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

1. **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?

2. 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.

3. 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).

4. 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

5. 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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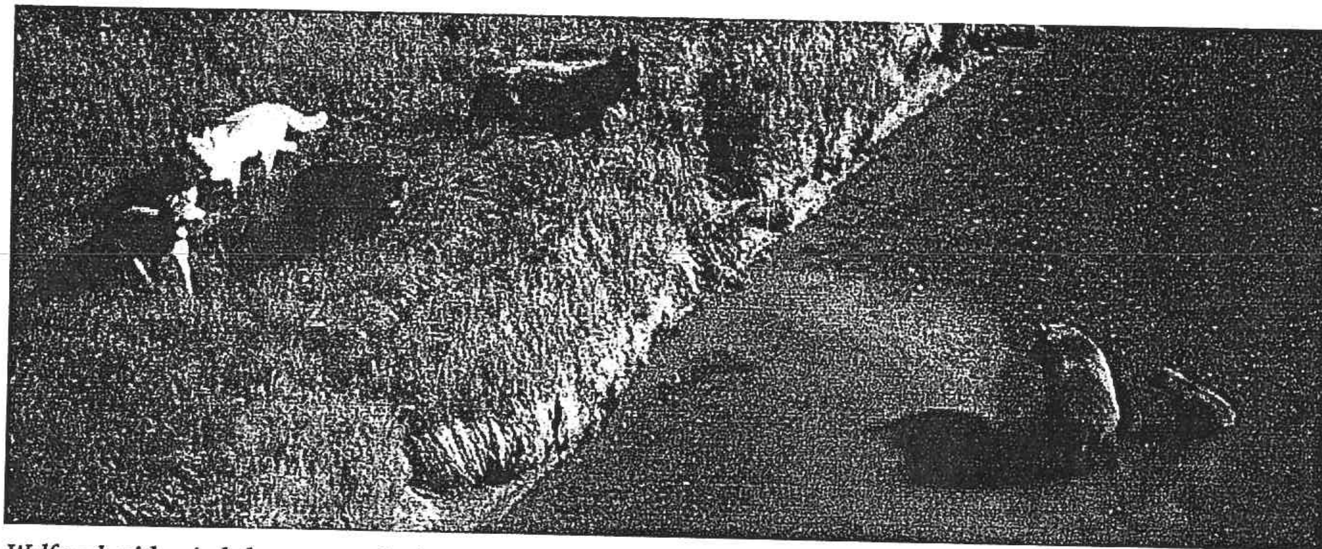


Wolf pack with grizzly bear sow and cubs. Interactions between wolves and grizzly bears have largely benefited grizzlies, although two grizzly cubs were probably killed by wolves. Photograph: Douglas Smith, National Park Service.

6, 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.

7. 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.

8. 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

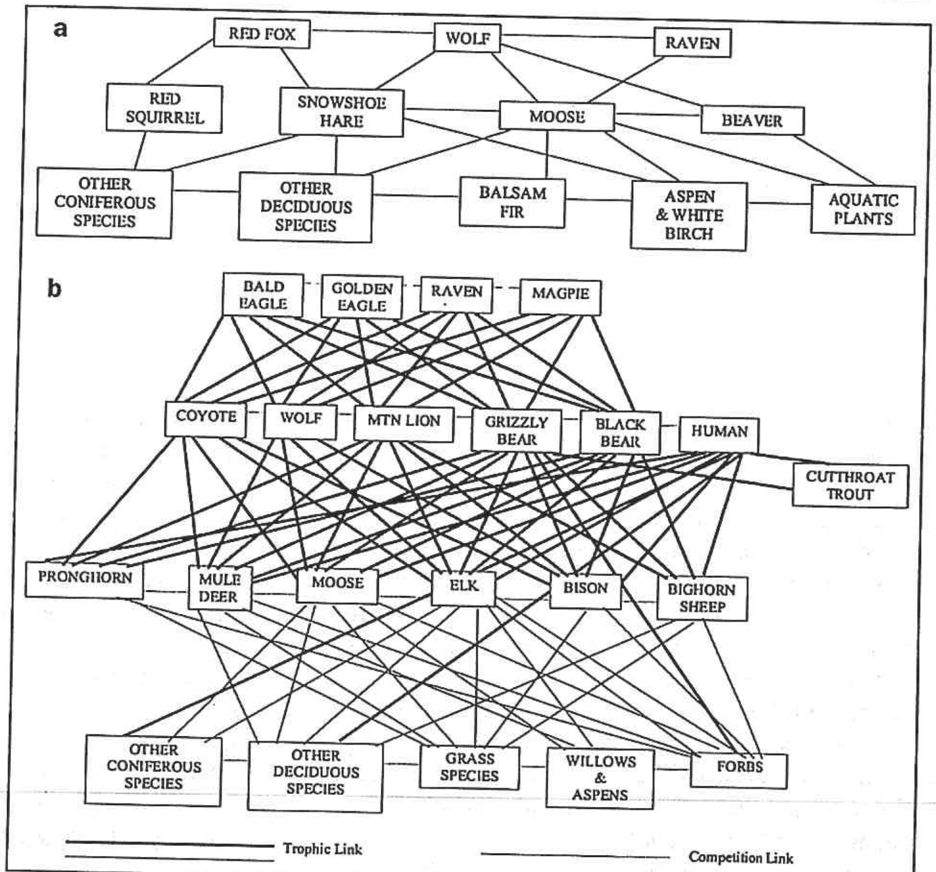


Figure 1. Yellowstone has more interacting species than does Isle Royale, which leads to greater complexity and makes scientific study and understanding more challenging. (a) Isle Royale; (b) Yellowstone.

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).

9. 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).

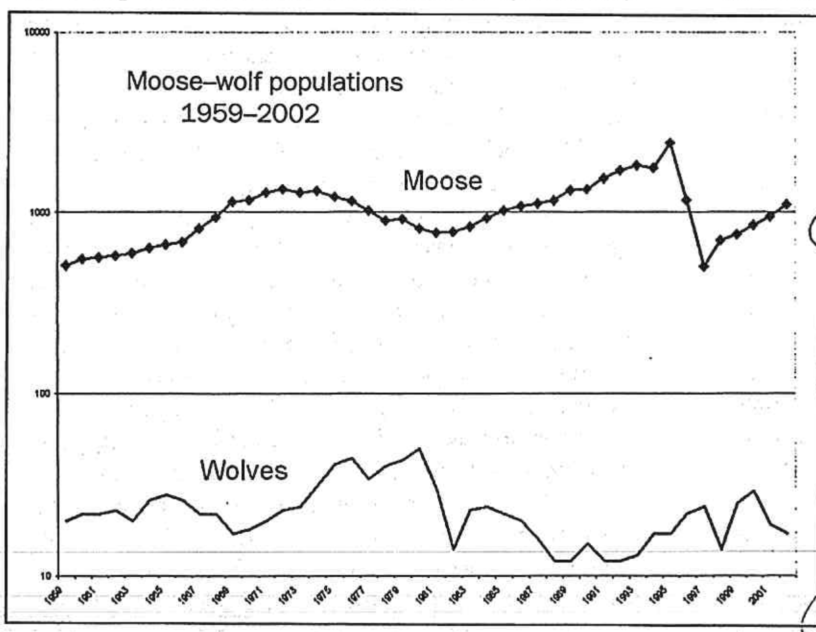


Figure 2. Fluctuations in the numbers of wolves and moose in Isle Royale National Park, 1958–2002. Wolf numbers were multipied by 15 to enable use of the same axis.

10. 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).

11. 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

12. 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?

13 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).

14 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

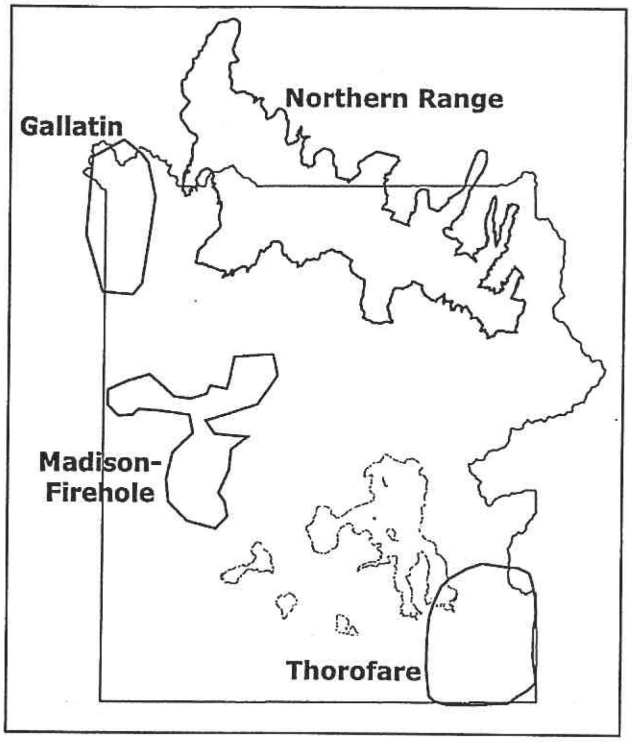


Figure 3. Before wolves were reintroduced, researchers predicted the wolves would settle in the four sites shown above.

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.

15. 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.

16 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.

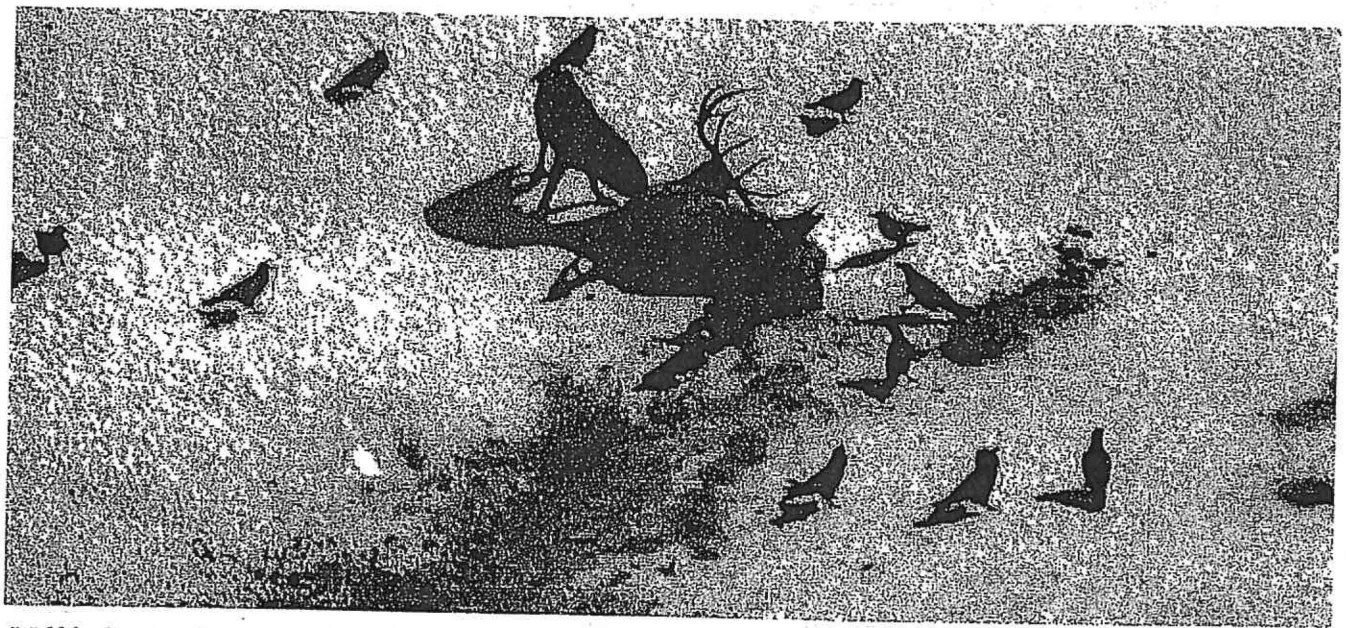
17 Both the historical record at Isle Royale and the predictions of Boyce (1993) for the northern Yellowstone elk underscore the dynamic future that will follow wolf recovery. Fluctuations in wildlife populations are normal; the renowned "balance of nature" at Isle Royale is decidedly dynamic. Wolf peaks 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).

18 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.

19. 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.

20 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.

21. 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).

22. 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.

23. 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.

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. I: Executive Summary; Vol. 2: Research and Analysis. Yellowstone National Park (WY): National Park Service.