Yellowstone after Wolves

DOUGLAS W. SMITH, ROLF O. PETERSON, AND DOUGLAS B. HOUSTON

With gray wolves restored to Yellowstone National Park, this ecosystem once again supports the full native array of large ungulates and their attendant large carnivores. We consider the possible ecological implications of wolf restoration in the context of another national park, Isle Royale, where wolves restored themselves a half-century ago. At Isle Royale, where resident mammals are relatively few, wolves completely eliminated coyotes and went on to influence moose population dynamics, which had implications for forest growth and composition. At Yellowstone, we predict that wolf restoration will have similar effects to a degree, reducing elk and coyote density. As at Isle Royale, Yellowstone plant communities will be affected, as will mesocarnivores, but to what degree is as yet undetermined. At Yellowstone, ecosystem response to the arrival of the wolf will take decades to unfold, and we argue that comprehensive ecological research and monitoring should be an essential long-term component of the management of Yellowstone National Park.

Keywords: wolf restoration, Yellowstone National Park, greater Yellowstone ecosystem, wolf–prey relationships

The reintroduction of gray wolves to Yellowstone National Park (YNP) surely ranks, symbolically and ecologically, among the most important acts of wildlife conservation in the 20th century. Once again Yellowstone harbors all native species of large carnivores—grizzly and black bears, mountain lions, and wolves. Before wolf reintroduction, there was a concerted effort to predict the ecological effects of wolves in Yellowstone (Cook 1993). Has reality, so far, met expectations? And does what we have learned in Isle Royale National Park, where wolves introduced themselves over 50 years ago, have relevance for Yellowstone in the future?

Gray wolves were restored to Yellowstone National Park in 1995–1996 with the release of 31 wolves captured in western Canada (Bangs and Fritts 1996, Phillips and Smith 1996). In the 7 years following their initial release, wolves have recolonized the 8991-square-kilometer (km^2) park and several adjacent portions of the 72,800 km^2 greater Yellowstone ecosystem (GYE). We use initial studies and field observations to determine the extent to which wolves may have already begun to restructure the Yellowstone ecosystem.

Although we consider wolves throughout the park, we focus on the 1530 km^2 northern Yellowstone winter range, an area dominated by steppe and shrub steppe vegetation that supports seven species of native ungulates (elk, bison, mule deer, white-tailed deer, moose, pronghorn antelope, and bighorn sheep), one nonnative ungulate (mountain goat), and five species of native large carnivores (gray wolf, coyote, grizzly bear, black bear, and cougar). Only about 65% of the northern range is inside the park; the remaining 35% is on public and private lands north of the park along the Yellowstone River (Lemke et al 1998).

Because many of the wildlife species on the northern range are hunted outside the park, we include humans as additional, formidable predators in the system. Although the National Park Service manages Yellowstone with an overall goal of minimal human intervention, allowing natural ecological processes to prevail inside park boundaries, wildlife populations may be profoundly altered by human actions, including hunting, outside the park.

Simplicity and complexity: Isle Royale and Yellowstone

We find it useful to contrast the Yellowstone system with that of Isle Royale National Park, a less complex ecosystem renowned for long-term studies of the interaction of gray wolves with moose (Peterson 1995, Peterson et al. 1998). Amid the complexity of Yellowstone, where might we expect to find the ecological footprints of wolves, and where might science make its greatest gains? We anticipate that long-term studies similar to those of Isle Royale will be required to understand the effects of wolves in Yellowstone. We could have picked other parks—Riding Mountain in Manitoba or Denali in Alaska, which are both multicarnivore–multiprey systems like Yellowstone—but long-term data (from the turn of the century to the present) on willdife population sizes from these other areas were lacking, and we do not have intimate experience with these parks. Often, what is important is subtle and detailed yet can account for the difference between an informed conclusion and one that is not. Where appropriate, we make comparisons to other wolf–prey systems.

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Wolf pack with grizzly bear sow and cubs. Interactions between wolves and grizzly bears have largely benefited grizzlies, although two grizzly cubs were probably killed by wolves. Photograph: Douglas Smith, National Park Service.

Isle Royale and Yellowstone provide opposite extremes in faunal and food web complexity. Isle Royale is a closed system with fewer species (one-third the species found on the adjacent mainland), and Yellowstone is an open system with greater diversity of both predators and prey (figure 1). Thus, Isle Royale should be more amenable to scientific scrutiny, with clearer cause-and-effect relationships among a few key species, a good starting point and example for interpreting Yellowstone.

There are surprising parallels in the histories of Isle Royale and Yellowstone during the past century, particularly in concerns raised over too many ungulates and their effects on their habitat. During a wolf-free period, both ecosystems saw ungulates increase to levels that alarmed some knowledgeable observers, and coyotes were numerous in both areas.

It is not only ecology that is complex at Yellowstone. Its bureaucratic history as the nation's first national park (Haines 1977) is long and rich. Management of Yellowstone's wildlife, particularly on the northern range, has a history of concern and controversy dating from the establishment of the park in 1872 (Pritchard 1999). Early on, extirpation of many native species was feared because of intense hide and market hunting. Understandably, this period was followed by one of progressively increasing husbandry of native ungulates, which eventually involved winter feeding and predator control. Gray wolves were effectively eliminated by the 1930s (Weaver 1978). During the extended drought of the 1930s, some ungulate species, particularly elk, were considered to be "overabundant" and "range deterioration" became an issue. This led in turn to

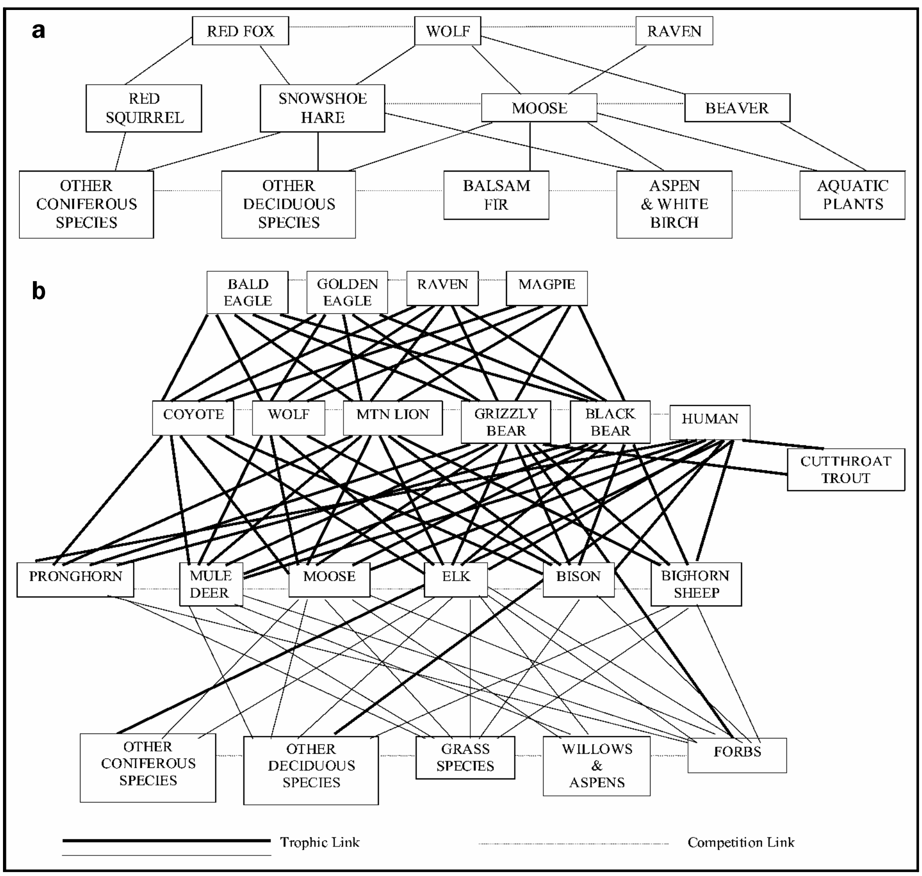

Figure 1. Yellowstone has more interacting species than does Isle Royale, which leads to greater complexity and makes scientific study and understanding more challenging. (a) Isle Royale; (b) Yellowstone.

intense and highly controversial reductions of elk, bison, and pronghorn populations by field shooting and trapping, aimed at testing the effects of reduced ungulate densities on vegetation conditions. By the late 1960s elk numbers had been reduced by perhaps 75%, to around 4000 animals (Houston 1982). In 1969 a moratorium on reductions was instituted in an attempt to rely more on natural regulation of ungulate numbers within the park and to restore hunting opportunities outside (reductions of elk within the park had essentially eliminated elk hunting outside). Those efforts to rely on more natural processes have, in one sense, culminated in restoration of the wolf. This brief outline of management history is treated in detail by Meagher (1973), Houston (1982), and Pritchard (1999).

Like Yellowstone, Isle Royale had a wolf-free era, which resulted in an overabundant moose population (Allen 1979). Instead of artificial reductions to control moose, the Park Service tried unsuccessfully to reintroduce zoo-raised wolves in 1952 (Allen 1979). But unlike in Yellowstone, wolves reintroduced themselves to Isle Royale in the late 1940s by crossing the ice of Lake Superior (Allen 1979). What did the arrival of the wolf mean for the Isle Royale ecosystem? Although the relative roles of bottom-up (nutrition and vegetation) and top-down (wolf predation) influences on moose population dynamics are not fully understood (Messier 1994, Peterson 1995), the historic chronology of moose numbers indicates that wolf predation tends to cap moose density (figure 2). The growth in moose numbers peaked in the early 1970s and ended when severe winters affected vulnerability (Peterson 1977), and the resulting increase in wolves kept the moose population low for many years. The greater number of wolves indirectly allowed forest recovery by reducing browsing by moose (top-down; McLaren and Peterson 1994). However, when wolves crashed in the 1980s—from 50 to 14 in 2 years—and were limited because of a canine parvovirus, a disease accidentally introduced by humans (Peterson 1995), moose numbers grew until catastrophic starvation hit in 1996 (one of the most severe winters on record; Peterson et al. 1998).

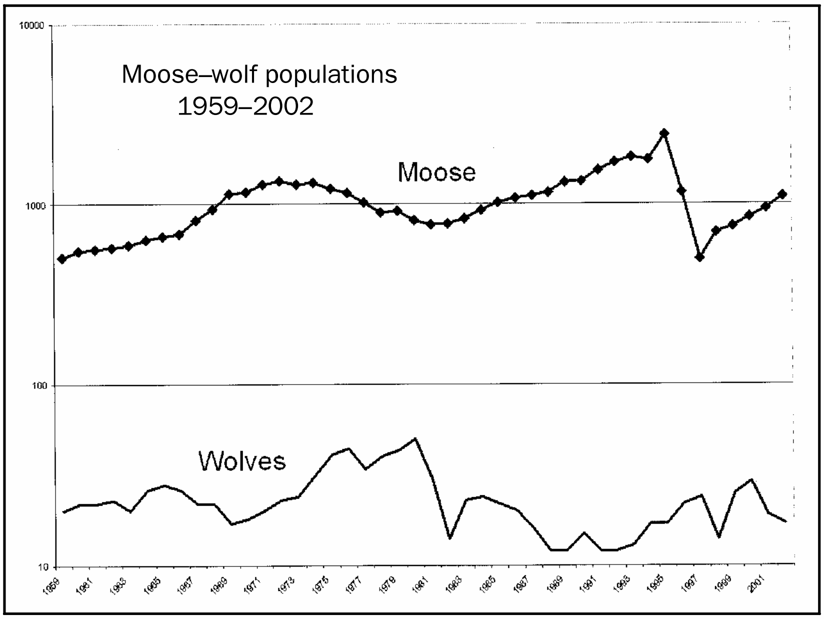

Figure 2. Fluctuations in the numbers of wolves and moose in Isle Royale National Park, 1958–2002. Wolf numbers were multipied by 15 to enable use of the same axis.

The rise and fall of Isle Royale's wolf population can be read in the growth rings of balsam fir trees—trees flourish when wolf numbers increase and moose are reduced (McLaren and Peterson 1994, McLaren 1996). The relative abundance of coniferous and deciduous trees, which is strongly influenced by moose browsing, further affects litter composition and nutrient cycling in the soil, so the ripple effect beginning with the arrival of wolves extends far and wide (Pastor et al. 1993). But it is not that simple. On one-third of Isle Royale, fir trees are able to escape moose browsing (because of thick, high-density stands) and grow into the canopy, but on most of the island, balsam fir trees are unable to grow out of the reach of moose (McLaren and Janke 1996).

Hence, moose remain a powerful force shaping forest succession, even with intense wolf predation. Variations in soil types, disturbance history (fire and wind), and light intensity complicate a system that, in comparison with Yellowstone, is easily understood. Even after a century with moose, the forest of Isle Royale has not reached equilibrium. One needs a long-term perspective and study to completely understand the dynamics of long-lived plants and animals. In the public perception, however, the arrival of wolves solved the problem of an overpopulation of moose.

Another look at predictions

Will wolves stabilize prey fluctuations in Yellowstone, especially those of elk (Boyce 1993), or will wolves destabilize elk fluctuations, exacerbating population fluctuations (NRC 2002)? How far will the ecological ripple extend? Moose no longer number 3000 on Isle Royale, as they did before wolves (Allen 1979), so will elk ever exceed 19,000, as they did before wolves and after the artificial reductions in Yellowstone?

Before wolf reintroduction, several studies used modeling to predict the future impacts of wolves on the Yellowstone ecosystem (YNP et al. 1990, Varley and Brewster 1992, Cook 1993, USFWS 1994). These were comprehensive efforts, prepared for Congress and the general public, that focused on the interaction of wolves with native ungulates, livestock, and grizzly bears. Simulations predicted between 50 and 120 resident wolves in YNP, with packs on the northern range, Madison-Firehole, and possibly the Gallatin and Thorofare areas (figure 3; Cook 1993).

All models suggested that elk would constitute the primary prey for Yellowstone wolves. Four models dealt with the impact of wolves on native ungulates (Garton et al. 1990, Vales and Peek 1990, Mack and Singer 1992, 1993, Boyce

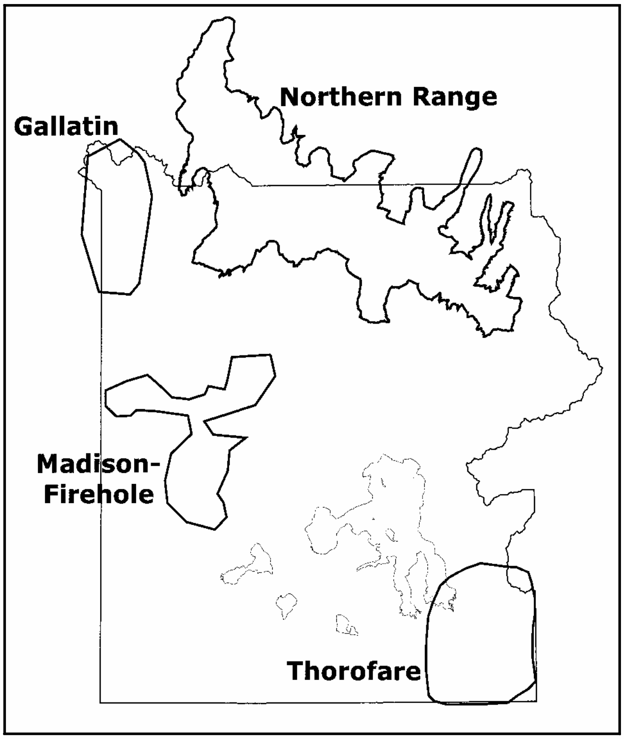

Figure 3. Before wolves were reintroduced, researchers predicted the wolves would settle in the four sites shown above.

1993); no simulation predicted large declines in ungulates following wolf restoration. The northern Yellowstone elk population was predicted to decline 5% to 30% over the long term, with levels of decline contingent on the extent of hunter harvest of female elk outside the park (Boyce 1993, Mack and Singer 1993). Boyce (1993) suggested that some reduction in the number of cow elk killed by hunters outside the park might be necessary over time, but restrictions on bull harvests would be unnecessary. Significant effects on other prey species (bison, moose, and mule deer) were not anticipated.

In contrast to most predictions based on modeling, Messier and colleagues (1995) suggested that elk might decline substantially following wolf recovery because of the number of predator species involved. In boreal ecosystems where moose deal with multiple predators, moose density typically declines with each additional carnivore species (including human hunters; Gasaway et al. 1992). According to this thinking, the exceptionally high density of moose at Isle Royale (averaging about 2 per km^2) occurs because there is only one predator—the wolf. Where wolves and bears coexist, calf survival is consistently reduced, and moose density is always less than 1 per km^2 and usually less than 0.4 per km^2 (Messier 1994). The only geographic region where moose density is comparable to that of Isle Royale is Fennoscandia, where humans are the predominant predator species (bears have a minor presence), or the Gaspe Peninsula in New Brunswick, where there are black bears but no wolves and no hunting is allowed.

Messier and colleagues (1995) believed that Yellowstone elk would decline significantly, more than the 5% to 30% predicted by Boyce (1993) and Mack and Singer (1993), especially where human hunting of cow elk was permitted. Focusing on the northern Yellowstone elk herd, at a prewolf winter elk density of more than 10 per km^2, they anticipated that elk numbers would decline during the inevitable severe winters and would not rebound because of relatively low calf survival. What will be critical for elk recovery after declines will be the level of human hunting of elk outside the park, the only mortality factor that can be completely managed.

Both the historical record at Isle Royale and the predictions of Boyce (1993) for the northern Yellowstone elk underscore the dynamic future that will follow wolf recovery. Fluctuations in wildlife populations are normal; the renowned "balance of nature" at Isle Royale is decidedly dynamic. Wolf peaks lag behind those of prey, and wolf declines follow prey declines. In the past four decades, two major declines in moose at Isle Royale have occurred when severe winters coincided with high moose density (> 3 per km^2; Peterson 1995). Predictions for the wolf–prey system at YNP were similarly variable over time (Boyce 1993).

Media attention and scientific debate have focused heavily on population size for northern Yellowstone elk. Average population size is an interesting statistic, but no one should expect elk to spend any time there. At most times, they will either be increasing or decreasing, and at any given time wolves and elk will probably show opposite trends.

Isle Royale moose have spent more time below the population mean, probably because of suppression by wolves. Possibly this reflects the resilience of wolves in the face of prey decline, and the antiregulatory (inversely density-dependent) influence of wolf predation that wildlife managers in Alaska have noted (Gasaway et al. 1992). An important question for Yellowstone, however, is to what extent wolves will prey on bison, a more formidable—and more difficult to kill—prey species (Smith et al. 2000). If wolves do prey on bison, which are widespread and abundant (4000 animals), predictions of wolf impacts on elk will certainly change.

For the threatened grizzly bear population of GYE, wolf restoration was predicted to have either no impact or a slightly positive impact (Servheen and Knight 1993). Wolf predation on bear cubs was expected to be offset by better feeding conditions as bears usurp wolf kills (Servheen and Knight 1993). Carcasses would be more evenly distributed for bears throughout their seasons of activity, rather than coming as a pulse in late winter and early spring—the prewolf condition. Bears would not have to risk killing elk themselves but could scavenge wolf kills, which are well distributed in space and time.

Although there was a general awareness of interspecific competition among native canids when the effects of wolf reintroduction were being assessed a decade ago, there were few predictions about exactly what wolf recovery would mean for coyotes, which on the northern range existed at one of the highest densities known for the species (Crabtree and Sheldon 1999). Some predicted that wolves would reduce coyotes

Wolf feeding on elk carcass. Elk are the primary prey of wolves in Yellowstone; so far, wolves have not significantly affected the elk population anywhere in the park. Photograph: Douglas Smith, National Park Service.

and that the coyote reduction would affect other species (YNP et al. 1990, Varley and Brewster 1992). On Isle Royale, where wolves and coyotes competed for all the same prey species, wolves eliminated coyotes in about 8 years (Mech 1966).

Before the reintroduction of wolves in Yellowstone, there were no predictions about possible responses in northern range vegetation caused by changes in distribution or density of ungulates, particularly elk. The forage for most ungulates wintering on the northern range—elk, bison, mule deer, bighorn sheep, pronghorn—is produced primarily in the extensive grasslands and shrub steppes. Grasslands are dominated by native species, although several alien grasses have been introduced (both accidentally and deliberately) and dominate local sites (YNP 1997, Stohlgren et al. 1999). A series of studies suggests that this grazing system is stable and highly productive; ungulate herbivory accelerates nutrient cycling and actually enhances productivity of the range (Houston 1982). Long-term changes in the vegetation (increased distribution and density of coniferous forests, increased abundance of big sage, decline in aspen and willow communities) seem to be associated with herbivory and suppression of natural fires, which occurred during a shift to a warmer, dryer climate (Meagher and Houston 1998). It is worth noting, however, that aspen and willow are minor components of northern range vegetation (less than 1% or 2%); Meagher and Houston (1998) explore the difficulty of basing management of the larger grazing system on minor components of the vegetation.

Another unresolved point, far too complex to realistically simulate, is the productivity of the northern range, which nourishes the elk in winter. This is a unique north temperate grassland, one that has been compared to Africa's Serengeti. A much higher proportion of plant biomass can be consumed by ungulate grazers than by ungulate browsers, which depend on the annual growth of twigs and buds of woody shrubs. It is possible that the bottom-up stimulation of productivity from this grassland system will sustain elk at high density with a full suite of predators, both wild and human. A review committee of eminent scientists recently focused on the condition of the northern range (NRC 2002), concluding that high ungulate density was not causing irreversible damage to this ecosystem. Now that wolves are present, this committee firmly endorsed the scientific imperative to monitor ecosystem status closely.

The unfolding Yellowstone story

In the summer of 2002, at least 216 free-ranging wolves (before the 2002 birth of pups) could be found in the GYE, with about 14 packs (132 wolves) holding territories in or mostly within YNP and 14 packs (84 wolves) outside (figure 4). About 77 wolves (in 8 packs) occur on the northern range (very close to the number predicted for this area; Boyce 1993, Mack and Singer 1993). The initial rate of increase for the wolf population was very high (figure 5), but population growth within YNP has slowed now, and most recent increases have occurred outside the park. Here we summarize the current status of wolves and their primary prey, the northern Yellowstone elk, and note some preliminary observations of other selected species affected by wolf recovery.

Wolf territories. The northern range, targeted during wolf reintroduction, is well-occupied by wolves: Virtually all potential wolf habitat in the park is occupied to some extent, including several areas that may not prove suitable for long-term occupancy (figure 4). Wolf packs have established year-round territories, despite the seasonally migratory nature of their ungulate prey. This was an important uncertainty before wolf introduction (Boyce 1993). The territories have been quite labile, and further subdivision seems likely, especially for the very large Druid pack (37 wolves in August 2000, split into four packs as of April 2002), which now dominates much of the northern range in the park and has forced some packs into peripheral areas. Across the park, wolf packs exist approximately in the places predicted by Boyce (1993; figure 3).

Wolf–prey relationships. As expected, elk are the primary prey for wolves in the park year-round, representing 92% of 1582 wolf kills recorded from 1995 to 2001. As elsewhere, wolf predation in winter has been highly selective; calves represent about 43% of wolf-killed elk, cows 36%, and bulls 21% (compared with the approximate winter population proportion of 15% calves, 60% cows, and 25% bulls). The adult elk killed by wolves have been very old, with a mean age of 14 years for wolf-killed cow elk (Mech et al. 2001). In contrast, human hunters outside the park kill female elk in their reproductive prime, at an average age of 6 years. Bull elk killed by wolves are taken primarily in late winter and average 5 years old, which is the same average age as for hunter-killed bull elk. Examinations of femur marrow from the wolf-killed elk on the northern range indicate that 34% (N = 494) had exhausted all fat reserves.

Although elk represent the primary prey for wolves throughout the park, bison are taken during late winter in interior portions of YNP (Smith et al. 2000) and moose are important along the southern boundary. Yet neither of these species represents more than 2% of the wolf diet in winter, though the figure is higher in some areas during late winter. Although wolves have killed some bison (Smith et al. 2000), so far most Yellowstone packs are supported almost entirely by elk.

Coyotes. Before wolf reintroduction, coyote population density on the northern range was about 0.45 per km^2, organized as packs with well-established borders (Crabtree and Sheldon 1999). Wolves began to kill coyotes soon after they were released in YNP. During 1996–1998, wolf aggression toward coyotes resulted in a 50% decline in coyote density (up to a 90% decline in core areas occupied by wolf packs) and reduced coyote pack size on the northern range (Crabtree and Sheldon 1999). In the Lamar Valley of the northern range, the coyote population declined from 80 to 36 animals from 1995 to 1998, and average pack size dropped from 6 to 3.8 animals (Crabtree and Sheldon 1999). With lower coyote density, litter size increased, but the increased production of pups has been insufficient to offset the effects of wolves.

Although data are preliminary, pronghorn fawn survival seems positively correlated with wolf density and inversely correlated with coyote density, as most fawn mortality is caused by coyote predation (John Byers, University of Idaho, Moscow, ID, personal communication, October 2003).

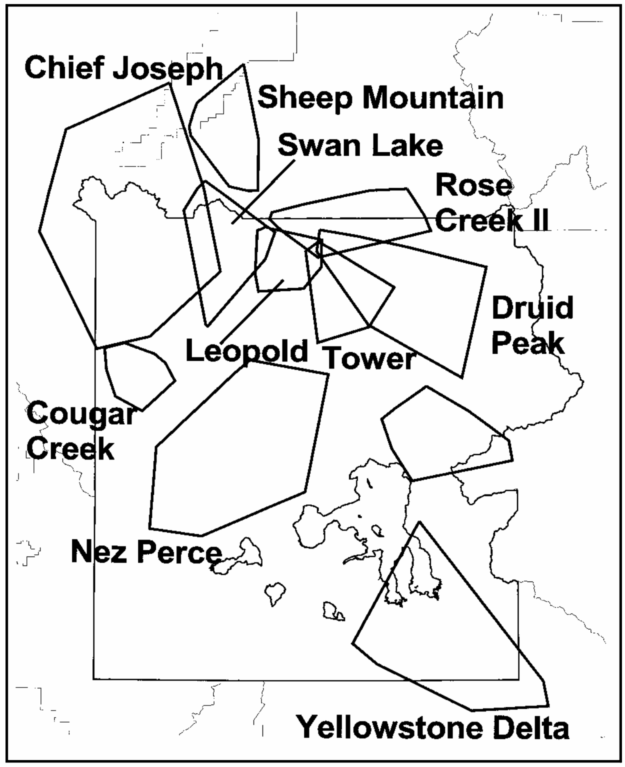

Figure 4. Wolf pack territories in Yellowstone National Park in 2001.

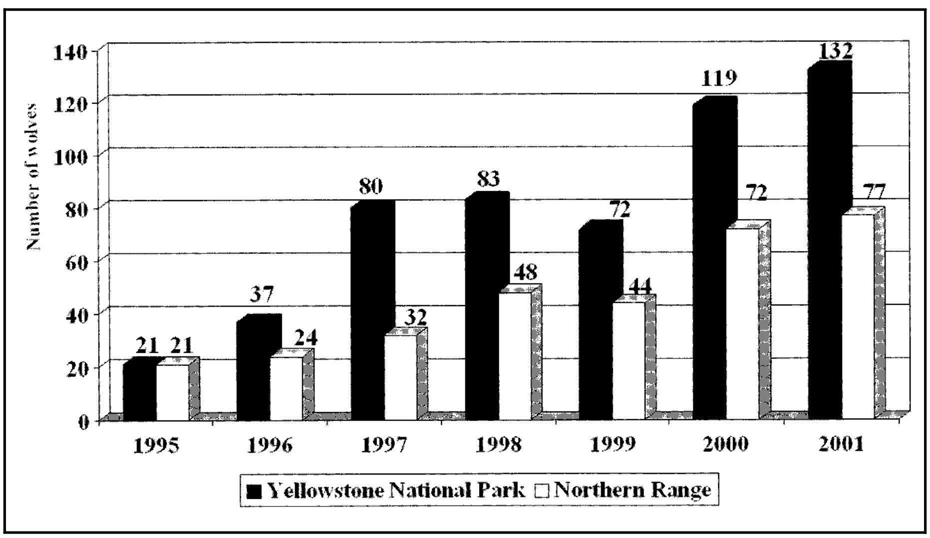

Figure 5. Population growth of wolves in Yellowstone National Park and on the northern range of the park, 1995–2001.

In about 84% of 145 wolf–coyote interactions observed at wolf kills, wolves prevailed over coyotes. Wolf kills clearly provide food for coyotes (virtually all winter kills are visited by coyotes), but coyotes that scavenge wolf kills risk death from wolves.

Scavengers. Besides coyotes, nine other scavenger species have been observed using wolf kills. All wolf kills are visited by ravens, magpies, and eagles. Many kills in the nonwinter months are visited by both species of bears (grizzlies and black bears). In winter, wolf kills are tremendous centers of activity for scavengers, and small packs of wolves lose large amounts of food to scavengers (Hayes et al. 2000). Kills are especially important to ravens—the average number of ravens per wolf kill was 29 and the largest number recorded was 135, a record in the literature (Stahler et al. 2002). Ravens follow wolves and discover wolf kills immediately, or even before the kill as they fly overhead while wolves pursue their prey (Stahler et al. 2002).

Grizzly bears. The grizzly bear population in the GYE has increased dramatically since the 1970s, although the bears are still listed as threatened under provisions of the Endangered Species Act. In 2001 the population was estimated at 354 bears, including 35 sows with cubs at heel (Haroldson and Frey 2001). Fifty-eight wolf–bear interactions have been recorded in YNP. Most interactions occur at wolf kill sites, where control of the carcass is hotly contested; typically, bears prevail in the encounter even though wolves outnumber them. In one case a bear held 24 wolves at bay. Although fully capable of killing ungulates, especially in spring, grizzly bears now appear to seek out wolf kills and are often successful at driving wolves from carcasses.

Cougars. The cougar population on the northern range has been monitored intensively through most of the 1990s (Murphy 1998). The present population on the northern range, roughly 25 animals, appears to have slowly increased during the 1990s and in the presence of wolves (Toni K. Ruth, Wildlife Conservation Society, Bozeman, MT, personal communication, October 2002). Documented interactions between wolves and cougars have been rare, seemingly because of separation of the habitats used by the two species (cougars inhabit rock outcrops and cliffs along rivers). Field observations suggest that cougars avoid wolves, are subordinate at kill sites, and are at risk of predation. In one incident, four cougar kittens were killed by wolves (Toni K. Ruth, Wildlife Conservation Society, Bozeman, MT, personal communication, October 2002).

Mesocarnivores. The effect of wolves on these animals has yet to be documented; we indulge in some speculation, however. Yellowstone has robust populations of some midsized carnivores (weasels, marten, badger) but low populations of others (fishers, wolverines, red fox, lynx, bobcat, otter). Several species may benefit from the advent of wolves. The red fox, for example, which competes more closely with coyotes than with wolves, may increase because of lower numbers of coyotes. Wolverines, which scavenge carcasses, also may increase.

Elk. From 1981–1982 through 1994–1995, winter numbers for the northern Yellowstone elk herd averaged 15,520 (± 2324, standard deviation; Lemke et al. 1998). Annual hunter harvests outside the park during the same 14-year period were variable but averaged 1823 (± 1022) elk, including 1192 (± 661) animals taken during the late hunt (65% of the total harvest; figure 6). The late hunt targets "antlerless" elk (females and calves of the year) that migrate from YNP; most elk harvested each year are females, followed by calves, with a quota limiting bull harvests to around 100 animals (Lemke et al 1998).

No elk counts were made during the winters of 1995–1996 and 1996–1997, just after wolves were released on the northern range (figure 6). The winter of 1996–1997 was severe; rain on deep snow during December and January was followed by subzero temperatures, sealing off the supply of winter forage. Record ungulate migrations from YNP were documented, and large numbers perished. A count in the following January (1998) tallied 11,736 elk in the northern herd, lower even than after the drought, fires, and severe winter of 1988–1989. Counts for the next four winters, 1999–2000 through 2002–2003, ranged from 11,742 to 14,539 (figure 6). While the elk population appeared to rebound slightly after the

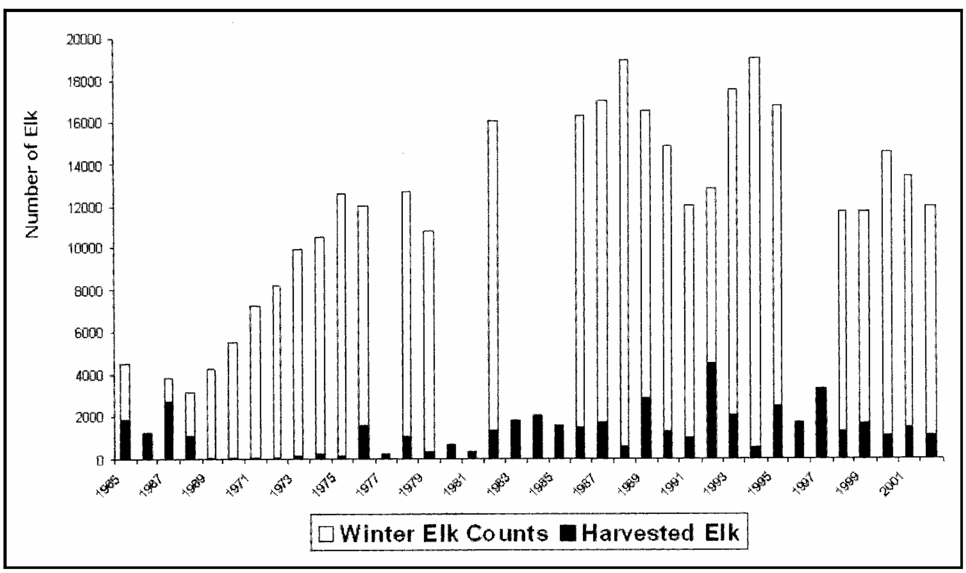

Figure 6. Elk population fluctuations and hunter harvests, 1965–2001.

Three wolves traveling. Wolf reintroduction ranks as one of the great conservation actions of the 20th century. Restoration of this top carnivore will very likely trigger a trophic cascade, restructuring the Yellowstone ecosystem. Photograph: Douglas Smith, National Park Service.

severe winter of 1996–1997, the pace of recovery was evidently very slow compared with the one that followed the die-off in 1989. Already media attention has abruptly switched from concern about too many elk for the northern range to concern about too few elk for human hunters outside the park.

It is worth noting that elk are the main prey for cougars, and cougars have a greater per capita kill rate than do wolves (Murphy 1998). Cougars kill an elk about every 9 days throughout the year (Murphy 1998). In winter, a wolf kills an elk about every 15 days on average (Mech et al. 2001); summer wolf kill rates are unknown. Elk calves are also seasonally important in the diet of coyotes and grizzly and black bears (Clark et al. 1999). Grizzly bears also kill adult elk and bison. Coyotes were estimated to take more than 1200 elk annually from the northern herd (about the same number as grizzly bears and cougars combined) before wolf restoration (Crabtree and Sheldon 1999). For all these predators, elk calves are a major dietary component. Thus, in a very real sense, the abundance and survival of cow elk, through their annual production of young, support major links in the Yellowstone food web and will determine the trajectory of the elk population in the future.

Population data for the approximately 500 nonmigratory Madison-Firehole elk in YNP suggest that their numbers have been relatively stable since wolf reintroduction (Eberhardt et al. 1998). This herd, surviving near warm geothermal "oases" in a region with very deep snow, could be at risk from wolf predation if packs hunt more intensively in that area. Data are sparse for the other six migratory herds that occupy YNP during summer (the total summer elk population is approximately 30,000 to 35,000), but they do not suggest that herds have declined since the arrival of wolves.

Bison. About 4000 bison occur throughout the park, with about 600 to 700 wintering on the northern range. Bison management has been controversial, because some animals harbor the bacterial disease brucellosis, and there is a remote chance the disease could be transmitted to livestock when bison migrate from the park (USDI 2000). Although wolves do kill bison (Smith et al. 2000), predation on bison is not yet widespread. One pack in Pelican Valley utilizes bison during late winter when bison are vulnerable and migratory elk are unavailable (Smith et al. 2000). Wolves are much less successful at killing bison than at killing elk; most bison stand their ground when confronted and this behavior seems to pose great difficulty for the attacking wolves. Bison carrion has been important wolf food during summers in the Lamar and Hayden Valleys whenever bulls die from injuries received during the rut. Bison carcasses attract concentrations of carnivores, including wolves, which scavenge extensively. Two grizzly bear cubs have probably been killed by wolves near these bison carcasses.

Moose. The moose population on the northern range, numbering only a few hundred, declined precipitously following the 1988 fires (Tyers and Irby 1995). This occurred because subalpine fir forests burned extensively, eliminating for many decades—if not centuries—these high-elevation winter habitats used by moose. Only 26 instances of wolf predation on moose have been recorded since wolf restoration.

Bighorn sheep. We do not expect wolves to affect the small population of about 175 bighorn sheep. Only one kill has been recorded since wolf reintroduction, and wolves spend very little time in the steep terrain commonly frequented by sheep.

Deer. We also do not expect wolves to affect deer populations significantly. The park does not contain good habitat for white-tailed deer, and the low deer numbers have not changed following wolf reintroduction. Wolves are not known to have killed any in the park. Mule deer are abundant, numbering about 2000 or 3000, but they migrate out of the park in winter, escaping some of the most intense wolf predation. Additionally, many mule deer winter in close association with humans in areas largely avoided by wolves.

Beaver. Beaver are widely but patchily distributed in Yellowstone. Most areas have few to none, although beavers are abundant in the Yellowstone River delta (south of Yellowstone Lake) and along the boundary of the park north of West Yellowstone, Montana. Systematic ground surveys began in 1988 and have continued at 5-year intervals; aerial surveys began in 1996 and have continued in alternate years. The 2001 aerial survey revealed 77 colonies distributed across the park.

During 1996, shortly after wolf reintroduction, there were no documented beaver colonies on the northern range. Since then, beavers have established four colonies in this portion of YNP, following recent beaver reintroductions on the adjacent Gallatin National Forest (Dan Tyers, US Forest Service, Gardiner, MT, personal communication, October 2002). Only two wolf pack territories—the Yellowstone Delta and Cougar Creek—contain substantial populations of beaver (figure 4). Wolves most likely prey on beavers in YNP as they do elsewhere, but we have documented only one beaver kill and have only rarely found beaver remains in wolf scats. Beavers are also closely associated with willow communities, a situation with relevance to wolves, as discussed below.

Vegetation. Interesting changes in willow and aspen growth occurred in the late 1990s. Increased height of some aspen stands has been attributed to elk redistribution following the arrival of wolves (Ripple et al. 2001), but the initial trend has ceased. Some stands of willow have also increased in stature, but it is still too early to know if this is attributable to wolves. Recovery of woody plants would be consistent with the speculation that some cottonwood stands dating from the 1880s could not recover until elk numbers were reduced or displaced, although this may be too simple an interpretation—the debate on this issue is intense (Meagher and Houston 1998, NRC 2002). No large stands of cottonwoods have been established on the northern range in the past 120 years. Currently very rare but in some places increasing since wolf reintroduction, willow and aspen are important for many bird species, small mammals, beavers, and moose. Ongoing research will continue to sort through this very complex issue, which could well turn out to be the most important aspect of wolf reintroduction to Yellowstone.

What next for Yellowstone? Science amid management and controversy

Predicting the future of the Yellowstone ecosystem is professionally hazardous—some would say foolhardy. Nevertheless, some initial patterns have emerged, and we deem this preliminary look ahead worthwhile. Predictions help frame research agendas and prepare the public, perhaps lessening some of the controversy that seems to engulf the management of Yellowstone.

At both Yellowstone and Isle Royale before the arrival of wolves, the condition of the vegetation was a source of concern and disagreement (Mech 1966, Pritchard 1999, NRC 2002). The controversy evaporated at Isle Royale when wolves were established and a natural "balance" was assumed to exist, although some people feared the wolves would kill all the moose and then start in on the people (Isle Royale National Park files, letter to the Superintendent, 1956). Similar letters in numerous newspapers in the Yellowstone area have appeared regularly. Based on the Isle Royale experience, we anticipate that the condition of the vegetation on the northern range will subside as a popular topic of debate in the media and that, in time, the fear that wolves will kill all the elk will also be put to rest.

Much will depend on the population trajectory for Yellowstone wolves. At what point will wolves have saturated YNP, particularly the northern range, and how will we know when that point is reached? There are indications that rapid population growth for wolves on the northern range has ceased, but wolves should continue to increase until chronic food limitation is evidenced through declining numbers and weights of pups and intraspecific killing. While this is hardly the case at present, body weight for young wolves born in the Druid pack was lower in 2002 than in previous years. Field evidence that wolves are approaching their carrying capacity at Yellowstone is also supported by increased levels of intraspecific strife in 2001 and 2002 and by a plot of wolf locations that indicates little vacant territory (figure 4). Isle Royale history and other studies indicate that there will be continual flux in pack territorial relationships (Fritts and Mech 1981, Mech et al. 1998).

Wolf–prey ratios may help indicate when wolves have saturated their Yellowstone niche. After wolf recovery, the average predicted elk-to-wolf ratio was 166, based on specific examples illustrated by Boyce (1993) for 100-year simulations, very similar to the elk-to-wolf ratio of 154 actually observed in 2002. At Isle Royale during 1959–2002, predator and prey have fluctuated around a mean moose-to-wolf ratio of 46, but this figure has fluctuated from 18:1 to 145:1 (Peterson et al. 1998). We speculate that the difference in prey-to-predator ratios between Isle Royale and Yellowstone may arise from the differences in body size (moose are twice as large as elk) and social behavior (elk live in groups, moose live singly). We stress that it will be some time before anything resembling a dynamic equilibrium at Yellowstone can be documented.

Before 1995, Isle Royale supported one of the highest year-round densities of wolves—42 per 1000 km^2— in the world. By 2002, wolves on Yellowstone's northern range had already reached a density of 50 wolves per 1000 km^2. Boyce (1993) predicted a mean population size of 76 wolves in YNP, primarily in the northern range, and a range from 50 to 120 under most management scenarios; in 2002 there were 77 wolves using the northern range and 132 wolves within YNP. The wolf population might overshoot equilibrium levels in a manner analogous to the irruptive pattern commonly observed for ungulate populations colonizing from low densities. The density reached by wolves in their initial period of rapid growth may indeed be very high, but this says little about the nature of the equilibrium that will be attained perhaps decades hence.

We are confident that form and function of the Yellowstone ecosystem will change because of wolf recovery. Reductions in the coyote population have already occurred, and elk numbers rebounded less after the severe winter of 1996–1997 but not to a degree that threatens the survival of either species in Yellowstone. A resulting trophic cascade will reverberate through the ecosystem. From the complicated food web that exists inYellowstone (figure 1), it is not hard to imagine that indirect effects of wolf recovery will be substantial. Although riparian willow habitats form a very small part of the northern range, any reestablishment of these woody shrub communities would increase biodiversity.

Wolf chasing a coyote. Wolves began killing coyotes immediately after the wolves' reintroduction. The wolves account for a 50% reduction in the coyote population on the northern range of Yellowstone. Photograph: Monty Dewald.

Although our expectations for wolf effects in Yellowstone are based on inferences from other studies and may seem self-evident, we realize that specific predictions may be wrong. Even in a system as simple as Isle Royale, predictability has been poor even after four decades of scientific scrutiny; none of the expectations for the moose herd, voiced in turn by Mech (1966) and Peterson (1977), actually transpired. Rather, external forces such as severe winters, summer heat, and outbreaks of winter ticks (driven by warm, dry spring weather) have caused the moose population to decline (DelGiudice et al. 1997). Surprises, like the arrival of the exotic disease that caused a wolf crash at Isle Royale in the early 1980s, are virtually guaranteed in the long term, and they will assuredly influence, and possibly determine, the outcome of the great natural experiment in wolf–elk dynamics now launched at Yellowstone.

Science will be challenged to clarify exactly which changes in Yellowstone have been prompted by the addition of wolves. No wildlife population response at Yellowstone can be attributed to the actions of just one species (although coyotes may be an exception) or to just one external event—such simplification of cause and effect is rarely possible in the science of ecology. Large perturbations, as with unique weather-driven events, will loom large in the future of Yellowstone. The 1988 fires burned about 36% of the land area of the park, affecting forage supplies for native ungulates (positively and negatively), but there is plenty of room for future fires in a climate that seems conducive to large conflagrations. Given time, the severe winter of 1996–1997 will be matched and exceeded. Climate change will magnify the scientific challenge (NRC 2002). The danger we perceive is that all changes to the system, now and in the future, will be attributed solely to the restoration of the wolf. Testing research hypotheses is particularly difficult in natural areas, where experimental manipulations are limited and controls are either absent or difficult to establish. In particular, the problem of multiple causation has plagued the testing of hypotheses in ecology and frequently confounded inferences derived from field studies. This stumbling block may be particularly troublesome in the complex Yellowstone ecosystem; the need to design research hypotheses that discriminate among potential competing causes is therefore very real.

As in the past, elk management decisions for areas outside the park will influence future population levels of elk inside the park. Some curtailment of midwinter shooting of cow elk outside the park might be necessary, because wolves and humans, though their hunting strategies are very different, compete over common prey. Successful coexistence of wolves and human hunters is a management conundrum that will test wildlife managers and challenge long-held beliefs. This is not the first time that the Yellowstone ecosystem has led us into uncharted waters, and our responses to this latest natural experiment will be no less interesting than the welter of ecological effects.

References cited

Allen DL. 1979. The Wolves of Minong: Their Vital Role in a Wild Community. Boston: Houghton Mifflin.

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

Boyce MS. 1993. Predicting the consequences of wolf recovery to ungulates in Yellowstone National Park. Pages 234–269 in Cook RS, ed. Ecological Issues on Reintroducing Wolves into Yellowstone National Park. Denver (CO): National Park Service. NPS/NRYELL/NRSM-93/22.

Clark T, Curlee AP, Minta SC, Kareiva PM, eds. 1999. Carnivores in Ecosystems: The Yellowstone Experience. New Haven (CT): Yale University Press.

Cook RS. 1993. Ecological Issues on Reintroducing Wolves into Yellowstone National Park. Denver (CO): National Park Service. NPS/NRYELL/NRSM-93/22.

Crabtree RL, Sheldon JW. 1999. Coyotes and canid coexistence. Pages 127–163 in Clark TW, Curlee AP, Minta SC, Kareiva PM, eds. Carnivores in Ecosystems: The Yellowstone Experience. New Haven (CT): Yale University Press.

DelGiudice GD, Peterson RO, Samuel WM. 1997. Trends of winter nutritional restriction, ticks, and numbers of moose on Isle Royale. Journal of Wildlife Management 61: 895–903.

Eberhardt LL, Garrott RA, White PJ, Gogan PJ. 1998. Alternative approaches to aerial censusing of elk. Journal of Wildlife Management 62: 1046–1055.

Fritts SH, Mech LD. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. Bethesda (MD): Wildlife Society. Wildlife Monographs 80.

Garton EO, Crabtree RL, Ackerman BB, Wright G. 1990. The potential impact of a reintroduced wolf population on the northern Yellowstone elk herd. Pages 3-59–3-91 in Yellowstone National Park, US Fish and Wildlife Service, University of Wyoming, University of Idaho, Interagency Grizzly Bear Study Team, University of Minnesota Cooperative Park Studies Unit. Wolves for Yellowstone? A Report to the United States Congress, Vol. 2: Research and Analysis. Yellowstone National Park (WY): National Park Service.

Gasaway WC, Boertje RP, Grangaard DV, Kelleyhouse DG, Stephenson RO, Larsen DG. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Bethesda (MD): Wildlife Society. Wildlife Monograph 120.

Haines AL. 1977. The Yellowstone Story. Boulder: Colorado Associated University Press.

Haroldson MA, Frey K. 2001. Grizzly bear mortalities. Pages 24–29 in Schwartz CC, Haroldson MA, eds. Yellowstone Grizzly Bear Investigations: Annual Report of the Interagency Grizzly Bear Study Team, 2000. Bozeman (MT): US Geological Survey.

Hayes RD, Baer AM, Wotschikowsky U, Harestad AS. 2000. Kill rate by wolves on moose in the Yukon. Canadian Journal of Zoology 78: 49–59.

Houston DB. 1982. The Northern Yellowstone Elk: Ecology and Management. New York: Macmillan.

Lemke TO, Mack JA, Houston DB. 1998. Winter range expansion by the northern Yellowstone elk herd. Intermountain Journal of Sciences 4: 1–9.

Mack JA, Singer F. 1992. Population models for elk, mule deer, and moose on Yellowstone's northern winter range. Pages 4-3–4-31 in Varley JD, Brewster WG, eds. Wolves for Yellowstone? A Report to the United States Congress, Vol. 4: Research and Analysis. Yellowstone National Park (WY): National Park Service.

———. 1993. Using Pop-II models to predict effects of wolf predation and hunter harvests on elk, mule deer, and moose on the northern range. Pages 49–74 in Cook RS, ed. 1993. Ecological Issues on Reintroducing Wolves into Yellowstone National Park Denver (CO): National Park Service. NPS/NRYELL/NRSM-93/22.

McLaren BE. 1996. Plant-specific response to herbivory: Simulated browsing of suppressed balsam fir on Isle Royale. Ecology 77: 228–235.

McLaren BE, Janke RA. 1996. Seedbed and canopy cover effects on balsam fir seedling establishment in Isle Royale National Park. Canadian Journal of Forest Research 26: 782–793.

McLaren BE, Peterson RO. 1994. Wolves, moose, and tree rings on Isle Royale. Science 266: 1555–1558.

Meagher MM. 1973. The Bison of Yellowstone National Park. Washington (DC): Government Printing Office. National Park Service Scientific Monograph Series no. 1.

Meagher MM, Houston DB. 1998. Yellowstone and the Biology of Time: Photographs across a Century. Norman: University of Oklahoma Press.

Mech LD. 1966. The Wolves of Isle Royale. Washington (DC): Government Printing Office. Fauna of the National Parks of the United States. Fauna Series 7.

Mech LD, Adams LG, Meier TJ, Burch JW, Dale BW. 1998. The Wolves of Denali. Minneapolis: University of Minnesota Press.

Mech LD, Smith DW, Murphy KM, MacNulty DR. 2001. Winter severity and wolf predation on a formerly wolf-free elk herd. Journal of Wildlife Management 65: 998–1003.

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

Messier F, Gasaway WC, Peterson RO. 1995. Wolf-Ungulate Interactions in the Northern Range of Yellowstone: Hypotheses, Research Priorities, and Methodologies. Fort Collins (CO): Midcontinent Ecological Science Center, National Biological Service.

Murphy KM. 1998. The ecology of the cougar *(Puma concolor)* in the northern Yellowstone ecosystem: Interactions with prey, bears, and humans. PhD dissertation. University of Idaho, Moscow.

[NRC] National Research Council. 2002. Ecological Dynamics on Yellowstone's Northern Range. Washington (DC): National Academy Press.

Pastor J, Dewey B, Naiman RJ, MacInnes PF, Cohen Y. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. Ecology 74: 467–480.

Peterson RO. 1977. Wolf Ecology and Prey Relationships on Isle Royale. Washington (DC): National Park Service. Scientific Monograph Series 11.

———. 1995. The Wolves of Isle Royale. Minocqua (WI): Willow Creek Press.

Peterson R, Thomas NJ, Thurber JM, Vucetich JA, Waite TA. 1998. Population limitation and the wolves of Isle Royale. Journal of Mammalogy 79: 828–841.

Phillips MP, Smith DW. 1996. The Wolves of Yellowstone. Stillwater (MN): Voyageur Press.

Pritchard JA. 1999. Preserving Yellowstone's Natural Conditions: Science and the Perception of Nature. Lincoln: University of Nebraska Press.

Ripple WJ, Larsen EJ, Renkin RA, Smith DW. 2001. Trophic cascades among wolves, elk, and aspen on Yellowstone National Park's northern range. Biological Conservation 102: 227–234.

Servheen CW, Knight RR. 1993. Possible effects of a restored wolf population on grizzly bears in the Yellowstone area. Pages 28–37 in Cook RS, ed. Ecological Issues on Reintroducing Wolves into Yellowstone National Park. Denver (CO): National Park Service. NPS/NRYELL/NRSM-93-22.

Smith DW, Mech LD, Meagher M, Clark WE, Jaffe R, Phillips MK, Mack JA. 2000. Wolf–bison interactions in Yellowstone National Park. Journal of Mammalogy 81: 1128–1135.

Stahler DR, Heinrich B, Smith DW. 2002. Common ravens, *Corvus corax,* preferentially associate with gray wolves, *Canis lupus,* as a foraging strategy. Animal Behavior 64: 283–290.

Stohlgren TJ, Schell DL, Vander Heuvel B. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. Ecological Applications 9: 45–64.

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

[USDI] US Department of the Interior, National Park Service. 2000. Bison Management Plan for the State of Montana and Yellowstone National Park: Final Environmental Impact Statement, Vol. I. Washington (DC): USDI.

[USFWS] US Fish and Wildlife Service. 1994. The Reintroduction of Gray Wolves to Yellowstone National Park and Central Idaho: Final Environmental Impact Statement. Helena (MT): USFWS.

Vales DJ, Peek JM. 1990. Estimates of the potential interactions between hunter harvest and wolf predation on the Sand Creek, Idaho, and Gallatin, Montana, elk populations. Pages 3-93–3-167 in Yellowstone National Park, US Fish and Wildlife Service, University of Wyoming, University of Idaho, Interagency Grizzly Bear Study Team, University of Minnesota Cooperative Park Studies Unit. Wolves for Yellowstone? A Report to the United States Congress, Vol. 2: Research and Analysis. Yellowstone National Park (WY): National Park Service.

Varley JD, Brewster WG, eds. 1992. Wolves for Yellowstone? A Report to the United States Congress, Vol. 4: Research and Analysis. Yellowstone National Park (WY): National Park Service.

Weaver J. 1978. The Wolves of Yellowstone. Washington (DC): National Park Service. Natural Resources Report no. 14.

[YNP] Yellowstone National Park. 1997. Yellowstone's Northern Range: Complexity and Change in a Wildland Ecosystem. Mammoth Hot Springs (WY): National Park Service.

[YNP et al.] Yellowstone National Park, US Fish and Wildlife Service, University of Wyoming, University of Idaho, Interagency Grizzly Bear Study Team, University of Minnesota Cooperative Park Studies Unit. 1990. Wolves for Yellowstone? A Report to the United States Congress, Vol. 1: Executive Summary; Vol. 2: Research and Analysis. Yellowstone National Park (WY): National Park Service.