets established by the states. Given that it would take wolves a considerable period of time to reduce the large elk herds of the ecoregion, we predict that wolves would not affect hunter success in the Southern Rockies until years after wolves establish, if ever. This prediction could change, of course, if a local or small elk population declined quickly and precipitously due to habitat problems induced by an overabundance of elk or disease such as chronic wasting disease (see chap. 10).

In summary, for the short term (and possibly longer) following wolf reestablishment, we predict that wolf predation on elk would not negatively affect hunter harvest. Quite simply, there appear to be ample elk in the Southern Rockies for both hunters and wolves. Over the long term (several decades), wolf recovery to the Southern Rockies could cause elk populations to decline. Such reductions, however, seem consistent with objectives established by state game agencies. Moreover, such reductions could help ameliorate the negative effects of high ungulate numbers on other flora and fauna and possibly reduce the spread of infectious diseases such as chronic wasting disease.

Options for Minimizing the Effect of Wolves on Native Ungulates

Managers should recognize the potential for elk and deer populations (especially small and localized herds) to remain low for long periods where wolves, bears, cougars, coyotes, and humans vie for the same prey (Gasaway et al. 1992; National Research Council 1997; Kunkel and Pletscher 1999) and where winter weather can greatly affect ungulate numbers (Bangs et al. 2001; Mech et al. 2001; National Research Council 2002; Smith and Ferguson 2005). Depending on their objectives, managers should be prepared to quickly reduce hunting pressure, especially on adult females, to prevent prey populations in such areas from potentially falling to low levels and remaining there for the long term (Fuller 1990; Gasaway et al. 1992; Boertje et al. 1996).

In addition to managing hunter harvests, predators can be managed. Evidence suggests that under certain circumstances reducing the size and distribution of wolf populations can facilitate an increase in ungulate populations (Mech 1985; National Research Council 1997). For example, Bergerud and Elliot (1998) reported that removing 505 wolves from northern British Columbia resulted in an increase of elk and moose. They argued that predator-prey management allows a greater biomass of wolves and ungulates than a laissez-faire approach. Management guidelines for wolves in the Northern Rocky Mountains permit controlling wolves to reduce predation pressure on local ungulate populations (Bangs 1994). State wildlife agencies, which will eventually acquire primary responsibility for wolf management, are considering recreational wolf harvests to control wolf numbers and their effects on prey species. If wolf control is being considered, we suggest that managers follow the recommendations of the National Research Council (1997). Most important, we agree with the council that decisions on wolf control require a comprehensive science-informed process that considers the effects of control on the entire ecoregion. Past decisions based only on the interaction of two species have proven disastrous for the larger system (Terborgh et al. 1999; Estes et al. 2001; see chap. 3).

Alternatives other than direct predator control exist for reducing the effects of wolf predation on ungulates (Boetje et al. 1995; Kunkel and Pletscher 2000; Kunkel and Pletscher 2001). For example, improving habitat and manipulating alternative prey may prove more effective at generating benefits for some prey populations than wolf control (Boertje et al. 1995; Kunkel 1997). Managers should strive to maintain wolf population dynamics within the variability seen in natural systems.

POTENTIAL EFFECTS OF WOLVES ON LIVESTOCK

Wherever wolves occur in the conterminous United States, conflicts with livestock (and pets) have occurred. Problems caused by these conflicts have been controversial, complex, and challenging (Mech 1995, 1996, 1999, 2001; Mech et al. 1996, 2000; Clark et al. 1996; Phillips and Smith 1998; Paquet et al. 2001). Assessing factors that predispose livestock to depredation by wolves is notoriously difficult. Some factors include the size and nature of livestock operations, the intensity of monitoring of livestock, age and health of the livestock, livestock carcass management practices, presence or absence of guard animals, size of the resident wolf pack(s), distance cattle graze from a residence, remoteness and habitat characteristics of pastureland or rangeland, and presence of elk in the pasture (Bradley and Pletscher 2005). Clear understanding of the patterns that characterize wolf depredations remains elusive (Mech et al. 2000; Oakleaf 2002). Consequently, we consider the issue of wolf and livestock interactions in the Southern Rockies Ecoregion in general terms.

DEPREDATION DATA FROM OCCUPIED WOLF HABITAT

It is critically important to note that the relatively high frequency of wolf control belies the actual magnitude of the wolf-livestock problem. For example, within the farm and ranch industry in the Great Lakes states (Minnesota, Michigan, Wisconsin) and the Northern Rockies, losses to wolf depredation have been insignificant compared to overall losses. Only about 1 percent of farms in wolf range in Minnesota experience verified wolf depredations (W. J. Paul, unpublished report, 1998, as cited by Mech et al. 2000).

Similarly, between 1987 and 2003, wolf depredations in northwestern Montana averaged seven cattle and five sheep annually (US Fish and Wildlife Service 2004). In contrast, between the years 1986 and 1991, livestock producers in Montana reported losing an average of 142,000 sheep and 86,000 cattle to all causes annually (Bangs et al. 1995; Montana Agricultural Statistics 1992). In the two reintroduction areas in the Northern Rockies, from 1995 to 2003 the average annual confirmed losses to wolves have been slight: thirteen cattle and forty-six sheep in the Greater Yellowstone Area and eight cattle and thirty-four sheep in Idaho (US Fish and Wildlife Service et al. 2004). Between 300,000 and 400,000 sheep and cattle graze summer pasture on public lands in each of these areas annually, and losses from all causes prior to wolf reintroduction ranged from 8,000 to 12,000 cattle and 9,000 to 13,000 sheep (US Fish and Wildlife Service 1994). A small fraction of these were predator-caused. While the number of livestock that are lost varies annually based on myriad factors, it is clear that wolf depredations are only a very small part of the challenge of raising livestock. The general pattern of wolf depredation on livestock notwithstanding, it is important to point out that some individual operators do experience significant problems.

IMPLICATIONS FOR THE SOUTHERN ROCKIES ECOREGION

The livestock industry in the Southern Rockies continues to dwindle as a share of the region's economic base. For example, recent data indicate that the entire agricultural sector (crops, livestock, forestry, and fisheries) accounted for roughly 0.5 percent of Colorado's gross output in 2006 (Colorado Office of Economic Development and International Trade 2006; see chap. 5). Nonetheless, resolving conflicts between wolves and livestock undoubtedly would be the most challenging management task if wolves are ever restored to the Southern Rockies Ecoregion. Patterns of low-density public lands grazing in the western United States increase the potential for livestock depredations, which would fuel animosity toward wolf recovery by livestock producers. A recent opinion survey indicates that public support for wolf restoration is maximized if these conflicts can be resolved in a manner that promotes wolf recovery and is respectful of the needs and concerns of ranchers (Meadow 2001; Meadow et al. 2005; see also chap. 6).

Extrapolating from the experience of other regions where wolves and livestock coexist, we do not expect that wolf depredations of livestock would affect the general economy of the Southern Rockies Ecoregion. Moreover, because on average wolf depredations of livestock are insignificant, we predict the economy of the regional livestock industry would not be affected by wolf recovery. Nonetheless, if not addressed quickly, wolf depredations can cause significant losses for individual producers and create great animosity toward wolf recovery.

Our assessment of the effects of wolves on livestock was greatly influenced by the work being carried out in the Northern Rockies. A detailed analysis of the potential effects of wolf reintroduction to central Idaho and the Greater Yellowstone Ecosystem predicted that 100 adult-sized wolves would kill about ten to twenty cattle and fifty to seventy sheep in each area annually (US Fish and Wildlife Service 1994). Depending upon their distribution, more than 100 adult-sized wolves would proportionally increase effects above those predicted in the Environmental Impact Statement (EIS) (US Fish and Wildlife Service 1994). The EIS for the central Idaho and Yellowstone projects further predicted that resolving conflicts with livestock would result in killing about 10 percent of the wolf population annually. Using cost estimates from Alaska, the cost of killing a wolf from the air can range from \$770 to \$873, excluding personnel costs (Ballard and Stephenson 1982 in Ballard et al. 2001). While the EIS predictions represent overestimates of actual livestock losses to date by 33 to 50 percent (US Fish and Wildlife Service 2002), they are nonetheless useful for describing the likely magnitude of effects of wolf-caused losses of livestock in the Southern Rockies.

We used the EIS predictions because throughout wolf range, wolves kill more livestock than are verified (Roy and Dorrance 1976; Fritts 1982; Bangs et al. 2001; Oakleaf 2002). Oakleaf (2002) determined the cause of death and detection rate of 231 radio-tagged livestock calves (out of 700 calves) on large, remote, and heavily forested US Forest Service grazing allotments near an active wolf den. After two years, natural mortality (pneumonia, etc.) killed the most calves (64 percent), but wolf predation was the second leading cause of death (29 percent). While the number of radio-collared calves that died each year was very small (nine calves in 1999 and five calves in 2000), wolves may have killed from two to six calves for every one detected by normal livestock herding practices (Oakleaf 2002). The calves killed by wolves were relatively small, less well guarded by people, and inhabited the most heavily forested areas closest to the wolf den. Oakleaf (2002) concluded that it was possible that wolves tested the calves and preyed on the most vulnerable animals.

We predict that a population of 1,000 wolves in the Southern Rockies Ecoregion (the approximate predicted biological carrying capacity of the region) (Carroll et al. 2003, 2006) would kill about 100 to 200 cattle and 500 to 700 sheep annually. As of 1997, the sixty-four counties in the Southern Rockies supported 2,181,389 cattle and 788,888 sheep (Oregon State University, 2003). Consequently, we predict that wolves would kill a maximum 0.009 percent of the cattle and 0.1 percent of the sheep in the Southern Rockies annually. The value of these losses would depend upon the market value for these animals at the time of depredation, which varies dramatically depending upon the type and age of the animal and current market conditions. If lethal control is used against depredating wolves, these conflicts could result in the killing of 100 wolves. If airplanes and helicopters were used for control activities, the annual cost could range from about $75,000 to $90,000 (excluding personnel costs). This level of depredation may overestimate the actual values. It seems unlikely that a restored wolf population in the Southern Rockies would achieve the size set by the biological carrying capacity of the ecoregion of about 1,000 wolves. Rather, we believe that the wolf population size would be set at a much lower level by human intolerance, with a consequent reduction in effects on livestock.

OPTIONS FOR MINIMIZING THE EFFECTS OF WOLVES ON LIVESTOCK PRODUCERS

We argue that the tension between promoting wolf survival and population expansion and killing wolves to resolve conflicts with livestock has been and will continue to be the greatest challenge to wolf recovery and conservation. Even though wolf depredations are relatively uncommon, livestock producers demand immediate and definitive action when problems arise. For example, as the Minnesota wolf population increased during the last several decades, the number of wolves killed to resolve conflicts with livestock increased from 21 animals in 1980 to 216 in 1997, but the number subsequently declined to an average of 128 wolves per year from 2000 to 2004 (Paul 2001; US Fish and Wildlife Service 2007a). From 1987 through 2005, 396 wolves were killed in control actions in the Northern Rockies (US Fish and Wildlife Service 2007b). These control actions represent by far the largest percentage of all wolf mortalities in that region (Bangs et al. 1998; US Fish and Wildlife Service 2007b). The second largest source of mortality has been illegal killings, of which there have been thirty (US Fish and Wildlife Service 2007b).

Nonlethal techniques for resolving wolf-livestock conflicts include translocating problem wolves, hazing, aversive conditioning, using guard animals to protect livestock, intensive monitoring of livestock, modifying livestock husbandry practices, and fladry, the practice of hanging flags around livestock use areas to deter wolves. For myriad reasons these techniques must continue to be viewed favorably, improved, and applied whenever practicable. Two nonlethal techniques seem to hold special promise. First, intensive monitoring of livestock has proven useful at reducing conflicts, but it has not been widely practiced because of logistic and cost constraints. Through a range riders program, young adults from local ranching communities could be hired to ride the range and closely monitor livestock to reduce conflicts with wolves (and other predators). The second management approach of note employs fladry, a technique based on the proper spacing of red flags to restrict and direct wolf movements. Fladry is a traditional technique for hunting wolves (by funneling them toward hunters) in Eastern Europe and Russia and recently has been used to live-trap wolves (Okarma and Jedrzejewski 1997). Musiani and Visalberghi (2001) contend that fladry has the potential to reduce conflicts between wolves and livestock. Fieldwork conducted in Alberta and southwestern Montana support this contention, and additional work is under way.

To date, however, both lethal and nonlethal options for managing wolf-livestock conflicts largely have been ineffective, cost prohibitive, and/or logistically unwieldy when applied over a large scale (Cluff and Murray 1995; Mech et al. 1996; Musiani et al. 2005). Musiani et al. (2005) found that wolf depredations were seasonal in Canada and the Northern Rockies and that lethal control did little to prevent future depredation of livestock. As such, they recommended more intensive use of nonlethal methods during seasons of high risk, although they add that in the long term, "eliminating 'problem individuals' (sensu Linnell et al. 1999)... might play a management role by facilitating elimination of genetic or behavioral traits conducive to depredation" (Musiani et al. 2005, 883). They go on to suggest that lethal control may help build support for wolf restoration among livestock producers. Similarly, Mech observed that

> because wolf-taking by landowners or the public is the least expensive and most acceptable to people who do not regard the wolf as special, there will be greater local acceptance for wolf recovery in areas where such control is allowed. Thus, if wolf advocates could accept effective control, wolves could live in far more places. (1995, 276)

Mech's observation may be valid, but only if livestock producers actually do increase their acceptance of wolf recovery, which remains dubious, especially given that lethal control does not appear to decrease livestock depredation.

Many livestock producers have cooperated with wolf recovery because they believed that wolf-induced problems would be resolved equitably. In this regard, monetary compensation for livestock losses has proven useful for reducing animosity toward wolves (Fischer 1989; Fischer et al. 1994). From 1987 to 2007, Defenders of Wildlife paid $769,455 in compensation to livestock producers in Montana, Wyoming, and Idaho who had experienced confirmed or highly probable wolf-caused losses (M. Johnson, Defenders of Wildlife, pers. comm.). This compares to an estimated $45 million in annual losses to all causes for livestock producers in Montana alone (Bangs et al. 1998). Defenders' average annual costs for compensation in the Northern Rockies and Arizona and New Mexico are about $42,000, which amounts to a little more than the 3 percent of the annual total spent by the Wildlife Services Division of the US Department of Agriculture to protect livestock from wolves (about $1.3 million). Even if officials document only one out of ten livestock depredations by wolves, the annual losses would amount to only $420,000. Wildlife Services in the Northern Rockies spends more than three times that on wolf management.

In areas where wolves and livestock coexist, ranchers sometimes report greater losses than can be confirmed. Under current management schemes, however, an instance of missing livestock does not initiate wolf control or compensation by Defenders of Wildlife. Even with intensive monitoring, for various reasons some wolf-induced losses will be unconfirmed. However, without some type of agency-confirmation process, any control or compensation program could be subject to widespread abuse. State-administered compensation programs for livestock losses to pumas, black bears, and grizzly bears in Idaho and Wyoming (Bangs et al. 1998) and to wolves in Minnesota (Fritts et al. 1992) require agency confirmation of reported losses. It is likely that some sort of compensation program would be an important component of any wolf-livestock management scheme in the Southern Rocky Mountains.

Finally, incentives promoting ecologically sound management practices benefit society as a whole (Farraro and Kiss 2002). But there must be a direct link between incentives and the cause of the problem. Incentives should thus aim to change underlying negative attitudes regarding issues such as threats to lifestyles, issues of control over public and private grazing lands, or traditional notions of land stewardship. Incentives that merely replace lost income only reinforce the notion that wolves are pests.

THE EFFECTS OF GRAY WOLVES ON LAND USE

A common concern voiced about wolf recovery is that it inevitably leads to public or private land use restrictions to ensure wolf survival. Yet land use restrictions have largely not been needed to advance wolf survival and recovery, primarily because the gray wolf is an ecological generalist that can survive in myriad settings. Indeed, human tolerance is probably the most important component of habitat quality for the gray wolf. Nonetheless, many opponents to wolf recovery believe that wolf restoration will lead to significant changes in land use. Some people believe that wolf restoration represents a battle in the War on the West that they claim environmentalists are waging. These individuals predict that the federal government will close vast areas of public land to promote wolf conservation.

Nothing in the rules governing reintroduced wolves supports fears of widespread land use restrictions. For example, plans governing the wolf reintroduction projects in the Northern Rockies only provide the option of restricting the use of public land beyond the boundaries of national parks or national wildlife refuges in the immediate area of active den sites (e.g., within about 1.6 km, or 1 mile) for a forty-five-day window of time during spring (mid-April through June) (Bangs 1994). Any such closures are not implemented when the wolf population exceeds six packs in the reintroduction area. Except for restrictions placed on the use of M44 cyanide devices used to kill coyotes, the presence of wolves has not changed public or private land use in the Northern Rockies (Bangs et al. 1998). Draft and approved state wolf management plans similarly do not require sweeping changes to public land use. Further, nothing in federal or state wolf recovery or management plans provides for restricting lawful activities on private land (see chap. 7).

In 1978, about 25,000 sq. km (9,653 sq. mi., or 6.2 million acres) of public land in Minnesota (about 11 percent of the total area of the state) was designated as critical habitat for the gray wolf per Section 4 of the Endangered Species Act (Nowak 1978; see chap. 7). Local offices of federal land management agencies in the area, including the US Forest Service and National Park Service, supported this designation. In 1992, the Eastern Timber Wolf Recovery Team recommended changes to the critical habitat designation (US Fish and Wildlife Service 1992). The designation of critical habitat in Minnesota did not impose any new restrictions on the movement or activities of private citizens or state agencies.

Although it might be necessary to restrict activities within the immediate vicinity of active wolf den sites for short periods of time during spring when the wolf population lies below some predetermined threshold (e.g., less than six packs), we predict that wolves would not affect lawful uses of public land. We also predict that wolf restoration in the Southern Rockies Ecoregion would have very little effect on current and lawful uses of private land.

POTENTIAL EFFECTS OF WOLVES ON HUMAN SAFETY

The following data are based on information compiled by the International Wolf Center (www.wolf.org), a nonprofit education organization that focuses on the wolf. Much of the original work can be found in Mech (1990, 1996a, 1998) and Route (1999).

Debate has raged over whether or not wolves pose a danger to humans. The Alaska Department of Fish and Game (2002) has documented only twenty-eight cases of humans being injured by wolf attacks since 1890, even though more than 60,000 wolves exist in Alaska and Canada. In North America from 1900 to 2000, no healthy wolf killed a human being (Alaska Department of Fish and Game 2002); however, wolves killed a Canadian man in northern Saskatchewan in 2005. Overall, the Alaska Department of Fish and Game (2002) found that wolves present very little threat to human safety.

Humans have historically persecuted wolves throughout much of their range. Perhaps because of this, most wolves remain shy and avoid humans. Yet, in rare cases wolves have become fearless of humans, leading to serious injury and, in some countries, even death. Fearless wolves represent a concern in India, where they roam freely around remote villages. In 1996, sixty-four children were seriously injured or killed on the outskirts of small villages in one area of the country. In some of these cases, evidence collected by a US-trained wolf biologist from India points to one or more wolves being involved. In 1997, officials implicated wolves in the deaths of nine or ten children in the same region.

It is important to keep wolf-human encounters in perspective. Most wolves are not dangerous to humans. Lightning strikes, bee stings, or car collisions with deer present a much greater chance of death than wolves do. Nonetheless, like bears and cougars, wolves are instinctive predators that people should respect and keep wild.

OPTIONS FOR MINIMIZING THE EFFECTS OF WOLVES ON HUMAN SAFETY

Because wolves generally avoid humans, most people will never see a wolf, let alone have a conflict with one. However, wolves can lose their fear of people through habituation and may approach camping areas, homes, or humans, increasing the possibility for conflict. The following guidelines help decrease the chance of wolf habituation to and conflict with people living in or visiting wolf country.

We recommend that people living in areas inhabited by wolves adhere to the following guidelines:

- Do not feed wolves or other wildlife (attracting any prey animal may attract wolves).
- Hang suet feeders at least 2 m (7 ft.) above the ground surface or snow.
- Feed pets indoors and leave no food outdoors.
- Dispose of all food and garbage in cans with secure lids.
- Do not leave pets unattended outside (dogs and cats are easy targets for wolves).
- If you must leave pets unattended in a yard, keep them in a kennel with a secure top.
- Install motion sensor lights, as they may help keep wolves away.

The following guidelines apply to camping in areas inhabited by wolves:

- Cook, wash dishes, and store food away from sleeping areas.
- Pack out or dispose of garbage and leftover food properly.
- Suspend food, toiletries, and garbage out of reach of any wildlife.
- Keep pets near you at all times.

Outdoor enthusiasts should adhere to the following guidelines when observing wolves:

- Do not feed wolves.
- Do not entice wolves to come closer.

- Do not approach wolves.
- Leave room for the wolf to escape.
- Do not allow a wolf to approach any closer than 91 m (300 ft.).

If a wolf acts aggressively (e.g., growls, snarls, or fearlessly approaches at a close distance) take the following actions:

- Raise your arms and wave them in the air to make yourself look larger.
- Back away slowly; do not turn your back on the wolf.
- Make noise and throw objects at the wolf.

CONCLUSIONS

Several factors influence wolf population dynamics, but research suggests that the two most important are the ungulate biomass in a region and the amount of human-caused mortality. Wolves also influence the population dynamics of other species, especially their prey and other carnivores with which they compete for prey. Interactions between wolves and competitors remain poorly understood, but carnivores do compete through direct interference and by exploiting mutually important resources.

Predator-prey interactions are somewhat better studied. Research from the Northern Rockies helps us predict that the Southern Rockies might support up to 1,000 wolves, but people probably would not tolerate that many. We predict that these wolves would consume a maximum of 22,000 elk and 3,500 deer each year. Yet, because the Southern Rockies boast such large populations of both elk and deer, we predict small if any impacts on hunter harvest. This is especially true because both Colorado and New Mexico are currently trying to reduce their elk herds.

Once restored, wolves in the Southern Rockies would likely depredate on livestock; however, evidence from other areas with established wolf populations suggests that the impacts would remain relatively low and localized. Of course, a small number of livestock operations affected by wolf depredation might experience significant losses. In such cases, a variety of mitigation actions are possible, including lethal control of depredating animals, a variety of nonlethal control actions, and compensation programs to pay for losses due to wolves. Finally, wolves generally pose little threat to human safety, but people should still adhere to certain readily available guidelines for minimizing conflict when living in or visiting wolf country.