Yellowstone Science

volume 13 • number 1 • winter 2005

Ten Years of *Yellowstone Wolves*

1995–2005

What Big Teeth You Have

As Roger Anderson assumes his new duties as branch chief of cultural resources, I am happy to serve as guest editor of *Yellowstone Science.* I believe this journal is a unique and important medium for communicating the wide variety of research projects that take place in Yellowstone National Park. The results of these studies are often educational, sometimes unexpected or groundbreaking—and occasionally controversial.

We decided to devote this entire issue to the story of the wolves, 10 years after the U.S. Fish and Wildlife Service's Congressionally mandated restoration program that placed Canadian wolves in the Greater Yellowstone Area and central Idaho. For some, the return of the wolf indicates progress, a change in attitudes toward predators and increased understanding of ecosystems. For others, the wolves' return is a backward step to a time when they felt less able to defend their livelihoods and families.

I live in the gateway community of Cooke City, Montana, and I remember the thrill of seeing the recently released Rose Creek pack as they crossed the road in my headlights late one night. That was back when everyone thought the elusive wolves would rarely be seen. Now, 20,000 people each year see a wolf in the park: they are highly visible, and intensely studied.

The Cooke City–Silver Gate area is just one that has benefited economically from the return of the wolf to Yellowstone, as wildlife watchers have found it to be a convenient place from which to base their Lamar Valley excursions. It is also a place where some blame wolves because they believe they are seeing less wildlife, and where you can read "Die Wolf" on the back of a truck.

Although one might expect that sentiment to quiet down as time passes and people readjust to living with wolves, feelings about wolves remain passionate. As wolves repopulate the area and leave the park, as research continues and conclusions are debated, as delisting looms—tensions continue to roil.

Love them or hate them, few people feel indifferent about wolves. As Yellowstone National Park wolf biologist Douglas Smith states in his article, it was a change in human attitudes that brought wolves back; their future will depend on us too.

YELLOWSTONE SCIENCE

a quarterly devoted to
natural and cultural resources

volume 13 • number 1 • winter 2005

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Bozeman, Montana
Printer

Yellowstone Science is published quarterly. Support for *Yellowstone Science* is provided by the Yellowstone Association, a non-profit educational organization dedicated to serving the park and its visitors. For more information about the association, including membership, or to donate to the production of *Yellowstone Science,* visit www.yellowstoneassociation.org or write: Yellowstone Association, P.O. Box 117, Yellowstone National Park, WY 82190.

For back issues of *Yellowstone Science,* please see www.nps.gov/yell/publications.

Submissions are welcome from all investigators conducting formal research in the Yellowstone area. To submit proposals for articles, to subscribe, or to send a letter to the editor, please write to the following address: Editor, *Yellowstone Science,* P.O. Box 168, Yellowstone National Park, WY 82190.
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Yellowstone Science is printed on recycled paper with a soy-based ink.

on the cover:
Wolf howl.
Photo © Bob Landis.

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Druid Peak wolf pups on an early outing.

FEATURES

DEPARTMENTS

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NEWS & NOTES

2004–05 Winter Count of Northern Yellowstone Elk

The Northern Yellowstone Cooperative Wildlife Working Group conducted its annual winter survey of the northern Yellowstone elk population on January 5, 2005. A total of 9,545 elk were counted during good survey conditions. Approximately two-thirds of the observed elk were located within Yellowstone National Park (YNP), while one-third was located north of the park. Biologists used four fixed-wing aircraft to count elk on the entire northern range during the one-day survey. The northern Yellowstone elk herd winters between YNP's northeast entrance and Dome Mountain/Dailey Lake in Montana's Paradise Valley.

This year's total of 9,545 elk was 15% higher than the 8,335 elk counted last winter, and slightly higher than the 9,215 elk counted in winter 2003. According to YNP wildlife biologist P.J. White, the increase in counted elk from last year most likely is a result of better survey conditions and detection of elk this winter, rather than an actual increase in elk numbers. Survey conditions were good, owing to a significant snowstorm on December 31, 2004, that covered the landscape and caused elk to concentrate in relatively open areas at lower elevations where detection was likely higher compared to count days during the last several mild winters.

The overall trend in counts still suggests that elk numbers have decreased substantially over the past decade. Predation by wolves and other large carnivores and human harvests during the Gardiner late elk hunt have been the primary factors contributing to decreasing numbers of northern Yellowstone elk since the mid 1990s. Other factors that have contributed to decreased elk numbers include a substantial winter-kill caused by severe snow pack during 1997 and, possibly, drought-related effects on pregnancy and calf survival.

The Gardiner late elk hunt was designed to reduce elk numbers outside YNP so that they do not cause long-term changes in plant communities or decrease the quality of their winter range. Tom Lemke, biologist for Montana Fish, Wildlife and Parks (FWP) said, "as elk numbers and calf recruitment have declined in recent years, FWP has reduced the hunter harvest by significantly reducing the number of elk permits issued. At this point, hunter-related elk mortality is the only mortality factor we have some control over." FWP has tentatively proposed reducing the number of elk permits further next year, due largely to the substantial decrease in elk numbers and poor calf recruitment.

The working group will continue to monitor trends of the northern Yellowstone elk population and evaluate the relative contribution of various components of mortality, including predation, environmental factors, and hunting. The group was formed in 1974 to cooperatively preserve and protect the long-term integrity of the northern Yellowstone winter range for wildlife species by increasing scientific knowledge of the species and their habitats, promoting prudent land management activities, and encouraging an interagency approach to answering questions and solving problems. The group is comprised of resource managers and biologists from Montana Fish, Wildlife and Parks, the National Park Service (YNP), U.S. Forest Service (Gallatin National Forest), and U.S. Geological Survey-Northern Rocky Mountain Science Center, Bozeman.

YCR Deputy Director Wayne Brewster Retires

On January 3, 2005, Wayne Brewster, Deputy Director of the Yellowstone Center for Resources, retired after 35 years of federal service in the U.S. Army, U.S. Fish and Wildlife Service (USFWS), and National Park Service (NPS). He and his wife, Lil, moved to Helena, Montana. Brewster came to work for Yellowstone in 1991 from Glacier National Park, where he had worked on wolf and grizzly recovery since 1988.

Prior to working for the NPS, Brewster had a long career in the USFWS. After receiving a Master's degree in Wildlife Biology from South Dakota State University, he began his career as a GS-7 in 1975. In 1979, Brewster was selected by the USFWS as the Endangered Species Team Leader for Montana and Wyoming. His boss during this period, the USFWS Area Manager, paid him a high compliment, "[Brewster] has never had a[n] [Endangered Species Act] Section 7 Biological Opinion overruled." In 1982, Brewster moved to Helena to become Field Supervisor for all Endangered Species Act (ESA) activities in Montana and Wyoming.

In these two crucial states, Brewster had primary responsibilities for ESA species including grizzly bears, black-footed ferrets, bald eagles, peregrine falcons, Kendall Warm Spring Dace,

NPS

gray wolves, whooping cranes, piping plovers, and least terns. Most of the species on that list have either been de-listed (bald eagle), are having proposals sorted out for their de-listing (peregrines, grizzlies, wolves, dace), or are clearly on the road to recovery (ferrets).

In Yellowstone, Brewster was the regional lead for wolf recovery planning for all parks. He was the taskmaster for the all-important four-volume set of research findings, *Wolves for Yellowstone? A Report to the U.S. Congress.* He was NPS spokesperson to the ill-fated, anti-wolf dominated Wolf Management Committee. These activities inevitably and logically led to his being named NPS czar (and taskmaster) for the joint Environmental Impact Statement (with the USFWS) evaluating restoration of wolves to Yellowstone and central Idaho. By late 1994, with wolves on the ground and Wolf Project Leader Mike Phillips in place, Brewster turned his efforts to advising the agency solicitors and Justice Department attorneys on the lawsuits brought by anti-wolf interests. In this role, he was singled out for praise by a number of people, including an especially nice letter from Attorney General Janet Reno to Interior Secretary Bruce Babbitt.

Brewster gradually transitioned out of wolves and into bison work. Again, he took on a laborious and frustrating multiple-agency EIS. The result was a hard-won compromise with other agencies that, given the opportunity, would manage Yellowstone's bison very differently than the NPS. Considering the alternatives, Brewster did very well on the park's behalf.

Brewster's career followed very closely the life to date of the Endangered Species Act, and YCR Director John Varley suggests that it was with those downtrodden species that Brewster's star shined brightest. His influence and talents have made an extraordinary difference on some of North America's most popular, but needy wildlife. There is probably no individual who has had a greater positive effect on these many species in the northern Rocky Mountains.

National Geographic's "Wolf Pack" Wins Emmy

"National Geographic Explorer," cable television's longest-running documentary series, took home two News and Documentary Emmy Awards at the National Television Academy's September 2004 ceremony. "Wolf Pack," a program based on Yellowstone wolves with footage by Gardiner, Montana, resident Bob Landis, won the Emmy for outstanding science, technology, and nature programming.

New Specimens Added to YNP's Herbarium

Yellowstone recently received four plant specimens collected in the park in 1899. The donation came from the Booth Herbarium (MONT) at Montana State University (MSU) in Bozeman. These specimens have undergone a saga since their collection by J.W. Blankinship, the first curator of the MSU herbarium. Soon after their collection, they were apparently displayed at a World's Fair, possibly in St. Louis. When returned, they were mistakenly sent to the University of Montana herbarium (MONTU). Apparently, cooperation between the two institutions was poor at that time, because the specimens were not forwarded to MSU. They were not all mounted or catalogued into the MONTU collection, but have simply been stored there for over 100 years.

They were recently re-discovered, and the MONTU herbarium checked with the MONT herbarium to see if these were duplicates of specimens at MONT. Surprisingly, they were not, so the material was finally returned to Bozeman. Since there was plenty of material, duplicate specimens were available for another institution. The good relationship between the Yellowstone and Booth herbariums resulted in YNP receiving duplicates. These four specimens are of western groundsel (*Senecio integerrimus*) and woolly groundsel (*Senecio canus*). When accessioned and catalogued into Yellowstone's collection, they will be the oldest specimens in the park's herbarium, superseding the previous oldest specimens, which were collected in 1910.

Update on the Spires in Yellowstone Lake

In *Yellowstone Science* 12(4), we reprinted the article "The Bridge Bay Spires: Collection and Preparation of a Scientific Specimen and Museum Piece" by Dr. Russell L. Cuhel et al. This article was originally published in 2002 in the proceedings from the 6th Biennial Scientific Conference on the Greater Yellowstone Ecosystem, *Yellowstone Lake: Hotbed of Chaos or Reservoir of Resilience?*. The article states that the USGS later discovered hundreds of much larger spires in the northern end of the lake. This is incorrect. When the area was investigated, it turned out to be a series of north–south trending hydrothermal fissures or cracks in the lake floor. Further mapping by the USGS and Eastern Oceanics has shown that the Bridge Bay area is the only place where spires are currently known to exist in Yellowstone Lake. YS

NPS/DOUGLAS SMITH

PERSPECTIVES

How Did Wolves Get Back to Yellowstone?

Ed Bangs

Rocky Mountain Wolf Recovery Program Coordinator,

U.S. Fish and Wildlife Service

THE WISDOM of eliminating wolves from Yellowstone National Park was discussed before the task was finished. In 1944, Dr. Aldo Leopold, arguably the father of modern wildlife science, said "There still remain...some areas of considerable size [Yellowstone] in which we feel that...gray wolves may be allowed to continue their existence...Yes—so also thinks every right-minded ecologist..." Unfortunately, at that time predators were not valued as wildlife, and the last known wolf in the Greater Yellowstone Area was killed that very year.

Yellowstone wolves, though, continued to live in the imagination of a growing number of people. In the 1960s, public reports of possible sightings increased, and biologists recommended wolf restoration to Yellowstone. The time was not yet right, and powerful political interests quickly crushed the concept. Despite this political trip to the woodshed, the park never lost sight of its mission to restore natural processes for the benefit of people and kept the symbolism of wolves alive through its informational programs for the next 30 years.

In 1974, wolves in Montana and Wyoming became protected under the new federal Endangered Species Act, and the U.S. Fish and Wildlife Service (USFWS) was mandated to achieve wolf recovery. In 1974, the State of Montana led a USFWS recovery team that recommended wolf restoration in the area stretching from Yellowstone National Park to the Canadian border. The Greater Yellowstone Area's 19,000 square miles of public land, wildness, abundant wildlife, and Yellowstone National Park core automatically leapt to the top of every list of potential wolf reintroduction sites. As wolf restoration continued to gain public support and momentum, Yellowstone became synonymous with wolf recovery.

Dr. John Weaver concluded his seminal 1978 report, "The Wolves of Yellowstone," by recommending a transplant of wolves from British Columbia or Alberta to Yellowstone. In 1980, the first northern Rocky Mountain wolf recovery plan was signed, and Yellowstone was foremost in the team's mind. In 1987, a revised recovery plan recommended that wolves be reintroduced to the Yellowstone area as an experimental population, which allowed extra management flexibility to address the concerns of the park's neighbors.

The idea of wolf reintroduction to Yellowstone continued to gather steam. In 1988, Congress mandated the National Park Service's *Wolves for Yellowstone?* studies, to investigate the possible impacts of wolf reintroduction. In 1990, Congress established a political Wolf Management Committee in an attempt to reduce public controversy over wolf reintroduction, and funded another round of *Wolves for Yellowstone?* studies.

In 1992, Congress directed the USFWS, in consultation with the National Park Service and USDA Forest Service, to prepare an exhaustive Environment Impact Statement (EIS) about wolf reintroduction. During that two-year process, 180,000 public comments were received. In 1994, the EIS was approved, and in 1995, wolves were reintroduced into both Yellowstone National Park and central Idaho. As predicted, wolves—with their great natural abilities—have flourished. Naturally, more than half of the 300 wolves in the Greater Yellowstone Area live in the park. Without Yellowstone's amazing ecological features and leadership, wolf restoration may not have been possible.

Barbee Retrospective

Yellowstone Wolf Restoration

NPS

Bob Barbee, Superintendent of Yellowstone National Park from 1983 to 1994

DURING THE LATE FALL OF 1982, I journeyed to Washington, D.C., for an interview with Interior Secretary James Watt, a prerequisite to an appointment as superintendent of Yellowstone. Amazingly, I passed, which was no small feat for someone of my ilk. The subject of wolves did not come up with Secretary Watt, but it did with Assistant Secretary G. Ray Arnett. He half-jokingly admonished me "to not even flirt with the idea of bringing wolves back to Yellowstone, or you will find yourself a park planner in South Yemen." I allowed that "I was glad to be able to smoke him out on that issue."

The notion of restoring wolves to Yellowstone had been around for a long time before I got there, but never seriously pursued. In 1983, resource issues in Yellowstone centered on efforts to keep the grizzly bear from sliding into a black hole, and wolves were not on the agenda. Still, there was background chatter about them. By the mid 1980s, William Penn Mott had become the Director of the National Park Service, and wolves found a voice in Bill Mott.

Mott had been Ronald Reagan's California State Parks Director and was an unabashed advocate for conservation in general and for parks in particular. We had many discussions about wolf restoration. He never missed an opportunity to bring up the subject and let it be known how he felt. Mott carried cards in his pocket with a picture of wolves and the inscription: "With your support we can bring wolves back to Yellowstone." He passed them out liberally. But while Mott was a superb advocate, he was not a coalition builder. He felt that if some particular thing was the right thing to do and had public support, it would happen. He absolutely enraged the Wyoming Congressional delegation and livestock interests by his outspoken support for wolf restoration.

Naturally, the environmental community had embraced the idea, and while they shared unanimous support for wolf restoration, how it was to be accomplished was bitterly disputed. Most greens, including the National Parks Conservation Association, the Greater Yellowstone Coalition, and especially the Audubon Society, believed in a "pure of heart" approach (let the wolves come to the park on their own or bring them in with full protection as endangered species). In the other camp, Hank Fischer from Defenders of Wildlife and Tom France of the National Wildlife Federation supported the National Park Service and the U.S. Fish and Wildlife Service (USFWS) approach for introducing an "experimental population" of wolves that had less stringent protection. Yellowstone's resource chief John Varley and I felt that the only way we could get our nose under the tent was using the experimental population designation. We felt it was necessary politically, and according to wolf experts, it would ensure a viable population of wolves and allow more flexibility in their management.

At the 1988 General NPS Superintendents' Conference at Grand Teton National Park, Bill Mott made wolves a cause célèbre by having wolf badges made that depicted a wolf face with lighted eyes that blinked and were inscribed with "The Eyes Have It." At the closing ceremony, which included a prominent anti-wolf Wyoming senator, Mott had the lights doused and almost all present turned on their lighted wolf buttons with grand smiles. But that summer, the great fires of 1988 eclipsed everything, and fires and fire aftermath consumed many of us for the next two years.

During the long march from a vague idea to wolves on the ground, many individuals stepped forward and worked tirelessly on the wolves' behalf. Renée Askins of the Wolf Fund personified the spirit of those individuals, with her disarmingly articulate and persuasive manner. By 1991, Congress appropriated money to do preliminary studies. Yellowstone's Wayne Brewster and USFWS's Steve Fritts doggedly worked on environmental process and a million details—without which, wolf restoration would never have happened. The stars and planets lined up when Bruce Babbitt became Secretary of the Interior. With the EIS work complete, and reparation assurances offered to the livestock interests, the stage was set. Secretary Babbitt personally stepped up to the plate, leading Clinton administration support, and the rest is history.

If there is a take-home lesson in all of this, it would have to be the value of patience, persistence, passion, and timing. In the fall of 1994, I transferred to Alaska as the NPS Regional Director, and several months later, from my Anchorage living room, unceremoniously watched on television as the wolves were released into Yellowstone. A closing poignant moment for me was watching Secretary Babbitt and Mollie Beattie, USFWS Director (who tragically died shortly afterward), help carry the crates of Canadian wolves up the snowy slope to the release site. I was there with them in spirit.

A Good Start


NPS

Dr. Rolf O. Peterson

Professor of Wildlife Ecology, Michigan Technological University, and Scientific Collaborator with the Wolf Project


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A Druid Peak wolf looks for a vulnerable elk in the Lamar Valley.

THE DECADE SINCE THE RESTORATION of wolves to Yellowstone has passed quickly, at least for me, and anyone with a link to the event and its aftermath is likely to have a unique set of recollections. Many will recall the blood, sweat, and tears, quite literally, involved in planning for and actually launching the wolves. For some people, the intense controversies lie in the past; for others, they still lie ahead. For researchers, there has been a tremendous effort to initiate and maintain scientific investigations. For tens of thousands of visitors, the memory of their first observation of a wild wolf will be indelible. Even seasoned wolf observers have found much that is new in the Yellowstone wolf story.

For me, beyond the fascinating wolf personalities that are threaded through the past decade, it is the prospect of indirect ecosystem effects that is most fascinating, perhaps because they were largely unanticipated. Two issues that come to mind involve plants and smaller carnivores. The first effect was introduced to me in March 2001, when my visit overlapped that of veteran elk researcher Doug Houston. After we discussed the perennial questions that focus on the "condition" of the northern range, Doug recommended that I go look at the willows up Blacktail Creek. When I started walking up this watershed from the road, I was so keen on measuring the impressive resurgence of willows that I completely missed the "Bear Closure" sign prominently posted in the pullout. I managed to backdate enough willows to convince myself that they had escaped from elk about the time wolves arrived. But my measuring was cut short by the arrival of a ranger, who pointed toward the sign and politely told me where to go (across the road, where there was no closure). No, you can't just let scientists run wild!

The second memory was just a fleeting glimpse, which I have to admit may mean nothing at all. As the Druid pack and a large grizzly fed for days on a winter-killed bison along Soda Butte Creek in March 2004, among the hoard of scavengers were *two red foxes*. These were the first foxes that I, a relative newcomer, have seen in Yellowstone, and I like to imagine that this single observation signals another important shift in the Yellowstone ecosystem—foxes squeezing in where coyotes used to roam.

My point, surely not lost on readers of *Yellowstone Science,* is that the scientific enterprise enabled by the establishment of wolves in Yellowstone far exceeds anything imagined in the planning and prediction phase of the early 1990s. Many ecosystem responses will depend on the population trend for northern range elk, which support most of the wolves. Beyond that, the questions quickly multiply, in myriad directions. That much of this unfolding story is visible to a careful observer simply driving the park roads means an unprecedented educational opportunity for visitors to Yellowstone, another unanticipated development. It is an exciting time to be alive, and I would argue that the Yellowstone wolf story has only just begun.

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A Swan Lake pack rally. Wolves howl for several reasons, one of which is social.

Ten Years of Yellowstone Wolves

1995–2005

JEANNE ROSS

Douglas W. Smith

Douglas W. Smith is Yellowstone National Park's Wolf Project leader. He holds a Ph.D. in Ecology, Evolution, and Conservation Biology from the University of Nevada at Reno. He has worked with many leading wolf biologists, including Dr. Rolf O. Peterson at Isle Royale National Park in Michigan, Dr. L. David Mech in northern Minnesota, and Dr. Erich Klinghammer in Indiana. Smith has been with the Yellowstone Wolf Project from its beginning in 1994. This spring, Lyons Press will release Decade of the Wolf *by Doug Smith and Gary Ferguson, Smith's second book. He lives with his wife, Christine, and their son, Sawyer, in Gardiner, Montana.*

Ten Years After: An Intimate Account of the Yellowstone Wolf Story

ONE OF THE LAST GREAT WILDERNESSES in the contiguous United States is located in the southeastern corner of Yellowstone National Park. This area, anchored by the Thorofare region, is farther from a road than any other spot in the continental U.S. Those who have traveled to the Thorofare know its grandeur, its mountains, its animals, its wildness. But for most of the twentieth century, few, if any, wolves traveled this vast landscape. The area's apex carnivore had been eradicated as part of a larger predator control campaign many decades ago. Was the Thorofare really wild, when what some consider the defining feature of North American wildness was absent? Many who have experienced wolf country feel it is like no other. Some believe that wolves make all the difference, and if you're open to it, you can feel the aura of wildness so intensely, it makes all other country seem dull.

Since the summer of 2001, visitors to the Thorofare area have reported hearing wolf howls virtually every night. Around dusk, when the calmness of evening sets in, the wolves let loose. From the depths of this great immensity, their ancient song rings out with amazing regularity. Canoeists and kayakers paddling across Yellowstone Lake from the north, backpackers and horseback riders coming from all directions—people hear the wolves. For some, this presence represents progress. Thorofare has recovered from an age-old wound, and this remote place has withdrawn a little farther away from civilization again.

Those echoing howls are not limited to Thorofare, but are now heard throughout the Greater Yellowstone Ecosystem (GYE). The effort to restore the howl took decades, involved many people, and culminated in the reintroduction of wolves to Yellowstone National Park in 1995 and 1996. The story of that restoration is unique, and represents an important effort to restore Yellowstone National Park to its natural conditions, a long-stated goal of the National Park Service. With the reintroduction of wolves to the landscape, one of the last great ecosystems on the planet is changing right before our eyes—an unprecedented opportunity for observation and research.

Predator Control and the Endangered Species Act

In many ways, wolves have been pawns in a larger cultural and philosophical battle. The last known wolf in Yellowstone National Park was killed in Lamar Valley in 1926. At that time, Congress sanctioned predator control in the park, and most people agreed with it. (Bears, though, were spared because of their contributions to visitor enjoyment and because most people, including park staff, didn't consider them predatory to any significant extent.) In part, predator eradication was "how the West was won;" the range was made suitable for livestock through predator removal.

The National Park Service ended the systematic killing of predators in 1933, but it wasn't until 1973 that Congress passed the Endangered Species Act (ESA), making restoration of endangered species to suitable habitat the law. This was a policy reversal for the federal government, from sanctioned eradication to restoration. The Rocky Mountain wolf (*Canis lupus irremotus*) was listed as endangered under this act in 1973, and in 1978 the entire species *Canis lupus* was listed as endangered in the lower 48 United States, except in Minnesota. The ESA was evidence that times were changing. Public tolerance for predator control was waning. Wolf restoration has, in large part, been about this change in attitudes. The future of wolves will depend on the same.

In 1980, the first U.S. Fish and Wildlife Service (USFWS) Northern Rocky Mountain Wolf Recovery Plan was signed, and it was updated in 1987. The goal was 30 breeding pairs for three successive years in three designated areas of Idaho, Montana, and Wyoming. Northwest Montana already had wolves through natural immigration from the Canadian Rockies, so the strategy was to nurture wolf populations there through protection, and reintroduce wolves from Canada to Idaho and Yellowstone. Upon achievement of the recovery goals, wolves would be removed from the endangered species list and turned over to the respective states for management, assuming that the states had federally-approved management plans in place (*see inset, "Wolves as an Endangered Species: Delisting"*).

In 1988, Congress directed the NPS to study the potential impacts of wolf reintroduction to Yellowstone. The *Wolves for Yellowstone? A Report to the U.S. Congress* studies were published in 1990. In 1991, Congress finally authorized funds and directed the USFWS, in consultation with the NPS and the U.S. Forest Service, to develop an Environmental Impact Statement on wolf reintroduction to Yellowstone National Park and central Idaho. The EIS was signed in June 1994, officially endorsing the restoration of wolves to Yellowstone.

In October 1994, Michael K. Phillips arrived in the park to be the leader of the Yellowstone Gray Wolf Restoration Project (*see inset, "Yellowstone Wolf Project Staff, 1995–2005"*), a position he held until May 1997, when the reintroduction phase of the wolf recovery program was complete and a monitoring plan was in place. Phillips then accepted a job with Turner Enterprises in Gallatin Gateway, Montana, where he still works as the Executive Director of the Turner Endangered Species Fund. At that time, I stepped up from wolf biologist under Phillips to Wolf Project Leader. Prior to his work in Yellowstone, Phillips was the coordinator of field projects for the Red Wolf Recovery Program in the southeastern United States. That program successfully restored the red wolf to parts of its former range. Phillips was also involved in another successful wolf reintroduction program after he left Yellowstone:

NPS/JIM PEACO

The first wolf was brought to the Crystal Creek acclimation pen by (left to right): Yellowstone Gray Wolf Restoration Project Leader Mike Phillips, Maintenance Foreman Jim Evanoff, U.S. Fish and Wildlife Service Director Mollie Beattie, Yellowstone Superintendent Mike Finley, and Secretary of the Interior Bruce Babbitt.

the USFWS's reintroduction of Mexican wolves to southeastern Arizona and southwestern New Mexico. Along with Yellowstone's program, these are the other main successful wolf reintroduction projects yet attempted.

Wolf Reintroduction

By 1995, more than 20 years after listing, wolf reintroduction was ready to begin. This is not to say the battle over wolves subsided. Despite some strong opposition, primarily from the local ranching and political communities, the USFWS and Canadian wildlife biologists captured a total of 31 Canadian wolves by darting them from a helicopter and shipped them to Yellowstone. Fourteen came from Alberta in January 1995, and 17 from British Columbia in January 1996. An additional 35 wolves from the same locations were shipped to central Idaho's Frank Church–River of No Return Wilderness. The Canadian source areas, situated along the Rocky Mountains, were similar to Yellowstone in terrain and prey type. In addition to the Canadian wolves, 10 wolf pups from northwest Montana (caught after their parents were killed in a control action due to livestock depredation) were released in Yellowstone in late winter 1997. The reintroduction of these pups was not very successful, as they spent the winter in a pen rather than learning in the wild. They were also released after one of the most severe winters on record, which made hunting for ungulates difficult; eight of the 10 were dead within four months. As of late 2004, the other two were still alive as part of the Nez Perce pack.

Release strategies differed between Yellowstone and Idaho. In Yellowstone, wolves were acclimated as family groups (packs) in pens and "soft" released; in Idaho, the USFWS "hard" released wolves, as individuals, directly onto the landscape. Part of the reason for the different techniques was the disparate nature of the recovery areas. The areas of Yellowstone where the wolves were

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Wolves as an Endangered Species: Delisting

NPS/JIM PEACO

When the first shipment of wolves entered the park in 1995, many people, including Gardiner School students, lined the road near the Roosevelt Arch to watch and cheer.

ONE OF THE GOALS of wolf reintroduction was to restore wolf populations so the species could be removed from the endangered species list. Originally, the U.S. Fish and Wildlife Service (USFWS), the agency responsible for endangered species, determined that having 10 breeding pairs in each of the three recovery areas (Yellowstone, central Idaho, and northwest Montana) for three successive years, would suffice to indicate a viable population and qualify wolves for delisting. Recently, the USFWS softened these criteria to 30 breeding pairs for three successive years with a relatively equal distribution in Idaho, Montana, and Wyoming combined.

"Breeding pair" has a very specific definition for the delisting criteria. To count as a breeding pair in a given year, an adult male and female wolf must raise at least two pups that survive until December 31 of that year. The male and female do not have to be the pups' parents; they just need to be with the pups. Many packs do not meet these criteria each year. For instance, if an adult male or female dies, a pack may not breed at all. In 2002, Idaho had 284 wolves in 24 packs, but only nine of the packs met the criteria. In addition, some packs may not count toward delisting simply because their composition is unknown.

The northern Rockies had 30 breeding pairs that met the delisting definition for the first time in 2000. The wolf population has grown since then, with 34 breeding pairs in 2001, 49 in 2002, 51 in 2003, and 111 in 2004. Because wolves have had adequate prey and protection from humans—the key conditions for wolf survival—wolf numbers are above the minimum needed to delist them. However, the other requirement for delisting is that the states involved have federally-approved wolf management plans in place. Although Idaho's and Montana's plans have been approved, Wyoming's has not. Wyoming's plan, as submitted, designated wolves as predators outside parks and wilderness areas. This is problematic because people who kill animals designated as predators are not required to report those kills. Thus, assigning wolves a predator designation would preclude the population monitoring required following a species' delisting under the ESA, and the USFWS rejected Wyoming's plan as unmanageable—primarily because the plan would make it impossible to determine when or if the wolf population fell below the minimum level of 15 packs in each state.

The State of Wyoming has contested the rejection in court; hence, the delisting process is being delayed by litigation. The USFWS believes their delisting approach is sound, and that wolf management will be turned over to the states in the future. At the time of this writing, the USFWS is in the process of transferring day-to-day management of wolves to the states that have approved management plans—Idaho and Montana. This will reduce USFWS involvement, paving the way for eventual delisting.

NPS

Deb Guernsey

NPS/KERRY GUNTHER

Deb, Dan, and Doug

NPS

Dan Stahler

NPS/DOUGLAS SMITH

Mike Phillips

NPS/DOUGLAS SMITH

Kerry Murphy

NPS/DOUGLAS SMITH

Rick McIntyre

Yellowstone Wolf Project Staff, 1995 2005

THE DESIGNERS OF THE WOLF RESTORATION PROJECT deserve credit for preparing the way, reaching out to and informing the public, and giving the wolves a solid structure within which they could thrive. Wayne Brewster, retired Yellowstone Center for Resources Deputy Director, is considered one of the main architects of the entire wolf reintroduction effort (the Yellowstone project was Wayne's third job in 20 years related to wolf recovery in the American West), as is noted biologist and Yellowstone Center for Resources Director John Varley.

There is also a dedicated team of professional scientists whose company I've been privileged to keep. Mike Phillips was project leader from the beginning until May 1997, when he accepted a job with Turner Enterprises in Gallatin Gateway, Montana, where he still works as the Executive Director of the Turner Endangered Species Fund. I started as the project biologist in 1994, taking over as project leader after Phillips.

Kerry Murphy, who had been working with cougars, became biologist after me, 1998 through 2000, and a year later the position was filled by Dan Stahler, who had worked with Mike Nelson and Dave Mech in Minnesota trapping wolves. Dan first came to Yellowstone to help with wolf den research and went on to work on various winter studies. He gained his Master's degree through the University of Vermont working with world-renowned raven researcher Bernd Heinrich, examining the relationships between wolves and ravens in Yellowstone. He now spearheads the project's scavenger research and GPS collar work.

Debra Guernsey, the project's biological technician, started out as one of the very first volunteers in April 1995 and worked her way up through the ranks, giving her all to this effort. Rick McIntyre works year-round for the Wolf Project, part of the year as a biological technician, and part as a volunteer. He has helped visitors and staff better understand wolves since 1994. In addition, there has been an ongoing stream of dedicated volunteers, too numerous to list here, but whose contributions have been invaluable.

released were less remote than those of central Idaho, so the wolves had less room to safely wander after release. The area where wolves were released in Idaho allowed more wide-ranging movements. In Yellowstone, acclimation was chosen because it has been known to curtail wolf movements and break their homing instinct. The Yellowstone road system and availability of park staff also made acclimation pens accessible, and therefore more feasible than in Idaho.

In 1995, the first three groups of wolves were placed in pens on Yellowstone's northern range at Soda Butte, Rose Creek, and Crystal Creek (Figure 1). In 1996, four groups were placed in pens, two of which were not on the northern range: one at Nez Perce Creek, and one on the southeast arm of Yellowstone Lake. In each pen was a group of wolves caught together in Canada. When a breeding pair could not be captured, Yellowstone Wolf Project staff "match-made" a pair in the pen, creating a pack. An adult male and female in a pen will almost always get along, and adding pups of either sex rarely causes problems. Introducing same-sexed adult wolves in pens, however, almost always causes fights or deaths. The Rose Creek pack, led by #9 and #10, was an example of a match-made pack; the Druid Peak and Lone Star packs were others.

The wolves were held 10 weeks, a period of time that Yellowstone National Park biologists estimated would be adequate for acclimation. Over two winters, Wolf Project and other park staff visited the 41 penned wolves minimally—twice a week to feed them road-killed deer, elk, moose, and bison. This allowed us to learn their characteristics and personalities well, which facilitated identification after release—a rare and relishable opportunity for wild wolf studies. Rangers patrolled the pens continuously from afar, yet close enough to protect the wolves from ill-willed human intent.

Wolf researchers traditionally name wolf packs for geographic features near where they live. Because these wolves didn't live anywhere yet, Wolf Project staff named them after

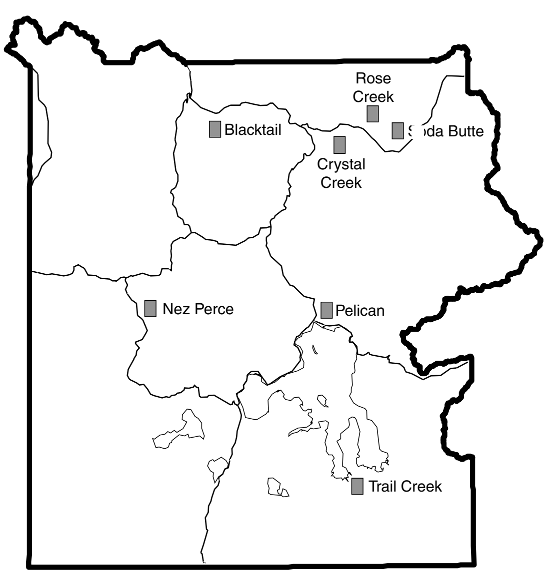

Figure 1. Location of wolf acclimation pen sites.

NPS/JIM PEACO

A Nez Perce wolf is released from the shipping container into the acclimation pen.

their pen sites. Since then, wolf packs have sometimes been named to commemorate someone important to wolf reintroduction. Pack names change when a pack no longer lives near the area after which it was named and all of the original members are dead. We numbered and radio collared all the wolves so we could identify individuals for study and management, but we did not give individual animals official names. Some have criticized us for this decision, but we did not want to humanize the wolves. Grizzly bears in Yellowstone are not named for the same reason. Some people informally name certain bears and wolves anyway, but apart from their collars, the wolves were autonomous from humans after release, except in extraordinary circumstances.

Release from the Pens

No one knew what would happen when we opened the gates to the pens. We assumed the wolves would run out immediately once they glimpsed freedom; people speculated on how far they would go before they stopped running. Cartoons in local newspapers had them "making a run for the border."

That did not happen. A video camera mounted in a tree at the Crystal Creek pen ran for about an hour when that pack was released. The alpha female, #5, approached and looked out

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Everyone expected the wolves to run toward Canada after release, but most wolves exhibited restricted movements.

the wide-open door six times in about 20 minutes, but never got close to it. The other wolves avoided the door. It took 10 days for the Crystal wolves to finally leave, but in the meantime, they snuck out at night, explored, and then slipped back in during the day. The Druid Peak pack, probably the best-known pack today (*see inset, "Wolf Watching"*), took the longest to leave—12 days—even though we opened two opposite sides of the pen.

The Soda Butte pack left the pen when the gate was opened, but only far enough to chew through the ropes on two deer carcasses that Wolf Project staff had tied to a tree. Then they dragged the carcasses back into the pen. This reluctance to leave the pens was surprising, but we designed subsequent releases so that the wolves would leave the pens when we were absent, thereby eliminating the added stress of human presence and possibly deterring widespread post-release movements.

However, part of the Nez Perce pack left immediately, as #27, the instigator of this rapid departure and of many other wide-ranging movements for her pack, took off with her three daughters. They fled at a pace that was blistering even by wolf standards. From near Old Faithful they traveled to Red Lodge, Montana, via a circuitous route in a few nights. At Red Lodge, the three siblings had had enough, and quit following their mother. Either Interstate 90, near Reed Point, Montana, or the new litter

Wolf Watching

NO ONE PREDICTED that the wolves would be so visible after reintroduction; in fact, some biologists thought the wolves wouldn't be seen at all. Few people catch even a fleeting glimpse of a wild wolf in other areas with wolf populations. In Michigan's Isle Royale National Park, a small island park compared to the vast Yellowstone, it is possible to hike 500 miles over the course of a summer and see but a single wolf. In Yellowstone, approximately 20,000 people see a wolf in the park each year. It is estimated that more than 153,000 different people have seen wolves in the park since restoration, and every day since February 8, 2001, at least one visitor has sighted a wolf in the park. Yellowstone National Park is the best place in the world to view wild wolves.


NPS/JIM PEACO

Wolf watching is a popular pastime in Lamar Valley.

Wolves this visible have been a benefit to some and a pleasure to many. The people who come to see wolves generate economic activity by eating out, staying in hotels, purchasing merchandise, and buying gasoline from local establishments. Some wildlife safari companies have formed, and others have expanded because of the interest in wolves. Groups from Italy, Japan, Norway, Sweden, Russia, South Africa, and Portugal, to name a few, have come to see wolves. Groups from England and Germany sponsor Yellowstone wolf-watching trips every year, sometimes two trips each. In the past, winter was not considered to be a prime wildlife-viewing season in the park, but now it is. Wolves have benefited local economies—just how much is currently being studied by the University of Montana.

On any summer morning or evening, 200 or more people may assemble in Lamar Valley to try and see wolves. Numbers are also growing in winter, when it is not uncommon for 50 or more people to gather along the roadside to "wolf watch." Wolf Project staff patrol roadsides, keeping people at a safe viewing distance. Providing people another opportunity to experience wildness first-hand in Yellowstone is one of the remarkable achievements of the reintroduction program that no one could quantify as another reason for wolf restoration.

The devoted "wolf watchers" and others learn to recognize individual wolves and learn their histories. Internet websites have blossomed to carry wolf news to people who are not in the park often enough to keep up with developments. Fan clubs have developed for different wolves; mourners exchange condolences when a favorite dies. Public interest in these wolves, and the emotional connections that many people develop for these wild animals, is intense, and may suggest that many people today desire personal experience with something "real"—something not orchestrated or mediated. In Yellowstone, people experience the wolves right in front of them, doing things some people may not like, or that are boring because there is no editor to clip out the "dull" parts. The scenarios may not always have "happy endings," but they are real, and partly for this reason, the wolves are loved by many.


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Although the plan called for three to five years of Canadian wolf releases, only two years were needed.

to which #27 gave birth finally caused her to stop; she denned alone near Nye, Montana. This settled her down only briefly. Our unsuccessful attempts to capture #27 and her new litter in order to relocate them to Yellowstone had them on the move as soon as the pups were able.

A year later, USDA Wildlife Services killed #27 after she preyed on livestock near Dillon, Montana, west of the park. This brought an end to a wolf whose wide-ranging movements were what many researchers had expected would characterize the reintroduction of wolves to Yellowstone. Three (#26, #29, and #30) of the four yearlings released from the Nez Perce pen survived to form new packs, breed, and contribute to the restoration. Wolf Project and USDA Wildlife Services staff captured wolf #48, the last surviving pup from the Nye litter, near Nye in February 1997 and relocated her to Yellowstone, where she is now the alpha female of the Nez Perce pack.

Number 27's mate, #28, and a male pup stayed in the pen until the day after we opened the gate, a delay that prevented the pack from reuniting. They attempted to follow #27's scent trail, but stalled, then split up. Number 28 wandered widely for about eight months and was later found dead from a gunshot wound, floating in the Madison River near Three Forks, Montana.

The Rose Creek pack also wandered widely. Initially, the pack was made up of three wolves; #9 and her daughter, #7, were introduced to male #10 in the pen (*see inset, "Important Wolves"*). But upon release, #7 traveled alone until January 1996, when she joined a lone male from the Crystal Creek pack, #2. This was the start of the Leopold pack, the first naturally forming wolf pack in Yellowstone's new wolf era. The name Leopold was used to commemorate the late conservationist Aldo Leopold, who suggested in 1944 that wolves be conserved in Yellowstone.

The Rose Creek pair traveled widely and eventually had a litter near Red Lodge. Around this time, #10 was shot by Red Lodge resident Chad McKittrick, who was convicted of killing a threatened species, and possessing and transporting its remains. Number 10's death precipitated the USFWS's decision to capture #9 and her litter, as it is rare for a female to raise pups alone, especially in unfamiliar country, and the pups represented 40% of the Yellowstone wolf population at the time. Wolf Project staff transported the wolves to the Rose Creek pen, where they remained until the pups could contribute to their own survival. This gave the Rose Creek pack a new start and led to #9's pairing with another Crystal Creek disperser, #8, who helped raise #9's eight pups.

We varied the release strategy as we learned from the wolves, modifying as the program continued. Several packs were acclimated at one site, and then moved to another for release (e.g., the Chief Joseph and Lone Star packs). Female #36 was released near Lone Star Geyser Basin, the location of some of the hottest springs in the park, in what appeared to be a successful release. However, shortly after she left the pen, she was scalded in a hot spring and did not recover. It took her 10 days to die, and at the time we were unaware of what had happened because her mate was in the area with her every time we located them, so we did not intervene.

The plan to restore wolves to the GYE via pen acclimation worked. Except for the Nez Perce pack, the goals of acclimation—to reduce post-release movements and maintain familial ties between wolves—were achieved. The plan called for three to five years of Canadian wolf releases, yet only two years were needed in Yellowstone and Idaho. There was some debate over whether even a second year of reintroductions was necessary, but to increase genetic diversity, wolves were brought from Canada a second year. At this point, one of the favorite "soundbites" of the project popped up: we were "ahead of schedule and under budget." Everyone liked that.

In retrospect, even the Nez Perce releases could be characterized as successful, because the pack's disintegration produced roaming wolves that paired with other lone wolves and formed new packs. Number 29 started the Gros Ventre pack, #26 the Washakie pack, and #30 the Thorofare pack. Including reproduction from the original Nez Perce pack, these wolves produced seven litters of pups—a significant contribution to wolf restoration in the GYE.

As it turned out, territorial expansion outside the park, such as that of the Nez Perce pack, played a role in how wolf monitoring and management is handled by the agencies cooperating in wolf reintroduction. The U.S. Fish and Wildlife Service was the lead agency for wolf reintroduction, no matter where wolves traveled or settled. Yellowstone National Park hired two people to monitor and manage wolves inside the park, but when wolves left the park early on, there was no nearby USFWS staff to track them. So from 1995 through early 1999, Wolf Project staff followed wolves wherever they went. We made numerous trips to Red Lodge, Jackson, Dillon, Sunlight Basin, and most often, Paradise Valley. In 1999,

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Rose Creek wolf #9, second from the front, was especially important in repopulating the Greater Yellowstone Ecosystem.

Important Wolves

MOST WOLF STUDIES begin with an existing population, making key contributions by individual wolves difficult to identify. Each individual wolf's role is diluted by those of many others, making it harder to determine if any one wolf exerts uniquely strong effects. This was not the case for wolf reintroduction in Yellowstone. Because there were no wolves in the park, and all of the reintroduced wolves were marked, it was easy to identify strong individual effects, and there were many.

Rose Creek wolf #9, who arrived with the first shipment of wolves from Canada, was the first wolf to produce a sizable litter—eight pups. These pups were extraordinarily important, in that they later dispersed and established new packs at a critical time. Of these wolves, #21 went on to be alpha male of the Druid Peak pack, producing many litters and becoming one of the most visible Yellowstone wolves. Number 18, his sister, took over the Rose Creek pack from her mother and went on to have 32 pups. Their sister, #16, founded the Sheep Mountain pack north of the park. Number 9 produced litters through at least 1999. At that time, we estimated that 79% of all wolves in the park were related to her—certainly a key contribution!

The original alpha female in the Crystal Creek pack, #5, was noteworthy because she moved her pack from Lamar Valley after the Druid Peak pack moved in, establishing a pack in central Yellowstone that provided a stepping stone for other pack formation. Number 7, who came from Canada with her mother, #9, gave birth to 34 pups, more than any other wolf. Her offspring helped establish at least three packs. The Soda Butte pack's alpha female, #14, established a wolf outpost deep in Yellowstone that opened the way for wolves south of the park in the Bridger-Teton/Gros Ventre area. Number 14 died while trying to take down a moose in 2000.

Males also played key early roles. Male #2 paired with #7, and they occupied Blacktail Deer Plateau for eight years (1996–2003). The Leopolds, as this pack came to be named, had one of the most stable territories and pack compositions in the park. After #9 of the Rose Creek pack lost her mate and was re-penned with her eight pups, #8 arrived and adopted the pups. He later mated with #9, and then with her daughters, #16 and #18. Number 8 remained alpha male of the Rose Creek pack until 2000. Shortly after his death, a long, slow decline began for the Rose Creek wolves.

The 1996 reintroduction also produced several key wolves. Female #42 had 32 pups and was mate to #21. She died in January 2004, at age eight, the last original reintroduced wolf to die. Number 42's sister, #40, was very aggressive, attacking many coyotes and other wolves, and was killed by her packmates. Female #27 was notable because she traveled widely, and one wolf in her 1996 litter became especially important: #48 helped establish the Nez Perce pack, has given birth to at least 23 pups, and is quite possibly still the pack's alpha female at almost nine years old.

The next generation of important wolves came from a litter born to the Druid Peak pack in Lamar Valley in 1997. Although wolves #104 and #107, both males, dispersed from the park, #103, #105, and #106 anchored the next generation of northern Yellowstone wolves. Number 103 formed the Agate Creek pack, #105 the Buffalo Fork pack, and #106 the Geode Creek pack, where she is still the breeding female.

Certainly, there are other important wolves. Number 302 slips in and out of the Druid Peak pack now that #253 is no longer around, breeding with its females, and appears to have permanently joined them. Sisters #151 and #152, daughters of #7, formed and still lead the Cougar Creek and Swan Lake packs, respectively. They have produced 30 pups between them. Number 44 and #126, both of the Soda Butte pack, are surviving second-generation wolves, still deep in the heart of Yellowstone. We can barely hear the radio collar on #44, only when we are directly above her. Born in 1996, she is, along with #48, one of the older wolves in the population. Number 126 has kept us in touch with the Delta pack, often being the only collared wolf in that pack.

the USFWS hired new staff and partnered with the Turner Endangered Species Fund and, later, the states of Montana and Idaho, to expand its operations into the GYE outside the park. Yellowstone National Park staff no longer monitor or help manage wolves outside the park.

Territoriality and Population Expansion

Wolves are territorial mammals that establish firm boundaries that they defend against other wolves. A family of wolves, a pack, which is the basic structure of wolf society, defends these territories. Few other mammals live and operate in such a way. Many mammals are solitary, and a group typically consists of a female with young, not an extended family. Numerous factors combine to determine how packs are organized and how big they get. One factor is the size of their primary prey—the larger the prey, the more food is available to eat, which leads to slightly larger packs. Wolves that live on deer tend to have packs of five to seven wolves, whereas wolves that prey on moose or bison tend to have packs of more than 15 wolves. In Yellowstone, with wolves primarily feeding on mid-sized elk, the average pack size during the first 10 years has been 11 wolves, but the range of pack sizes was 2–37.

Wolf pack composition is another factor that guides how packs operate and territories are defended. Simple packs are made up of a breeding pair with pups; a complex pack is a breeding pair with several generations of offspring. In complex packs, the experience level of the wolves is high. Sometimes, in addition to the breeding wolves, there are yearlings as well as two- or three-year-old wolves in the pack. In this case, not every task undertaken by the pack has to be accomplished by the breeders or dominant wolves (historically, these wolves have been referred to as the alphas). Older, subordinate wolves are very capable of contributing their effort. For example, when a pack with breeders and pups attempts to bring down an elk, the adult wolves have to do all the work, as the pups know nothing about this very risky job. In a complex pack, several animals possess this knowledge, so achieving the kill is not completely up to the breeding wolves. We have seen cases where the best hunter is a non-breeding subordinate: wolf #106, when she lived in the Druid Peak pack, was a prime example.

Most wolf packs in North America are probably simple packs—breeders or alphas with pups. This is due to the unstable nature of wolf packs in environments where humans kill wolves. The vast majority of wolf packs in North America are in Canada and Alaska, where wolves are hunted. In some cases, they are hunted very hard, which results in packs that break apart, preventing them from retaining older wolves and accumulating experience.

Unlike other packs in North America, most Yellowstone packs are complex and very stable. Six packs that formed in 1995 and 1996 still exist: Crystal Creek (now called Mollie's, after the late Director of the USFWS, Mollie Beattie), Delta, Rose Creek, Druid Peak, Leopold, and Chief Joseph. As of late 2004, 17 of the 19 packs that had formed in the park were extant (Table 1). This stability and structure has important

Pack	Year Formed	Currently Exist?	Tenure (yrs)	Comments
Agate Creek	2002	Yes	3	
Bechler	2002	Yes	3	
Biscuit Basin	2004	Yes	1	
Buffalo Fork	2002	Unknown	1	Killed by other pack
Chief Joseph	1996	Yes	9	
Cougar Creek	2001	Yes	4	
Crystal/Mollie's	1995	Yes	10	
Druid Peak	1996	Yes	9	
Geode Creek	2002	Yes	3	
Gibbon Meadows	2004	Yes	1	
Leopold	1996	Yes	9	
Nez Perce	1998	Yes	7	
Rose Creek	1995	Yes	10	Moved north out of park by other pack
Slough Creek	2002	Yes	3	
Soda Butte/Yellowstone Delta	1995	Yes	10	
Specimen Ridge	2004	Yes	<1	Alpha male, probably dead
Swan Lake	2000	Yes	5	
Thorofare	1996	No	2	Killed by other pack
Tower	2001	No	2	Alpha male died
19 Packs		**79%**	**mean = 4.9 years**	

Table 1. Count of all wolf packs that have formed and their tenure since reintroduction.

implications for how wolves operate in the Yellowstone area and in their own packs. Wolf Project staff have been able to detect some of the differences as the structure of packs has matured from simple to complex. In simple packs, the alpha wolves dominate leadership decisions (when to travel, where to go, what to hunt, who hunts). In complex packs, it is less clear who is calling the shots, as many wolves participate in pack activities. This makes the decision-makers harder to identify.

In the beginning, Yellowstone's mostly simple wolf packs established territories relatively rapidly after release (Figure 2), but there was some confusion and conflict as they divided land among them. When the Druid Peak pack was released in 1996, they had no territory, but they had a territorial mentality, having come from British Columbia where wolves fiercely contest their space. The Druids roamed the landscape, engaging in fights with two other packs that resulted in two wolf fatalities and at least two other injuries. They eventually evicted the Crystal Creek wolves from their territory in Lamar Valley, an event that has had long-term consequences. The Druid Peak wolves still reside in Lamar Valley, while the Crystal Creek pack fled to Pelican Valley, in the middle of the park, where they still reside and were renamed Mollie's pack (Figure 3).

Following these early—and not unexpected—skirmishes, established territories were quickly defined. They varied greatly in size, ranging from a tiny 53 square miles (Cougar Creek) to a gigantic 553 square miles (Chief Joseph). Packs occupying

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The Slough Creek pack chasing the Druid Peak pack.

the prey-rich northern range tended to have smaller territories (average = 113 square miles), while packs where prey was less abundant had larger territories (average = 340 square miles). Such disparity makes it hard to estimate an "average" pack territory. Some of the variability is probably also due to the migratory behavior of seven of the eight elk herds that use the park. Most elk leave the park in the winter, strongly affecting wolf movements and territory size.

Mollie's pack ranges widely in winter, following major elk migrations, but not in summer, when Pelican Valley is a

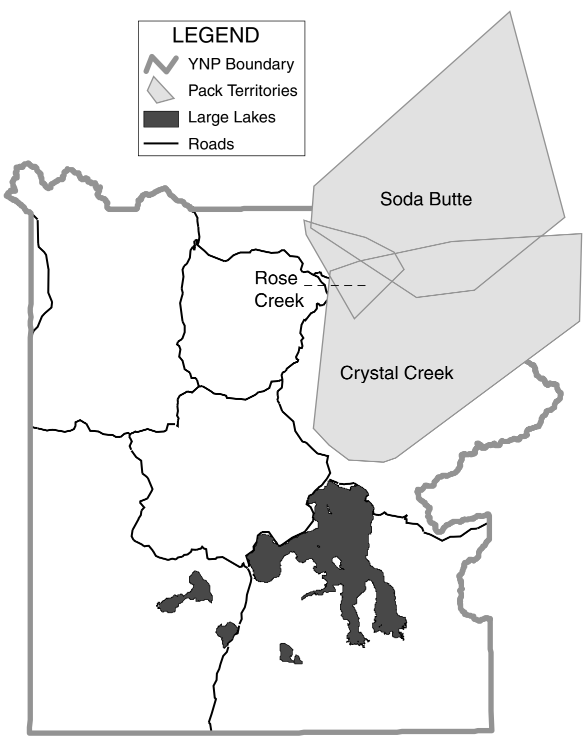

Figure 2. The 1995 Yellowstone National Park wolf territory map included three packs. Notice the large territories and large overlap between packs.

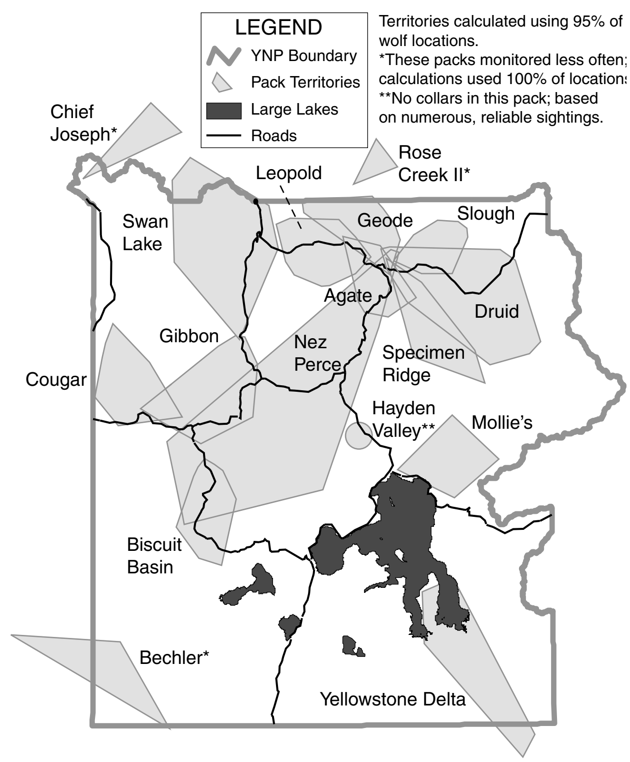

Figure 3. The 2004 wolf territory map included 16 packs. Notice the smaller territories with less overlap, although some packs overlap a great deal.

paradise for wolves. The elk-less winters (almost all elk migrate out of Pelican Valley) force the wolves to either leave the park in search of elk or prey upon bison, which are far more dangerous for wolves to kill. As soon as elk move because of accumulating snow, usually around early December, Mollie's pack moves too. While their departure is predictable, their direction is not: they have been detected in Hayden Valley, the North Fork of the Shoshone River, and the east side of Yellowstone Lake searching for prey. Some bison remain in Pelican Valley, where they tend to be invulnerable to wolf attack in early winter. In late winter, though, Mollie's pack returns from its wanderings and focuses on the winter-weakened bison. Epic battles can ensue, with both bison and wolves suffering casualties. The wolves kill enough bison to last them until spring, when elk migrate back into the valley.

The Soda Butte pack (now called the Yellowstone Delta pack) and the Chief Joseph pack also travel widely in winter, following migrating elk. The Nez Perce wolves have begun wandering during the last few winters, as have the Druid Peak wolves on occasion—always around the time when elk migrate from summer to winter ranges. These wanderings have produced clashes between resident and trespassing packs. One Druid wolf (#253) still limps from such an encounter.

The Bechler region was one of the last places in the park to be reoccupied by a pack of wolves. Because typically harsh winters prevent year-round occupation by elk or moose, wolves have had trouble living there. Four wolves were found in Bechler, however, during the summer of 2002, and have remained there during the last two mild winters. A return to harsher winters may move these wolves out of the park in search of migratory prey. Another tough place in the park for wolves to establish a year-round territory is the Mirror Plateau, although they do use it in the summer when elk are at high elevations.

Since they drove out the Crystal Creek pack, the Druid wolves have aggressively maintained their territory in Lamar by killing four more interlopers and wounding several others. Eventually, they killed their own alpha female, #40. Their numbers and strength have dwindled, and long-time alphas #21 and #42 have died, so the pack's future is uncertain, but Lamar Valley will continue to be a wolf stronghold because of its rich prey. As of this writing, the Slough Creek pack has made significant overtures into Druid territory in a possible takeover of the Lamar.

Pups

One reason for the tremendous success of the reintroduction program was the wolves' early and successful reproduction (Figure 4). Four of the seven reintroduced packs bred in the pens, leaving them with a pregnant female upon release. This was completely unexpected. Most wolf biologists had predicted that the wolves would be too stressed to show natural breeding behavior while confined, so the initial plan had scheduled acclimation and release to occur before February in order to avoid the breeding season. However, litigation ended up delaying the capture and transport of the wolves to pens, moving acclimation from early to mid-winter, and release from before to after the wolf-breeding season. Combined with wolves' natural fecundity, the fact that they bred in the pens jump-started the population, giving it an immediate foothold. No such beginning was recorded in Idaho, where wolves were not held in captivity during the breeding season.

In the Rose Creek pack, #9 gave birth under a tree (she didn't have time to dig a den) outside Red Lodge, Montana. These pups took advantage of their first-born status and went out to settle the Yellowstone landscape. In 1999, our genetic

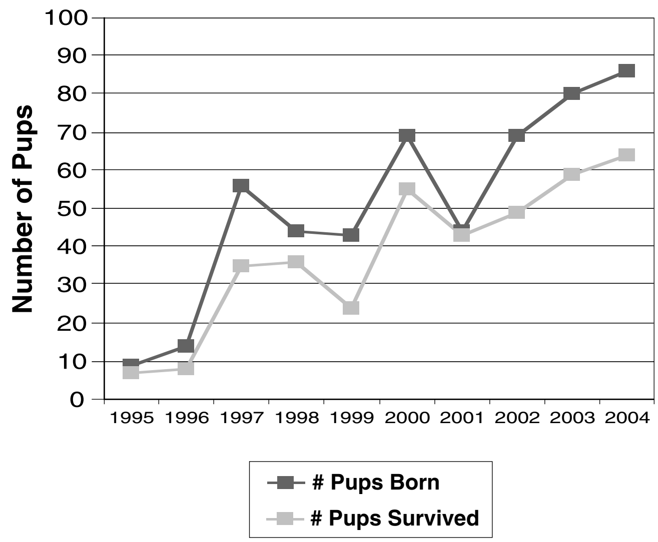

Figure 4. Number of pups counted in May and June (born) versus November and December (survived). Pup survival was typically 75–80%, except in 1999, when a likely parvovirus outbreak reduced pup survival to 60% (40% on the northern range, where the outbreak occurred).

ISAAC BABCOCK

Wolf pups are born in April. Since reintroduction, pups have been born progressively earlier in April, probably because of Yellowstone's lower latitude compared to Canada.

studies found that 79% of all wolves in Yellowstone National Park were related to #9. Wolf #21, who was observed by thousands of visitors to Lamar Valley, was from this litter. From the other 1995 litter, only one pup was known to have survived (for four years), born to #14 in the Soda Butte pack. This pup, #24, stayed with her natal pack for three years—fairly long compared to most wolves. She eventually dispersed south and started the Teton pack near Jackson, Wyoming.

These two 1995 litters were born into a nearly wolf-less landscape where, when the wolves were old enough, opportunities to start new packs were abundant. Young wolves typically encounter a sea of other wolf packs and territories, making breeding vacancies tough to come by, and a young wolf may die trying to find one. But these first Yellowstone pups merely had to move next door.

Although breeding vacancies were available in those first years, mates were largely not. Consequently, pups bred in the wild. This had previously been recorded only in captive wolves, but the circumstances under which one would predict such an occurrence in the wild were present in Yellowstone: abundant food, available territories, and few other wolves with which to breed. In 1996, female pup #16 (from #9's litter) bred with #8. Then in 1998, in the Dome Mountain area north of the park, male pup #165 bred #16, probably for the same reason—a shortage of mates.

Wolves also began having multiple litters per pack. Wolves are typically monogamous, having only one litter per pack. However, when conditions permit (typically when there is abundant food), more females breed. Genetic analysis has shown that multiple females bred within packs, not multiple males. Another condition contributing to multiple litters was the presence of several unrelated wolves in the same pack. Because wolves avoid inbreeding, and most members in a pack are related, the adult male breeder usually has only his unrelated mate to breed with. This limits the number of litters per pack. Match-made packs in pens changed this dynamic, and produced a few situations in which the alpha male was not related to any of the females in the pack. As a result, he bred with all the females. In 2000, this circumstance produced the spectacular number of pups for the Druid Peak pack—21 in three litters, catapulting their pack size to 37 wolves and making them one of the largest wolf packs ever recorded. The Rose Creek, Chief Joseph, Geode Creek, Swan Lake, and Leopold packs also produced multiple litters, but most only did so once. Most other packs in Yellowstone had only one litter per year, averaging, at first count in May and June, 4.7 pups. As of 2004, there were 106 documented litters of pups born in the park since reintroduction.

Survival and Mortality

Two key parameters of any animal study are estimations of survival and mortality. They reveal a great deal about how well a population is doing, and what management actions may be necessary to increase or curtail population growth. Initially, the Yellowstone wolves did well because mortality was low and survival was high. This was unexpected. Most biologists felt, as many studies indicated, that the mortality rate for reintroduced wolves would be high, and from many causes.

Overall wolf survival during the first eight years was about 80%, and survival rates increased with age: 60% for pups, 70% for yearlings, and 80% for adults. Experience seems to keep wolves alive, to a point; survival tended to increase to middle age, and then decrease as the wolves grew older. Males and females had equal survival rates. These data represent only information gathered from radio-collared wolves (*see inset, "Radio Collars"*). Pup survival data is not collected until after collaring, which occurs at between eight and nine months of age.

The average age at death for a wolf in Yellowstone is 3.4 years old. If a Yellowstone wolf lives past five years old, it is doing well. The oldest was male #13, who died at 11.9 years. The longest-lived females were #7 and #42, who lived to be eight years, but #44 and #48 are still alive at eight. Females, on average, have lived four months longer than males.

Research has shown that wolf populations that experience mortality of less than 30% per year tend to grow. If mortality rises much higher than that, the population will decline. Wolf survival has been high enough, and mortality low enough, that wolf population growth since reintroduction has been positive (Figure 5). From 1995 to 1998, when the Wolf Project was bringing wolves into the park, the annual population growth rate was 40–50%. From 1998 to 1999, however, the growth rate was –14%. Although pup survival is normally >75%, in 1999, pup survival was only 60% (40% on the northern range), which was the lowest annual survival rate since reintroduction. Parvovirus, a disease that may be transmitted to wolves

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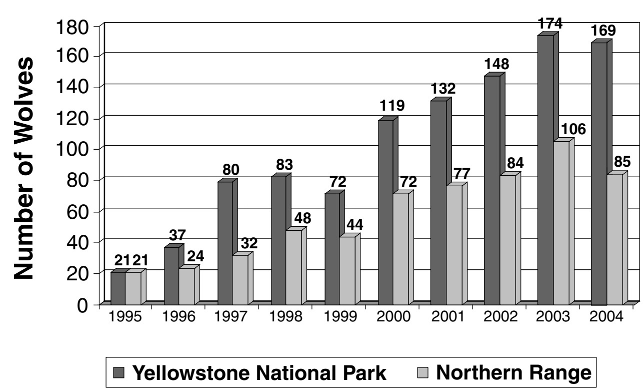

Figure 5. Initially (1995–2000, except for 1999), wolf population growth was rapid, about 40–50% per year. Growth slowed to 10–15% in 2001–2004, and to 0% in 2004. The negative growth in 1999 was likely due to disease (canine parvovirus).

Radio Collars

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Helicopters help Wolf Project staff to locate and dart wolves with tranquilizers in preparation for capture and collaring. All wolf monitoring and research in Yellowstone depends on maintaining a marked population of wolves.

A WOLF'S RADIO COLLAR is similar to a standard dog collar, but a little heavier because a tracking device is attached where a dog's tags would typically hang. This device emits beeps that Wolf Project staff can tune in with telemetry equipment, enabling us to locate the wolves. Initially, every wolf released in Yellowstone wore a radio collar. No previous wolf study had enjoyed such a luxury, and we were excited because of the unprecedented amount of information that we could gather on each wolf and the entire wolf population.

But not everybody was pleased. To be collared, wolves must be captured and handled by humans, and some people believe this is inappropriate for wild animals, or just don't like to see collars on wildlife. Others feel that collaring wolves is too intrusive, an insult to the wolf's wildness, asking too much for the sake of research. Wolf Project staff tranquilize the wolves for handling by darting them from a helicopter, which also causes concern for the animals and for Yellowstone's visitors, who may be annoyed to hear a low-level helicopter in a national park. At least, some people said, the wolves should be left alone eventually—completely alone, with no collars. They asked us to learn what we could early on in the restoration, then to eliminate the radio-collaring program one day.

Certainly, viewpoints such as these have led Yellowstone Wolf Project staff to much soul searching about why we continue to collar wolves. On the other hand, virtually everything we know about wolves today comes from radio-collaring studies. There are a few exceptions, such as Adolph Murie's work in Denali National Park, Alaska, during the 1930s and 1940s, and various Isle Royale National Park wolf studies from 1958 to 1988 (after that year, wolf researcher Dr. Rolf O. Peterson switched to using radio collars, and still uses them to this day).

Also, solid, scientific information is needed not only for the delisting process, but also to help resolve the controversies related to the wolf reintroduction. Debates over wolves continue, and it is necessary for the Wolf Project to continue to have access to information about the wolves' locations, numbers, and reproductive, survival, and mortality rates, as well as how many elk and other prey (including livestock) they kill each year, and their effects on those populations. History and experience have demonstrated that in the absence of information, tall tales will fill the void; few other animals have had as many false stories spread about them as wolves.

Our own assessments have shown that the radio collars have little, if any, effect on the wolves. During helicopter darting, wolves are rarely forced to run farther than the average distance they might run when chasing down an elk. Post-capture monitoring has shown that the majority of wolves are back with their packs within a few hours. In several cases, they have gone on to kill an elk the same day, and once they killed an elk while the helicopter was still following them!

Finally, surveys conducted as part of Alice K. Wondrak's 2002 Ph.D. dissertation found that of a random sample of 150 Yellowstone visitors, 83% did not have negative feelings toward seeing collared wildlife in the park (see *Yellowstone Science* 10:3).

The goal of the Yellowstone Wolf Project is to take all views into consideration and seek compromise. The wolves are still captured, and still wear the marks of human intervention—radio collars. The helicopters and aircraft used for tracking intrude upon the silence of Yellowstone. These are legitimate concerns that we respect, and even share. In fact, not all of the wolves are collared anymore; since year three of the project, no more than 40% of the population has been collared. Typically, only 25–30% of the wolves are collared now. Most capturing and collaring activities are conducted in winter and during shoulder seasons, when fewer people are in the park. We also do not ear-tag wolves, which is standard practice in the work of most wildlife biologists.

These are examples of compromises that still allow us to gain vital information. They may not provide perfect solutions, but are an attempt to improve the chances for successful science as well as visitor enjoyment in Yellowstone.

by domestic dogs, was likely a significant cause of pup deaths that year, and the reason for the negative growth rate. From 1999 to 2000, the growth rate was again 50%, due mainly to the unusually big litters of the Druid Peak pack. From 1999 to 2004, the growth rate dropped to about 10–15%, still high compared to other North American wolf populations, which typically grow at a rate of 0–5%. Wolf population growth in the park may be waning, as the population estimate in 2004 was down 3% (–20% on the northern range). The high initial growth rate is comparable to growth rates found for other wolf populations after they have been reduced through wolf control and are expanding at a maximal rate (Figure 6).

Wolves in Yellowstone have died from a variety of causes (Figure 7). Not unexpectedly, and like virtually all other wolf populations in North America, human-caused mortality has been the leading cause of wolf death in the GYE. The second major cause has been other wolves. Wolves are fiercely territorial, and when trespasses occur, wolves usually die.

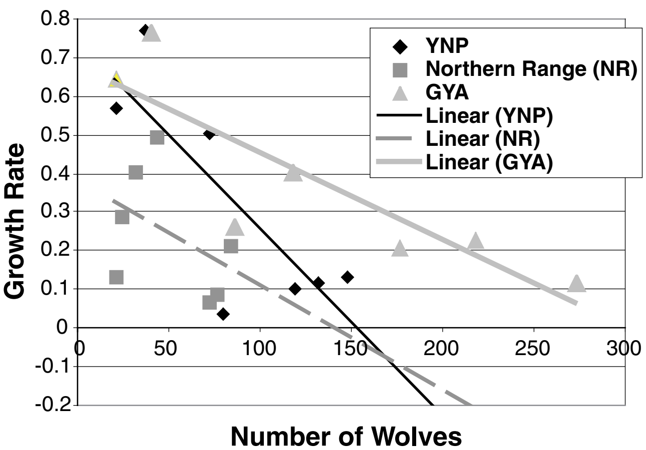


Figure 6. The rate of wolf population growth has been declining since reintroduction.

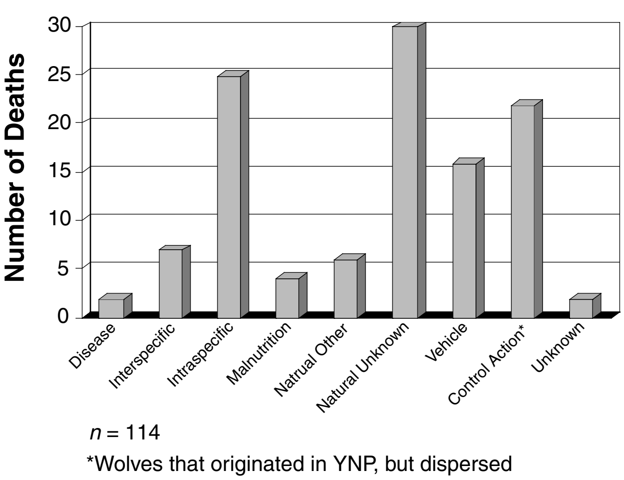
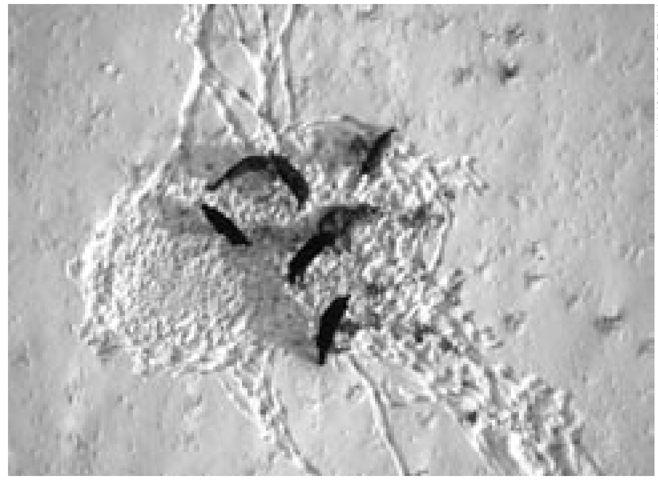


Figure 7. Human actions are a leading cause of death for wolves nearly everywhere (e.g., vehicle and control action, above). The leading known natural cause of death is wolves killing other wolves (e.g., intraspecific, above).



NPS/DOUGLAS SMITH

Druid Peak wolves kill a Rose Creek trespasser. Intraspecific strife has increased in the last two years on the northern range.

One vivid example of this occurred in 1997. The Soda Butte pack (now the Yellowstone Delta pack), which was released in October 1996, settled around Heart Lake, denning in a cave near the thermal features of Witch Creek. In early 1997, the Thorofare pack formed and occupied an area south of the southeast arm of Yellowstone Lake. In summer, Badger Creek was a hotspot for them. Their den was close to the Yellowstone River. Summer passed uneventfully, with the two packs never coming close to each other.

In summer, the area occupied by both packs pulsates with several thousand elk. By winter, most of these elk have migrated south or east, a few north, to winter range. However, deep snow did not come until December that year, later than normal, delaying the elk migration. Once the snow came, the elk moved, and so did the wolves. The Soda Butte pack, four adults with four pups, moved into the territory of the Thorofare pack, which had two adults with six pups. In a pack-to-pack confrontation, a number of factors typically play a role in determining the winner: whose turf is it (whether a pack is trespassing or defending), which pack has more wolves, and the level of experience possessed by those wolves. In this case, the Soda Butte pack was trespassing, which put them at a disadvantage, but they had an equal number of wolves and more experience, likely giving them an edge. Because none of the pups would be of help, this battle would be four-on-two.

The two packs clashed in late December. As is typical, the Soda Butte wolves attacked an alpha, male #35. They caught him along the shoreline of Yellowstone Lake and tore him to shreds, leaving nothing but hair, blood, and urine. Wolf Project staff could see where he made his last stand, as the story was told in the tracks in the snow. It appeared that the other wolves in his pack had fled when the attack started. In his effort to survive, #35 had dived below a fallen log on the shoreline, where he found a deep hole, likely hollowed out by strong lakeshore winds. He had backed himself up against the onslaught in this hole, but his defense had been futile. I walked over to an area nearby and picked up his radio collar, placed as if someone had laid it on the snow. Most collars in these situations are found still on the animal.

Two other wolves probably died as a result of this encounter. It appeared that the surviving wolves fled south along the Yellowstone River. The alpha female, #30, and a pup, #127, turned up Escarpment Creek into steeper terrain. It was the first time Wolf Project staff had located them there, and the area was probably unfamiliar to them. This route proved fatal, as #30 and her pup were killed in an avalanche. After mortality signals alerted us to this cluster of dead wolves, we flew in by helicopter to try to sort out what had happened. We attempted to dig #30 and #127 out of avalanche debris, but after we had dug down well over our heads and seen no sign of either wolf, we decided to defer searching until the snow was gone. When we returned by horseback that summer, all that was left were two wolf skeletons surrounded by bright blue harebells near a clear pool at the bottom of a small waterfall. A third collar was recovered up the Thorofare River. It had been chewed off, but no wolf was found.

NPS/DOUGLAS SMITH

Summer wolf work in Yellowstone uses the time-honored tradition of travel via horseback, as Jerry Mernin and Mike Ross show here on the Mirror Plateau.

The Thorofare pack had been broken apart, and both alphas were dead. The remaining pups traveled in a loose coalition for the rest of the winter, but split up in the spring. Some of these pups went on to form other wolf packs—the Washakie and Gros Ventre packs south of the park—again showing the resilience of wolves.

As of the end of 2004, Wolf Project staff have documented 103 interpack conflicts, resulting in 21 wolf deaths. Results like this make it easy to understand many statements in the wolf literature describing wolf populations as self-regulating: wolf populations control themselves through wolves killing other wolves. We expect such intrawolf conflict to be strongly influenced by the abundance of prey. As elk numbers decline, wolves will get hungry, travel in search of prey, trespass on other wolf territories, and fight with other wolves. This is, at least, the general pattern documented by long-term wolf research projects. In the meantime, we will continue to monitor such encounters; the rate of interpack encounter is already increasing on the northern range.

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The Howl Restored

In August 2002, I was on a horseback trip with Gerald Mernin, a retired park ranger whose long career in Yellowstone had been mostly wolf-less. We traveled through Pelican Valley, up Astringent Creek to Fern Lake cabin, and into Raven Creek via the "back way." Jerry had not taken the route since the mid 1970s, and he remembered much grizzly bear use then. On this trip, he wanted to see what the place was like now that wolves had returned.

I never pass up a chance to take a horseback trip with Jerry, one of the great wilderness minds of Yellowstone's history. The kind of knowledge he possesses was earned through long years spent on the land, and his wisdom helps us better observe and interpret this magnificent landscape, including changes since wolves were reintroduced. My NPS colt, Joker, also benefits from the backcountry work and exposure to grizzlies, getting good training in the company of Jerry's horse, Scott, who never flinches from a grizzly and can even be cantankerous with one.

That night in camp, after the horses were tended to and we were relaxing over beers and stories, we heard something outside the cabin. We stepped out, and down Pelican Creek we heard the deepest wolf howl one could ever hope to hear. We sat quietly and listened in the waning light, to the wavering howl, for more than 15 minutes. After a while, Jerry turned to me and said, "Everything is as it should be."

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Bison are significantly more difficult for wolves to kill than elk.

© MARK MILLER

The Swan Lake pack, traveling single file as wolves often do, especially in deep snow.

Ten Years After: What We're Learning About Wolves in Yellowstone

Restoring wolves to Yellowstone has provided researchers with extraordinary opportunities for understanding wolf ecology and behavior. Few places in the world offer the view into wolf life that researchers are afforded here. L. David Mech and Luigi Boitani, both world-renowned wolf researchers, have published the most comprehensive book on wolves to date, *Wolves: Behavior, Ecology, and Conservation*. The book was published too soon to include much of what has been learned about wolves in Yellowstone, but in the preface, the authors noted the remarkable nature of what is being learned in the park: "The ongoing studies of the biology of the reintroduced wolf population in Yellowstone National Park are particularly productive and will greatly promote our understanding of the wolf."

During the last 10 years, more wolf–elk, wolf–grizzly bear, and wolf–coyote interactions have been seen in Yellowstone than just about everywhere else combined. Current knowledge of how wolves attack and bring down prey has been vastly improved by observations of hundreds of wolf–elk encounters. More than 100 wolf–grizzly interactions have been witnessed in Yellowstone. The views into wild wolf behavior in the park are equally unique, allowing Wolf Project staff and researchers the opportunity to watch how packs make decisions, and how the breeding season melee plays itself out as numerous individuals vie for breeding opportunities. With new technology, wolf–prey interactions in the summer are just beginning to be understood. (*See inset, "Current Research."*) The first 10 years have been remarkable. As wolves expand out from Yellowstone, the knowledge gained through research will be critical to future wolf management decisions.

Wolves and the Structure of Ecosystems

The Greater Yellowstone Ecosystem (GYE) evolved in the presence of large carnivores. Wolf-like canids have been around for about 40 million years, making them one of the most ancient of all carnivores. The first modern wolf, *Canis lupus*, appeared during the Pleistocene, about one million years ago. Since European settlers in North America eliminated wolves from most of the United States, most ecosystems have functioned with the top level of the food chain lopped off. Even before 1926, when the last known wolf in the park was killed, wolves were absent as an ecological force throughout the Greater Yellowstone.

Research has indicated that wolves are the most dominant large carnivores in North America, and played highly important roles in the original structuring of ecosystems. They act as a top-down influence, indirectly affecting plants through their direct effects on animals that eat plants (herbivores). Because they occur at low densities, yet are so important, wolves have been described as a keystone species. With the return of the wolf, these structural processes are being researched in Yellowstone.

Wolf–Prey Relationships

Elk. The effects of wolves on prey, particularly elk, may be the most pressing of all controversies swirling around the restoration of wolves in the Yellowstone area (Figure 8). Outside the park, elk are a valued economic resource for sport hunting, and many fear—reasonably so—that the return of the wolf is affecting elk numbers.

Of the eight Yellowstone-area ungulate species, wolves most often prey upon elk (Figure 9). Of the 1,275 documented winter-kills by wolves, 90% have been elk. The proportion of elk calves, cows, and bulls killed on the northern range by wolves is 38%, 36%, and 26%, respectively (Wolf Project staff were not able to classify the remaining elk to sex and age class). This shows strong selection for calves, which comprised only about 18% of the available elk on the northern range from 1995 to 2000. It also represents strong selection against cows, as they comprised roughly 60% of the available prey during this period. Wolves have killed bulls in proportion to their availability.

These are not surprising figures. Young-of-the-year, no matter what the species, are usually a large part of a carnivore's diet. Carnivores typically take the easiest prey to kill, and young animals are easier targets than more experienced animals. Mortality of young is a basic evolutionary tenet of natural selection. Darwin characterized it as "overproduction of offspring," i.e., the idea that animals "overproduce" offspring because only the strongest will survive. Predation by wolves has played a large role in eliminating the weaker young animals.

Even further selectivity is evident. During the first 10 years of wolf restoration, the average age of wolf-killed cow elk on the northern range was 14 years. Work by Yellowstone National Park researchers and others has shown that at around 14 years of age, the pregnancy rate of cow elk drops significantly. This suggests that older elk do not have a calf every year, making them less productive than prime-age elk (elk 2–14 years of age). Therefore, some researchers believe that wolf predation on these older cows has lesser impacts on the population as a whole than removal of elk that are likely to produce many more calves in their lifetimes; this point is debated. The average age of elk killed by hunters north of the park is six years. These are elk in their reproductive prime, and in recent years, as elk numbers and calf recruitment have declined, the Montana Department of Fish, Wildlife and Parks has reduced the number of elk permits issued in areas near the park. Further reductions have been proposed.

Wolves were just as selective with bull elk. Bulls are the most difficult and dangerous segment of the elk population for wolves to kill. Wolves have typically killed few bull elk early in the winter, when their focus is on calves and old cows. As winter wears on, wolves begin killing more bulls because they become easier to kill. Long winters hurt bulls more than cows because the elk rut occurs just before winter's onset, sapping the bulls' energy. During the rut, bulls may not eat for days, possibly weeks; meanwhile, cows are eating. Thus, bulls begin the winter in poorer shape than cows do, and become weaker more quickly; wolves take advantage of this. Although Wolf Project studies have found that wolf kills of bull elk have usually coincided with the times of year when bulls are weakest and most vulnerable, data gathered in late 2004 ran contrary to this pattern. Many bulls and few calves were taken during early winter. It is hard to say what this means yet, but fluctuations and differences like this are to be expected over the course of long-term research.

The conclusion drawn by the Wolf Project and many others studying wolf–prey relationships is that wolves do not kill at random. If they did, they would likely be killed more often themselves, and would kill off all their prey, which has rarely been recorded. Prey are known to have killed nine wolves in Yellowstone since wolf reintroduction. The bottom line is that

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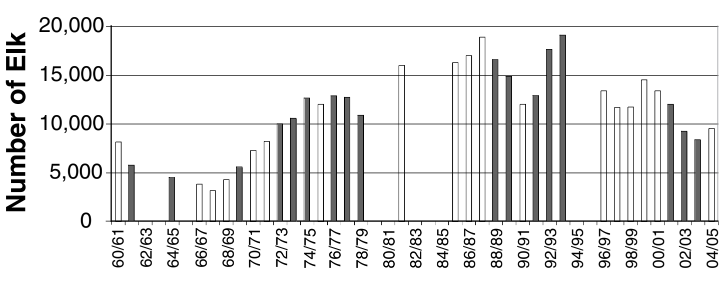

Figure 8. Since wolf reintroduction, the northern Yellowstone elk herd has declined about 50%. Reasons for the decline are multiple: wolves, other carnivores, human hunting, and possibly drought. Counts are conducted once a year in either December or January. Gaps in the graph show years when no count was conducted.

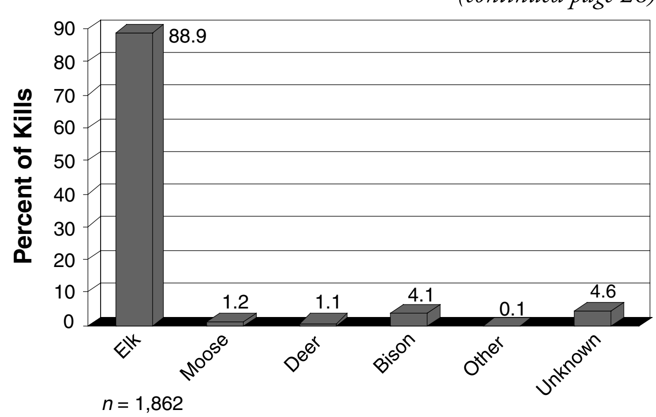

Figure 9. The winter (1995–2004) diet of wolves has been primarily elk, although seven of the eight ungulates present have been taken (no white-tailed deer are known to have been killed). The low, but increasing use of bison will be important to future wolf–prey ecology.

Current Research

NPS/DANIEL STAHLER

Wolf research in Pelican Valley requires patience and winter camping skills.

YELLOWSTONE NATIONAL PARK'S WOLF PROJECT and the Yellowstone Park Foundation provide support for the following research projects currently being conducted by park staff.

Yellowstone Wolf Project Staff Research

1. Population dynamics of Yellowstone wolves
   - Northern Rocky Mountain survival analysis
2. Wolf–prey interactions
   - Winter and summer prey selection
   - Winter and summer kill rates
3. Behavioral studies
   - Wolf pack leadership and dominance relationships
   - Social behavior during the breeding season
   - Den attendance
4. Wolf–carnivore interactions
   - Grizzly bears, black bears, cougars, coyotes
5. Population genetics
   - Wolf population pedigree
   - Evaluation of maternity and paternity
   - Gene flow between Rocky Mountain recovery areas
   - Identification of unknown wolves
6. Disease
   - Assessment of major wolf diseases
7. Wolf–scavenger interactions – "Food for the Masses"
8. Denning ecology
   - Observation of wolves at dens
   - Den site characteristics

Other Yellowstone Staff Wolf Research

1. Historical research on the history of wildlife presence in Yellowstone.

The Wolf Project and the Yellowstone Park Foundation provide direct and indirect support for collaborative research with scientists at other institutions, primarily universities. Most of these studies represent pioneering work on wolves within the topic of interest.

Collaborative Research Projects

Graduate Projects

Leadership: ecological implications of social behavior in gray wolves
Michigan Technological University
Committee Chair: Dr. Rolf O. Peterson
Graduate Student: Amy Jacobs

The predatory sequence in the wolf
University of Minnesota
Committee Chair: Dr. L. David Mech
Graduate Student: Daniel MacNulty

Spatial and temporal variation in wintering elk abundance and composition, and wolf response on Yellowstone's northern range
Michigan Technological University
Committee Chair: Dr. Rolf O. Peterson
Graduate Student: Carrie Schaefer

Common ravens following gray wolves as a foraging strategy in Yellowstone National Park
University of Vermont
Committee Chair: Dr. Bernd Heinrich
Graduate Student: Daniel Stahler

Homesite attendance as a measure of alloparental and parental care by gray wolves in northern Yellowstone National Park
Texas A & M University
Committee Chair: Dr. Jane Packard
Graduate Student: Linda Thurston

The disposition of carrion biomass: energy flow and ecological relationships between wolves, wolf-killed prey, and scavengers
University of California, Berkeley
Committee Chair: Dr. Wayne Getz
Ph.D. Candidate: Chris Wilmers

Adult cow elk seasonal distribution and mortality post-wolf reintroduction in Yellowstone National Park, Wyoming
University of Minnesota
Committee Chair: Dr. L. David Mech
Graduate Student: Shaney Evans

Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park, Wyoming
University of Alberta, Canada
Committee Chair: Dr. Mark S. Boyce
Graduate Student: Julie Mao

An analysis of Yellowstone National Park's northern range elk herd
Michigan Technological University
Committee Chair: Dr. Rolf O. Peterson
Graduate Student: Gregory Wright

Other Collaborative or Indirect Assistance Projects

Wolf–cougar interactions
Hornocker Wildlife Institute/Wildlife Conservation Society
Lead Collaborators: Drs. Howard Quigley and Toni Ruth

Wolf–coyote interactions
Yellowstone Ecosystem Studies
Lead Collaborators: Dr. Robert Crabtree, Jennifer Sheldon

Wolf–elk relationships in the Madison–Firehole watershed
Montana State University
Lead Collaborator: Dr. Robert Garrott
Graduate Students: Rose Jaffe, Eric Bergman, Claire Gower, Matt Becker

Wolf stress hormones
Montana State University
Lead Collaborator: Dr. Scott Creel
Graduate Student: Jennifer Sands

Wolf–scavenger relationships
University of California, Berkeley
Lead Collaborators: Drs. Wayne Getz and Chris Wilmers
Yellowstone Ecosystem Studies

Wolf–carnivore–human interactions
Hornocker Wildlife Institute
Lead Collaborator: Dr. Howard Quigley
Interagency Grizzly Bear Study Team
Lead Collaborator: Dr. Charles Schwartz
U.S. Forest Service, Gallatin National Forest, Gardiner District
Lead Collaborator: Dr. Dan Tyers
Montana Department of Fish, Wildlife and Parks
Lead Collaborator: Kevin Frey

Wolf–bear interactions
Interagency Grizzly Bear Study Team
Lead Collaborators: Dr. Charles Schwartz, Mark Haroldson, Kerry Gunther

Wolf howling
University of Waterloo, Canada
Lead Collaborators: Dr. John Theberge, Mary Theberge

Wolf–pronghorn interactions
University of Idaho
Lead Collaborators: Drs. John Byers and P.J. White

Wolf–aspen (cottonwood)
NPS
Lead Collaborator: Roy Renkin
Oregon State University
Lead Collaborator: Drs. William Ripple and Robert Beschta, Eric Larsen
University of Montana, University of Wisconsin-Stevens Point
Lead Collaborator: Matt Kaufman

Wolf–willow studies
NPS
Lead Collaborator: Roy Renkin
USGS
Lead Collaborator: Drs. Francis Singer, Tom Hobbs, David Cooper, and Don Despain
University of Alberta
Lead Collaborator: Drs. Mark S. Boyce and Evelyn Merrill

Wolf trophic cascades
USGS
Lead Collaborator: Dr. L. David Mech
University of Alberta, Canada
Lead Collaborator: Dr. Mark S. Boyce
Michigan Technological University
Lead Collaborator: Dr. Rolf O. Peterson

Wolf predation
Michigan Technological University
Lead Collaborators: Drs. Thomas Drummer and John Vucetich

Wolf survival
Trent University
Lead Collaborator: Dr. Dennis Murray

Wolf–elk calf mortality
University of Minnesota
Lead Collaborators: Drs. L. David Mech and P.J. White
Ph.D. Candidate: Shannon Barber

A behavioral analysis of the effect of predator and prey densities on wolf predation
University of Minnesota
Committee Chair: Dr. Craig Packer
Ph.D. Candidate: Daniel MacNulty

if a wolf is not selective, it may die or be severely injured while obtaining food; hence, wolves search for vulnerable prey, rather than just any prey.

A pattern of selectivity reveals itself again in how often wolves make a kill. Early in the winter, when prey are in good condition and harder for the wolves to bring down, the rate at which they take prey is usually less than in late winter (Figure 10). During the first five years after restoration (1995–2000), each wolf killed an average of 1.4 elk over 30 days (the length of the Wolf Project's intensive study period) in early winter, and 2.2 elk during a 30-day period in late winter, for a winter average of 1.8 elk/wolf/30 days. However, since about 2000, wolf kill rates have not increased in late winter, and overall, wolves are killing fewer elk (1.1 elk/wolf/30 days from 2000 to 2004).

There is not yet a conclusive explanation for this. It may be that there are fewer vulnerable elk; other data hint at various drought effects, as the area is in its seventh year of drought. A mathematical modeling effort led by Dr. John Vucetich from Michigan Technological University has elucidated some interesting hypotheses on what drought effects on the northern range ecosystem might be. His findings show that over the last six years (a drought period with high elk density and heavy hunting), the effect of wolf predation on elk mortality may have been compensatory—meaning that an elk killed by wolves would have died anyway, or that one elk death promoted the survival of another—and therefore negligible relative to the overall elk population. This theory is dependent on the conditions for that time period. Underscoring the importance of long-term research, a different set of conditions in the future could cause predation mortality to be either compensatory or additive, meaning that the elk mortality rate is higher than it would be without wolves present. Vucetich also found that during this period of drought, the elk population would likely have declined regardless of whether or not wolves were present. When he hypothetically modeled "normal" climatic

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Two Druid Peak wolves test a cow elk. The neck is a common attack point on cow elk, unlike larger prey, which are more likely to be attacked from behind.

conditions, in which precipitation did not decline from 1998 through 2004, he found that the elk population would have increased over those years, assuming that hunting pressure was light.

This analysis caused Wolf Project staff to look more closely at our data, wherein we discovered another aspect of wolf predation: any variation in the wolf-kill rate, like the one mentioned above from early to late winter, has been due to fluctuation in the kill rate on calves, old cows, and bulls—not prime-age cows. As drought stressed the elk population, the young, old, and bulls felt the most pressure, not the prime-age cow elk, which are the key population drivers. This supports the idea that weather may be an important driver to the elk–wolf interaction. Other evidence for this was seen in the winter of 1996–1997. Thousands of elk died that winter due to severe weather, drastically reducing the elk population.

It is important to note that not everyone concurs with this interpretation, and scientists are just beginning to sort out

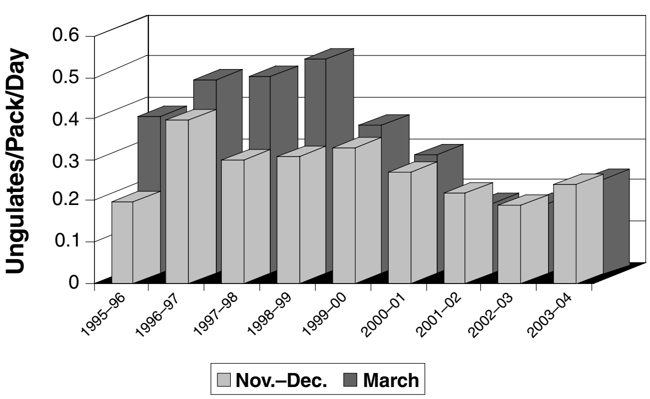

Figure 10. How often wolves kill, early winter compared to late. Killing frequency has changed over the last five years. Early on, wolves killed more frequently in late compared to early winter, a trend no longer true for 2000–2004.

NPS/DOUGLAS SMITH

Escape to water is a common strategy for elk, and in this case, it worked against the Mollie's pack wolves.

these complex relationships. Other models have found wolf predation to be mostly additive during the drought years rather than compensatory. Competing models and disagreements are productive, as more scrutiny will help reveal the subtle and complicated nature of the wolf–elk relationship.

Our findings on wolf–elk relationships have caused us to conclude that there are two wolf–prey systems in Yellowstone: one on the northern range, and one in the interior. The northern range is lower in elevation than the interior, there is less snow, thermal areas are rare, and elk are abundant year-round. Conditions in the interior are the opposite: elevation is higher, snow is deep in winter, thermals are abundant, and elk (except for the Madison–Firehole herd) migrate out of the area, making them seasonally rare. Wolves have adapted to these different conditions. On the northern range, elk are the primary prey of wolves throughout the winter. In the park's interior in late winter, after many of the elk have left the park, wolves also kill bison and sometimes moose. Wolves in the interior use thermal areas to their advantage. Prey face deep snow outside the snow-free thermal areas, stranding them and making them vulnerable to wolves.

The differences between the park's northern range and the interior also result in much higher wolf density on the northern range. Abundant elk in the north allow wolf territories to be smaller and to abut or overlap each other. In 2003, 41% of the area included in northern range wolf pack territories was in more than one pack's territory, whereas interior wolf pack territories were mostly isolated and rarely overlapped. As a result, wolf-to-wolf conflict and kills have been much higher on the northern range than in the interior. In the north, the wolves are smaller, and the population has declined an average of 30% during the winter (due to death and dispersal), compared to the nearly stable interior population.

Prey other than elk. Bison comprised only 2% of the wolves' diet during the first 10 years of wolf restoration, but their consumption has increased in the last few years, reaching 6% in 2004. Most bison are taken in late winter, and 54% of those are calves. Wolves are even more selective with bison than with elk because the risk of injury is much greater. One aspect common to bison and elk is that if they decide to stand their ground against wolves, wolves have a harder time killing them, and typically do not succeed. It is safer for wolves to move in and kill prey that are running than those that face the attack head on. However, even when elk run, they still outrun wolves 80% of the time; only one in five wolf attacks is successful.

Wolves are more successful with elk than bison because bison typically stand their ground. Bison are most important to wolves in Pelican Valley (Mollie's pack), the Madison–Firehole (Nez Perce pack), and Cougar Creek (Cougar Creek pack), the areas where most bison in Yellowstone congregate, especially in winter. Their involvement with bison has made the stories of these packs slightly different from those of other Yellowstone packs because of the extreme difficulty they have in killing such large, dangerous animals.


NPS/DOUGLAS SMITH

Prey that run are more likely to be killed by wolves, but elk still outrun wolves 80% of the time. Only one in five wolf attacks is successful.


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Prey that stand their ground are even harder for wolves to kill, and they typically get away.


NPS/DOUGLAS SMITH

Bison stand their ground more often than elk, and wolves are less successful per encounter at killing them.

Bison, however, may come to play a very important role in future wolf–elk dynamics. If the wolves become more adept at killing bison, the bison may maintain the wolf population even if elk numbers dwindle. Such behavior is called "prey switching," and it has been documented in other wolf populations. If wolves don't figure out how to kill more bison, declining elk populations will probably mean declining wolf populations as well.

Other than elk and bison, wolves take little other prey in winter in Yellowstone. Most of the mule deer that use the park in the summer migrate out of the park in winter to lower elevations. Summertime scat collections show that as the deer migrate back into the park, wolves start using them again. About 25% of the wolves' summer diet is mule deer (Figure 11).

Wolves have taken few pronghorn, probably because they are far too fast for wolves to catch (top speed for a pronghorn is 60 mph, vs. 35 mph for a wolf). Preliminary study indicates that wolves may actually be having a positive effect on the Yellowstone pronghorn population. Work done by Dr. John Byers of the University of Idaho has indicated that pronghorn fawn survival in Yellowstone is highest near wolf dens, presumably because these fawns are less subject to coyote predation. Pronghorn fawns are an important prey for coyotes, but not for wolves, and coyotes avoid wolves (see "Cooperative Studies of Carnivore–Carnivore Interactions," page 30). Yellowstone National Park ungulate biologist Dr. P.J. White is leading an effort to continue this pronghorn research.

Wolves occasionally take moose, but like bison, moose are very difficult for wolves to kill. Wolves are known to have killed only 33 moose in Yellowstone from 1995 to 2004. Nine of these kills happened in the Thorofare area, where moose densities are higher than in the rest of the park.

All other prey species taken by wolves comprised less than 1% of the wolves' winter diet during the first 10 years. It is frequently speculated that bighorn sheep, an animal of concern in Yellowstone because of declining populations, have been affected by wolves, but there is only one documented sheep kill, and wolves spend very little time in bighorn sheep habitat, suggesting little if any use of bighorn sheep.

Summer studies. Most of the available information on wolf kills comes from data gathered in the winter, or from scats collected at dens and rendezvous sites in summer. No parallel study examining kill rates and prey selection has been conducted in the summer, in Yellowstone or elsewhere. However, most estimates conclude that wolves eat less in the summer—as much as 30% less. Summer is pup-rearing time, which means that adult wolves are anchored to the den and travel around it "like spokes on a wheel."

It is more difficult to determine what wolves are killing in the summer. Because some wolves usually stay with the pups, hunting units in summer are typically comprised of singles, duos, and triples instead of larger units. In addition, summer prey often includes animals too small to leave a carcass to trace—fawns, calves, beavers, even ground squirrels—and is often widely-distributed in areas without snow to aid in detection of kills.

But technological advances are making it easier for Wolf Project staff to track wolf movements, even in the summer and at night. Global Positioning System (GPS) collars that communicate with satellites can download data from the field, enabling us to receive data while the collar is still on the wolf. In the summer of 2004, two wolves wore GPS collars programmed to record their locations 40 times during each 24-hour period. (*See inset, "GPS Collars."*)

With this location data, we could create detailed maps of where those wolves went. We hiked to each point where they spent several hours and often found kills. By combining these data with information about how many hunting groups a pack has, estimates for summer kill rates can be refined. For example, we saw four of the six adult wolves in the Geode Creek pack hunting together, including the GPS-collared wolf. The other two were breeding females, so they probably did not

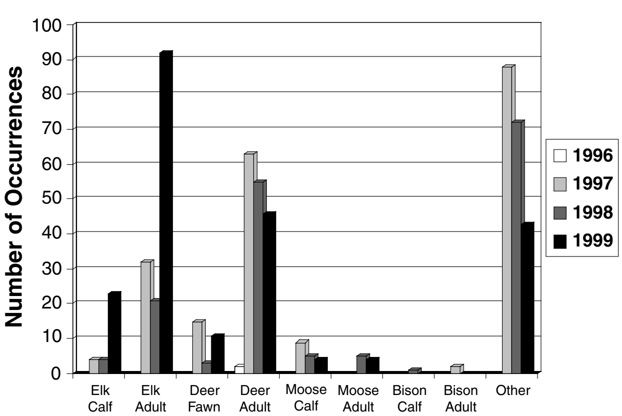

Figure 11. In summer, scat analyses indicate that elk are still important, but due to an influx of migrating mule deer, mule deer use increases. Other food sources include small rodents, beavers, ground squirrels, and vegetation.

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Wolves are social mammals with a dominance hierarchy.

GPS Collars

BECAUSE the newer GPS collars offer so many advantages over traditional radio collars, some people ask why the Wolf Project doesn't just use them instead of telemetry collars, which require human legwork to locate the animals. There are several reasons why not. First, GPS collars are expensive; one collar can cost around $3,200, compared to $300 for a conventional radio collar. Second, GPS collars last only about 10 months, compared to about five years for other radio collars. This is a big drawback, because catching wolves for collaring is difficult and expensive. If all collared wolves were fitted with technology that lasted just 10 months, we would quickly lose contact with most of them, because re-collaring efforts could not keep up. Third, with the GPS collars, we don't see the wolves! Instead, they become dots on a computer screen. Good biological practice cannot substitute solid fieldwork with fancy technology—rather, technology can provide tools to be used in conjunction with a variety of techniques. Visual observations remain invaluable, enabling us to count the wolves and their pups, study their behavior, and observe interactions between wolves and other animals.

hunt much early in the summer. At the sites where the GPS-collared wolf was located, the evidence of predation that staff found probably provided a fairly accurate representation of what and how much the pack was killing.

We also found that the Geode pack wolves were killing fewer elk in the summer, and that when the calves were born, the wolves only took them opportunistically. They did not begin killing the calves exclusively, or even mostly, as some people thought they did. These findings corresponded with those of collared elk calf studies being conducted concurrently in the park.

Wolf Project Scavenger Studies

What happens to the carcasses of animals killed by wolves? Do the wolves eat everything? A wolf's stomach can hold about 20 pounds of meat, so the average Yellowstone pack of 10 wolves can eat about 200 pounds at a time. A cow elk may weigh 500 pounds, a bull elk 750, and a bison 1,500. That can leave a lot of leftover meat, and scavengers are taking advantage of it. Wolf research in the Yukon Territory suggests that small wolf packs have to compete with scavengers to such an extent that they may have kill rates as high as those of larger packs just to make up for the food they lose.

Wolf Project staff have documented 12 scavenger species that use wolf kills, not including the many invertebrates that ultimately clean up the carcasses. The easiest way to find a wolf kill is to look for raven activity. Dan Stahler, of the Yellowstone Wolf Project, and Bernd Heinrich, a raven expert from the University of Vermont, studied the relationship between Yellowstone wolves and ravens from 1997 to 1999 and, for the first time, quantitatively documented that ravens follow wolves. In fact, Stahler and Heinrich found that ravens were reluctant to visit a carcass unless wolves or other scavengers were present. Ravens avoided human-provided carcasses, sometimes just looking at them as they flew over. While ravens did not feed on any of the non-wolf-killed carcasses, they fed on wolf kills without hesitation, usually starting as soon as the prey was killed. The longest it took a raven to appear after a wolf kill was two minutes. Ravens quickly recruited more ravens, and within minutes, there would be a cacophony of raven cries. The average number of ravens per kill on the northern range is 28; 135 ravens is the highest number ever recorded at a kill site.

Many wolf-kill sites also attract magpies, bald and golden eagles, and coyotes. Coyotes visit wolf kills at their peril, as wolves often kill them. However, they cannot resist the banquet wolves provide, and nearly every recorded case of a coyote killed by a wolf was in the vicinity of a wolf kill.

Black and grizzly bears visit wolf kills when they are not hibernating, and grizzlies have forcefully expelled wolves from kill sites. Although all Yellowstone wolf packs must deal with bear competition, Mollie's pack in Pelican Valley is particularly vulnerable to bear raids. When ravenous grizzly bears emerge from their dens in Pelican Valley, typically in March, they now tend to zero in on wolf kills. In the last three years,

Wolf-provided carcasses have been a significant alteration to the Yellowstone landscape, providing food for vertebrate and invertebrate scavengers.

every observed kill made by Mollie's pack from March through October was taken over by grizzly bears. Wolf Project observations of these interactions show that within a few hours of wolves' killing an elk or bison, bears sniff it out and chase the wolves away. On one occasion, NPS staff saw 4 wolves and 12 grizzly bears near a bull elk that wolves had killed. The largest grizzly bear controlled the carcass, holding the other bears and wolves at bay. A year later, at almost the same site in Pelican Valley, park staff found 10 wolves and 4 grizzly bears near a bull elk carcass. Again, the largest grizzly bear controlled it. In another case, one bear was observed holding 24 wolves at bay from a wolf-killed bull elk. Some of the wolves were pups, but the number is still extraordinary. As Wolf Project staff watched, wolves darted in, unsuccessfully trying to hassle the bear from the kill. The bear stood on top of the carcass, which he had begun to bury, not budging. We expect these wolf–bear–carcass interactions to be an important aspect of the grizzly bear story in the Yellowstone area in future years. In late 2004 and early 2005, it appeared that Mollie's pack might be breaking apart. This may be largely due to the death of their alpha male and female in December 2004, but loss of food to grizzlies may also be a factor.

We also expect more rare animals to take advantage of wolf kills. Wolverines, for example, do not typically migrate to lower elevations in winter, and they rely primarily on carrion to survive. Wolves often make kills on high ridges (e.g., Specimen Ridge) in winter because bull elk often stay high on windblown slopes, surrounded by deep snow. These kills could serve as food sources for the rare wolverine. Examples like this show the effects that wolves may have on other species, increasing Yellowstone's biodiversity. One thing is certain, though—nothing from a wolf kill goes to waste.


NPS/DOUGLAS SMITH

Wolf–grizzly interactions typically favor bears, which are more dominant at carcasses. Mollie's pack, in Pelican Valley, typically has grizzlies visit all of their kills, as seen here, where six bears and a wolf compete for access to a wolf-killed elk.

Cooperative Studies of Carnivore–Carnivore Interactions

The Yellowstone area has one of the most diverse assemblages of large carnivores in North America, and these species all feed on elk at some point during the year—black and grizzly bears, cougars, coyotes, wolves, and humans. While wolf–prey relationships and the benefits of wolf kills to scavengers are the main focuses of Yellowstone Wolf Project studies, we are also involved in cooperative studies to help us understand carnivore–carnivore interactions.

Wolf reintroduction has affected coyotes more dramatically than any other carnivore, as reported by Crabtree and Sheldon (see *Yellowstone Science* 7:2, 1999). Within eight years after wolves reestablished themselves in Isle Royale National Park in 1948, they had killed all of the coyotes. Biologists don't predict coyote extinction in Yellowstone, but reduced densities have already been recorded by Crabtree et al. across the northern range. Fewer coyotes and/or redistributed coyotes will have other effects on the park's ecological communities.

Observations indicate that wolves are benefiting grizzly bears by providing carcasses for them to scavenge. When whitebark pine nuts, a key pre-hibernation food source for bears, were scarce in the autumn of 2002, an unusually large number of grizzly bears were observed feeding on wolf kills parkwide. Black bear interactions have been fewer, and wolves seem to dominate black bears. Other wolf populations have been recorded driving black bears out of their denning areas, and in one case, wolves treed a black bear that ventured too close to their den.

Wolf–cougar interactions have rarely been observed. Most of the information the Wolf Project has on these interactions comes from analysis of radio-tracking data with the Yellowstone Cougar Project, sponsored by the Wildlife Conservation Society and led by Dr. Toni Ruth (see *Yellowstone Science* 12:1, 2004). Some displacement of cougars by wolves seems to be occurring, but these findings are preliminary.

A pilot study including the National Park Service, U.S. Forest Service, U.S. Geological Survey, the State of Montana, Montana State University, and the Wildlife Conservation Society has shown how wolves, cougars, and grizzly bears respond to the elk-hunting season north of the park. Bears seem to be attracted to the hunting activity, taking advantage of the gut piles, while cougars retreat into the park. Wolves travel in and out of the park, unaffected by the hunting season. The Wolf Project plans to continue this

DALE AND ELVA PAULSON

Wolf #21, alpha male of the Druid Peak pack, investigates a coyote den in Lamar Valley, despite attempts from the resident coyotes to dissuade him. In this case, no coyotes were injured, but in at least three other cases like this, coyote pups were killed. Wolves have dug into coyote dens numerous times without killing any coyotes.

study, as it offers great promise for managing and living with carnivores. The next step is to use satellite radio telemetry on wolves, cougars, grizzly bears, and black bears. The objective will be to locate these carnivores more often, each species at the same time during each 24-hour period and at night. (Typically, only one location per day or week is taken.) Overlaying such detailed data will take us to the next step in understanding how these carnivores use and apportion the greater Yellowstone landscape during the hunting season and in general.


NPS/DOUGLAS SMITH

One of the most debated research topics in the park right now is, Why are some willow suddenly growing taller? Some believe this to be a wolf-triggered "trophic cascade."

Trophic Cascade

All of this wolf research culminates in one overarching question: What will Yellowstone be like 30 years from now, after the full ecological effects of wolves are felt? One hypothesis is that wolves are centrally important to the functioning of the ecosystem—a keystone species, and that their return will trigger a trophic cascade (a succession of indirect effects) involving every part of Yellowstone National Park. Some researchers predict, for example, more songbirds due to riparian regrowth as elk change their browsing behavior because of wolves (similar studies to the north in Banff National Park and to the south in Grand Teton National Park have documented such connections). These studies in Yellowstone are in their infancy, and these ideas are only hypotheses. One thing most researchers agree on is that willow are "releasing," or growing taller, in some areas, and that elk behavior is changing, but cause and effect have yet to be determined and will continue to be debated. What the effects of these changes are and will be is also debated (*see inset, "A Wolf-Triggered Trophic Cascade?"*). Assessing the ecological effects of wolf reintroduction involves complex, interacting factors. This may be one of the most dynamic research subjects in the park, affecting overall concepts of ecosystem functioning and restoration. YS

A Wolf-Triggered Trophic Cascade?

ONE OF THE MORE EXCITING aspects of wolf restoration in Yellowstone is the collaborative nature of the research taking place. Many people are involved, bringing wide-ranging expertise and support to an array of projects. Probably the best example of this approach—and a hot ecological question for the Yellowstone ecosystem today—is the work investigating the possibility of a wolf-triggered trophic cascade.

Ecosystems can be said to function at different levels. Driven by the sun, energy works its way up through the levels—from plants, to herbivores, to carnivores and scavengers, to decomposers. This is an oversimplification, but at each level above the bottom, many animal species exist. In the Yellowstone system, elk are the main herbivore, and wolves are an important carnivore. The central question for those who hypothesize a wolf-triggered trophic cascade is, "How will wolves affect elk, and how might those effects, in turn, impact species at other trophic levels?" Numerous researchers have joined in this work, and they frequently disagree; that is often how science advances!

Trophic cascades deal with indirect effects. For example, what might happen if wolves affect elk behavior, which alters where elk choose to eat and spend time, which then affects plant growth? If a plant species' growth is affected, the other plants and animals that interact with that species may also be affected. It might be theorized that wolves reintroduced to Yellowstone are like a stone thrown into a calm pond, sending out ripples in every direction. One might also picture a rock that has been sitting on the edge of a cliff for some time. Wolves did not put it there, but they may be the force that comes along and kicks it off, triggering a set of observable impacts. The wolves are not entirely responsible for the cascade, but it might not have happened had they not exerted their force.

At the center of the current trophic cascade debate are the park's willows. One thing upon which nearly all scientists can agree is that willow growth has improved since the time of wolf reintroduction. After decades of suppressed production, why the increase now? For many years, it was believed that an overabundance of elk had overgrazed the park's willows, leading to their dearth. However, although elk reduction efforts took place for more than 30 years in Yellowstone in an attempt to prevent overgrazing, anecdotal evidence has it that willow growth was still suppressed during those years. The current willow release is happening with roughly three times as many elk on the landscape as there were then.


NPS/DOUGLAS SMITH

Douglas Houston and Rolf Peterson, two noted Yellowstone researchers, contemplate the recent willow surge near the Druid Peak den in Lamar Valley.

This combination of circumstances has spawned the notion of the "wolf effect," but there is not universal agreement that wolves are a key factor. Many intertwining, interacting factors are likely involved. One theory is that it may be elk *behavior*, rather than elk numbers, that makes the difference. Wolves are now always present on the landscape, and they hunt at night. Elk have responded by keeping themselves on the move. Elk reduction was always done as quickly as possible, and only during the day, so it likely did not stop elk from browsing willow patches.

The willow story is not simple. Willow decline through the middle of the last century caused stream courses to deepen, reducing the areas where willows could become established. The 1988 fires produced a brief spurt in willow establishment, but it was short-lived. The effects of moose, a big but declining consumer of willows since the 1988 fires, need to be accounted for, but wolves may also affect moose distribution. Elk browsing, besides reducing willow size, has affected seed production. Near-record floods in 1996 and 1997 changed stream courses, which may have affected willow colonization, and that happened to be when wolves were reintroduced. Climate must also be considered. The last six years, when water-loving willows have really taken off, have actually been drier on the northern range than was the preceding period, but temperatures above freezing have also started earlier and lasted later in the season. The lately mild winters have allowed elk greater browsing ability. What will happen if hard winters return? The presence of beavers and their ponds may be another reason why willows are doing better now. It is also possible that wolves have been the catalyst that has stirred up the whole process.

Whether or not wolves are responsible, the recovery of willows, if it continues, could produce major ecological ripples. Animals that use willows might move in and increase. For example, Slough Creek inside the park had no beaver colonies in 1996, but there were seven in 2003. Lamar Valley also has its first beaver colony in decades. The Gallatin National Forest reintroduced beavers in the early 1990s, increasing the abundance of that species on the park's northern range. Willow resurgence helped the new colonies to become established. Back sloughs dammed by beavers could attract more waterfowl, boreal chorus frogs, other amphibians and reptiles, trout, voles, shrews, insects, and so on. Lush willows can also benefit songbirds such as Wilson's and yellow warblers, and possibly moose.

Wolves may be involved with several trophic cascades. Carcasses provide meat for a host of scavengers. The wolf-mediated decline in coyote densities may ripple through to affect animals preyed upon by coyotes, including the red fox and other small mammals. Grizzly bears can readily steal wolf kills, wolverines will have more carrion, and on and on. Altogether, it is not hard to see why some believe that wolves will restructure the GYE, increasing the biodiversity of the entire system.

This spring, a PBS series called "National Geographic's Strange Days on Planet Earth," episode three: "Predators," will focus on this idea of how predators affect ecosystems. Hosted by Edward Norton, the program investigates what happens to areas from which predators have been removed. It includes a segment on the wolf reintroduction in Yellowstone, and discusses some of the trophic cascade research that is taking place.

Acknowledgements

Many individuals and agencies were involved with the reintroduction of wolves to the Yellowstone area; too many to mention in this issue. Numerous individuals helped with the creation of this article, and I would like to recognize them. First and foremost are Tami Blackford and Roger Anderson. Many individuals read the article and offered critical comments. They are as follows: Ed Bangs, Wayne Brewster, Gary Ferguson, Mary Ann Franke, John Good, Deb Guernsey, Terry McEneaney, Rick McIntyre, Jerry Mernin, Tom Olliff, Rolf Peterson, Glenn Plumb, Dan Stahler, Roy Renkin, Paul Schullery, Alice Wondrak Biel, John Varley, and P.J. White. Deb Guernsey produced the graphics. Photographers William Campbell, Bob Landis, Mark Miller, Dale and Elva Paulson, and Jeanne Ross donated images from their collections. Over the years I have benefited from the work and insights of my colleagues on the Wolf Project: Mike Phillips, Kerry Murphy, Dan Stahler, Deb Guernsey, and Rick McIntyre. Many volunteers and technicians on the wolf project have been supported through grants to the Yellowstone Park Foundation, and this too has been critical to the success of wolf work in Yellowstone. All of the above, often without knowing it, helped improve what we know about wolves.

A Swan Lake pack wolf.

Yellowstone After Wolves

Environmental Impact Statement Predictions and Ten-Year Appraisals

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In 1988, the Senate-House Interior Appropriations Conference Committee appropriated funds for the National Park Service and U.S. Fish and Wildlife Service to address concerns regarding the restoration of wolves to Yellowstone National Park, including impacts on ungulate populations, hunter harvest, domestic livestock, and land use. These agencies made a concerted effort to predict effects in and near Yellowstone National Park using extensive literature surveys, independent investigations by university scientists, and consultations with experts from around the world and with the wildlife agencies of Idaho, Montana, and Wyoming. Summaries of these evaluations were presented in *Wolves for Yellowstone? A Report to the United States Congress,* Volumes I–IV, published by the National Park Service in 1992. The expected ecological and economic effects from wolf restoration were also described in the *Final Environmental Impact Statement for the Reintroduction of Gray Wolves to Yellowstone National Park and Central Idaho,* published by the U.S. Fish and Wildlife Service in May 1994.

Prediction of the future is an inexact science, at best, as weather forecasts frequently demonstrate. Thus, natural resource managers inevitably need to act without the luxury of complete knowledge, using the best available information to evaluate the range of possible future effects and weighing the potential benefits and costs of alternate management actions. However, scientific knowledge progresses by predicting the effects of alternate actions and rigorously monitoring actual effects and progress toward an objective after an action is implemented. Ongoing and future management actions can then be refined, as necessary, based on the effective feedback of information between monitoring and conservation efforts as the system evolves through time and new findings are uncovered.

In the following table, we evaluate whether reality has met expectations regarding the restoration of wolves to Yellowstone National Park. Predictions were obtained from the *Final Environmental Impact Statement for the Reintroduction of Gray Wolves to Yellowstone National Park and Central Idaho* and categorized into the following sections: wolf recovery, impacts on ungulate populations, impacts on hunter harvest, impacts on domestic livestock, impacts on land use, impacts on visitor use, and impacts on economics. We focused our assessment on northern Yellowstone elk because most of the pre-wolf restoration predictions focused on this world-renowned population. The list of predictions is by no means comprehensive, but is intended to address the range of concerns identified prior to wolf restoration.

This article evolved from our interest in understanding what the EIS predicted compared to the current conditions. It is important to note that the EIS predictions were based on a recovered wolf population of approximately 100 wolves in 10 packs, and this threshold was passed four or five years ago. The appraisals here describe what has happened to date—10 years after reintroduction—with a wolf population of 301 wolves in the Greater Yellowstone Recovery Area. The following appraisals should not be treated as final outcomes of wolf restoration. The Yellowstone system will continue to dynamically adjust for decades; these appraisals only reflect the *current* situation in relation to pre-wolf restoration predictions. The relative importance of, and interactions between, various factors (e.g., climate, harvest, predation) that influence elk numbers may become more apparent over time as the abundance, kill rates, and prey selection of wolves change in response to decreasing elk numbers, the harvest is further reduced, the current seven-year drought ends, and occasional severe winters occur. Thus, it is imperative that monitoring and research regarding the ecological implications of wolf recovery continue to elucidate the long-term effects of this systems-level restoration.

EIS Prediction	Ten-Year Appraisal
WOLF RECOVERY	
A recovered wolf population in the Greater Yellowstone Recovery Area will consist of approximately 100 wolves in 10 packs. However, wolf numbers will fluctuate substantially between 50 and 120 animals under most management scenarios.	By 2004, there were 301 wolves in the Greater Yellowstone Recovery Area, including 167 wolves in 16 packs using Yellowstone National Park. It is uncertain if this density of wolves represents an irruptive pattern in which wolves overshot equilibrium levels, or a density that can be supported given the decreasing abundance of ungulate prey.
Wolf recovery will be attained in eight years.	Biological recovery criteria were met for removing Northern Rockies area wolves from the Endangered Species List in eight years (i.e., 1995–2002).
Few wolves will be outside the park or adjacent wilderness areas during the first five years following restoration.	Few wolves traveled outside the park or adjacent national forest lands during the first five years following reintroduction.
Most wolves will avoid low elevation areas with high levels of human activity.	Most wolves avoided low elevation areas with high human use, but some individuals did travel there.
Wolves will have positive, long-term effects on ecosystem functions and re-establish more complete predator–prey relationships.	Wolves are altering the abundance, distribution, group sizes, movements, and vigilance of elk. There are some indications that these interactions may be contributing to a "release" of woody vegetation from the effects of herbivory. However, cause and effect relationships have yet to be rigorously demonstrated.
IMPACTS ON UNGULATE POPULATIONS	
Wolves will prey on several ungulate species.	Wolves have preyed on bighorn sheep, bison, elk, moose, mountain goats, mule deer, and pronghorn.
Elk will be the primary prey for wolves.	Elk are the primary prey for wolves, comprising 92% of kills during winter.
Bighorn sheep, pronghorn, and mountain goats will not be significant prey for wolves.	These species comprise <0.5% of wolf kills during winter.
During early stages of wolf recovery, effects of predation on ungulates will be undetectable.	Predation effects were not detected during the early stages of wolf recovery because the range of elk counts during 1995–2000 (11,000–17,000) was similar to 1980–1994 (12,000–20,000). During later stages of wolf recovery (2000–2004), elk counts significantly decreased.
Seventy-eight to 100 wolves will reduce numbers of northern Yellowstone elk by 5–30%, contingent on a 27%	Counts of elk significantly decreased by >50% from 16,791 in winter 1995 to 8,335 in winter 2004 as the number of

(continued page 36, first column)

(continued page 36, second column)

EIS Prediction	Ten-Year Appraisal
reduction in the antlerless elk harvest.	wolves on the northern range increased from 21 to 106. Factors contributing to this decrease include bear and wolf predation, increased human harvests, winter-kill (1997), and drought-related effects on pregnancy and survival.
Mule deer numbers will decrease 3–19% following wolf restoration.	There is no apparent increasing or decreasing trend in spring counts of northern Yellowstone mule deer. Counts during 1995–2003 were within 1% of the 17-year average of 2,014 deer.
Wolves will reduce moose numbers by 7–13%.	There are not reliable estimates of moose abundance following wolf restoration. Moose numbers decreased in the northern portion of the park after the fires of 1988 burned important winter habitat (i.e., mature spruce/fir forests).
Wolves will reduce bison numbers by <15%.	Wolves have not reduced the abundance of bison. Rather, the bison population grew at 15% per year during 1998–2003, after accounting for removals.
A recovered wolf population of 100 wolves in 10 packs will kill 1,200 ungulates at a rate of 12 ungulates per wolf per year.	Kill rates by wolves during winter have been closer to 22 ungulates per wolf per year, which equates to 2,200 ungulates for 100 wolves. Summer kill rates are unknown, but likely lower than winter rates for adult ungulates.
There are no conditions in which wolf predation will have devastating effects on elk populations.	Counts of northern Yellowstone elk will likely continue to decrease until levels of harvest and/or predation decrease sufficiently to enable increased survival and recruitment of calves to breeding age. If the current, relatively high rate of decrease (4–9% per year) continues, then predation may prevent rapid recovery of the elk population.
Following wolf recovery, ungulate populations will continue to fluctuate in response to winter severity, habitat condition, hunter harvest, predation, and other environmental factors. However, population highs will be lower and population lows will not be as low as prior to wolf recovery.	Ungulate populations have continued to fluctuate in response to these factors. It is anticipated that elk numbers will decrease toward a lower equilibrium owing to a combination of multiple predators, human harvests, and occasional severe winter-kills.
Winter mortality of ungulates will be less than prior to wolf restoration.	The number of deer and elk carcasses observed during spring helicopter surveys in the low-elevation, Gardiner basin portion of the winter range for northern Yellowstone elk has decreased since wolf restoration, with the exception of 1997, during which there was a severe winter-kill.
Wolf predation will not comprise more than 21% of the total predator-caused mortality of adult ungulates.	Since 2000, wolves have accounted for 45% (n = 18) of the total deaths for which the cause of death was known (n = 40), and 75% of the predation deaths (n = 24; not including

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EIS Prediction	Ten-Year Appraisal
	human harvest), of radio-collared adult female elk (*n* ~ 111) on the northern range. For comparison, human harvest and winter-kill accounted for approximately 30% (*n* = 12) and 8% (*n* = 3) of the total known deaths, respectively.
IMPACTS ON HUNTER HARVEST	
Effects of wolf predation on hunter harvests will be undetectable during the initial years following wolf restoration.	The average annual harvest of 1,372 elk during the Gardiner late elk hunts from 1995 to 2004 was higher than the long-term average of 1,014 elk during 1976–1994. Hunter success during 1995–2004 (mean = 65%; range = 43–97%) was similar to success during 1976–1994 (mean = 64%; range = 10–96%).
Following wolf recovery (10 packs, 100 wolves), hunter harvest will be reduced 27% for antlerless elk, 100% for mule deer, and 50% for moose.	Contrary to expectations, harvests were not reduced appreciably concurrent with wolf restoration, but instead remained similar to pre-wolf restoration years. However, Montana Fish, Wildlife and Parks gradually reduced antlerless permits for the Gardiner late elk hunt by 51% from 2,882 to 1,400 during 2000–2004. They recently proposed 100 permits for 2006, a 96% decrease from the 2,660 permits issued in 1995, owing to decreasing abundance and low recruitment. No reductions in permits, animals harvested, or hunter success for mule deer or moose have occurred as a result of wolf restoration.
Bighorn sheep and mountain goat harvests will not be affected by wolf recovery.	There has not been a reduction in permits or harvests of these species since wolf restoration.
IMPACTS ON DOMESTIC LIVESTOCK	
During the first five years following reintroduction, few wolves will be in areas that contain livestock, and losses to wolves will be few.	During 1995–1999, *confirmed* wolf depredation in the Yellowstone Recovery Area averaged 2 cattle (range = 0–5) and 20 sheep (range = 0–67) per year.
During years 5–10 following reintroduction (based on a recovered wolf population of 100 wolves in 10 packs), depredation rates on livestock will be similar to those in northwestern Montana, Minnesota, and Alberta, Canada.	During 2000–2003, *confirmed* wolf depredation in the Yellowstone Recovery Area averaged 27 cattle (range = 7–45) and 79 sheep (range = 39–117) with wolf numbers ranging between 177 and 301. Depredation in the Northwest Montana Recovery Area averaged 8 cattle (range = 6–10) and 6 sheep (range = 2–13) with wolf numbers ranging between 64 and 92.
Long-term depredation rates by a recovered wolf population will average 19 cattle per year (range = 1–32),	During 2002 and 2003, *confirmed* wolf depredation on livestock in the Yellowstone Recovery Area averaged 39

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EIS Prediction	Ten-Year Appraisal
with 85% being calves. Long-term depredation rates by a recovered wolf population will average 68 sheep per year (range = 17–110). Losses of lambs and adult sheep will vary widely but, on average, will be nearly the same.	cattle (33 in 2002 and 45 in 2003). About 85% of this depredation was calves. During 2002 and 2003, *confirmed* wolf depredation on sheep in the Yellowstone Recovery Area averaged 81 sheep (71 in 2002, and 90 in 2003). Losses included adults and lambs.
Depredation rates will be highly variable among years and areas. Depredation rates on sheep will be higher and more variable than for cattle.	During 1995–2003, *confirmed* wolf depredation on sheep was higher (average = 46 sheep per year) and more variable among years (range = 0–117) than on cattle (average = 13; range = 0–45) in the Yellowstone Recovery Area.
Cattle and sheep will likely constitute 95%–100% of livestock killed or injured by wolves.	Cattle and sheep accounted for 98% of the 547 *confirmed* livestock depredations in the Yellowstone Recovery Area during 1995–2003.
Wolf depredation will not have a measurable effect on livestock production for the industry as a whole, but annual losses of livestock will not be evenly divided among livestock operators and a few individual operators may be quite adversely affected in any one year. A few operators may sustain chronic losses.	Wolf depredation did not have a measurable effect on the livestock industry as a whole averaging <1% loss to wolves per year. Livestock losses were not evenly divided among operators, and annual or chronic losses did adversely affect some operators.
Annual losses of livestock to wolf depredation on national forest lands that are seasonally grazed will likely be about 8 cattle (range = 1–13) and 68 sheep (range = 38–110).	Approximately 55% of livestock losses have been on public land and 45% on private.
Most livestock depredation by wolves on public lands will occur during the summer and early autumn.	Peak livestock kills by wolves were in August and September, but kills occurred in all months of the year.
Wolf predation on domestic dogs will be infrequent. This predation will occur near rural residences or at the edge of small rural communities in areas where wolf densities are high.	Wolves killed 1–8 dogs per year (confirmed total = 25) in the Yellowstone Recovery Area during 1995–2003. Predation generally occurred on guard or herd dogs protecting livestock in rural areas.
Losses of livestock from wolf predation will not average more than 0.1% of any class of livestock in the analysis area and no cumulative impact on livestock populations is expected.	Livestock losses to wolves did not exceed 0.1% per year for any class of livestock.

IMPACTS ON LAND USE

EIS Prediction	Ten-Year Appraisal
Land management agencies may restrict public access around active wolf den sites from April 1 to June 30 when there are five or fewer breeding pairs. About 5 mi^2 (13 km^2) could be affected. No land use restrictions will be employed after six breeding pairs of wolves are established.	Land use restrictions occurred around active wolf dens inside national parks. The area of use affected was approximately 2 mi^2 (4 km^2). These restrictions have continued after six breeding pairs of wolves were established.

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EIS Prediction	Ten-Year Appraisal
Public access to wolf confinement/release sites will be restricted about 1 mile (1.6 km) around the facilities to prevent harm and avoid habituation.	Public access to wolf confinement/release sites was restricted about 2 mi^2 (4 km^2) around the facilities.
Most wolves (7–11 packs) will live in the northern third of Yellowstone National Park.	Most wolves lived in the northern third of Yellowstone National Park during the early years following restoration. By 2005, however, only 50% of the population lived in the northern third of the park, while the remaining wolves were spread throughout the park.
Wolves will select denning areas to avoid traffic and noise.	All dens but one were located in secluded locations. One den was within one-half mile of the road and received much visitor attention.
No measurable limitation on visitor use is expected because little backcountry activity occurs until late June and commercial outfitting begins after July 1. No adverse effects to reintroduced wolves are expected from visitor use.	No measurable limitation to visitor use occurred and wolves have not been adversely affected by visitors.
Limits on public use to protect den areas will not affect initiation of grazing on national forest allotments. Livestock grazing areas will not be adjusted to accommodate wolf occupancy if conflicts develop.	No restrictions on livestock grazing have been implemented because of wolves.
It is unlikely that closures to protect wolf dens will preclude a measurable portion of annual timber harvest. Some sales could be delayed if they were proposed during April 1–June 30.	No timber sales have been precluded or delayed because of wolves.
Access to national forest lands will not be significantly affected during the wolf denning period.	Access to national forest lands has not been restricted because of wolves.
The presence of wolves may limit/suspend the use of M-44 traps on several of the 185 farms and ranches near the park during any one year, but no cumulative effects are expected.	M-44 use has not been restricted because of wolves.
No changes in public land use levels or patterns are expected.	No changes in public land use levels or patterns have been recorded.
IMPACTS ON VISITOR USE	
A slight long-term increase in visitor use will occur because people want to see or hear wolves in a wild setting.	Based on responses to a 1999 visitor survey, 4.9% of winter visitors and 3.5% of residents and nonresidents (states outside ID, MT, WY) would not have made their trip to Yellowstone if wolves were not present in the park.

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EIS Prediction	Ten-Year Appraisal
Visitors to the park will have the opportunity to see or hear wolves, or see their sign.	To date, approximately 153,000 park visitors have seen wolves. The park is now acknowledged as the most likely place in the world to see wild wolves.
IMPACTS ON ECONOMICS	
The primary costs of wolf recovery will include: a) wolf management costs, b) foregone hunter benefits (the economic value hunters derive from their hunting experience), and c) the costs of wolf predation on domestic livestock.	Wolf management costs, impacts on hunters, and wolf predation on livestock have proved to be the primary costs of wolf recovery.
Wolf management costs associated with reintroduction in the GYE were estimated to include $3,077,500 for a five-year reintroduction effort (1994–1998) and about $1.3 million for monitoring and wolf control (1999–2002), or about $320,000 per year. Reintroduction in central Idaho (1994–1998) was expected to cost about another $2 million.	Wolf reintroduction proved to be less costly and speedier than anticipated. Actual wolf reintroduction took only two years, not five, and cost only about $870,000 for both Yellowstone and Idaho combined ($585,000 in the first year and $285,000 in the second year). However, the combined annual continuing costs of wolf monitoring and management are now substantially higher than earlier estimates, even when corrected for inflation. For example, the U.S. Fish and Wildlife Service estimates the additional continuing cost to taxpayers until delisting will be about $1.5 million per year.
Reduced hunter harvest of elk, mule deer, and moose in the Greater Yellowstone Recovery Area could result in foregone hunter benefits of $187,000 to $465,000 per year. The first estimate is specific to Yellowstone's northern range and associated hunting districts in Montana. It was anticipated that a foregone harvest of up to 9 moose, 122 antlerless mule deer, and 280 elk in adjoining hunting districts in Montana would lead to a loss of 2,300 hunter days annually. The loss specific to elk hunting was estimated to be about $97,000 annually, or about 50% of the total value of foregone hunting opportunities.	Elk hunter harvests in the Gardiner, Montana, late hunt from 1995–2004 were on average 35% higher than the long-term pre-wolf average (1976–1994). No wolf-related changes in deer or moose harvests have been identified in this period. However, the late hunt elk permits have been sharply reduced in the last few years, to 1,100 antlerless permits for 2005. The antlerless harvest in January–February 2005 was 392 elk, about 625 fewer elk harvested compared to the pre-wolf average. Associated foregone use is estimated to be about 2,900 hunter days, valued at an estimated $280,000 (using 1994 EIS economic parameters).
Wolf-related livestock depredation losses in the Yellowstone area were expected to be between $1,887 and $30,470 per year. This is derived from predation rates in Minnesota, northwestern Montana, and Alberta, Canada; relative numbers of livestock at risk; and an assumption of 100 wolves in a recovered population. From 1 to 32 cattle were expected to be lost each year, at a 1993 market value of $715, and from 17 to 110 sheep per year, at a market value averaging $69.	In the period 1997–2000, when there were roughly 80 to 175 wolves in the recovery area, there were on average 35 sheep, 7 cattle, 3 dogs, and 1 horse taken by wolves annually (including both confirmed and probable losses). The Defenders of Wildlife compensation fund paid an estimated market value specific to each depredation incident, averaging about $11,300 per year in this period. Now that wolf populations have approximately tripled to around 300 wolves in the recovery area, losses and payments have increased. In 2003, Defenders paid about $32,000 for about 137 sheep and 66 cattle; in 2004, payments were a little
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EIS Prediction	Ten-Year Appraisal
	over $70,000 for 209 sheep, 57 cattle, and 6 other animals. The latter costs, per 100 wolves, are within the range of the 1994 EIS prediction.
The primary benefits of wolf recovery will include both values derived from direct experience and values derived from knowing that wolves exist in the park.	Wolves have proved to be unexpectedly visible to Yellowstone National Park visitors. From a sample of 1,143 winter visitors to Yellowstone in 1999, 35.9% reported that "seeing or hearing wolves was one reason for making the trip to the Greater Yellowstone Area." About 42% of summer visitors in 1999 (n=1,291) also agreed with this statement. A total of 46.5% of visitors agree with the statement: "I would derive satisfaction from just knowing wolves are present in Yellowstone National Park," while 41% disagreed. A total of 59.1% agreed that "I would like it if visitors to Yellowstone National Park had the opportunity to hear or see wolves."
The mean net economic value associated with wolf recovery in the Yellowstone area is estimated to be $8.3 million (95% confidence interval of $6.7 to $9.9 million).	This is an area for further research. However, the underlying demographic and attitudinal causes of economic demand for wolf conservation appear to be trending upward, including income, increasing familiarity with livestock depredation funds, and indications that people are valuing just knowing that wolves are present in the park.
Visitors will place value on seeing and hearing wolves.	Respondents to a park visitor survey conducted in 1990 ranked wolves ninth among the animals they would most like to see on a visit to the park (after grizzly and black bear, moose, bighorn sheep, elk, mountain lion, eagle, and bison). By 1999, park visitors ranked wolves as the number one animal they would most like to see on a winter visit to Yellowstone, and summer visitors ranked wolves second only to grizzly bears (58% ranked grizzly in the top three they would like to see, compared to 36% for wolves).
Wolf reintroduction will result in positive regional economic impacts in the Yellowstone area through a projected increase of $23 million per year in visitor expenditures, based on an estimated increase in visits of 10.4% for regional (ID, MT, and WY) visitors ($3.3 million), and 4.8% for nonresidents ($19.7 million).	There is not yet enough data to report regional economic impacts, but based on responses to a 1999 visitor survey, 4.9% of winter visitors and 3.5% of both resident and nonresident summer visitors would not have made their trip to Yellowstone if wolves were not present in the park.
Wolf recovery in Yellowstone will be a case where the benefits exceed the costs by a substantial margin.	Presuming that the estimated benefits for wolf recovery are relatively accurate (and corrected for inflation since 1994), wolf management costs and foregone hunter benefits would have to increase more than fourfold from their current estimated levels to approach even the lower range of the benefit estimate.

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Call for Papers

8th Biennial Scientific Conference on the Greater Yellowstone Ecosystem

GREATER YELLOWSTONE PUBLIC LANDS

A Century of Discovery, Hard Lessons, and Bright Prospects




The goal of the conference is to generate, in non-technical language, a publicly-oriented discussion of the mandates, "cultures," relationships, and accomplishments of the numerous local, state, and federal management agencies responsible for Greater Yellowstone's public lands. Are the "conflicting mandates" of these agencies really the problem they've been portrayed to be? What are the prospects for long-term planning, scientific information exchange, sustainable recreation, and community prosperity? What new social and ecologic paradigms and perspectives may serve the needs of the region?

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The program committee invites all qualified parties to submit abstracts for papers, panels, and posters on the following topics:

Agencies and Communities ◆ History of management agencies (the fate of rivalries and partnerships) ◆ Management agencies and indigenous peoples ◆ Symbology of ecosystem-related concepts in the evolving conservation ethic ◆ Development and effects of advocacy groups across the political spectrum ◆ Community partnerships

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FROM THE ARCHIVES

"There still remain, even in the United States, some areas of considerable size in which we feel that both the red and the gray [wolves] may be allowed to continue their existence with little molestation."

—Aldo Leopold
The Wolves of North America, *1944*


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In April 1922, rangers shot a female gray wolf and captured her litter of pups. The pups were kept and shown at park headquarters at Mammoth Hot Springs for a week, after which they were destroyed by order of Yellowstone Superintendent Horace Albright in keeping with park policy.

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