YELLOWSTONE'S NORTHERN RANGE

COMPLEXITY & CHANGE IN A WILDLAND ECOSYSTEM

An introduction to ecology, management, and controversy in the world's first national park

Yellowstone's Northern Range fills an important gap in our information about this dynamic and complex land. It is presented here in a format that does justice to its significance, as it takes its place in the annals and literature of this great park.

We share this publication with gratitude to Canon U.S.A., Inc. During Yellowstone's 125th anniversary, Canon made possible the largest public/private sector wildlife conservation program in the park's history, "*Expedition Into Yellowstone.*" In addition to a series of critical species and habitat initiatives that will assist us in planning for the long term well-being of the majestic wildlands and animals here, Canon has funded this study's printing.

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We thank them for their generosity, and the selfless spirit with which their donation was made.

1872 - 1997

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Yellowstone's Northern Winter Range

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Yellowstone National Park
National Park Service
Mammoth Hot Springs, Wyoming

1997

Suggested citation:
Yellowstone National Park. 1997. Yellowstone's northern range: complexity and change in a wildland ecosystem. National Park Service, Mammoth Hot Springs, Wyoming.

Book design by Renée Evanoff. Color photographs courtesy National Park Service files, Renée Evanoff, and Nathan Varley.
Printed on recycled paper.

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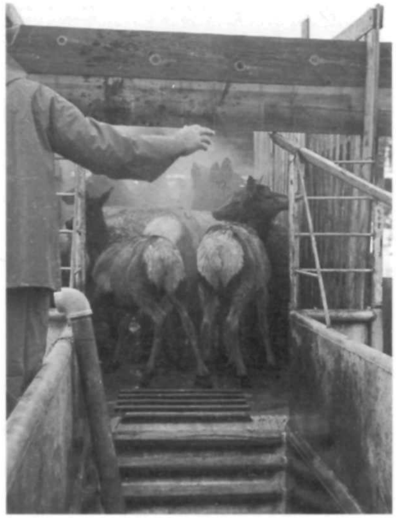
FOREWORD



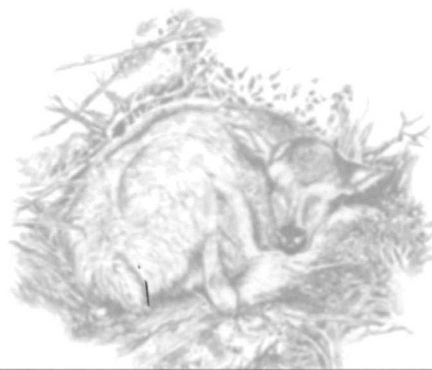
Yellowstone's northern range has inspired one of this century's most productive, if sometimes bitter, dialogues on the management of a wildland ecosystem. This book contains a vast amount of new scientific research about the range and forever changes that dialogue because it synthesizes a vast amount of new information that has previously been available only in highly specialized and technical journals. This book interprets and summarizes the work of dozens of ecologists and other researchers from across the scientific community, and it provides you with the formal administrative position of Yellowstone National Park on the northern range grazing issue.

This is an enormously exciting and challenging time for all of us who care about Yellowstone's northern range and the spectacular assortment of wildlife that inhabit the range. As knowledge accumulates, and as we better understand just how complex and subtle nature can be in a large wildland ecosystem, our job becomes more difficult rather than less. More new research on the northern range has been published in the leading scientific journals in the past 15 years than in the entire previous history of this world-famous landscape, and that research has shaken the foundations of traditional ideas, not only about Yellowstone, but about other similar wildland ecosystems. In time, we think this research will be of benefit to managers of other kinds of ranges as well, including livestock ranges; Yellowstone serves us in many ways, but one of the most important is as a "control site" against which we can measure our effects on other landscapes managed for other purposes.

Recent research may have changed many things, but it will not change the controversial nature of the northern range, which will always attract people with differing values that they would prefer to have applied to the management of this unique resource. Though it is far from the last scientific word on the northern range, this report can serve all viewpoints by elevating the dialogues to a previously impossible level of knowledge. It is only through a common awareness of the range's history and ecology that we will work together to give it the best care possible.

Mike Finley, Superintendent, Yellowstone National Park

EXECUTIVE SUMMARY



The condition of the winter range of the northern Yellowstone elk herd (referred to here as the northern range) of Yellowstone National Park has been of concern to the public, managers, and scientists for more than 70 years. Before 1970, almost all observers regarded the range as overgrazed due to an overpopulation of elk. Other problems thought to have been caused by high elk numbers included declines in woody vegetation, especially willow and aspen, declines in white-tailed deer and beaver, and increased erosion. These concerns led to increasingly aggressive attempts to control elk herd size, which peaked in the 1960s, when thousands of elk were slaughtered. The agency's control actions resulted in a monumental public outcry and U.S. Senate hearings that led to the termination of elk control in the park.

Because of changing attitudes about natural systems in the scientific community and growing uncertainty over how ecological processes worked in Yellowstone National Park, National Park Service (NPS) managers and biologists decided to test the common assumption that the elk were inevitably inclined to overpopulate the range and, alternatively, to determine if the elk herd might be "naturally" regulated, or regulated by its environment. Natural regulation of animal populations was an established topic in ecology by the 1950s. In the 1960s and 1970s, by applying prevailing ecological theories relating to natural regulation, NPS scientists provided substantial evidence that traditional views of the range as overgrazed were either erroneous or based on incomplete information.

During the 1980s, concern over the condition of the range continued among the public and the scientific community. In 1986, Congress funded a major study initiative to address the overgrazing issue. Researchers noted that commercial range managers defined an overgrazed range differently than did wildland ecologists. Use of commercial

range criteria to judge a wildland grazing system, as was done from the 1920s to the 1960s, was a primary cause of confusion over the condition of the range. During the study years 1987-1990, the bunchgrass, swale, and sagebrush grasslands of the northern range did not appear to be overgrazed by any definitions of overgrazing. In fact, production of grasses was not reduced or, in some cases, was actually enhanced by ungulate grazing in all but drought years. Protein content of grasses, growth lengths of big sagebrush, and seedling establishment of sagebrush were all enhanced by ungulate grazing. Overgrazing typically reduces root biomass and results in more dead bunchgrass clumps, but neither of these signs of overgrazing was observed.

Photographs of riparian areas on the northern range in the late 1800s show much taller willows in some locations. Studies have shown that virtually no aspen have escaped ungulate browsing and reached tree height since the 1930s. Some researchers have attributed these changes in willow and aspen success to overbrowsing by ungulates, while others ascribed the changes to more complex interactions of climate, fire suppression, and ungulate use. Aspen history was clarified by the discovery that since the early 1800s there has been only one period, between about 1870 and 1895, when aspen have escaped browsing and grown to tree height on the northern range. The inability of aspen to grow to tree height in the period between about 1800 and 1870 suggests that then, as now, elk may have been abundant enough to contribute to the suppression of aspen regeneration; other factors that may have contributed to such suppression include fire. This discovery, that aspen only successfully reached tree height during one period in the park's history, casts a new light on today's elk browsing of aspen, suggesting that perhaps the failure of aspen to reach tree height in recent years should not be solely regarded as proof of elk overabundance, but perhaps instead that the lack of aspen is due to a complexity of factors that include elk, but also climate change, especially to a more arid state (Romme et al. 1995), fires, and predator abundance. More research will be needed to improve our understanding of woody vegetation on the northern range.

Erosion and heavy sedimentation in northern range rivers was traditionally attributed to an abrupt increase in elk numbers around the turn of the century. However, numerous recent studies of historical and modern erosion indicate that there are several highly erodible areas in northern range drainages that historically and currently contribute most of the sediment to local watercourses. These erosion sources apparently operate independently of ungulate influence. One area of potential concern is that grazed sites have less litter, more exposed surface (11 percent more), and slightly higher soil compaction. We interpret these trends as logical consequences of ungulates consuming vegetation and just moving about. Most grasslands sampled contained enough protective groundcover to protect them from accelerated erosion. Experimental sedimentation work found no significant difference attributable to grazing. The study of sediments in eight small lakes on the northern range indicated no measurable recent change in erosion patterns that would result from sudden increases in ungulate use of the lake shores. Erosion rates in riparian areas have not yet been comprehensively studied, though it is visually obvious that ungulate use of these areas likely contributes to the movement of soil on some streamside banks through their trailing, wallowing, and rubbing. Visual evidence, however, is not scientific quantification; more research is needed, especially with respect to riparian erosion systems.

Paleontological, archeological, and historical evidence indicates that elk and other ungulates, as well as large predators, were present and common on the northern range for thousands of years prior to the establishment of Yellowstone National Park. Several alternative scenarios have been proposed explaining their past and present abundance, and for the influences that Native Americans had on wildlife populations. Further work in these fields is needed as well.

The northern Yellowstone elk herd cannot be regarded as increasing without control. Population regulation mechanisms are evident in the northern Yellowstone elk herd; the herd is naturally regulated by a combination of forces.

From 1987 to 1990, combined summer predation by grizzly bears, coyotes, black bears, and golden eagles averaged 31 percent of elk calves born on the northern range, and winter mortality, mostly due to undernutrition in the very young and very old elk, averaged 20 percent. "Density dependence" (the measure of a population's response to higher numbers with lower growth rate) was well-documented for the northern elk herd. Over-winter calf mortality, yearling elk mortality, and adult bull mortality all increased with higher elk density. Pregnancy rates of both yearling and adult cow elk also declined at higher elk densities. Population increases in the 1970s were due to release from the extreme elk reductions in the 1960s, and increases in the 1980s were due to a series of mild winters and wet summers, plus acquisition of more than 10,000 acres of additional winter range north of the park. A third of the northern winter range is on public and private lands north of the park, where elk often compete with livestock for grazing lands. The northern Yellowstone elk herd counts have not increased significantly since 1991, varying with conditions between 16,000 and 20,000 animals. We conclude the addition of wolves to the predator community may reduce the herd by 8 to 20 percent at some time in the future, if, according to three independent modeling efforts, 75 to 100 wolves eventually occupy the area. A minority opinion among the scientists who studied the situation was that up to 200 wolves may occupy the northern range which, if it happened, might reduce elk up to 50 percent.

For the most part the fates of other ungulate species do not seem tied to elk numbers. Five other ungulate species that coexist with elk increased in the 1980s. Only moose did not. Bighorn sheep status is complicated by a disease outbreak in the early 1980s that reduced the population, but they too have been recovering since that time in the face of high elk numbers. There is considerable overlap in forage between sheep and elk, so the possibility of competition between these two species must be considered; but competition between species is a fact of life in nature, and does not necessarily prove something is inherently "wrong."

Supposed "declines" of beaver and white-tailed deer after 1920 were based in good part on inaccurate historical interpretations. Beaver persist at low levels on the northern range, with more abundant colonies living in suitable habitat elsewhere in the park. White-tailed deer are sighted regularly on the northern range in summer, in very low numbers perhaps similar to those at the time of the park's establishment.

Pronghorns, once extremely abundant throughout greater Yellowstone but heavily controlled and reduced by managers well into the 1960s, exist on the northern range in a small and apparently isolated population that is in some danger of disappearance. Competition with elk does not appear to be a significant limiting factor for the pronghorns. Diet and habitat overlaps between elk and pronghorns were minimal. For example, pronghorns increased at a very rapid pace in the 1980s in spite of very high numbers of elk. Similarly, a decline in pronghorns in the 1990s appears unrelated to elk numbers.

Grizzly bears and other predators, including black bears, mountain lions, wolves, and coyotes, rely heavily on elk for food. A human-caused reduction of the northern elk herd would almost certainly place some of these predator populations in jeopardy. This is also true of a host of scavengers such as ravens, eagles, and foxes, plus many small birds, mammals, and insects.

Over the almost 30 years since its inception, many elements of the natural regulation policy have undergone repeated tests, and additional work is necessary to clarify the ecological consequences of the policy. However, research conducted to date, which amounts to one of the largest and most comprehensive issue-oriented research programs in the history of the National Park Service (or in North America), has demonstrated that natural regulation is not only the most valid management option of the northern range (of the several options available), but is also the option that promises to teach us the most about wildland ecosystems in both the short and long term.

CHAPTER ONE

HISTORY OF NORTHERN RANGE RESEARCH AND MANAGEMENT

The condition of the winter range of the northern Yellowstone elk herd (referred to here as the northern range) of Yellowstone National Park has been of concern to the public, managers, and scientists for more than 70 years. During that time, many different interpretations of its condition have been put forth; the majority of opinions offered prior to 1970 agreed that the range was to some extent overgrazed. Many observers regarded overgrazing as severe. Overgrazing was almost always attributed to high elk numbers, but bison and pronghorn were implicated as well. Other problems thought to have been caused by high elk numbers included declines in woody vegetation, especially willow, aspen, and several sagebrush species, declines in white-tailed deer and beaver, and accelerated soil erosion.

Changing perspectives in management and in the ecological sciences in the past 30 years have resulted in an intensive reconsideration of past views, and have also resulted in renewed controversy over the range and its management. This report summarizes the long history of this issue, especially the tremendous surge in scientific research in the past decade, research that has changed the nature of the overgrazing debate in Yellowstone National Park, and promises to have far-reaching effects in the management of other wildland grazing systems as well.

Today's natural resource managers and users are recipients of a rich legacy in national parks. The legacy includes not only the resources themselves but also the array of policy, regulations, and management directions that have grown during the institutional history of the parks. The National Park Service's Management Policies (1988) have summarized this legacy as follows:

> The natural resource policies of the National Park Service are aimed at providing the American people with the opportunity to enjoy and benefit from natural environments evolving through natural processes minimally influenced by human actions. The natural resources and values that the Park Service protects are described in the 1916 NPS Organic Act (16 USC 1 et seq.) and in the enabling legislation or executive orders establishing the parks. These resources and values include plants, animals, water, air, soils, topographic features, geologic features, paleontologic resources, and aesthetic values, such as scenic vistas, natural quiet, and clear night skies. Some of these resources and values are protected both by NPS authorities and by other statutory authorities, such as the Clean Air Act (42 USC 7401 et seq.), the Clean Water Act (33 USC 1251 et seq.), the Endangered Species Act (16 USC 1531 et seq.), the National Environmental Policy Act (42 USC 4321 et seq.), and the Wilderness Act (16 USC 1131 et seq.).

This generous and ambitious statement of purpose is the result of more than a century of experience, struggle, and experimentation in national park management that began in Yellowstone National Park in 1872. The park was created prior to the development of the professions of wildlife management and range management in North America, and at a time of great waste of wildlife and other resources. With little or no funding and even less specific legislative direction, early park managers began the park's 125-year struggle to come to terms with managing this large, complex wildland.

EARLY MANAGEMENT

Figure 1.1. Photographer William Henry Jackson, a member of the 1872 Hayden Survey, took this photograph along the Yellowstone River in Yellowstone National Park about three miles from the Lower Falls. It shows Hayden Survey hunter Fred Bottler (center) and companions with five freshly killed bull elk. Until 1883, park visitors were legally entitled to hunt and kill wildlife for food, but the industrial slaughter of market hunters led to the prohibition of hunting in the park. NPS photo.

From 1872 to 1883, public hunting was legal in the park, partly because there were few services available to visitors, who often killed park wildlife to supplement their provisions (Figure 1.1). According to early regulations, hunting was limited to sport or subsistence killing by visitors, but the market hunting that swept many western gamelands in the 1870s and early 1880s did not miss the large wildlife herds of Yellowstone (Schullery in press). Market hunting probably started in the Yellowstone Valley north of the present park around 1869-1870, and soon was occurring within the boundaries of the newly established park. The park's early civilian administrators (1872-1886), who spent only the brief tourist season in residence (and some years did not visit at all), were not equipped or funded to prevent industrial-scale slaughter of park wildlife, which usually took place in early spring. This slaughter began before the park was established, and seemed

to abate in the late 1870s, gradually tapering off further in the early 1880s. Little information has survived on the number of animals killed, but Schullery and Whittlesey (1992) reviewed contemporary informal accounts of the slaughter of a minimum of 8,000 elk on portions (though by no means all) of the northern range in 1875. Most of these were killed in the park, including 4,000 reportedly killed in 1875 in the Lamar Valley. Thousands of other animals—bison, deer, pronghorn, and bighorn sheep—were also killed, most for their hides, while their carcasses were poisoned to kill predators and scavengers. Schullery and Whittlesey (1992) suggested that by 1883, when public hunting became illegal in Yellowstone National Park, wolves and other carnivores may already have been seriously reduced, more than two decades prior to the well-known federal predator-control program of the early 1900s.

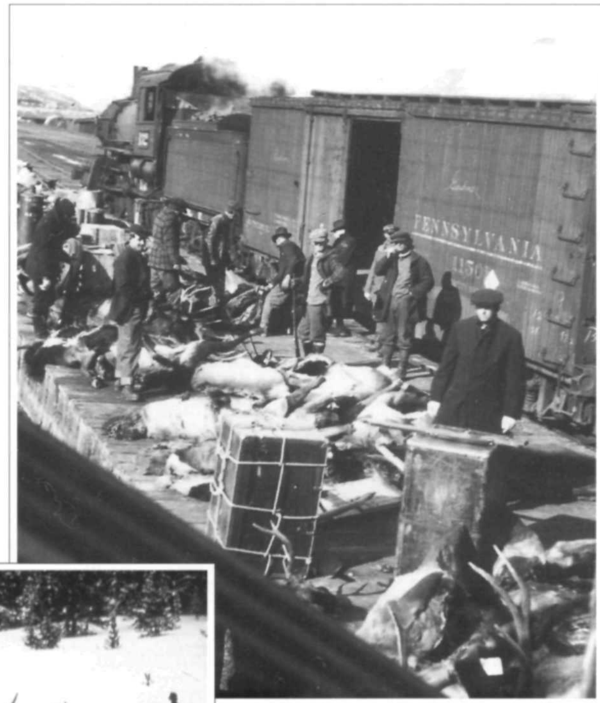


Figure 1.3. Hunters loading elk at the Gardiner Depot, 1919. Once they were protected by Yellowstone National Park and Montana game laws, migrating members of the northern Yellowstone elk herd supported an important sport hunt in southeastern Montana. NPS photo.

Figure 1.2. Deep snow made elk easy to reach, for both poachers and early visitors. Haynes photo from the NPS files.

In 1886, the U.S. Cavalry was assigned to protect Yellowstone National Park, and did so until 1918. The National Park Service was created in 1916, but did not assume control of park management until 1918, and at first continued the wildlife-management policies developed by the army. Wildlife-management practice and philosophy has undergone many changes in Yellowstone National Park, which has been a primary testing ground for new ideas and approaches (Haines 1977, Wright 1992, Schullery in press).

THE ERA OF INTENSIVE MANAGEMENT AND EARLY RESEARCH

From the arrival of the army in 1886 to the 1930s, wildlife management in Yellowstone National Park was in good part seen as protecting the grazing animals and other herbivores from poachers, predators, and other threats, including winter mortality. As early as the 1880s, conservationists, especially sportsmen, had recognized that the park could serve as a reservoir of game to restock surrounding lands with an endless supply of elk, deer, and other popular species, so the 1883 prohibition of hunting in the park received wide support from hunters in the then-young conservation community (Schullery in press). As the animals became less wary and easier to see, the park became recognized as one of the world's foremost wildlife sanctuaries, which in turn meant that the animals became an important attraction and a significant part of the visitor experience (Figure 1.2).

But at the turn of the century, wildlife biology was in its infancy, and there was little available expertise in how best to manage the wildlife of a large wilderness reserve (Figure 1.3). Management mostly came down to protection of the "good" animals, which even included feeding them in winter. Much of what was "known" about these animals was in fact folklore or misconcep-

tion. There was not only uncertainty over the numbers of mammals, especially elk, but also great confusion and inconsistency in early reports of those numbers (Appendix B) (Tyers 1981, Houston 1982). Houston (1982) reviewed early "census" reports from the army period (1886-1918) and the early National Park Service administration. He demonstrated that estimates of elk numbers, which typically ranged from 15,000 to 40,000 but sometimes as high as 60,000, "in some cases were seemingly based on little more than the previous estimate," and often included very different combinations of at least eight elk herds that lived seasonally or all year long in the park.

Toward the close of the army period, after about 1910, more serious attempts were made to accurately census the northern herd, but again, Houston (1982) has demonstrated that flaws in methods used led some park administrators to continue estimating 25,000 to 30,000 elk, while professionally conducted counts yielded smaller numbers: 9,564 elk actually counted (from the ground) between the upper Lamar Valley in Yellowstone National Park and Dailey Lake in Paradise Valley, Montana in 1916, and 10,769 elk actually counted between the upper Lamar Valley and Stands Basin (northwest of Dome Mountain, in Paradise Valley) in 1917. Unfortunately, even today some scientists persist in using the most inflated early estimates (Wagner et al. 1995*a*), rather than the better-documented counts. The first regular aerial surveys of elk began in 1952, and that is the beginning of the era when elk counts can be accurately compared between years.

The question of numbers of elk has been central to dialogues over the condition of the northern range throughout the rest of the century. Perhaps the most famous early episode in the history of Yellowstone's northern herd was the supposed "crash," or massive winterkill, in the winter of 1919-1920, when second-hand reports of as many as 14,000 elk dying of undernutrition were circulated and have since made their way into modern wildlife management literature as fact. This spectacular die-off of elk seems not to have happened; the most alarming accounts of it were written by people far from the scene. Houston (1982), in the most thorough review of the actual counts made of elk prior to and following that winter, reported that in the spring of 1920, field personnel reported winter mortality of 700 to 1,500, with another 3,500 killed or crippled by hunters north of the park in the fall of 1919. Houston's clarifications of these and other historical numbers of elk have not been challenged in the scientific literature, and are accepted for the

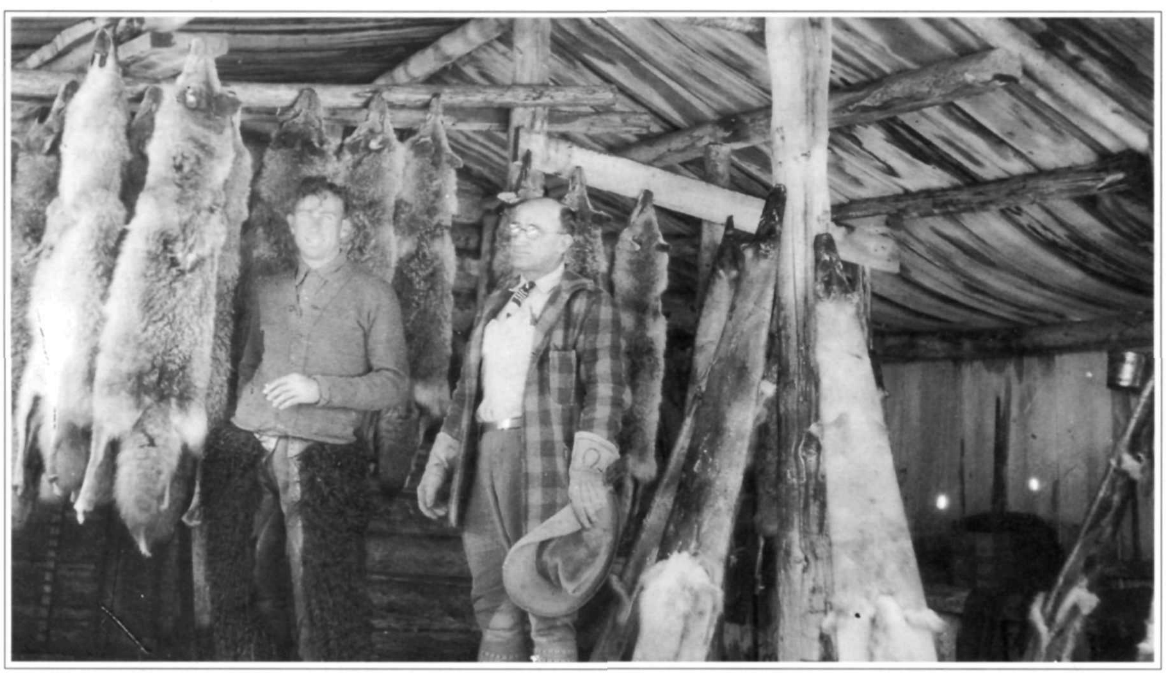


Figure 1.4. Rangers with predator hides during National Park Service predator control era in the 1920s. NPS photo.

purposes of this overview.

By the 1920s, several ideas had emerged that would guide wildlife managers in their thinking about the management of the northern herd. The most important of these ideas was that there were now "too many" elk. This conviction was based on the assumption that elk and other large grazers were not native to Yellowstone National Park, or at least did not inhabit the park in large numbers until the 1870s, when they were "crowded farther back into the mountains" by human settlement pressures (Graves and Nelson 1919). With this fundamental assumption driving their thinking, managers and other observers spent the first seven decades of this century expressing alarm over the high numbers of elk. Until the 1920s, such expressions were limited mainly to concern for the large numbers of elk that might die in a given winter. This concern was focused on the seeming waste of game animals. But by the 1920s, more concern was expressed about overgrazing of the range and other effects the elk were thought to be having on their habitat.

A comprehensive history of American wildlife management is beyond the scope of this book, but it must be kept in mind that other factors were at work in the development of management practices in Yellowstone National Park. National predator control initiatives, aggressively fostered by the ranching community and just as aggressively carried out by various state and federal agencies, were further complicating the relationship of many herbivore populations with their environments; in Yellowstone National Park, many predators were poisoned even in the park's first years, and between 1900 and 1935, more than 100 wolves and mountain lions and more than 4,000 coyotes were killed (Figure 1.4) (Murie 1940, Weaver 1978). Similarly aggressive predator-killing campaigns were conducted on the lands surrounding the park, where livestock operators' concerns led to the extermination of some predators and the drastic reduction of others.

At the same time, most of the park's grizzly and black bears were inadvertently "trained" to feed on garbage rather than search out native foods (Figures 1.5, 1.6). They were effectively "divorced" from their native feeding regime for a significant part of the year, and their behavior and habitat use was altered in the process (Schullery 1992, Craighead et al. 1995).

Increased human settlement of winter ranges throughout the west was in fact reducing the available winter forage of many herds. As early as 1917, biologists recognized that Yellowstone's northern winter range included the entire river valley from the park boundary 11 miles north to Dome Mountain, much of which would become unavailable to the elk in the succeeding decades as human development in wildlife migration corridors proceeded.

During this time, ongoing climatic changes seemed to complicate efforts to understand range conditions. The ending of the Little Ice Age in the mid-1800s meant that the park's climate was in a transition period of some significance even as it was being established. The wet period of 1870-1890 came when white people were developing their first impressions of Yellowstone's climate, but the drought of the 1930s displayed the variability of the area's climate. Against this backdrop of a dynamic system, managers attempted to determine what condition the park's range "should" be in when in fact the ecosystem was offering evidence that there was no such specific condition.

Traditionally, managers of national parks have tended, either formally or unofficially, to regard the establishment date of a park as a kind of

Figure 1.5. Garbage-fed bears were a major tourist attraction in the 1930s, when hundreds of people gathered nightly to watch bears at the dump a few miles south of the Canyon area. NPS photo.

Figure 1.6. Grizzly bears and gulls at the Canyon dump, 1930. In the 1960s and later, ecological research would indicate that the dumps dramatically altered the behavior, movements, and other activities of Yellowstone bears. NPS photo.

baseline against which to measure and judge later changes in that landscape, but this view has fallen out of favor more recently, because of the inherent variability of ecosystems and because it is now known that influences of Euramericans on landscapes often predated their actual arrival (see Chapter Two). Even recognizing the shortcomings of attempting to establish a baseline date by which to judge later conditions in a national park, it should be pointed out that the year 1872 was an especially bad choice for making such judgments. Not only had the park area just recently emerged from the Little Ice Age, and not only had the park experienced extensive fires in the 1860s (Romme and Despain 1989*b*), but also the park was just then at the beginning of a two-decade period of unusually high precipitation (Houston 1982). Park managers and observers, who for generations have attempted to understand the park's ecology in terms of its establishment date, were slow to recognize the many consequences of relying on such a simplistic approach.

Human manipulation of the vegetation further complicated the picture. Fire, today recognized as an essential element in the shaping of most North American ecosystems, was regarded as an evil to be prevented at all costs. Historical evidence suggests that the only place firefighters were regularly able to suppress natural fire in Yellowstone National Park was in the grasslands, where the fire-return interval (about 25 years) was much more frequent than that of the surrounding forests (200 to 300 years), so it is possible that fire suppression had significant effects on northern range vegetation (Houston 1982, Romme and Despain 1989).

Underlying these difficulties were other beliefs that have since been challenged, if not discarded, by advances in scientific thinking. Perhaps the most important, if rarely articulated, was the assumption among the public that a primary goal of wildlife management was to provide consistency of production, whether the product was elk available for hunter harvest or grasslands available for grazing. Through the first half of this century, nature was perceived by many leading ecological thinkers as tending toward a stable state that managers could predict and maintain: the public was taught to think in terms of some ideal "balance of nature" that humans alone could disturb. The complexity of wildland grazing systems appreciated today was not yet grasped in the early 1900s. The implicit goal of most management actions prior to the late 1960s

was to regulate and manage Yellowstone's northern range so that its production of elk was more or less unvarying and predictable, and so that winter mortality did not occur or was kept to some ideal minimum.

In the 1920s and 1930s, concern over the condition of the range grew, as the elk population was repeatedly described as too large. Other aspects of the northern range came to the attention of observers. Skinner (1929) reported a decline in the park's white-tailed deer population, from 100 at the beginning of the 1900s to essentially none by the late 1920s. In 1931, Talbot reported an increase in exotic plant species and erosion, attributing these to overgrazing (Tyers 1981).

The most important of these investigations was conducted by U.S. Forest Service biologist W. M. Rush (1927, 1932). Based on horseback trips through part of the northern Yellowstone elk winter range in 1914 and 1927, Rush concluded that drought and grazing had lowered range carrying capacity, that erosion was widespread, that exotics continued to invade, and that all browse species would be lost if something were not done. Houston (1982) pointed out that "Rush recognized the cursory and subjective nature of his range assessments, a fact which seems to have been overlooked in subsequent references to his findings." Tyers (1981) and Houston (1982) summarized the work done by subsequent National Park Service biologists, especially R. Grimm and W. Kittams between 1933 and 1958, both of whom generally supported Rush's conclusions. By the early 1960s, the "Yellowstone elk problem" had become one of the longest-standing dilemmas in American wildlife management history. In June 1963, Cooper et al. made a 12-day survey of the northern range and estimated a winter elk carrying capacity of about 5,000, in keeping with several earlier estimates and using standards usually applied to domestic livestock grazing (Cooper et al. 1963).

From the 1920s to the 1960s, northern Yellowstone elk were trapped and shipped alive to re-stock depleted game ranges all over North America (Figure 1.7). In attempts to control or reduce the elk population (see carrying capacity, below) elk were also shot by park rangers and the meat was shipped to Indian reservations. In all, 26,400 park elk were removed from 1923 to 1968. From the mid-1930s to the mid-1960s, bison and pronghorn were also reduced in numbers or otherwise manipulated on the northern range.

The long-term monitoring conducted by Kittams until the late 1950s was followed by more

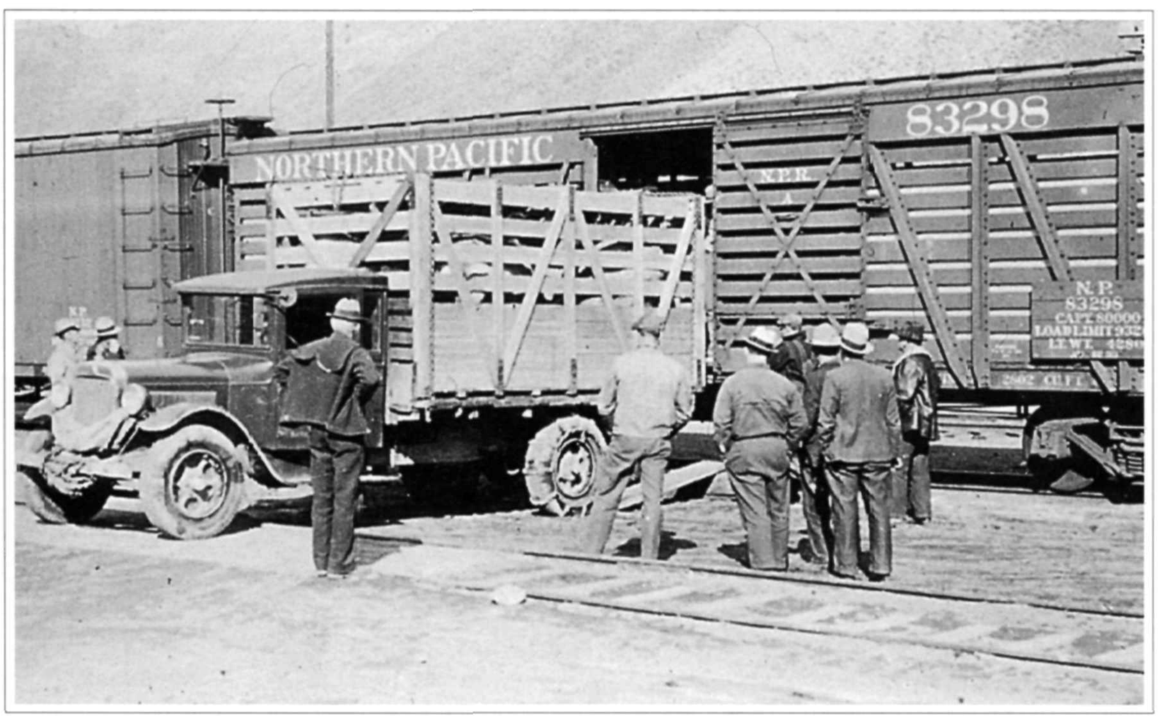


Figure 1.7. Loading live elk at the Gardiner Depot, 1935. Elk were transported live from Yellowstone to restock elk ranges in many other parts of the United States. NPS photo.

Figure 1.8. Elk killed during the herd reductions of the 1960s were distributed to regional Indian tribes. NPS photo.

comprehensive work (1962-1970) by Barmore, who examined interspecific relationships among the ungulates of the northern range (Barmore 1980). In 1963, Meagher began to study the life history, ecology, and management of bison; her work continues (Meagher 1973, 1976, 1989*a*, 1989*b*). From 1970 to 1979, Houston investigated history and ecology of the northern Yellowstone elk winter range (Houston 1982).

THE NATURAL REGULATION ERA

Houston began his work at a time of dramatic change in National Park Service management philosophy (Wright 1992). Traditional approaches to wildlife husbandry in parks were challenged, and new scientific approaches were emerging. Perhaps the most important event in the changing nature of Yellowstone elk management took place in the early 1960s, when Yellowstone's managers, on the advice of commercial range management authorities (Cooper et al. 1963), increased the intensity of their elk control and began killing thousands of elk in the park (Figures 1.8-1.13). At the time, consensus among managers and biologists was firmly in support of this action, but public outcry against the killing was so intense that hearings were held on Yellowstone elk management by U.S. Senator McGee (Wyoming) in 1967. Out of these hearings came a cessation of elk slaughter in Yellowstone National Park (and a brief period of intensive trapping and shipping of animals to other areas).

Even before the elk reduction crisis reached its well-publicized peak in 1967-1968, changing views of park resource management had been articulated in the now-famous Leopold Report, the statement of a panel of independent ecologists published in 1963 (Leopold et al. 1963). This group's work has been subjected to countless reinterpretations over the years. While some see their work as more or less reinforcing traditional policies, others interpret the Leopold Report as a bold new perspective for its time. With its advocacy of a much higher role for science in park management, and its numerous eloquent recommendations for such things as sustaining vignettes of primitive America, and a "reasonable illusion" of a wild system, the Leopold Report was to many minds at the time a revolutionary document, one that influenced Yellowstone's managers as they sought to resolve the apparently endless elk problem.

Superintendent Jack Anderson, appointed in 1966, and chief park biologist Glen Cole faced a difficult challenge in the elk management controversy. The public was opposed to killing elk in the park. Many hunters and the surrounding state wildlife-management agencies favored opening the park to hunting. Ranchers near the park wanted elk reduced to prevent range competition with livestock. The National Park Service, legally and traditionally opposed to hunting in parks, resisted continued manipulation of animal numbers in the park, while the scientific community largely agreed that the elk population must be controlled. The Senate hearings confirmed a strong public disapproval of elk reductions in Yellowstone National Park, but National Park Service leadership still believed they had the option of killing elk, however

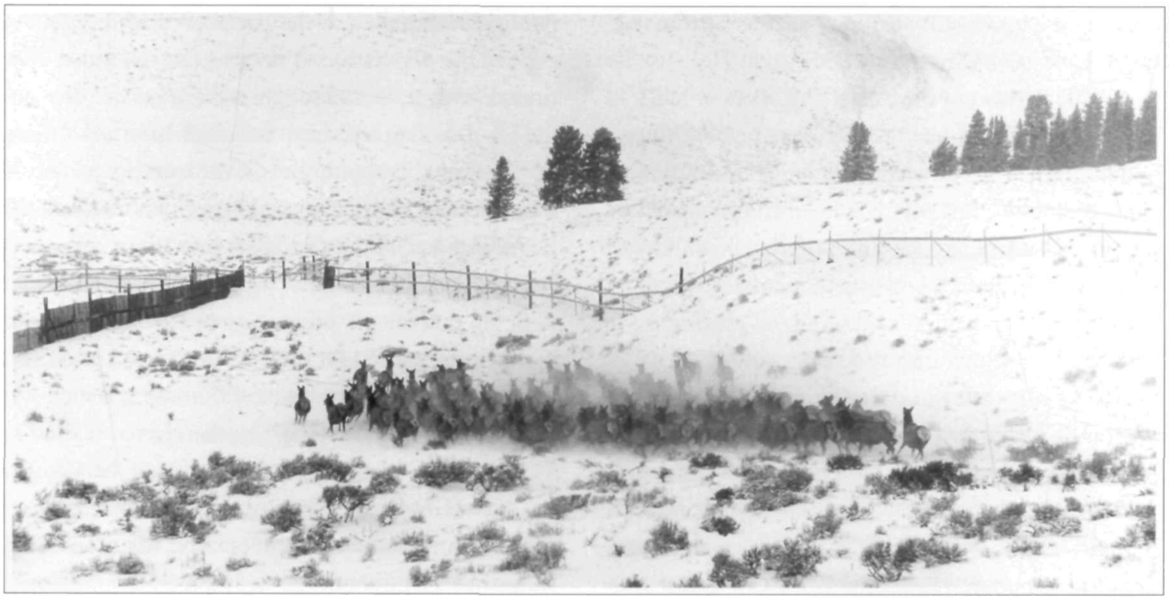


Figure 1.9. Helicopter pilot's view of herding elk into a corral at Daly Creek during elk reductions, 1964. NPS photo

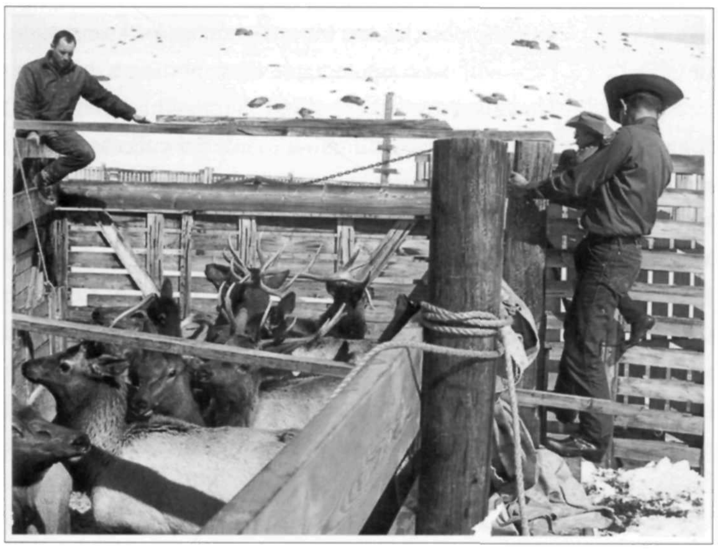


Figure 1.10. Live-captured elk were sorted by sex during preparation for translocation to other elk ranges. NPS photo.

Figure 1.11. A "squeeze chute" made it possible to tag and handle captured elk prior to translocation. NPS photo.

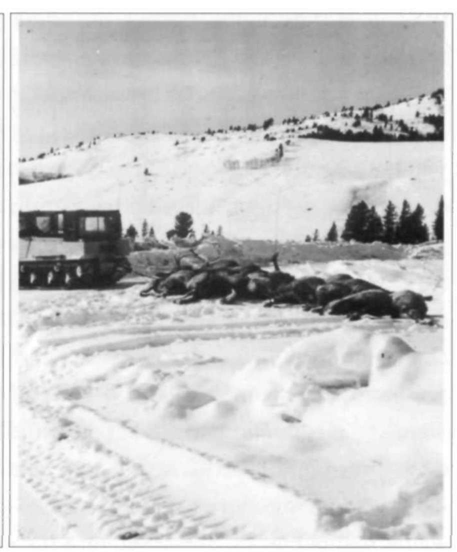


Figure 1.12. Captured elk were run through a dip tank to treat them for parasites prior to translocation (1963). NPS photo.

Figure 1.13. Elk killed during reductions were dragged to loading point by a tracked oversnow "weasel." NPS photo.

unpopular or politically difficult such an action might have been (Pritchard 1996).

The authors of the Leopold Report in 1963 had supported continued reduction of the elk population, but there was a growing distrust among some biologists, including Cole, of traditional interpretations of the condition of the range. There was little data from unexploited ungulate populations or from unmanipulated wildland grazing systems to apply to the Yellowstone situation, so managers were at a disadvantage in trying to determine just how a naturally functioning elk population might interact with its range. Cole and Anderson realized Yellowstone was a place where it might be possible to find out how a large ungulate population interacts with its environment, and at the same time make advances in understanding the park's oldest and most bitter wildlife controversies. Thus was born the natural regulation policy.

The development of the natural regulation policy has sometimes been mistakenly portrayed as an "only-option-left" approach, in which National Park Service managers were simply stonewalling, or buying time by doing nothing (Chase 1986). The natural regulation policy has been rhetorically cast in many other lights, from a great experiment in progressive wildland management to a simple effort to avoid confronting an elk overpopulation. However, a careful review of the administrative records of this period, as well as a review of the scientific literature, reveals that in fact National Park Service managers chose from among several options, and did not choose the easiest. Pritchard (1996) has reviewed the decision-making process by which natural regulation was chosen in the 1960s and early 1970s. Besides continued killing of elk, managers considered other options, including wholesale trapping and redistribution of elk, experimental neutering of animals, and hunting by sportsmen. Moreover, by 1967, Yellowstone's chief biologist Glen Cole believed that if the northern Yellowstone elk herd, whose migrations were at the time shortstopped at the park boundary by a "firing line," were instead allowed to restore their migratory pattern down the Yellowstone River Valley, enough of them would leave the park that public hunting outside the park could readily control the population as needed. At the same time, however, Cole brought a fresh perspective on the elk population's size. Based on his knowledge of other animal populations, Cole questioned the longstanding belief that the elk population was too large, and forced the dialogues into a new stage, from which they have not yet emerged. In short, noticing that the elk population had somehow been regulated naturally for thousands of years prior to the arrival of whites, he asked if it might not be naturally regulated now, given the chance (Cole 1971).

One interesting dimension of natural regulation that has made it controversial is that it in effect raises questions about the widespread assumption in traditional wildlife management circles that wildlife populations must be hunted by humans or they will overpopulate and destroy their habitat. However, the National Park Service has never displayed any inclination to use the success of natural regulation as a device to criticize hunting on other public lands. Indeed, historically, hunting of animals after they leave the park has been accepted and encouraged by the National Park Service as an appropriate use of those wildlife resources.

The idea of natural regulation had not originated in Yellowstone National Park or in the National Park Service. In the 1940s and 1950s, a number of ecological researchers had explored how populations were regulated; the most notable of these may have been David Lack, whose book *The Natural Regulation of Animal Numbers*, was published in 1954 (Botkin 1990, Porter 1992, Pritchard 1996). When Cole came to Yellowstone and began reconsidering traditional interpretations of the elk population's demographics, behavior, and of the condition of the northern range, he drew Yellowstone National Park into an ongoing debate over what regulates animal populations and how such regulation functions. Now, 30 years after Cole's arrival, scientists are still debating many elements of natural regulation theory (Boyce 1991, Patten 1993, Krebs 1995, Wagner 1995*a*, Coughenour and Singer 1996*a*), and Yellowstone National Park has become a prominent testing

ground for theoretical exercises in this field, as well as a continuing forum for debate.

In the early years of the natural regulation period, National Park Service managers and biologists decided to test fundamental beliefs about the northern range by seeing if the elk, left to seek their own population level, would be "naturally" regulated. In other words, Cole and his colleagues, thought that there were possibly two things operating to control the elk population. The first was self regulation (the result of some combination of behavior, physiology, and genetics), which might work to keep the population at some level lower than the food supply would allow. The second was the notion that a combination of environmental factors, especially winter and food supply, would act to limit population numbers (it is interesting to note that they did not consider predation on elk by native carnivores a significant factor, but did recognize the importance of human hunting of elk wintering outside the park).

Allowing the elk population to grow to whatever size it chose allowed biologists to study what controls might exist on that population, and to test ideas about what the most important regulating factors were. Houston (1976) designed a set of criteria by which to judge the success or failure of this test, in terms of changes in vegetation and interactions between the elk and other grazing species.

Natural regulation, a term applied to many wildlife management situations outside of Yellowstone, has been a hotly contested policy since its initiation in the park (Cole 1971; Beetle 1974; Peek 1980; Houston 1982; Despain et al. 1986; Kay 1990; Boyce 1991; Patten 1993; Wagner et al. 1995*a*; McNaughton 1996*a*, *b*). The essential issues in the natural regulation experiment revolved around the extent to which the elk population would grow, how that growth would be regulated by range and other environmental conditions (especially climatic ones), and the effects of the larger elk population on vegetation.

From 1970 to 1979, National Park Service ecologist Houston (1982) conducted the first monitoring and research analysis of the northern Yellowstone elk herd under natural regulation. A host of other questions, including the effects of the elk on other native ungulates and predators, the fate of other wildlife populations when they were naturally regulated, and the best long-term management goal of the park, have also been important, and have all to some extent been addressed by numerous investigators (Barmore 1980; Singer and Norland 1994; Coughenour and Singer 1996*a*, 1996*b*, 1996*d*).

Houston's work is now regarded as pivotal in the process by which earlier management directions were reconsidered. His book *The Northern Yellowstone Elk: Ecology and Management* (1982), summarized a largely new perspective on the range and its ungulates, and, as already mentioned, challenged many previous interpretations of historical information and ecological conditions. A central theme of Houston's work was that the truly primitive (that is, uninfluenced by European humans) wildland grazing system was a thing of the past in almost all of the United States by the time wildlife ecology and range management were professional disciplines. He pointed out that scientists who had been attempting to measure the condition of the northern range had never been exposed to native grazing systems with the full complement of grazers in place, and therefore had no clear idea of how those systems worked or what they typically looked like. He noted that by the time the first rangeland researchers began working in the United States, the native grazing system was already gone, in most cases replaced by domestic livestock operations with entirely different goals and effects on the landscape. Out of this realization later came the idea that a few places like Yellowstone, though themselves somewhat altered by Euramerican activities (such as introduction of exotic plants and the exclusion of fire), were probably our best window on the past of North American grazing systems (Frank 1990, Boyce 1991, Schullery and Whittlesey 1992, Knight 1994).

Houston found that the conclusions made by earlier authors on how the range "should" look, based on commercial grazing criteria rather than on any clear knowledge of an unmanipulated wildland range, lacked supporting data. He noted that

earlier Yellowstone investigators studied only certain locations, especially near Gardiner, Montana, where former livestock pastures, elk, deer, and pronghorn feedgrounds, and other damaged or altered sites were used to exemplify the condition of the entire northern range. Many of these sites were in the Boundary Line Area (BLA), a later addition of 12,108 acres (4,900 ha) of land along the park's north boundary. In these sites, which had been heavily grazed by livestock for many years, it was easy to identify signs of excessive erosion or overgrazing. Houston said that "range sample units and narrative accounts showed that earlier interpretations of deterioration of vegetation on the northern range were based primarily upon the decrease of aspen, the appearance and utilization of herbaceous vegetation on ridgetops and steep slopes characteristic of about 3% of the area, and the decrease of big sagebrush in the 1932 addition to the BLA."

Houston and Meagher reviewed many historical photographs of the northern range, returning to those sites to re-photograph them, and were unable to find evidence of overgrazing in the photographs. They noticed that steep erodible slopes that were major sources of sediment (e.g., Mt. Everts, Parker Peak, the Grand Canyon of the Yellowstone River) into northern range streams looked the same in the early 1870s as they do today, suggesting that natural erosive processes were responsible for these local conditions; unstable slopes would erode whether heavily grazed or not, and in fact, most of these slopes are too steep to be grazed at all. Houston wrote, "The available evidence does not support interpretations of widespread or accelerated erosion on the area," and "Certainly the evidence does not support the interpretation of progressive pathological range deterioration." With the possible exception of the BLA, which was added to the park after half a century of commercial livestock grazing and farming had perhaps irreversibly affected its vegetation, Houston could not find convincing visual evidence of overgrazing:

> The term "overgrazed" was loosely used throughout this period [1930-1958] to refer to everything from heavy *utilization* of cured grass leaves and of individual plants to presumed *retrogressive* succession. The term, as used, was really a subjective assessment that had little clear biological meaning (Houston 1982).

THE RECENT RESEARCH INITIATIVE

A hiatus occurred in northern range research following the completion of Houston's fieldwork in 1979. Funding was at last provided to hire a new ungulate ecologist in 1985. In the meantime, continued public and scientific attention focused on the range and the elk. Houston's work had little impact on public knowledge of the overgrazing question, because it was published in a technical form and not widely interpreted for a large audience, and because some people in the scientific and range management communities continued to be vocal in their disapproval of elk management in Yellowstone National Park. Due to this continued attention, in 1986, the United States Congress mandated a major new research initiative to answer fundamental questions about the condition and trend of this important park resource.

Fortunately, in 1984, Yellowstone staff had submitted a proposal for special funding of such research, and their proposal was selected to be funded in 1985, so fortuitously, the Congressional mandate—which was not directly funded by Congress—could be fulfilled. Congress directed the National Park Service to "start a study on Yellowstone to see whether there is evidence of overgrazing [and] what should be done to avoid that." The funding allowed for a number of contract researchers from outside of federal agencies to take part in these new investigations of the range. This was the first time in the history of the northern range issue that funding existed for this broad a research initiative.

In the mid-1980s, a series of expert panels drawn from the university communities of North America, were convened to define the researchable questions relating to grasslands, riparian areas, elk, deer, and pronghorn. The resultant elk study plan,

for example, was reviewed and commented on by 43 scientists. To further facilitate this initiative, the Northern Yellowstone Range Working Group, consisting of representatives of the National Park Service, U.S. Forest Service, and the Montana Department of Fish, Wildlife and Parks, was established to guide research priorities, share information, and coordinate ongoing monitoring of ungulate populations.

The process of selection of the university researchers to receive Congressional funding was turned over to the University of Wyoming/National Park Service Research Center. This research initiative, one of the largest in the history of the National Park Service, involved scientists from many universities, institutions, and agencies, and once again challenged traditional views of the range. Approximately 60 percent of the funds were spent on university research projects, with the rest going to agency projects. In many cases, research projects were cooperative ventures between university researchers and agency researchers.

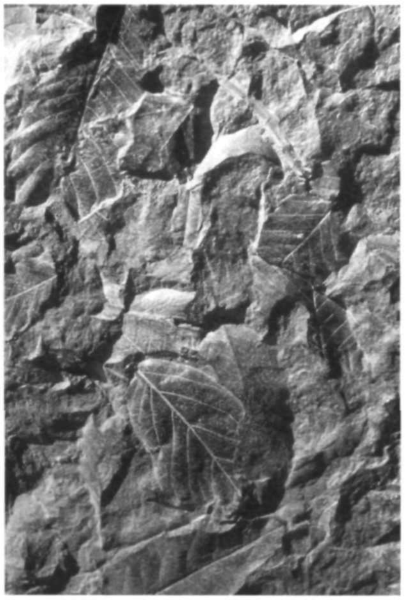
In 1986, the National Park Service initiated a multidisciplinary, team approach to researching questions about the success or failure of the natural regulation experiment. More than 40 projects were conducted, combining work by resident National Park Service biologists, university contract researchers, and researchers from other federal and state agencies (Figure 1.14). Several other projects have been funded through sources outside the National Park Service. Out of this original round of research came additional work and many additional scientific publications. Investigators initially funded by the National Park Service have continued their work with other funding (including the National Science Foundation). The reference list at the conclusion of this book attests to the extent and productivity of this work. In only ten years, more peer-reviewed journal articles and book chapters were published on the northern range than had appeared in the previous 75 years, and the production of new publications is on-going.

As an adjunct to this research initiative, and to facilitate both communication among researchers and with the public, the National Park Service hosted a series of workshops and discussion on the northern range beginning in 1988 (Appendix A). In 1991, the National Park Service, with several cosponsoring agencies and institutions, launched a biennial scientific conference series, held at Mammoth Hot Springs. The first conference, devoted to "plants and their environments," resulted in the foremost volume of new research findings on the northern range published to that time. The second conference (1993), devoted to fire research, and the third conference (1995), devoted to predators, added substantially to those aspects of studies concerning Yellowstone.

Figure 1.14 A radio collaring study of elk calves in the late 1980s revealed that predators were responsible for significant reduction in the annual calf crop. U.S. Forest Service photo by Dan Tyers.

In December 1992, the research division of Yellowstone National Park completed a large volume of northern range research reports, submitted by the various investigators funded under the 1986 initiative. Agency cutbacks and reorganizations resulted in a four-year delay in the release of this report, which is being published at the same time as this book. In the meantime, many of the papers in the report were submitted to peer review, accepted, and published by professional journals, so despite the delays, much of the science was made available to managers and the scientific community. The following sections deal with prehistoric and historic conditions on the northern range, especially related to climate and abundance of wildlife; grasslands; woody vegetation; erosion and related watershed issues; ecosystem and wildlife population questions; and other species of special concern in northern range management.

CHAPTER TWO



THE PREHISTORIC AND EARLY HISTORIC SETTING

CLIMATE AND THE NORTHERN RANGE

When discussing the northern range and its issues, the popular and scientific press have devoted most of their attention to the animals and plants that inhabit the range. But the fundamental force shaping the native plant and animal communities of the earth is climate. Because "climate is the primary determinant of vegetation" (Forman and Godron 1986), it is also the factor controlling herbivorous animals an ecosystem can support, and therefore what predators can thrive there as well.

Ecologists sometimes describe an ecosystem as a complex set of "feedback loops" in which the various elements of the setting interact and influence one another. For example, climate may dictate what vegetation can grow in an area, but the vegetation, by shading the soil from sunlight (thus creating various "microclimates" within the plant canopy), as well as by providing organic matter to the soil in the form of dead plant matter, "feeds back" into the climate-vegetation-soil system. As the soil is affected and enriched, it hosts different proportions and abundances of vegetation species. Ultimately, vegetation can even affect climate (Forman and Godron 1986); many vegetation communities, from the wildest tropical rainforest to the most carefully cultivated cornfield, may influence atmospheric conditions.

Northern range researchers cannot begin to fully understand the current climate (or the climate of the last half of the last century) in Yellowstone without studying the prehistoric climate, which Pielou (1991) summarizes succinctly:

> The most distinctive climatic interval of the recent past is the Little Ice Age, which lasted from about 1350 to 1870 A.D....Glaciers and ice caps expanded, the ranges of tree species changed, and human beings adapted to the sudden cold that followed the Little Climatic Optimum.
>
> Many Rocky Mountain glaciers advanced between one and two kilometers, injuring trees in the process. Many of the trees scarred by ice are still alive....Trees were also overridden and killed; broken stumps of some of them are now exposed where glacier snouts have receded again, in the climatic warming that began a little over 100 years ago.
>
> The only perennial ice yielded by the Little Ice Age was that which was added to preexisting glaciers and ice caps. Elsewhere, winters were colder, summers cooler, and precipitation greater. Ecosystems of all kinds were affected, including those with human beings as members.

It is one of the confounding complications of understanding Yellowstone vegetation in historic times that the park was established just as the Little Ice Age was ending. The park landscape was emerging from the effects of the colder winters, cooler summers, and greater precipitation of the Little Ice Age just as the first scientific observers arrived. These observers saw, described, and photographed a Yellowstone that still looked like a Little Ice Age environment, but was about to change in response to a new climatic regime.

Yellowstone's climate today is characterized by long, cold winters and short, cool summers. Total annual precipitation is greatest (about 70 inches annually) in the southwest corner of the park. Elsewhere, the park is mostly in a rain shadow and annual precipitation is lower and averages from 30 to 50 inches, depending on elevation. The north entrance at the park's lowest elevation (5,265 feet) is decidedly semiarid and only receives 10 to 12 inches of annual precipitation (Despain 1990). Most of the northern range, to a greater or lesser degree, falls in the semiarid category, which of course is what defines this landscape as ungulate winter range.

Climate's influence on a landscape reaches far beyond the effects on individual plants and animals. Climate can cause great fluctuations in ground water levels and springhead outflows that can favor or discourage particular plant species (Figures 2.1, 2.3). Climate is also probably the foremost factor in a landscape's fire history. Evidence of fire history as reflected in sedimentation (due to postfire mudflows and other large movements of soil and other material) in northeastern Yellowstone National Park, along with studies of historic climate records, "imply that the intensity and interannual variability of summer precipitation are greater during warmer periods, enhancing the potential for severe short-term drought, major forest fires, and storm-generated fan deposition" (Figure 2.2) (Meyer et al. 1995). This and several other studies of that portion of the park should, incidentally, provide some reassurance to people who were concerned about mudslides having long-term disastrous effects following the fires of 1988; such debris flows have been typical postfire events for thousands of years here but have since revegetated and are rarely recognized as disastrous events (Balling et al. 1992*a*, 1992*b*; Meyer et al. 1992, 1995; Meyer 1993; Bingham 1994; O'Hara 1994).

Rangeland climate is a function of temperature, moisture, and wind. Climatic variations from century to century, decade to decade, year to year, and even day to day, can have significant effects on the prosperity of a range and its animal inhabitants. The park's climate has undergone significant variations over the past 12,000 years since the end of the last ice age (Figure 2.2) (Hadly 1990, 1995; Engstrom et al. 1991, 1994, 1996; Whitlock et al. 1991, 1995; Whitlock 1993; Whitlock and Bartlein 1993; Barnosky 1994, 1996; Mullenders and

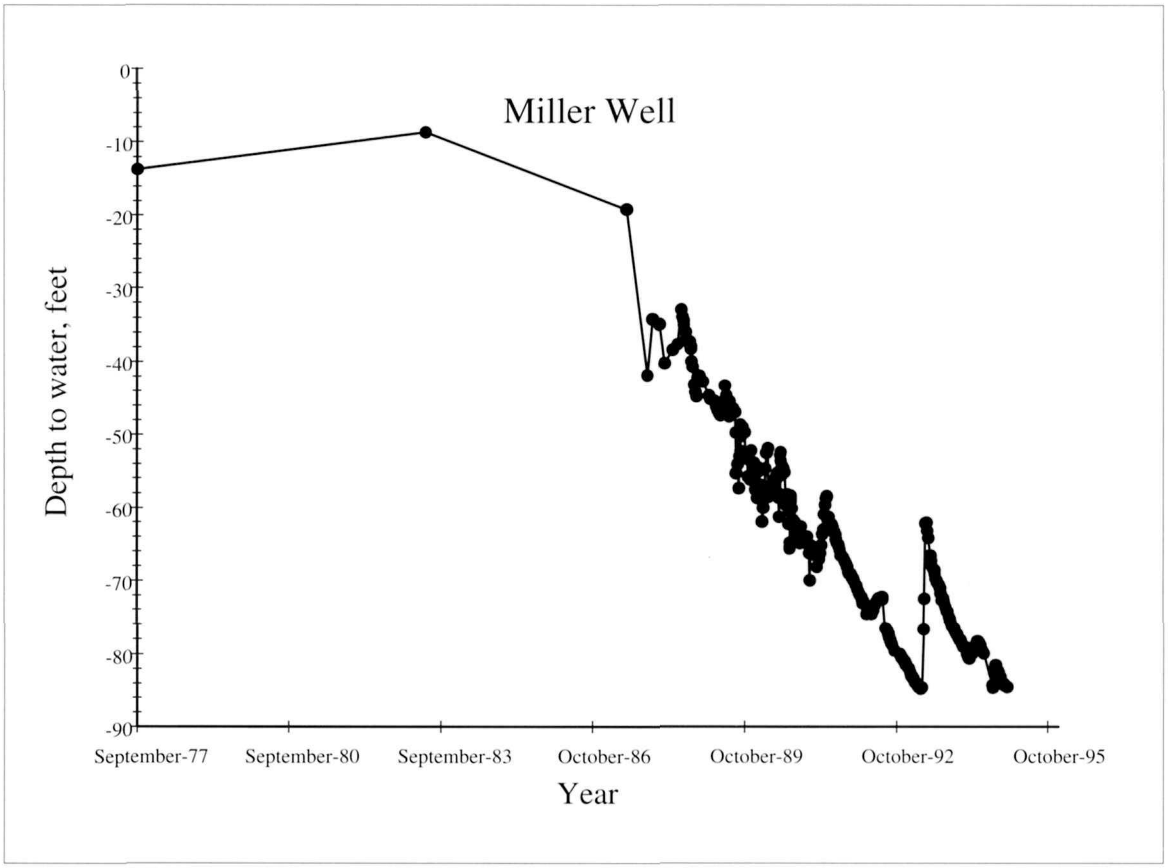


Figure 2.1. Decreasing groundwater levels on the northern range, at the Miller Well (3 miles north of Gardiner, Montana), reveal the apparent effects of the 1980s drought. Data courtesy of Irving Friedman, U.S. Geological Survey, retired.

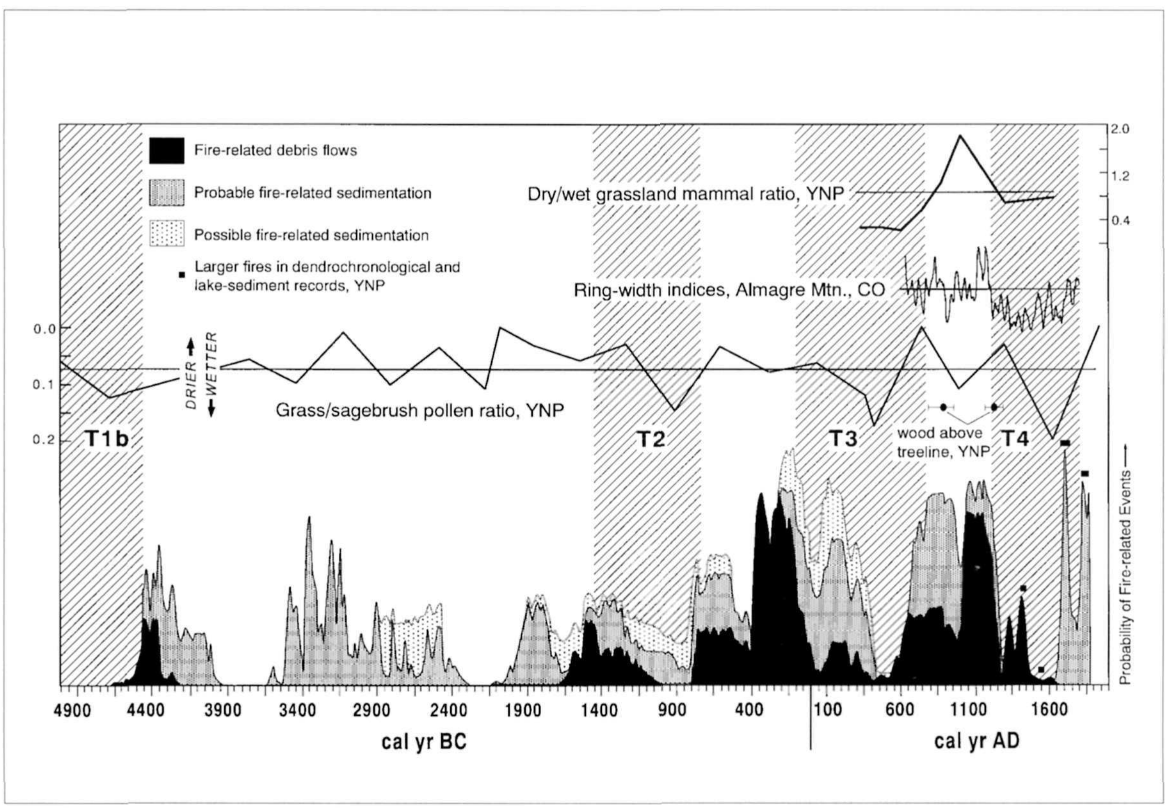
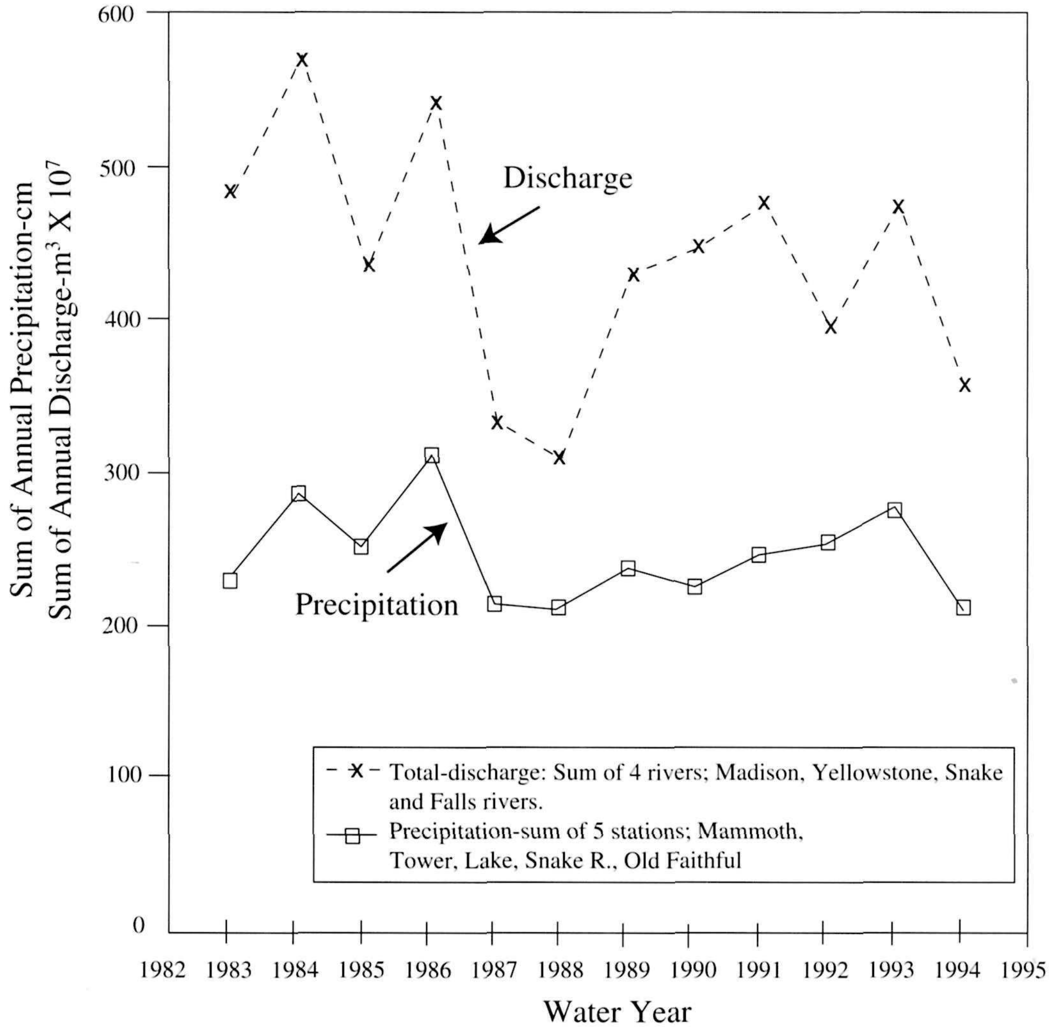


Figure 2.2. Calibrated calendar-year chronology of the variability of alluvial activity in northeastern Yellowstone National Park for 6,100 years before present. Note wetter and drier climate cycles as expressed by changing sagebrush-grass pollen ratios, and by large variations in alluvial transport. Adapted with permission from Meyer et al. (1995).

Figure 2.3. Sum ot total annual river discharge and precipitation from four rivers and five weather stations in Yellowstone 1983-1994. Note relatively flat precipitation, but declining river discharge. Figure courtesy Irving Friedman and Daniel Norton.



Coremans 1996; Mullenders et al. 1996).

But the changes in climate can be surprisingly abrupt and localized. Yellowstone National Park is large enough and topographically diverse enough to be characterized by significantly different climatic regimes in different areas (Despain 1987, Meyer et al. 1995, Whitlock et al. 1995). At the same time, within a given area the variations from year to year can be striking:

> Summer "monsoonal" precipitation is highly variable on small spatial and temporal scales; thus the potential exists for severe drought and large fires followed within a few years by intensive convective-storm rainfall (Meyer et al. 1995).

The timing of precipitation within a given year has had profound effects on plant growth. Studies of Yellowstone sagebrush-grasslands further indicated that relative productivity of those areas was more dependent upon winter precipitation than upon temperature and precipitation during the growing season (Merrill et al. 1993).

It is in this context of great climatic variability, both long- and short-term, temporal and spatial, that several generations of ecologists and managers have attempted to understand the northern range and its vegetation-ungulate interactions. It is only recently, however, that investigators have fully appreciated the unpredictability of climate, and have attempted to incorporate that unpredictability into their thinking. Though public attention on the

northern range is still focused primarily on animal numbers, it has become clear to scientists that those numbers are largely a response to varying climatic conditions.

Though an appreciation for climatic variability and its influences on ecological processes is essential to an understanding of the northern range, certain types of variability have attracted more attention among modern researchers than others. As will be seen in the following sections of this report, a key factor being considered in several northern range issues is changes in climate since the park's establishment. The long-term condition of several key species of plant communities are tied by investigators to possible effects of changing climate in Yellowstone.

Long-term precipitation changes can have profound effects on plant communities we see on the landscape today. For example, there are few young Rocky Mountain juniper among stands of old-growth (400+ years) juniper below 6,500 feet elevation on the northern range. Rocky Mountain juniper in the intermountain west are much studied, and it is well known that they survive best in landscapes that receive between 16 and 22 inches of moisture a year (Springfield 1976). The established old-growth juniper stands on the northern range are currently living in a precipitation zone that receives less than 14 inches of moisture a year. However, upslope, between 6,600 to 7,000 feet elevation, juniper are found in many age groups, including very young plants. It is logical to assume then, that the 400+ year-old junipers were established at a time when they were in a zone that received more than 18 inches of precipitation. This suggests that the 18-inch precipitation isobar has moved upslope from several hundred years ago, and the juniper have followed it.

A similar manifestation of the variability of climate on Yellowstone's plant communities is found in the current status of tall and robust stands of willows. In general, tall stands of willows occur in the park above 6,800 to 7,200 feet, in areas with at least 20 inches of annual precipitation. Tall and robust willow stands generally occur above 7,600 feet, in areas with about 30 inches of annual moisture. Historical photographs of northern range in the park in the late 1800s, at a time when at least several thousand elk were wintering in the park, show tall willows well below 6,800 feet, where they do not currently exist. This change in willows might indicate a decline in the annual amount of moisture over the past 100 years.

While there is considerable uncertainty about what effects such climatic changes may have on northern range vegetation, there is no longer any question that these changes are real and continue today. Yellowstone is blessed with having detailed climatic data for the past century (Farnes 1997), and a variety of other data sets, such as those found in tree-ring studies, complement the information base on the park's climate since its establishment in 1872. Study of these records indicates that over the course of the twentieth century, summer (i.e., fire season) temperatures have been increasing, January-June precipitation is decreasing, and the likelihood of major fire seasons is increasing (Figure 2.4) (Balling et al. 1992*a*, 1992*b*). Their results indicate a decline of 1.6°F (16.9°C) and a decline of 2.4 inches of precipitation over a 95-year period.

While these declines may seem small and insignificant in the Yellowstone area, small numerical changes may have large effects. As noted earlier, the difference between 16 and 18 inches of precipitation may be the difference whether seedling junipers survive or not. Permafrost has been observed and studied in, and adjacent to the park in the Beartooth, North Absaroka, Washburn and Gallatin ranges (Pierce 1961), at least as low as 6,600 feet elevation. The mean monthly air temperature in the Lake Yellowstone area averages 32.8°F (‹1°C), and if Yellowstone's famous geothermal heat were ignored for this example, would mean that the Lake area is only 0.8°F from being permafrost. In actuality, geothermal heat is fairly common around the lake so that the mean annual soil temperature at Fishing Bridge, for example, is 42.1°F (5.6°C) (Friedman and Norton 1981).

Winter range soil temperatures are generally cool. Average annual soil temperatures taken for several years in the mid-1970s on the northern

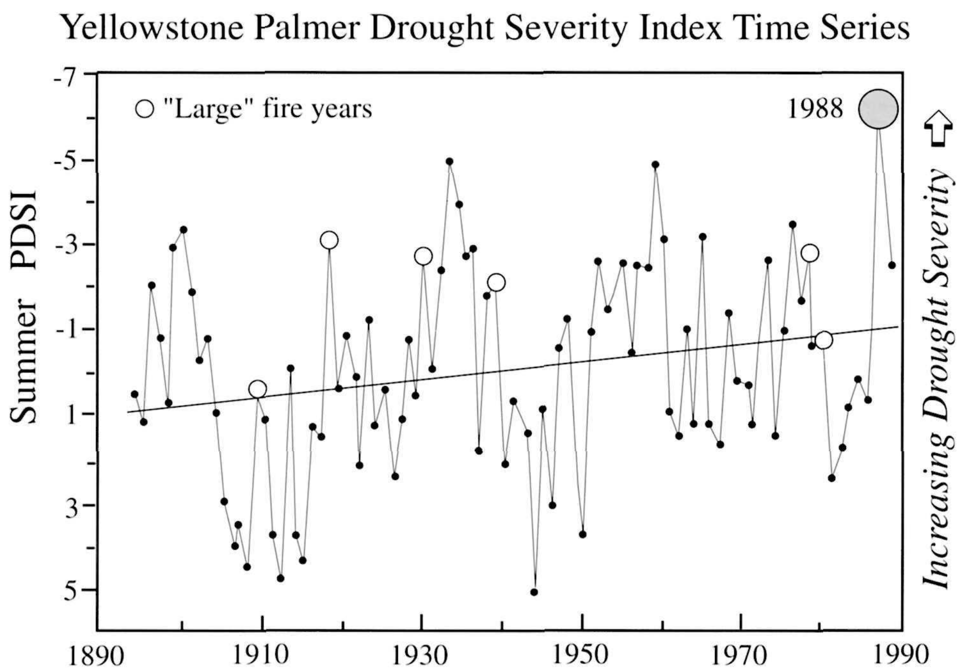


Figure 2.4 Tracking of the Palmer Drought severity Index (a commonly used indicator of fire risk) over the past century in Yellowstone shows a gradual drying trend, which may have a variety of effects on vegetation communities, as discussed in this chapter. Note especially the extreme and historically unprecedented dryness of 1988, when Yellowstone experienced fires on a scale apparently not equalled since about 1700. Courtesy of Grant Meyer, Middlebury College.

range in Lamar Valley vary widely; from 39°F (3.9°C) at the Lamar Ranger Station, to 40.5°F (4.7°C) at Pebble Creek, to 48.1°F (8.9°C) at the east end of Lamar Canyon (Friedman and Norton 1981).

It is a matter of some interest whether or not the changes in climate experienced by Yellowstone during the 1900s are in part the result of human influence on the atmosphere. Romme and Turner (1991) have proposed a series of alternative scenarios that may arise in the greater Yellowstone ecosystem as human-caused global climate change progresses in the future. These scenarios feature significant changes in vegetation communities, with consequences ranging from minor to grave for various mammal species. For example, a slight warming and drying of the park's climate will almost eliminate whitebark pine, an important food species for grizzly bears and other animals. Yet another reason to continue the present investigations of the northern range is the opportunity this research provides to establish baseline information against which to measure such changes.

CLIMATE: RESEARCH RECOMMENDATIONS

Over the past 20 years much of greater Yellowstone has been subjected to intense scrutiny using palynological methods to reconstruct paleoclimates. Particularly well-studied is the area from central Yellowstone south through the Grand Tetons. Research needs to be expanded to the north and east of Yellowstone, especially to understand more about the very important prehistoric variations in the Great Plains monsoonal pattern, and how it has affected the northern range in the past. A lake on the northern range has been identified as one of the very few "varved lakes" known in North America. Research on this lake could yield patterns in annual weather and vegetation, at the very least, back to the Pleistocene. Daily weather records from many stations in the park are archived in original hard copy at a facility on the east coast. These records need to be accessioned and computerized so that the weather during the historic period can be better understood.

FIRE AND THE NORTHERN RANGE

Yellowstone National Park features a variety of substantially different fire regimes (Despain 1990). These differences might most easily be shown in the length of a given plant community's "fire-return interval," that being "the amount of time between successive fires on the same site" (Despain 1990). The fire-return interval is largely determined by the age of the vegetation and the rate at which fuel accumulates, so in a slow-growing forest the fire-return interval is much longer than in a shrub community or a grassland. About 80 percent of the park's forests are lodgepole pine, which on Yellowstone's infertile central plateau have a fire-return interval in excess of 300 years (Romme and Despain 1989*b*). Barrett (1994) reported a considerably shorter fire-return interval, with a mean interval of 200 years, for lodgepole pine on more fertile andesitic mountain terrain in northeastern Yellowstone, and a mean interval of more than 350 years for high-elevation whitebark pine forests.

Houston (1973) sampled 40 fire-scarred trees on the northern range "to reconstruct the frequency and size of fires during the past 300 to 400 years in northern Yellowstone National Park." Houston, by aging fire scars on trees adjacent to northern range plant communities, was able to measure the frequency of fires in the grasslands adjacent to the trees, because the trees regularly survived such fires and continued to grow.

Houston (1973) estimated "mean adjusted intervals of 20-25 years between fires" on the northern range, and suggested that this fire frequency may have been in part the result of fire-related activities by Indians, who are believed to have set fires in other parts of North America for a variety of purposes, including game drives and vegetation management (there is as yet no evidence that Indians regularly set fires in Yellowstone, either in the grasslands or in the park's forests). But fire was suppressed whenever possible on the northern range after the establishment of Yellowstone National Park in 1872, and fire has been to some extent excluded from exercising its influence on the range since then:

> The best interpretation may be that much of the area would have burned at least one to four times since the establishment of the park were it not for the actions of modern man. Changes that have occurred in the vegetation seem best explained by a reduction in fire frequency but have also occurred within a fluctuating climate regime…and with concomitant foraging by ungulates (Houston 1973).

FIRE: RESEARCH RECOMMENDATIONS

There have been important advances in sampling techniques and statistical analyses since the publication of Houston's (1973) fire history study of the northern range. These advances are significant enough to justify a new and more ambitious fire history study on this range, incorporating Houston's (1973) findings. This new study should have a larger sample size, and the collections must be well referenced spatially so that we can better map the approximate extent of individual fires in the past. It is possible to collect fire scar samples from large Douglas-fir trees without killing the tree, and new

Figure 2.5. Additional research in fire history should shed light on the complex interactions of herbivores, climate, and fire in shaping vegetation communities. NPS photo.

dendrochronological techniques make it possible to determine not only the year of a fire but the season. New statistical models permit calculations of the probability of fires of various sizes occurring in any particular year, or the expected interval between successive fires of various sizes. Such a study is needed to provide the detailed, site-specific information on dates of fire occurrence and intervals between successive fires that is required if we are to effectively disentangle the relative roles of elk and fire in suppressing aspen tree regeneration during the early 1800s (Figure 2.5).

PALEONTOLOGY, ARCHEOLOGY, AND HISTORY OF THE NORTHERN RANGE: INTRODUCTORY COMMENTS

Since the turn of the century, a number of naturalists, ecologists, and other observers have proposed prehistoric and historical scenarios of wildlife abundance in the Yellowstone National Park area. Though there are variations among the viewpoints, two common positions have emerged. One is that large mammals were rare or absent prior to the arrival of European humans in the greater Yellowstone area, particularly on the northern range. According to this view, elk and other ungulates became more abundant on the northern range after 1870, due to growing human influences (specifically, Euramericans who settled the Yellowstone area starting in the 1860s) and loss of preferred ranges outside the park. The other view is that large mammals had been abundant in the present park area for many centuries prior to 1872, using the habitat as climate would allow.

Among the important variants of these viewpoints are differing positions on how much these animals used the park in winter. Some writers, for example, have held that elk were indeed common in the park area in summer, but that prior to the settlement of the Yellowstone River Valley north of the present park, the elk migrated as much as 70 miles down the valley to lower country each winter (Cahalane 1941). However, this seems highly improbable given the available winter range much closer to and inside the park (Houston 1982).

The paleontological, archeological, and historical record of early Yellowstone wildlife must be used cautiously. Paleontological research on mammals has just begun, and Cannon (1992) recently estimated that "less than one percent of the park (0.19 percent) has been intensively inventoried for archeological sites." Despite this slight information base, many writers have spoken with great confidence about what the historic or prehistoric record "proves" about the park's wildlife populations prior to 1872, but it is rarely safe to lift single statements out of a specific publication or source, whether an archeological study or a historical account, and use that statement to support a sweeping generalization about prehistoric wildlife conditions. The work that has been done so far is, however, revealing and at times suggestive, and offers important clues, not only to prehistoric conditions but also to future questions.

THE PALEONTOLOGICAL RECORD

Whitlock et al. (1991) and Whitlock (1993) analyzed pollen records from greater Yellowstone ponds to determine the pattern of revegetation following glaciation, and subsequent vegetation up to the present. Discussing northern range vegetation, Whitlock et al. (1991) summarized the pollen record as follows:

> The long-term pollen record suggests that over the past 14,000 years the magnitude of vegetation change has been quite great. For the first millennium after glacier retreat, the region was covered by tundra. As the climate warmed, spruce, then fir and pine, formed a subalpine forest, which was maintained for more than 2,000 years. Subsequently, with warmer, drier conditions and frequent fires, lodgepole pine forest predominated. The present-day parkland developed in the past 6,700 years, and more directly in the

> last 1,600 years. From this record, we can infer that climate changes do ultimately drive the ecosystem.

Millspaugh and Whitlock (1995), based on studies of charcoal in lake sediments in central Yellowstone, discovered that even in the shorter span of the past 750 years, the fire regime, and by inference the climate, has changed through time:

> Small areas in central YNP burned between c. 1840 and 1987. From c. 1220 to c. 1440 and from c. 1700 to c. 1840, intermediate areas of the region burned. Between c. 1440 and c. 1700, large areas burned in c. 1700, c. 1560, and c. 1440; these episodes were separated by periods of little burning. This particular regime, consisting of punctuated episodes of severe fires, may have been reestablished in 1988.

Hadly (1990, 1995; Barnosky 1994) conducted the first paleontological study of the northern range's prehistoric vertebrate community from 1987 to 1993 at Lamar Cave, located in the upper northern winter range about two-and-a-half miles (four km) east of Tower Junction (Figure 2.6). This site, discovered in 1986, provided a record of the past 3,200 years of faunal activity near the cave site, as reflected in 10,597 identifiable vertebrate bones (out of hundreds of thousands of bones present) brought into the cave by pack rats and a variety of other scavengers and predators (Hadly 1990, 1995; Barnosky 1994).

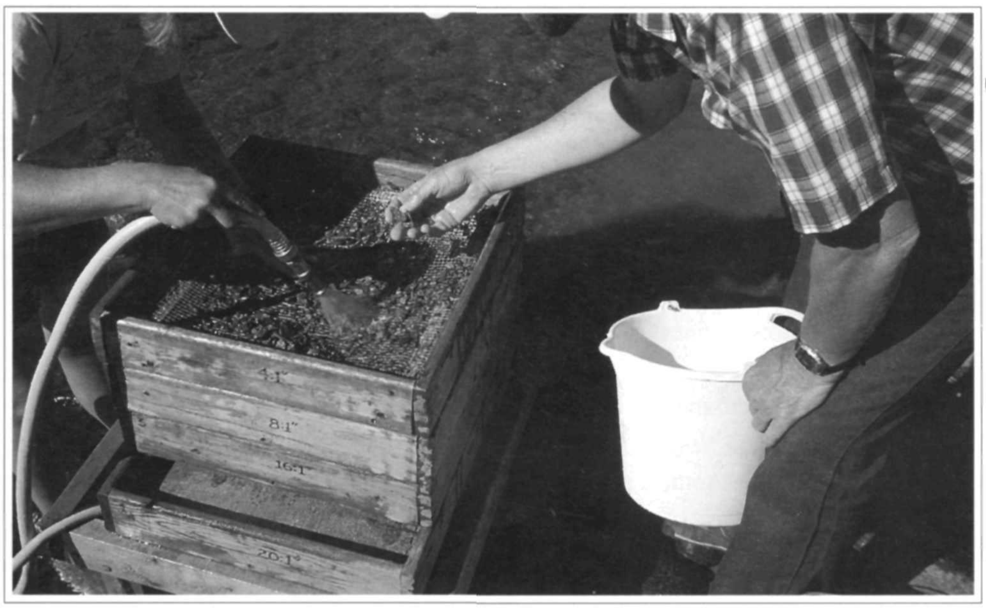


Figure 2.6. Collection of vertebrate remains at Lamar Cave: material excavated from the cave is washed through progressively finer screens in order to separate all sizes of bone, from large mammal leg bones to the finest shrew teeth. NPS photo.

Lamar Cave bones suggest a persistent community of mammals remarkably similar to today's, with "6 orders, 16 families, 31 genera, and 40 species" represented (Hadly 1995). In keeping with local habitats around the cave site and with typical relative abundance of various species, the most common mammals were small: montane vole, Uinta ground squirrel, pocket gopher, bushy-tailed wood rat (packrat), and deer mouse. "Large mammals, such as ungulates and carnivores, are diverse but present in low frequency much as they are in the present mammalian community" (Hadly 1995). Elk, bison, antelope, bighorn sheep, and mule deer are all present in numerous levels of the cave strata. Grizzly bear, coyote, beaver, and wolf all appear in multiple levels as well. Lamar Cave thus provides incontrovertible evidence that the large mammals currently occupying the northern range are native there, and have used the area for thousands of years as environmental conditions allowed.

Interpretation of the bones of small mammals at the site suggest that, though environmental conditions have changed over the past 3,200 years, there is no reason to doubt that the environment remained hospitable to continued occupation by the large ungulates. Additional evidence that elk used the area much as they do now is provided by the elk bones themselves, most of which are from young calves, "suggesting past use of the area around the cave for calving, much as it is used

today" (Hadly 1990).

Wagner et al. (1995*a*) claimed that Hadly's (1990) evidence supported a recent increase in elk numbers in the Lamar Valley, because the majority of the elk bones were found in the top layers of the cave excavation, but this claim is apparently the result of ignorance of the taphonomy of such collections, in which the sample size of the larger bones is insufficient to make such specific interpretations (E. Hadly, Mont. State Univ., pers. commun.). The Lamar Cave study does not provide us with the means to comparing elk numbers at some prehistoric time with elk numbers now; it only allows us to establish that elk were present prehistorically, and that they used the site much as they use it now.

Other paleontological studies have addressed issues of vegetation community persistence, climate, erosion, and fire history, and will be covered below.

THE ARCHEOLOGICAL RECORD

The archeological record, though still comparatively slight, agrees with the paleontological record that a large variety of native fauna used the northern range prehistorically. Human occupation of the greater Yellowstone ecosystem began more than 10,000 years ago, and the existing archeological record indicates that humans have at times used the area's resources in many ways, from hunting and gathering to mining obsidian and other materials for use in weapons and tools (Haines 1977).

Archeology in Yellowstone dates to the park's first decade, when Superintendent Norris noted many remains of Indian structures, some used for hunting ungulates, but professional archeological work in the park is a much more recent development. Malouf (1958) and Hoffmann (1961), in early surveys of park archeological sites, reported elk bones of unknown age at a wickiup site on Lava Creek. Hoffmann (1961) suggested that the lack of bones in the sites he studied might be the result of soil conditions; "the sites where such bone was found are mainly in the northern part of the Park along the Lamar, Gardner and Yellowstone Rivers." He also collected "stone gravers, tools used to incise bone, from sites along the Yellowstone River in the area where it leaves the northern park boundary." Taylor (1964) expanded on the work of Malouf and Hoffmann, reporting few bones but many hunting-related tools, such as scrapers and projectile points. The presence of such tools indicates that these early residents were in fact hunters, and further suggests that a native fauna must have been present. Wright (1984) regarded elk as rare prehistorically in southern Yellowstone and Jackson Hole. At sites on Swan Lake Flat, south of Mammoth Hot Springs, Wright found mule deer remains, and along the Gardner River near Mammoth Hot Springs he found ungulate and beaver bones (Wright 1982).

Since these preliminary studies, most of which investigated only surface finds, more recent work has begun to reveal a more complete portrait of prehistoric fauna in and near present Yellowstone National Park (Figures 2.7 and 2.8). Cannon (1992) summarized archeological investigations along the shore of Jackson Lake in 1986-1988 that identified bison bones common at several locations, as well as elk, moose, mule deer, and

Figure 2.7. Archeological excavation in 1996 of a cutbank along the Yellowstone River in northern Yellowstone National Park revealed a bed of butchered ungulate bones. Recent archeological investigations are exposing numbers of ungulate bones left by prehistoric hunters at several locations. NPS photo.

Figure 2.8. Archeologists excavating bison skull from a site near that shown in Figure 2.7, along the Yellowstone River in northern Yellowstone National Park. NPS photo.

several predator species. These sites date within the past 1,500 years. Cannon (1992) also reported on a prehistoric (about 800 years ago) bison kill site recently excavated along the north shore of Yellowstone Lake, and an archeological investigation near Corwin Springs that revealed elk, bison, deer, and a canid of unknown species. He found a variety of ungulate bones, including elk and bighorn sheep, at sites in excess of 1,000 years old along the Yellowstone River near Gardiner, Montana. Allen (U.S. For. Serv., pers. commun.) reported a variety of ungulate bones at a site on Sphinx Creek, in Yankee Jim Canyon north of Yellowstone National Park. More recently, analysis of blood residue on prehistoric stone artifacts collected in Yellowstone National Park has revealed blood from bison, deer, elk, sheep, and rabbit, as well as from ursids, canids, and felids, at various dates over the past 9,000 years, further proof of human use of faunal resources (Figure 2.9) (Cannon and Newman 1994, Cannon 1995, *Yellowstone Science* 1995).

It appears, then, considering the preliminary stage of our understanding of Yellowstone archeology, and considering the appearance of ungulate bones in a number of sites on the northern range, that prehistoric large ungulate presence is further established by the archeological record. Additional paleontology and archeology would be useful, however, because another interesting and longstanding archeological issue is the relative abundance of large mammals in greater Yellowstone prehistorically.

Several archeologists who have worked in the greater Yellowstone ecosystem have stated that elk were rare there prehistorically (Frison 1978, Cassells 1983, Wright 1984). More broadly, a number of paleontologists, archeologists, and other investigators have pointed out that elk are relatively rare in sites in Montana, Wyoming, and Idaho (Walker 1987, Hadly 1990, Kay 1990, Cannon 1992). It is uncertain, however, if rarity in archeological sites is proof of actual rarity during the times the sites were actively used by humans. Kay (1990) argued that rarity in archeological sites reflected actual rarity of elk in the region. Connor

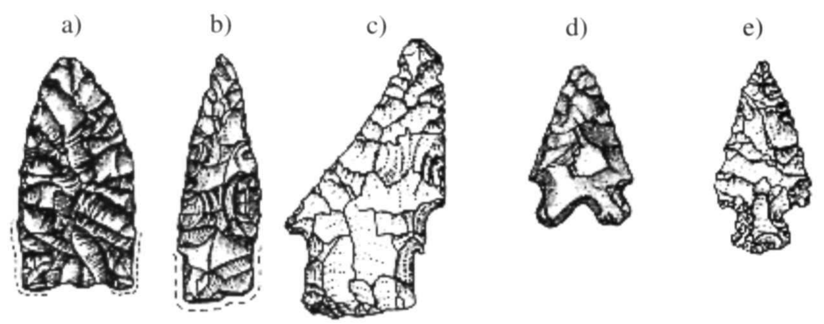


Figure 2.9. Five Yellowstone Lake-area projectile points that tested positive for various mammal species' blood antisera: a) Late Paleoindian obsidian point, 9,000 years BP (Before Present), tested positive for bear; b) Late Paleoindian chalcedony point, circa 9,000-10,000 years BP, tested positive for rabbit; c) chert Cody knife, about 9,000 years BP, tested positive for bison; d) basalt Oxbow-like point, about 5,000 years BP, tested positive for deer; and e) obsidian corner-notched point, 1,380-1,500 years BP, tested positive for canid. Dashed lines along bases of first two points indicates extent of grinding where points were reworked at some time following their original construction. Drawings by Janet Robertson, courtesy of Kenneth Cannon, Midwest Archeological Center.

et al. (1991) said that in Wyoming sites, the lack of elk remains may mean that elk were rare, or it may mean that the people occupying these sites preferred other species, or that the locations of the sites were not in elk habitat and were therefore "not conducive to the deposition of elk." Cannon (1992) surveyed the ethnographic literature and offered a number of reasons why elk were relatively rare in the archeological record. He said, for example, that "the mountain hunting pattern, as described for the Shoshone, would tend not to produce numerous elk remains due to transport cost of elements." In lay terms, this means that single human hunters might have de-boned meat where a large animal fell, rather than trying to carry the entire carcass to a distant camp. Furthermore, Hadly (1990) has suggested that relying too heavily upon archeological evidence has led to "simplistic interpretation of limited data." Hadly pointed out that elk appear in most levels at Lamar Cave, and are in fact "the most common ungulate in the Lamar Cave faunal assemblage."

A related question involves the extent to which Indians affected the numbers of elk and other animals. Hadly (1990), Cannon (1992), and Kay (1994*b*) all show that elk numbers increased in the archeological and paleontological record in the northern Rocky Mountains at some time in the past several hundred years. Whether this meant that elk numbers were actually increasing, or that humans were an important factor in controlling elk herd sizes, is a matter of debate. Cannon (1992) said that "a peak [in elk numbers] in the Late Holocene may reflect increased numbers through time, an increase in human predation, or simply sampling bias." Lahren (1976) believed it was "improbable, during any time of the year, that the hunter-gatherer populations ever operated at a level which significantly affected the evidently large biomass" of their prey in the upper Yellowstone River Valley.

More dramatically, Kay (1994*a*, 1995*a*) has proposed that prehistorically, predation by humans and other carnivores suppressed ungulate numbers in Yellowstone to extremely low levels. Kay (1995*a*) and Wagner et al. (1995*a*) point to recent estimates of the Native American human population of North America in 1492 being as high as 100,000,000 as an indication that humans were indeed numerous enough to suppress ungulate numbers to very low levels. However, their own citations do not support them. Wagner et al. do not provide sources for their statement, but probably relied on Kay (1995*a*), who cites Dobyns (1983) and Ramenofsky (1987) in support of his statement that "North America was not a 'wilderness' waiting to be 'discovered,' but instead was home to more than 100 million Native Americans before European-introduced diseases decimated their numbers." But these citations say no such thing. Dobyns (1983), for example, whose pre-Columbian population estimates have been the most extreme and controversially high (Denevan 1992), estimated that the human population *of the entire New World*—that is North, Central, and South America—was around 100 million, most of whom lived in Mexico, Central and South America. Dobyns (1983) estimated that the pre-Columbian population of North America was about 18 million, most of whom lived in the east, in the Mississippi Valley, or along the west coast (Dobyns estimated 722,000 lived in Florida alone). Perhaps Kay misread Dobyns' estimate for all of the New World as an estimate for only North America, and Wagner et al. then copied Kay's error. It is important to note, in addition, that pre-Columbian population estimates as high as Dobyns' are not the most favored among historians, anthropologists, and archeologists. A more typical estimate of the North American human population in 1492 would be "nearly seven million" (Kennedy 1994), most of whom lived on the Atlantic seaboard or in the Mississippi Valley.

Exercises that provide plausible scenarios for pre-Columbian human influences on wildlife populations and therefore on ecosystems in general are important and should be pursued. To date, however, they are all hypothetical or conjectural, and none are yet supported by convincing evidence in the case of Yellowstone, a high, isolated, and relatively unpopulated region when compared to the east and west coasts of North America. Janetski (1987) quotes Larocque, a French-Canadian trapper who visited Crow Indian villages north and east of the present Yellowstone National

Park in 1805, as reporting that European smallpox had by then reduced the Indians of that region from 16,000 to 2,400. Such reductions would have effects on regional ecological processes, but even the larger number of Crow Indians, spread over a substantial area, does not appear to be more than a small fraction of the human population numbers and densities required to suppress Rocky Mountain elk herds to practically zero. Additional study and evidence may provide clarification on this issue.

Even if such numbers are eventually clarified, the question remains how they should be applied to Yellowstone's elk management questions. North American human populations did not remain constant during the roughly 11,000 years during which the archeological record suggests that humans were inhabiting the Yellowstone area. The densities and effects of these people were no more constant than was the climate or any other element of the setting.

THE HISTORICAL RECORD

Analysis of early written accounts of the Yellowstone National Park area has been by far the most frequently employed method of attempting to determine prehistoric wildlife abundance. As Schullery and Whittlesey (1992) and Kay (1994*a*) have suggested, there are numerous pitfalls in assuming that conditions described in the early historical record (from the period roughly 1800 to 1880) are a reflection of "primitive" time, that is, a time prior to pre-Euramerican influence on the region. Old World wildlife diseases, epidemics of Old-World human diseases, Euramerican-introduced horses, Euramerican firearms and other weapons, and Euramerican trade incentives were among the forces present in the northern Rocky Mountain region by 1800, and any or all of these could have influenced Indian use of local resources.

However, the historical record is of great interest, because it is our most detailed picture of the Yellowstone National Park area prior to its creation and development by Euramericans. As mentioned earlier, by the 1920s it was widely believed that large mammals were scarce or absent in present Yellowstone National Park prior to the creation of the park in 1872 (Skinner 1928, Bailey 1930, Rush 1932, Grimm 1939). This position was challenged by Murie (1940), who offered the most thorough consideration of the early historical record to that date, and who was supported by later writers (Cole 1969, Lovaas 1970, Gruell 1973, Meagher 1973, Houston 1982, Barmore 1987). Murie (1940) took various positions on the side of large mammals being common, though not necessarily as numerous as in modern times.

Kay (1990), on the other hand, used the same early accounts to suggest that large mammals were rare in the period prior to 1876. Many writers used only a few historical accounts to prove their case; none used more than about 20. More recently, Schullery and Whittlesey (1992), in an analysis of 168 accounts of the greater Yellowstone ecosystem prior to 1882, concluded that such small information bases are simply insufficient to gain a trustworthy idea of wildlife abundance, and even their much larger information base was insufficient to give more than a general idea of wildlife conditions. They also concluded that large ungulates and their predators were present and numerous throughout the area during the period 1800-1882, and were using the park as both summer and winter range.

Perhaps most important in the context of wildlife abundance, Schullery and Whittlesey (1992) reported that more than 90 percent (51 of 56) of all observers prior to 1882 who commented on the abundance of wildlife expressed the belief that it was very abundant. This is in striking contrast to the common perception by the early 1930s, which held that large mammals were prehistorically rare in the area. This surprisingly quick switch from believing in abundance to believing in scarcity may have been a product of many things, including the general destruction of large game in many parts of the west between 1870 and 1900; most of the people residing in the Yellowstone region by 1920 had no memory of anything other than wildlife scarcity everywhere but the park. This may have led them to assume that the wildlife had always been scarce, and that the park, rather than being representative of an

earlier time, was an aberration from some imagined "normal" condition.

The overwhelming testimony of contemporary travelers and residents that large animals were common before 1882 offers us an important lesson in historiography: one must use a large amount of this anecdotal material in order to gain even a general impression of conditions. It has been a common tactic among supporters of the scarce-ungulate viewpoint to quote a few notable early accounts that can be used to suggest wildlife scarcity. For example, at one point during his first survey season in the park (1871), Ferdinand Hayden said that "our hunters returned, after diligent search for two and a half days, with only a black-tailed deer, which, though poor, was a most important addition to our larder" (Schullery and Whittlesey 1992). This quotation is usually invoked by writers attempting to prove that wildlife was rare prior to 1872 (Chase 1986). But Hayden's next sentences belie that argument: "It seems that during the summer months of August and September the elk and deer resort to the summits of the mountains, to escape from the swarms of flies in the lowlands about the lake. Tracks of game could be seen everywhere, but none of the animals themselves were to be found."

There is a consistent pattern to most of these early accounts, of considerable animal abundance. Nothing short of a full quoting of all sources makes the point completely, but a few examples (focusing on elk) may be offered here to suggest the reason why almost all early observers believed large animals were common (all of these are quoted from Schullery and Whittlesey 1992, who provide full citations). Trapper Joe Meek said that in 1830, the Yellowstone National Park area "abounded not only in beaver, but in buffalo, bear, elk, antelope, and many smaller kinds of game." In August, 1837, trapper Osborne Russell, who made many observations of abundant wildlife, entered the park area from the east and traveled to Yellowstone Lake, "where we found the whole country swarming with Elk ...." In 1863, a large party of trappers under Walter DeLacy "encountered many bands of elk" on the west side of the Gallatin Mountain Range in the present park. In 1869, David Folsom camped on Rescue Creek, east of Mount Everts, where he wrote in his diary that "this is a hunter's paradise. We saw the tracks of elk, deer and sheep in great abundance, and for several miles were scarcely out of sight of antelope." In camp one September night near Calfee Creek in the upper Lamar Valley, his party heard "the elk whistling in every direction." Between 1866 and 1871, prospector A. Bart Henderson frequently traveled in the park area, reporting in his unpublished diary on an abundance of wildlife, especially elk. Kay (1990) attempted to discredit Henderson as an unreliable observer, but Henderson's observations are buttressed by others. For example, in July, 1870, moving from Pilot Peak to the Lamar Valley, Henderson reported in his diary that his party traveled through "buffalo, elk & bear—all very tame." More recent research has revealed that one of Henderson's companions, James A. Gourley, also kept a diary, which reported on the same occasion that when they entered the Lamar Valley, "there were hundreds of Elk so tame that they only moved a little distance to the side of us." In 1870, the Washburn-Langford-Doane expedition, though sometimes unsuccessful in their attempts to kill game, repeatedly emphasized the abundance of wildlife in the area, as in Langford's observation that "the river is filled with trout, and bear, elk, deer; mountain lions and lesser game roam the plains, forest and mountain fastnesses," and Hedges' comment near Mount Washburn that there was "plenty of good feed and so of game, bear and elk very plenty." South of Yellowstone Lake, Doane observed that "the ground was trodden by thousands of elk and sheep." In 1872, C.C. Clawson reported that near Yellowstone Lake, "elk in bands flew away at the sight of us or stood in groups until the crack of the riffle [*sic.*]."

These are only a few representative reports of elk abundance, involving all parts of the park rather than just the northern range, but they serve to show how common the experience of encountering elk or evidence of elk was among early travelers. The fact that some or even several observers did not see wildlife proves only that they were unsuccessful at doing so; it does not necessarily prove that the wildlife was not there, any more than the success

or failure of a given group of hunters today proves that the game is present or absent. The key information is the positive evidence provided by those who saw animals. There were many such people in Yellowstone, and they left many reports of abundant elk and other wildlife.

CONCLUSIONS

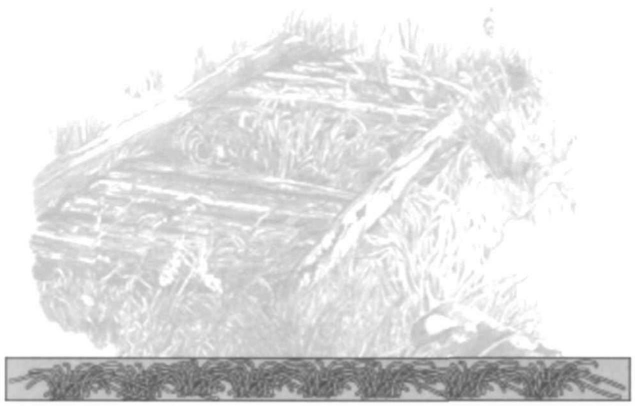
Yellowstone's long-term climatic record suggests that the native plant and animal communities are dynamic and respond to changing environmental conditions. The paleontological, archeological, and historical records, though they have important limitations that must be recognized, combine to suggest that these plant and animal communities, though they have been affected by these changes in climate, are quite resilient. Relatively few species, in fact, very few, are eliminated by the variations that the park area has experienced over the past 10,000 years. The region's biodiversity, then, seems to hold up well, but specific biodiversity issues will be discussed later in this report.

The paleontological, archeological, and historical evidence provides a picture of pre-1872 Yellowstone as a place continuously inhabited by essentially the same wildlife community as today. These three lines of evidence provide abundant proof that today's native ungulates and their predators were common residents of the park area for thousands of years, and provide equally strong proof that humans were an active part of this setting for nearly as long.

It is again important to point out, however, that the paleontological, archeological, and historical evidence does not permit us to make precise estimates of wildlife population sizes. Though the historical record suggests that large animals were common, we cannot yet use this material to prove that they were more common, as common, or less common than today. In fact, they may have been less common then than now, simply because of different environmental conditions. The period 1800-1872 represented the end (and the most severe years) of an extended cold and wet period (circa 1500-1850) known as the Little Ice Age. If the Little Ice Age resulted in deeper snows and harsher winters, then there were almost certainly fewer ungulates and predators wintering there then than now. Moreover, computer models suggest that the northern elk population size might be reduced from 8 to 20 percent when wolves are restored (Boyce 1990, 1993, 1995*a*; Garton et al. 1990; Mack and Singer 1992*a*, 1992*b*, 1993*a*, 1993*b*); wolves were present prior to 1872, and presumably played an important role in elk population size then. Environmental conditions, including the influences of Native Americans, change over time; there is no specific date or period in the past that can serve us as a model for how the Yellowstone landscape should look today. The highest value of the prehistoric and early historical record of Yellowstone may be in showing us the range of past variations in that landscape.

CHAPTER THREE

GRASSLANDS



The grasslands have occupied center stage in the long history of the northern range controversy. No other element of the setting has been the subject of as much discussion or research. The grasslands on the winter range have been at the center of this issue; the much larger and higher elevation summer ranges have not been judged unhealthy in these dialogues. As already explained, many investigators and observers described the winter range grasslands as overgrazed, especially since the drought of the 1930s. More recently, the relationship of herbivores to their grazing lands, and the concept of overgrazing itself, have undergone intense scrutiny in the scientific community. It has become clear that what a wildland ecologist might consider normal grazing effects, a livestock manager might consider unacceptable. Recent scientific investigators have approached the subject of overgrazing from a broader and more ecosystem-oriented perspective, and it is from that perspective that most of the recent research on northern range grasslands has proceeded.

DEFINING OVERGRAZING

Since the beginnings of range management science early in this century, the various scientific disciplines involved have changed greatly. There is now even considerable disagreement over many aspects of how livestock ranges should be managed. Much of this confusion results from our changing understanding of how rangeland ecosystems function. From the 1920s to the 1950s, it was widely believed that most vegetation

systems—range or forest—tended to reach a stable state, a sort of idealized equilibrium, that would be relatively easy to manage. In recent decades, however, instability has become more apparent as a fundamental characteristic of wild ecosystems, and has become especially important to students of wild ranges that are grazed only by native ungulates. Paleontology, as well as practical experience over the past 120 years, has shown us that ecological processes are far less predictable, and far more unruly (by human standards), than was previously supposed. This realization has led at least some observers, including park managers, to be more cautious about pronouncing a range "overgrazed, "unnatural," or "damaged," because we now realize that even without human influences, the conditions on a given range are far more variable than was once thought.

Earlier assumptions about the nature of wildlands have been challenged as ecologists have realized that nature has little regard for the range management and wildlife management textbooks written earlier in this century. Research in wildland grazing systems, that is systems in which wild ungulates use the landscape with relatively little interference from humans, have focused on sites like Yellowstone's northern range—large nature reserves. The researchers report many interesting things, some of which are reviewed below. Perhaps most important of all, they report that a wild rangeland, grazed only by free-ranging native ungulates, may not look the same as a commercial livestock rangeland. Wild ungulates will not use the range in the same way that livestock do; they will use the plants differently and to a different extent, they will move as the seasons dictate rather than when humans decide to move them; their numbers will vary—sometimes dramatically—with environmental conditions; and the range's appearance will depend upon many environmental factors rather than upon close supervision by a human manager whose primary goal is to maintain the highest sustainable level of livestock production on that range.

For all their localized imperfections in terms of human disturbances, reserves such as the northern range, are the closest modern humans can come to seeing truly wild ranges in today's intensively farmed world.

This is not to say that either type of range should somehow be regarded as better looking, or better managed. One of the reasons Yellowstone National Park's policies have been drawn into range management controversies is that natural regulation is perceived as a threat to traditional range management beliefs. Though there are lessons commercial range managers can learn from wildland range ecologists, it has never been the intent of the National Park Service to place a value judgment on natural regulation that would rank it qualitatively above or below other range management practices or philosophies.

On the other hand, Yellowstone's experience after nearly 30 years under the natural regulation policy suggests that for a commercial livestock specialist to come into Yellowstone National Park and judge its northern range by the standards of livestock management practices is as inappropriate as it would be for a wildland ecologist to expect a livestock range to resemble a wildland grazing system. Without a deep familiarity with local conditions—history, climate, soil, native plant composition prior to settlement, and other factors—these environments do not easily yield accurate assessments of their conditions. The notion that all ranges, regardless of their history and their management goals, can be judged by some standard "cookbook" approach will not work well in Yellowstone. Unfortunately, some participants in the dialogues over the condition of national park ranges are not aware of the importance of this philosophical difference in goals.

This problem of perception is central to the Yellowstone northern range issue. Until the two differing perspectives are recognized, grim pronouncements from the livestock industry about Yellowstone's rangelands will continue, just as a host of wildland ecologists will continue to extol the health and wonder of the northern range and criticize the appearance of commercial ranges.

These philosophical complications aside, there remain the fundamental scientific questions about the northern range, questions that have been asked and re-asked by generations of researchers.

Among the complications affecting northern range research today is the fact alluded to by Houston (1982), that North American grazing systems were not studied until their native grazers had been manipulated or, in many cases, entirely removed. In Yellowstone, modern studies of herbivory are being conducted after a century of ongoing climate change, as well as varying manipulation of herbivores and their range; even a several-year study of vegetation trends in the 1980s or 1990s, cannot fully inform us about the condition of that vegetation in earlier times. For example, the long-term vegetation exclosures on the northern range were not constructed until after the drought of the 1930s; they do not necessarily reflect historic or ancient conditions in those areas.

In the following paragraphs, we summarize some of the recent research findings regarding the northern range. Keep in mind that much work is still underway; there is still much to be learned about this complex ecosystem. Thus, what follows is only a summary of the recent work on the northern range. Readers interested in learning more should consult the many scientific papers, reports, and publications cited at the conclusion of this book.

First, the concept of overgrazing required clarification. In many recent dialogues about the northern range, different participants meant different things by the term "overgrazing," resulting in great confusion and frustration. To test different concepts of overgrazing and how they might apply to the northern range, Coughenour and Singer (1991, 1996*c*) compared the Yellowstone natural regulation hypothesis to four other models or concepts of overgrazing. They noted that even among traditional professional managers, definitions of the term "overgrazing" vary greatly. Coughenour and Singer compared the concept of overgrazing as viewed by "a range manager, a wildlife manager, a model of natural regulation..., the Yellowstone natural regulation hypothesis, and a model of natural regulation that is less dependent on equilibrial assumptions." They did this by comparing the criteria of each of these definitions—in other words, they compared precisely what range conditions each viewpoint used to define overgrazing, and discovered that, by any of these definitions, it would be difficult to judge the northern range as overgrazed.

Coughenour and Singer concluded that the concept of overgrazing in Yellowstone has been significantly influenced by the perceptions of range managers and ecologists of the historical periods they have represented. For example, the climate of the 1930s added greatly to a perception of overgrazing at that time, though it was a random environmental event—an extended and severe drought—that set up the conditions observed at the time, rather than the short-term actions of the grazing animals. Coughenour and Singer agreed with Houston (1982) that the perception of an overgrazed northern winter range was predicated on the assumptions that: 1) elk populations increased due to protection within the park; 2) few elk wintered in the park prior to 1878, and that instead, most elk had migrated out of the park each winter; and 3) human development and ranching outside the park excluded elk from winter ranges, and unrestricted hunter harvests on the park boundary further eliminated migration patterns. They further concluded that early acceptance of the idea that the northern range was overgrazed followed directly from principles of range management published in the 1940s, though these principles were only applicable to domestic livestock.

GRASSLAND SPECIES COMPOSITION AND ABUNDANCE

Changes in species composition (that is, the assortment of species present on a given site) can be seen as a sign of overgrazing. Studies therefore addressed this condition. On low-elevation winter range sites, no differences in species composition were documented between grazed sites outside and ungrazed sites within exclosures protected from any grazing since the late 1950s (Reardon 1996, Singer 1996*a*). Large ungulate herds and intensive grazing do not appear to be negatively affecting native or Alpha diversity (Singer 1996*a;* Coughenour and Singer, Colo. State Univ., and U.S. Geol. Surv., unpubl. data). The evidence

indicates the number of grass, forb, and shrub species on the northern range was the same in grazed and ungrazed sampling plots. Shannon's index to plant species diversity was very similar; 2.38 in ungrazed grasslands compared to 2.30 in grazed grasslands. Community or Beta diversity on the northern range, however, may have experienced a slow decline in the past century due to the decline in aspen and willow stands, but this is somewhat unclear due to the greater Alpha diversity outside the exclosures versus inside the exclosures (Singer 1996*a;* Coughenour and Singer, Colo. State Univ., and U.S. Geol. Surv., unpubl. data.)

Wallace (1991) monitored community structure of five northern range sites, on summer, winter, and transitional ranges, collecting data both inside and outside of exclosures. She found "no significant correlations between changes in diversity and grazing intensities," and concluded that "climate has a stronger control on system structure than does grazing."

However, one study of mid-elevation willow communities and nearby grasslands reported significantly more plant species outside the exclosure than inside (Chadde and Kay 1988). According to this study, there were a total of 17 species inside the exclosure: 1 tree, 5 shrubs, 7 forbs, and 4 graminoids. There were 35 species outside the exclosure: 2 trees, 6 shrubs, 16 forbs, and 11 graminoids. If only native species are considered, there were 15 native species in the ungrazed inside and 31 in the grazed outside. This does not suggest that ungulate grazing decreases species diversity, and seems to suggest that grazing allows for more diversity.

In mid-elevation grasslands, climatic variation from year to year caused greater variation in plant species composition than did grazing (Wallace and Macko 1993). In one study, bison and elk grazing were found to be complementary, the two grazers selecting different plants and plant parts (Wallace 1996).

Three investigations focused on determining plant species changes after 30 years of protection from grazing in exclosures (Coughenour et al. 1994, 1996; Reardon 1996; Singer 1996*a*). Minor changes in species abundance (based on biomass measures) due to grazing were found in the first study (Singer 1996*a*). Two grasses resistant to grazing, Junegrass and thick-spiked wheatgrass, were more abundant on grazed sites. There was a slight tendency for Sandberg's bluegrass and Hood's phlox to be less abundant on grazed sites, even though Hood's phlox is not known to be a grazed plant. No effects on 127 other plant species were found. A second investigation that monitored plant basal areas found no effect upon any species that could be attributed to grazing (plant basal area is the area occupied by the root crown of the bunch grasses; it is regarded as a more useful long-term indicator of the plant's success than is the area covered by the canopy formed by the plant's leaves, because the canopy is more dramatically affected by yearly variations in moisture) (Reardon 1996).

A third study based on plant frequencies showed that total plant frequency, Idaho fescue frequency, and Junegrass frequency increased on grazed areas over the 1958-1981 period, even while elk numbers increased fourfold (Coughenour et al. 1994). As mentioned above, in the 1960s, elk numbers were artificially reduced to less than 4,000 on the northern range. Bison numbers were reduced to 400 parkwide at the same time. Since then, the northern range herds of elk and bison have increased substantially, to as many as an estimated 22,000 elk and 900 bison, their numbers varying depending upon a variety of environmental conditions. Coughenour et al. (1994) found that "dominant perennial grasses either maintained their relative abundance or increased. Forbs (broadleaf, herbaceous plants that are neither grasses nor shrubs) decreased in relative abundance, and increased after 1986 both in and out of exclosures, in response to drought. Total plant cover decreased after 1981 due to climatic conditions, as shown by parallel declines both inside and outside exclosures." The authors concluded, "On the basis of these trends, we conclude that elk grazing has not degraded the Yellowstone northern winter range."

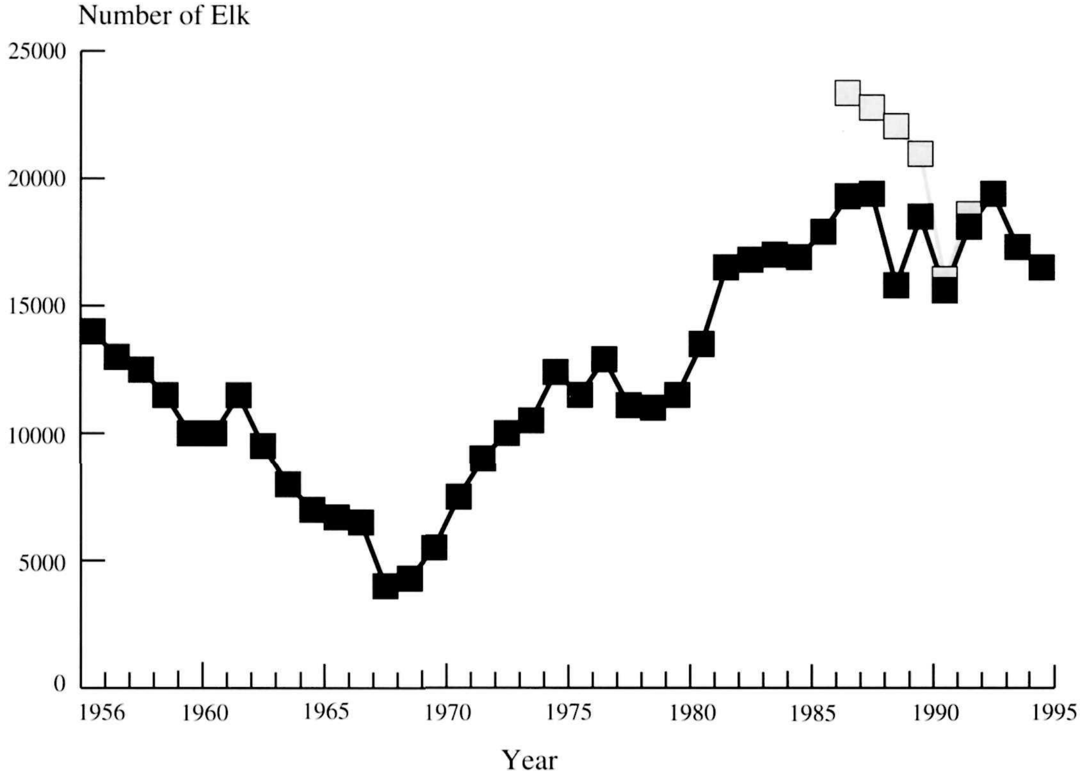


Figure 3.1a. Recent elk numbers on Yellowstone's northern range. Dark squares: minimum estimated number of elk in the fall. Grey squares: total estimated midwinter population as corrected for elk sightability, which varies due to differing winter conditions, adapted from Coughenour et al. (1994) and Singer et al. (1997).

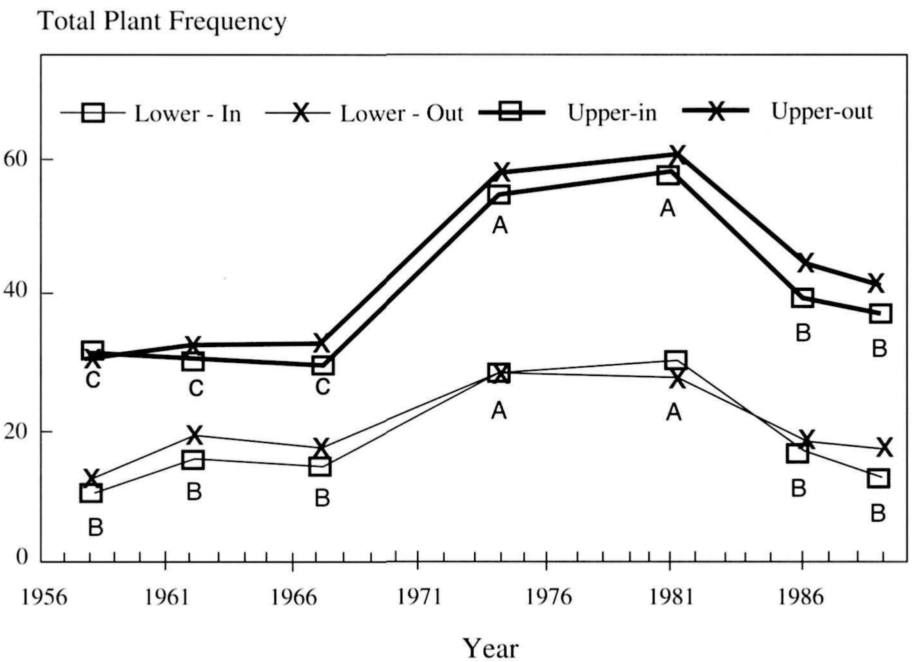


Figure 3.1b. Total plant frequencies inside and outside of elk exclosures on lower and upper elevation sites on the northern range. Note the lack of correlation between elk numbers and plant frequencies, suggesting that climate, rather than elk, is the determinant of the condition of plant communities. Adapted from Coughenour et al. (1994).

GRASSLAND PRODUCTION

The question of the effect of ungulate grazing on the abundance or biomass of grassland vegetation is central. Several research projects investigated vegetation biomass on a variety of locations and seasonal ungulate ranges (Frank 1990; Frank and McNaughton 1991, 1992, 1993, 1996*a*, 1996*b*; Merrill and Boyce 1991, 1996; Singer 1996*a*).

Data were gathered for two standard rangeland measures. One was net aboveground production. This is the total of all green annual production for the growing season, and includes an estimate of the production that is removed by grazing ungulates during the growing period. A second measure taken was peak standing crop biomass. This single measure includes the total vegetation biomass produced during the current season still standing at the peak of the growing season.

Peak standing crop biomass on summer range was not correlated with elk numbers. Biomass fluctuations apparently were related to climate and snowpack changes (Merrill and Boyce 1991, 1996). Peak standing crop biomass on lower elevation winter ranges was less on grazed sites in one study in 1986, but no difference was detected in 1987, 1989, or 1990 (Singer 1996*a*, Singer and Harter 1996). Grassland production was stimulated by elk and bison grazing on a wide variety of sites and elevations (Frank 1990, Singer 1996*a*, Wallace 1996), except that production was not stimulated on some sites during the severe summer drought of 1988 (Frank and McNaughton 1992, Wallace 1996).

Frank and McNaughton studied the interactive ecology of plants, large mammals, and drought on the northern range (Frank 1990; Frank and McNaughton 1991, 1992, 1993, 1996*a*, 1996*b*). They concluded that the park's ungulates, because of their high mobility and ability to make all their own decisions regarding forage choice, track young vegetation as it grows across the Yellowstone landscape. Elk and bison consumption rates of yearly grass production was found to be high, about 45 percent (Frank 1990). Peak consumption was linked to peak periods of plant growth. Nutrient cycling, that is, the return of minerals necessary for plant growth to the soil, occurred at a high rate on heavily grazed sites. Ungulates excrete 90 percent of the phosphorus they ingest, and 65-95 percent of their ingested nitrogen. By consuming and excreting plant matter at this scale, grazers stimulated aboveground production of their preferred food plants. This is a milestone scientific finding in Yellowstone, but it has been substantiated in other large wildland ranges, such as the African Serengeti. The discovery that grazers stimulated aboveground production of their preferred plant foods dramatically reverses traditional views by demonstrating that not only do wild ungulates not harm the plants, they facilitate and enhance plant growth:

> In Yellowstone, herbivores stimulated production at sites that were explicitly selected at the beginning of the study for their high herbivore use. Moreover, stimulation occurred in 1988 when elk and bison populations were at their highest levels in recent history. The only exception was the summer range site, mentioned above, where the drought was the severest and, notably, grazers had no effect on production. Some...have argued that the increase of northern range elk since Yellowstone Park's implementation of the "natural regulation" policy in 1969...has led to grassland deterioration in the northern range. These data clearly refute this argument by demonstrating no evidence for ecosystem process degradation, and show that quite the contrary, even during a year of unusually high elk and bison numbers, grazers stimulated grassland production in the northern range (Frank 1990).

It should be pointed out that some livestock managers are now discovering similar responses to grazing. When these managers move dense herds of their stock in an attempt more nearly to mimic the concentrations and seasonal movements of wild ungulates, they find that some plant species respond with vigorous growth (Dagget 1995).

Timing of ungulate use of the northern range was another critical element in understanding grazing there. Frank (1990) determined that use of plants on the northern range is timed to allow the plants to sustain heavy use year after year. The elk follow the "growth pulse" of greenup as it moves from winter ranges to higher elevation summer ranges. Unlike fenced, penned, or even herded livestock, elk do not remain on any given range for long, but move as environmental conditions dictate. This means that they seldom graze winter

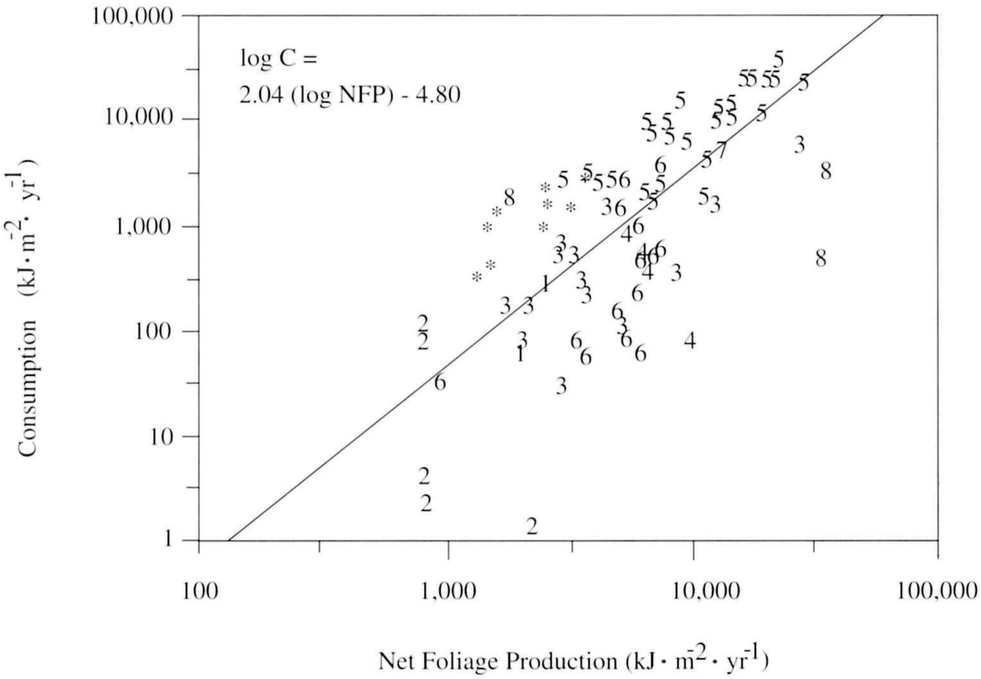


*Figure 3.2. The relationship of herbivore consumption, C, to net foliage production, NFP, for a variety of terrestrial ecosystems. Numbers on the graph are coded as follow: 1=desert; 2=tundra; 3=temperate grasslands; 4=temperate successional old field; 5=unmanaged tropical grassland; 6=temperate forest; 7=tropical forest; 8=salt marsh; 9=agricultural tropical grassland; and *=Yellowstone grassland. Note that consumption by herbivores on Yellowstone grassland falls well within the realm of other ecosystems, and is significantly less than the unmanaged tropical grassland. Adapted from Frank and McNaughton (1992).*

range forbs and grasses during the critical and most vulnerable growing period of those plants. As elk move across the range, they graze plants during their initial "greenup" phase, but move to higher elevations before the plants flower. The following fall, by the time the elk return from higher elevation summer ranges to the winter range, the plants have stored their essential energy reserves in their root systems, and the elk eat the aboveground plant matter without affecting the plants' ability to regrow the following year. Another way of saying this is that, while on the winter range, the ungulates are eating the "standing hay" that was able to grow while they were on the summer range.

Despain (1996) documented the natural coordination of elk movement with plant growth, in a separate study of the flowering dates of bluebunch wheatgrass. He observed that elk moved off bluebunch wheatgrass communities just as the grass began to flower and was at its most easily damaged stage of growth.

Concern has long been expressed over the magnitude of forage consumption on the northern range. Although the rate of ungulate herbivory on the northern Yellowstone elk winter range (45 percent) is higher than for small temperate grassland reserves with few ungulates, it is lower than the 62 percent average consumption reported on African game reserves that still have large segments of their native large herbivore fauna (Frank and McNaughton 1992) (Figure 3.2). These results suggest that high herbivory rates may have been characteristic of many North American grassland ecosystems dominated by large grazers prior to the Euramerican settlement of the continent.

Frank (1990) found that elk and bison stimulated grass production 36-85 percent at four sites in 1988, when compared to fenced vegetation. The degree of stimulation declined in 1989, apparently in part because of declines in ungulate populations and because of greatly reduced consumption of grassland vegetation in 1989; fewer ungulates resulted in less stimulation of vegetation production. At a site that saw severe summer drought in 1988, ungulates had no effect on production in either 1988 or 1989.

Spring grazing by ungulates was negligible on the lower winter range (Singer and Harter 1996), but spring offtake averaged about 26-30 percent on the upper winter range in Lamar Valley (Frank 1990; Merrill et al. 1994*a*, 1994*b*, 1996; Wallace 1996). Grass species compensated for this spring defoliation by the end of the growing season when grass biomass was equivalent between

grazed and ungrazed sites (Merrill et al. 1994*a*, 1994*b*, 1996). In other words, grasses grazed in winter and spring "caught up" with their ungrazed counterparts by the end of the growing season.

Singer and Harter (1996) studied the effects of long-term protection of plants from elk grazing, "at 8 large...exclosures constructed in 1958 and 1962:"

> Winter grazing by elk resulted in less standing crop biomass of grasses only in 1986, following a drier than normal spring. Total grasses were not influenced by grazing in any other year, and total forbs were not influenced by grazing in any year....

Use of exclosures (that is, ungulate-proof fences) to study plant communities on the northern range has been quite productive, but it has also caused considerable confusion. Critics of park management sometimes publish photographs of these exclosures showing that inside the fence the plant growth is taller; if the exclosure contains shrubs and other woody vegetation, the difference is even more dramatic. These exclosures are easily seen at several locations along the road from Mammoth Hot Springs to the Lamar River Valley, on the northern range. The implication of the publishers of the photographs is that the vegetation condition inside of the fence is what a "healthy" range should look like, when in fact the vegetation inside the fence only shows what the range would look like *if it had no large mammals grazing it at all.* As already noted, at least one researcher (Kay 1994*a*) believes that there were very few if any large animals on the northern range prior to 1872; if that were the case, then it might be argued that the exclosures represent the "natural" condition of the range. However, until evidence is presented to demonstrate such a paucity of grazers prehistorically (evidence that will have to overcome a mounting body of documentation indicating that grazers were present and abundant), the exclosures must be regarded as maintaining the artificial protection of plants from all large, native herbivores.

Last in the discussion of grassland production, Pearson et al. (1995) concluded that in the first few years after the fires of 1988, elk preferred to graze in burned areas, "presumably because burning had enhanced the abundance of forage," but that "fire effects on northern Yellowstone ungulates are likely to be relatively short-lived, and in the long term, may have minimal impact on population dynamics compared to winter conditions." Tracy (1997) found increased aboveground net primary productivity and forage consumption on transitional and winter range sites used by elk. But, results suggested that burning effects, if present at all, persisted for no more than three years postfire in most Yellowstone grasslands. Fire had either positive or neutral effects on aboveground production and the cycling of nutrients.

FORAGE QUALITY

Grazing enhanced the protein content of the three most common native northern range grasses (bluebunch wheatgrass, Junegrass, and Idaho fescue) between 10 percent and 36 percent (Singer 1996*a*). Grazing enhanced nitrogen content of forage plants in three other independent studies (Coughenour 1991, 1996; Mack and Singer 1992*a*; Merrill et al. 1994*a*, 1996). Grazing slightly enhanced other nutrient concentrations (calcium, phosphorus, magnesium, and potassium) in selected grasses.

NUTRIENT CYCLING

The nutrient dynamics of wildland ecosystems are quite complex. They are influenced by a variety of forces, including climate, soils, and the plant and animal species that inhabit the setting. Frank et al. (1994) examined the mechanisms surrounding the sustainability of grazing ecosystems such as the northern range through the study of nitrogen cycling. They reported that ungulates were a "particularly important component" of the nitrogen budget of the northern range, noting that the nitrogen flow from the animals to the soil was about 4.5 times that found in senescent plants. Their results suggested that herbivores increased both aboveground and belowground production.

Mammalian grazers, such as elk and other ungulates, process plant matter through their digestive systems with significantly different results for the ecosystem than if those plants were allowed to simply die and accumulate on the surface of the soil as litter. Grazers accelerate and enhance the cycling of nutrients through the soil system by consuming and digesting plants and then producing feces and urine that are cycled back into the system; they also do it by returning their dead carcasses to the system. A major difference between a wild native grazing system and a commercial livestock operation is that virtually all of the organic matter in the bodies of the wild grazers makes its way back into the system (often through the digestive tracts of predators and scavengers, who add another layer to the processing), while virtually all of the organic matter in the bodies of a commercial livestock herd is taken from the system to be consumed and processed elsewhere, usually through human digestive tracts.

An interesting side note to this recycling theme is the relational dimension of how nutrients move from the summer to the winter range. Since ungulates grow so rapidly and gain so much weight and fat on the summer range, and then lose weight and mostly die on the winter range, they probably move nutrients down the elevational gradient (F. Singer, U.S. Geol. Surv., pers. commun.).

GRASS SIZES AND SHAPES

In a study of the effects of elk herbivory on northern range grasslands, heights of seed stalks and vegetative leaves were taller on grazed winter range sites than on ungrazed sites in three of four years (Singer and Harter 1996). Vegetative leaves were shorter on grazed sites than on ungrazed sites in one year, 1986, apparently when growth conditions were sub-optimal, possibly due to a very early melting of the winter's snowpack (Singer 1996*a*, Singer and Harter 1996). No increases in bunchgrass mortality, no differences in species diversity, and no differences in soil moisture due to winter elk herbivory were documented (Singer and Harter 1996). Morphological parameters of grazed plants were reduced on summer range where plants were grazed through the active growing season (Wallace 1996). This might be evidence grazing effects on plant morphology does not necessarily damage the plants or their production.

LITTER

Accumulated organic litter was about 3.5 times greater in ungrazed sites within exclosures (Frank 1990, Singer 1996*a*). As a result of the increase in litter and soil crust lichens over a period of 24-28 years of protection from grazing, exposed surface (bare ground and rock combined) was 11 percent higher on grazed surfaces.

GRASS ROOTS

Coughenour (1991, 1996) studied root biomass and nitrogen responses to grazing of upland steppe on the northern range, and determined that, "grazing had no effect on root biomass, ...an important measure of the fitness of long-lived perennial grass genets." Coughenour emphasized the importance of climatic conditions in affecting grazing responses of plants. Root biomass on grassland sites was not affected by grazing (Merrill et al. 1994*a*). There were more root-feeding nematodes (roundworms) in the soil of grazed areas, and they probably increased nitrogen mineralization rates (Merrill et al. 1994*a*, 1994*b*, 1996).

FORBS

The forb biomass technique was used to gather data on forbs because it is most closely tied to the productivity of the site. The results of forb biomass analysis showed some variability between years and study sites. At the Blacktail Plateau exclosure, there was less forb biomass on grazed sites in two of three years of sampling. However, a study of six exclosures on the northern range found that there was no statistically significant difference in forb biomass in 1986 or 1987. Coughenour (1991), in an independent sampling of the same six exclosures in 1987, found no difference in forb biomass on grazed and ungrazed plots, and in 1988 found more forbs on grazed plots. Singer (1995)

showed that grazing selected against some species and for others. For example, there was less rosy pussy toes (85 percent less) and fringed sage (33 percent less) on some grazed sites, but there was a great deal of site-by-site variation. On the other hand, another native forb, *Arabis holboelii*, was found on grazed plots but on no ungrazed plots.

No consistent effects of grazing on forbs was revealed, as measured either by plant frequency or by plant basal cover. When plant frequency was measured, forbs were more often encountered on grazed sites in 8 of 14 comparisons, and less often encountered on grazed sites in 6 of 14 comparisons (Coughenour et al. 1995). Plant basal cover was less for forbs on grazed sites at the Blacktail and Lamar exclosures, but greater on grazed sites at the Gardiner exclosures (Reardon 1996).

From the evidence collected to date, there was no consistent response of forbs to ungulate grazing on the northern range. Green forb biomass was reduced by grazing at some locations, years, and sites but the reverse of this was also commonly measured. Some of the annual variations observed may have been related to variations in precipitation. Coughenour et al. (1995) felt that "forbs responded positively to high spring rainfall and, in those years, forbs became increasingly competitive with grasses. While some reductions in forbs were observed, they were usually non- or marginally-statistically significant, not consistent between years, and no species of forb was being eliminated or reduced to a low level."

SOILS

No consistent trends were found in soil nitrates, soil organic matter, or soil nutrients between grazed and ungrazed sites (Lane 1990, Lane and Montagne 1996). Soil surface bulk densities were consistently higher on grazed sites (Lane 1990, Lane and Montagne 1996). High surface bulk densities may restrict movement of air and water through the soil; higher densities are usually the result of soil compaction. Some soil compaction is a logical consequence of the hoof action of ungulates on the soil surface. But several studies verified that soil moisture levels were not affected by grazing (Lane 1990; Coughenour 1991; Merrill et al. 1994*a*, 1996; Lane and Montagne 1996; Singer and Harter 1996).

For more on soils, see Chapter 5 .

RESEARCH RECOMMENDATIONS: GRASSLANDS

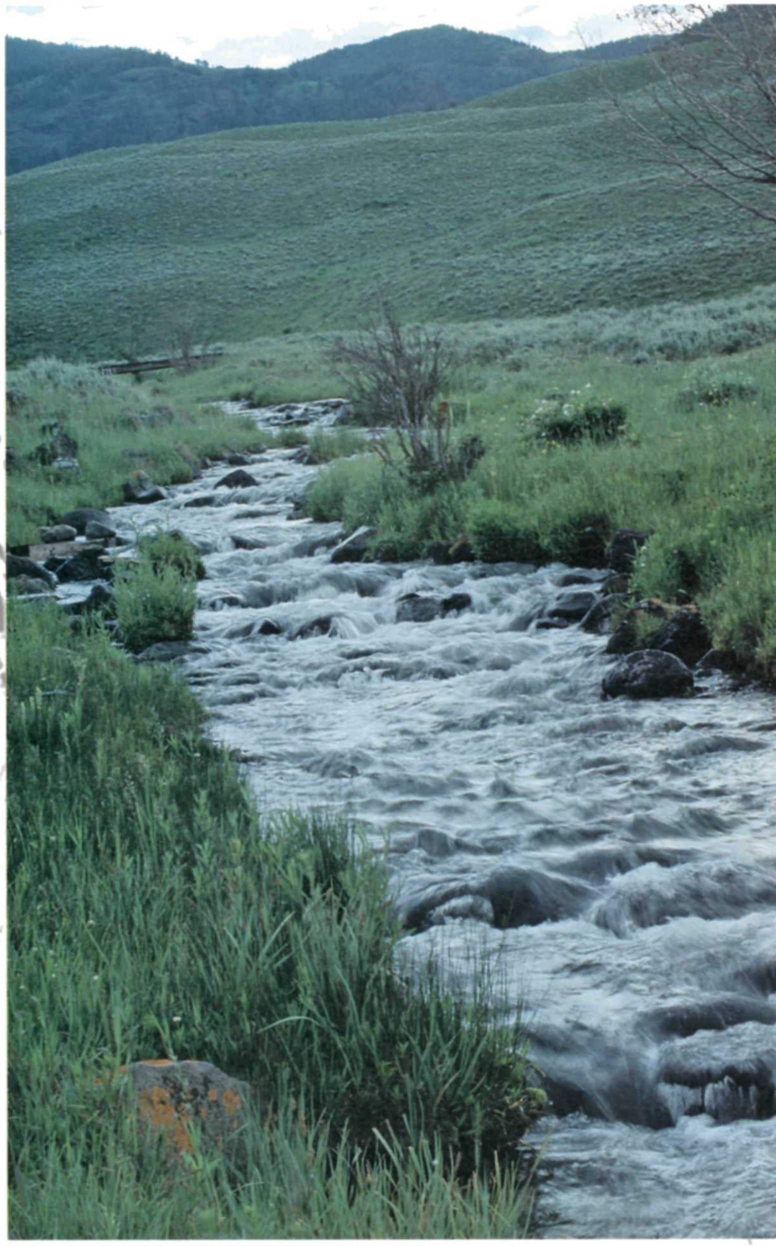
The area of greatest emphasis during the most recent research initiative concerned grazing effects on grasslands. While we now understand the grasslands better than the other components of the winter range, continuation of some aspects of grassland research is strongly recommended. First, a more intensive and consistent monitoring program for grassland production, grassland nutrient content, and climatic changes is needed. Second, the effects of the mechanisms of grazing on grasslands need to be better understood. For example, what factors contribute to the apparent stimulation of aboveground and belowground production and nutrient cycling by grazing? Third, fitness of some grasses may be enhanced by grazing, and this question should be pursued. Other important topics requiring further investigation include system functioning, the role of grasshoppers, nematodes and other invertebrate herbivores, and the role of small mammals such as pocket gophers in soil disturbance and plant succession (Gruell 1973, Houston 1982). Research is also needed to develop methods of restoring native grasses to areas now dominated by such non-native species as smooth brome, crested wheatgrass, timothy, and cheatgrass.

CONCLUSIONS

Houston (1982) wrote that, "the effects of herbivores upon the vegetation of the park require another look, because preoccupation with ungulates gives a distorted view of their herbivory in ecosystem dynamics." An important aspect of the studies conducted since Houston published that statement is their attention not only to ungulates but also to many other environmental factors. Rather than focus on the immediate effects of

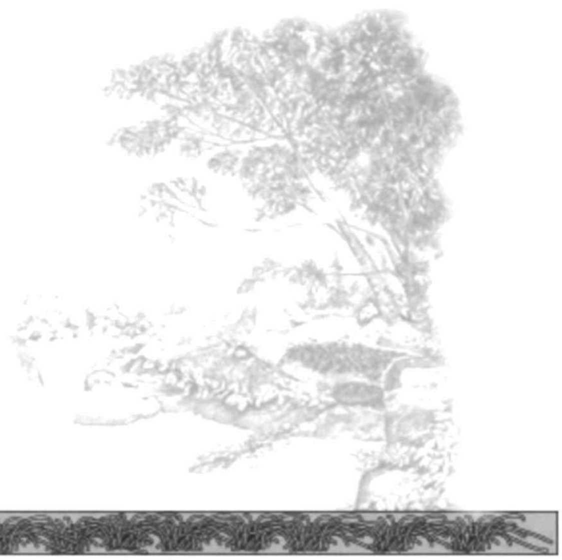
ungulate grazing alone in a given year, scientists instead measure other important factors, especially climate, that appear to be fundamental in controlling ungulate grazing and population levels. This approach allows for a more thorough, ecosystem-based analysis than past studies could.

Frank and McNaughton (1992) have written that "climate is the principal driving variable of ecosystems processes." In this light, the elk, bison, and other grazing animals on the northern range might be seen as one force among many in the northern range's ecological processes, rather than as the only force shaping those processes. The grazers, by converting green and dried plant matter to feces and urine, enable and accelerate the cycling of energy through the system. The system is further stimulated through the incidental tilling of the soil by the grazers' hooves, and the enrichment of the nutrient supply when cycled through predators and scavengers or by means of decaying ungulate carcasses. By conceptually integrating the grazing animals into the northern range's grassland ecosystem, rather than perceiving those animals as an independent force that acts arbitrarily on that ecosystem, we can gain a more clear and useful perspective on how the northern range functions. Based on these studies, it is apparent that the ecological processes of the northern range grasslands are functioning well within the range of variations known for such wildland systems elsewhere in the world (Frank and McNaughton 1992).



CHAPTER FOUR

WOODY VEGETATION



SAGEBRUSH

Sagebrush's history in the intermountain west is the subject of great debate. Disagreements center on whether or not sagebrush has increased in abundance since Europeans arrived in the New World (Mehus 1995). Managers in various areas deal with this issue as they attempt to formulate management plans. Sagebrush was a species of concern in the early years of the northern range overgrazing issue, and the dialogue featured this very question of the historical abundance of the species.

Big sagebrush-ungulate interactions vary dramatically between two areas of the northern range in the park. These two areas are the upper northern range, above Undine Falls (on Lava Creek), and the lower portion of the northern range between Mammoth and the north boundary, primarily in the Boundary Line Area (BLA) (Figure 4.1). Rush (1932) and Cahalane (1943) reported that sagebrush was declining on the BLA, and Kittams (1950) reported that it was declining at higher elevations as well.

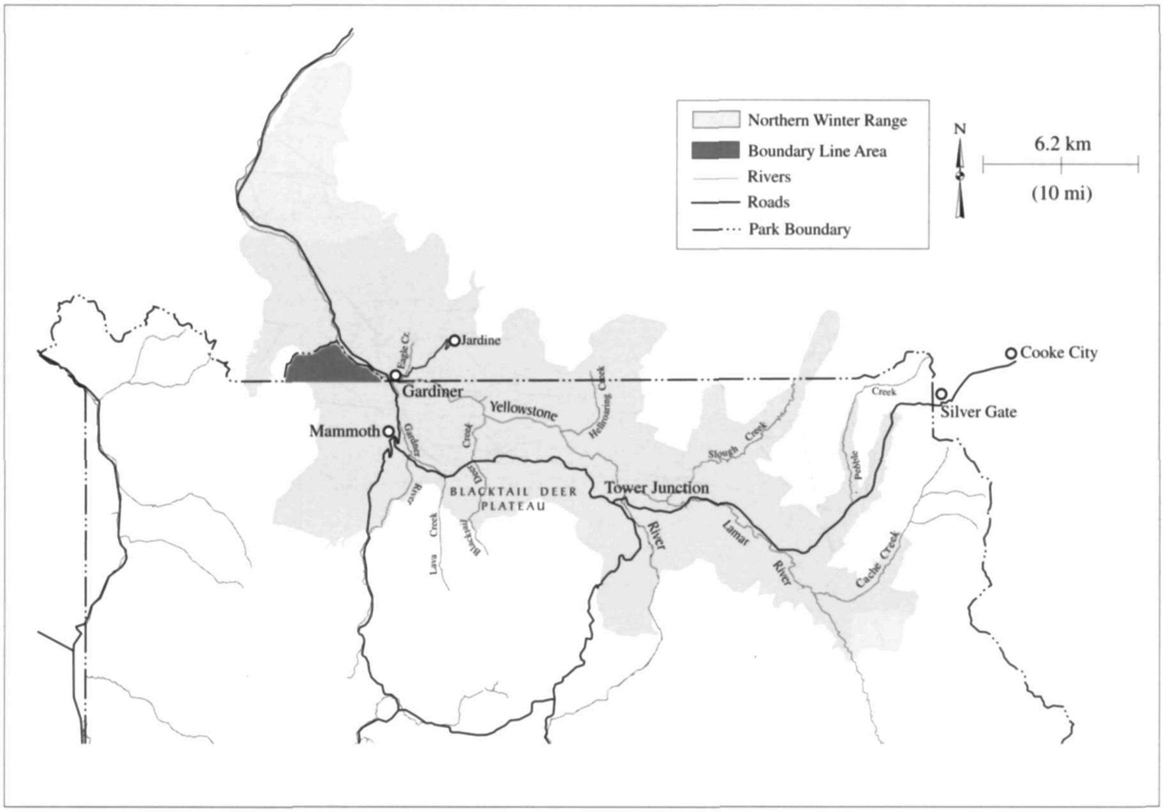


Figure 4.1. Northern range, showing Boundary Line Area (BLA), a later addition to the park (1932), west of Gardiner, Montana. A variety of human influences have affected the vegetation of the BLA more than most other parts of the northern range. Much of the BLA was heavily grazed or overgrazed by livestock before being added to the park, and intensive feeding of wild ungulates concentrated animals in limited areas where they severely affected native vegetation. Map by Yellowstone Spatial Analysis Center and the Yellowstone Center for Resources.

In the upper area, snows are deeper and only elk and bison use the grasslands in winter. This area encompasses the majority (about 91 percent) of the winter range in the park. Elk consume few sagebrush here (about 4 percent of their diet), and bison consume almost none (0.1 percent). As a result, big sagebrush plants are consumed at a low rate of about 9 percent of their current annual growth. Houston (1982), based in part on an examination of early photographs of the area (1870s and later), concluded that since the park's establishment in 1872, sagebrush had in fact increased over this higher elevation portion of the northern range. Between 1958 and 1990, big sagebrush increased dramatically on this area of the northern range, both on grazed and on ungrazed sites (Singer and Renkin 1995). Individual grazed big sagebrush and rabbitbrushes were shorter, and crown sizes were smaller, than ungrazed ones. However, grazed shrubs had longer average flower stalks, twigs, and leaves; therefore, annual production was equivalent between grazed and ungrazed stands. More big sagebrush and rabbitbrush seedlings became established on grazed sites. Shrub population dynamics were different on grazed than ungrazed sites, with smaller individual shrubs, but with more biomass produced per unit of shrub, and more recruitment of young shrubs on grazed sites, at least during the study years 1958-1988 (Singer and Renkin 1995). Houston, who attributed the increase in sagebrush on higher elevation sites to fire suppression by park managers since the 1890s, documented a mean fire-return interval on northern range grasslands of 20 to 25 years in the 300 to 400 years prior to the 1890s (Houston 1973).

The situation is quite the opposite in the lower northern range, which encompasses about 9 percent of the winter range in the park, specifically on the BLA, where heights and reproduction of big sagebrush were suppressed. Here, snows are shallower and three ungulates consume significant amounts of big sagebrush: elk, mule deer, and pronghorn. Singer and Renkin (1995) found that the pronghorn diet on the northern range was 81 percent shrubs. Mule deer diet was 50 percent shrubs, elk was 8 percent, and bison was 1 percent. Big sagebrush made up 49 percent of the prong-

horn diet, 23 percent of the mule deer diet, 4 percent of the elk diet, and 0.1 percent of the bison diet during the winters 1985-1988. But the declines were restricted mostly to the Wyoming subspecies, as well as to the mountain subspecies of big sagebrush; these declines occurred mostly on rolling upland topography. Sagebrush on lower slopes, swales, and drainages, which is mostly the basin subspecies, was as tall and vigorous as it was across most of the northern range. Thus, detailed study at three exclosures in the lower area and five exclosures in the upper area, as well as extensive foot and horseback reconnaissance of the rest of the northern range, indicates that big sagebrush is suppressed by ungulates and declining on about 3 percent of the range in the park, and is either holding its own or increasing on the other 97 percent.

Mehus (1995) found that on the northern range outside the park, big sagebrush was "the most significant item in mule deer diets, averaging 33 percent of the diet across 9 sites." It is not possible to attribute this high level of winter use of sagebrush to the elk population; Mehus (1995) found that big sagebrush averaged 3 percent of the diets of elk in the same area, and winter use of sagebrush was equally high in the 1960s when elk and pronghorn were reduced to about 25 percent of their late-1980s numbers (Singer and Renkin 1995). It should be noted that because elk are so much more abundant than pronghorn on the northern range, even very low consumption rates of sagebrush by individual elk could result in a large cumulative amount of sagebrush consumed. But again, it must be pointed out that competition between these native ungulate species is not in itself proof that something is wrong.

Declines in big sagebrush in the BLA will reduce the area's potential as winter range for mule deer and pronghorn. Mehus (1995) concluded that "because big sagebrush is a critical cover and browse species for wintering ungulates in the study area [the northern range north of the park], habitat management should focus on protection of these habitat types. Fire negatively influences non-sprouting browse species like big sagebrush that are already declining under intense browsing pressure." Conversely, Clark (1991) looked at the effect of fire on seed germination and concluded that sagebrush seed germination was stimulated by temperatures of 122°F (50°C). Subsequent work has shown that sagebrush is re-establishing well on most of the areas burned in the 1988 fires (D. Despain, U.S. Geol. Surv., pers. commun.).

Houston (1982) noted that the BLA was a later addition to the park that had been heavily used by livestock from before the turn of the century until 1932. Houston (1982) and Singer and Renkin (1995) also suggested that at times the BLA has hosted unnatural and artificially high numbers of ungulates "due to animal avoidance of hunting outside the park" (Singer and Renkin 1995). The historical presence of livestock and the continued influences of hunting on animal movements must be considered when evaluating trends in sagebrush on the BLA. For example, Mehus (1995) attributed declines in sagebrush on the BLA to high ungulate numbers and concluded that it will be necessary to reduce herbivore numbers "for browse species to persist even at their currently reduced abundance," but Houston (1982) interpreted the decline of big sagebrush in the BLA area as a return to more pristine conditions following the removal of livestock in the 1930s, because heavy livestock grazing promotes big sagebrush. Thus there is some question if the decline in sagebrush on the BLA is a departure from prehistoric conditions or an artifact of human activities in the area in the period of early white settlement.

RESEARCH RECOMMENDATIONS: SAGEBRUSH

Future research on sagebrush should focus primarily on the BLA. Continued high levels of human activity in and near the BLA, such as bison management operations at and near Stephens Creek, continued year-round pronghorn use in the BLA, and both livestock grazing and hunting just outside the park, can affect all native ungulates and their use of the BLA in the future. The reintroduction of wolves to Yellowstone National Park may affect prey species numbers (Singer 1991*a*), and

has led to predictions of decreases in coyote numbers (R. Crabtree, Yellowstone Ecosystem Stud., pers. commun.), which may permit an increase in pronghorn (Berger 1991), the ungulate species most dependent upon sagebrush, and currently regarded as a species of special concern on the northern range (see pronghorn research recommendations, Chapter Seven). Further research into the ecology of the various sagebrush species across the northern winter range is needed, especially into the factors contributing to the decline of the Wyoming subspecies, and the apparent thriving of the basin subspecies. The role of pronghorn in the vitality of sagebrush and climate change appears crucial. Continued monitoring of all of these interactive forces in the BLA seems warranted.

WILLOWS

About one-half of one percent (0.54 percent) of the Yellowstone Park's willow communities are on the northern range (Figure 4.2). The greatest concentrations of willows in Yellowstone National Park are south of Yellowstone Lake, the southwest corner of the park in the Bechler River area, and near the west boundary north of the Madison River. Willow abundance in the park is almost entirely defined by elevation and precipitation; areas that are above 7,000 feet and have more than 20 inches of annual precipitation comprise 74 percent of the park's willow communities, and areas that are above 7,000 feet and/or have more than 20 inches of annual precipitation comprise more than 99 percent of the park's willow communities. These are high-elevation sites, not on the winter ranges of ungulates, except possibly that of moose.

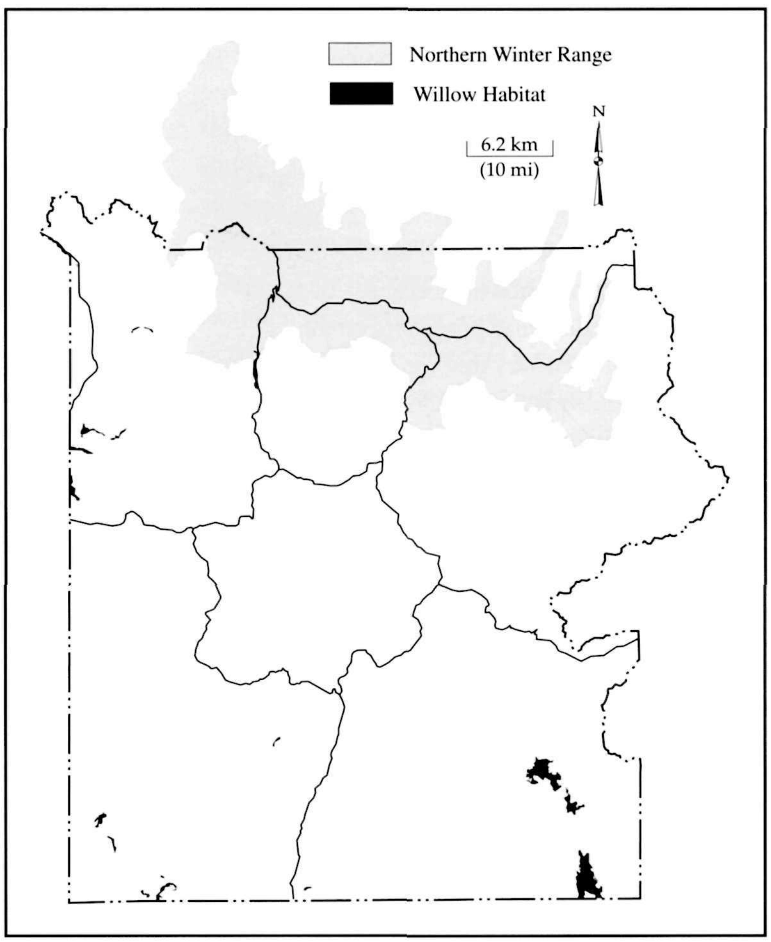


Figure 4.2. Willow distribution in Yellowstone National Park. The largest concentrations of willow are south of Yellowstone Lake along the upper Yellowstone River, in the southwest corner of the park, and in tributaries of the Madison River near the west boundary. Map by the Yellowstone Spatial Analysis Center and the Yellowstone Center for Resources.

Willows have been described as an "insignificant component" of the Yellowstone area for at least the past 20,000 years (Mullenders and Coremans 1996, Mullenders et al. 1996). That should be taken to mean that they occupy comparatively little area. It should not be taken to mean that they do not have significant ecological effects on northern range plant and animal communities, a subject dealt with later in this section.

Declines in willows were noted early in the northern range's written history. Houston, based on comparison of historic photographs with modern retakes, estimated that during the past century, willows may have declined in area from about 0.8 percent of the northern range (that is, slightly less than 1 percent) to about 0.4 percent (that is, less than half of 1 percent). Houston (1982) and Chadde and Kay (1991) published photographic evidence of heavier willow growth along some park streams prior to 1900.

There are approximately 24 species of

willows in Yellowstone National Park. Some are difficult to identify when specimens are available for examination. Thus, historic photographs rarely allow for species identification, but do provide gross evidence of changes in abundance or distribution. Many observers have attributed the decline in willows on the northern range to overbrowsing by elk (Grimm 1939, Kay 1990, Chadde and Kay 1991, Wagner et al. 1995*a*). Other suggested causes include declines in beaver since the 1920s (Singer et al. 1994), the colonization of the northern range by moose early in the 1900s (Houston 1982; Chadde and Kay 1988, 1991), fire suppression activities by park managers since the late 1800s (Houston 1973, 1982), and climatic variations, especially the drought of the 1930s, which, through changes in groundwater levels or other processes, might have either directly killed the plants or reduced their ability to produce secondary defensive chemical compounds that make them less palatable to grazers (Houston 1982; Singer et al. 1994, 1996*b*).

Figure 4.3. Willows are protected from all ungulate browsing in the Junction Butte exclosure. Casual observation of this and other exclosures has led to a mistaken impression that all vegetation on the northern range "should" have the same appearance as that inside exclosures. The only way the vegetation within the exclosures could be replicated across the whole northern range would be by completely eliminating ungulates from the range. NPS photo.

Elk are usually the proximal factor in the decline of willow stands (Figure 4.3). Elk very likely accelerate willow declines that might be due to other causes. However, not all declines in willows are due to ungulate browsing. Houston (1982) pointed out that an entire stand of willows on the lower northern range was defoliated by *Disonycha pluriligata*, a native beetle whose presence on the northern range was unknown until his study; he suggested that it would have been easy for the casual observer to mistake the after-effects of this defoliation for heavy browsing by ungulates. In another instance, willow stands and individual willows died in the summers of 1988-1989 apparently as a consequence of the severe drought of 1988. Those dying stands were measured for water pressure in 1988 and had the lowest measurements of any of the many willow stands measured that year, verifying the drought stress (Singer et al. 1994).

A third alternate factor in willow declines is fire. Willows on several marked transects burned and were either killed outright in 1988 or never resprouted or recovered (Norland et al. 1996). This is contrary to what others have observed. According to Wolff (1978) and MacCracken and Viereck (1990), willows virtually always vigorously resprout and reseed following fire. Some burned Yellowstone willow stands were immediately replaced with grasslands or forb vegetation. We interpret this as additional evidence that willows cannot recruit in many areas of the northern range and are failing on some sites under existing climate conditions or because of low surface/ground water control.

Popular perceptions of willows, as with aspen (see next section), seem to be of a progressively declining group of species that has been fading from the northern range since early in this century. However, over the course of this century, most willow declines on the northern range occurred in the 1930s. Most of these occurred during the extended drought of that period, and in the face of elk numbers much lower than at present (Houston 1982, Singer 1996*b*). These declines included the disappearance of some willow stands and suppression of the heights of some other willow stands. Since then, there has been little change in willow status, perhaps lending credence to the idea that climatic forces, rather than ungulate browsing, may be the most important factor in

Figure 4.4. In 1893, tall willows were abundant along watercourses in Yancey's Hole, near Tower Junction, and have since largely disappeared. Kay (1990, 1991) has proposed that elk were solely responsible for this disappearance, but historical evidence indicates that as early as 1883, 5,000 elk were wintering on the northern range, and probably more by the 1890s. In the 1960s, fewer than 5,000 elk were able to suppress willow growth on the northern range (Barmore 1980), leading to the question of why elk were unable to suppress tall willows at locations like Yancey's Hole in 1890s. Changes in climate since the 1890s may have reduced the willows' ability to defend themselves from browsing. NPS photo.

determining the fate of the willows. During the elk reductions of the 1960s, when the northern elk herd was suppressed to less than 5,000 for at least five years (and less than 4,000 for at least two years), willows were still heavily browsed (Barmore 1980, Singer et al. 1994, 1996*b*).

This episode of elk reduction in the 1960s provides a useful window on earlier times in the park's history as well. Kay (1990) has published historic photos (such as Figure 4.4), which show robust willow growth on the northern range in the period 1893-1897, and has suggested that unnatural increases in elk on the northern range were the cause of declines or disappearance of these willow stands. It is known that elk numbers were suppressed during the industrial-scale hide-hunting era in Yellowstone in the 1870s, but it is unclear from the historical record precisely how extreme this suppression was, or how long it lasted (Schullery and Whittlesey 1992, 1995; Schullery in press). However, as early as 1883, local observers reported a minimum of 5,000 elk wintering on the northern range in the park, and by the 1890s it appears that the number of wintering elk may have been considerably higher than that (Houston 1982, Schullery and Whittlesey 1992). During the period 1883-1896, then, elk were more abundant on the northern winter range in the park than they were during the period 1963-1969, but as historical photographs such as Figure 4.4 clearly show, willow growth in the 1880s and 1890s continued to be robust and tall in the presence of large numbers of wintering elk. This should raise the question of what had changed between 1896 and 1960: why did willows thrive between 1883 and 1896, in the presence of at least 5,000 elk, when willows were suppressed by even fewer elk between 1963 and 1969? As discussed below, changes in climate, with consequent changes in the willows' ability to defend themselves from browsing, are now considered by some investigators to be a likely answer to this question.

Because elk and bison, the most important ungulates on a biomass scale, eat mostly grasses and sedges (80 to 97 percent of the diet) and because the condition of northern range grasslands has been the primary concern of managers and investigators since the 1920s, willow research was not initially as high a priority as grassland research.

Only two willow studies were conducted between 1986 and 1990. Singer et al. (1994, 1996*b*) reported that suppressed-height willows were found in roughly one-third of the northern range willow stands. Intermediate and tall willow stands appeared to be healthy and vigorous; most management concerns focus on willows whose height is suppressed by browsing. Investigations suggested that suppressed willows were more common at lower elevations that are warmer and drier. Suppressed willows were more sought out as forage by ungulates and had lower levels of secondary defense compounds, lower levels of protein, and less water stress than taller willows. Suppressed willows produced only 12 percent the current annual growth of tall willows; even after 29 years of protection from all ungulate grazing, suppressed willows still produced only 33 percent as much growth as tall willows. Suppressed willows apparently grew on sub-optimal sites.

As mentioned earlier, willow production was positively correlated with higher precipitation and elevation on the northern range. Most tall stands

grow at higher elevations. Intermediate height stands are found at a wide variety of locations. Although less water stress was detected in suppressed willows, some of the willow communities on marginal sites may already have died, or may have failed from too much browsing. Shoot:root ratios of the remaining suppressed stands may have adjusted to a more favorable relationship for water balance. An interaction between climate, water tables, and willow herbivory was suspected. For example, death of many willow plants in two intermediate height stands was documented following the drought of 1988. Only about half of marked willow communities responded positively to burning in the fires of 1988. This suggested that some willow stands are on poor sites, because willows are reported to be stimulated by burning in nearly all other studies. There is a possibility that a warmer (1.6°F [16.2°C] higher average temperature) and drier (2.4 inches less precipitation) climate this century has contributed to the decline in abundance and stature of willows (Balling et al. 1992*b*, Singer et al. 1996*a*).

Willow status on the northern range was relatively stable or even improving during the past three decades (Chadde and Kay 1988; Singer et al. 1994, 1996*b*). Heights, stem numbers, and total cover of browsed willows on permanently marked transects were stable or increased slightly (Chadde and Kay 1988; Singer et al. 1994, 1996*b*). Nearby protected willows increased two to five times in cover since 1958, but the number of stems from protected willows declined and heights declined since 1986 (Singer et al. 1994, 1996*b*). Willows inside exclosures provide a dramatic example of the consequences of complete protection from ungulate browsing, but exclosures represent only one extreme point in the spectrum of ungulate herbivory. As noted earlier, one study showed significantly higher plant diversity outside a willow exclosure than inside it (Chadde and Kay 1988). In fact, the willows inside the exclosures have suggested to us that they are growing in what might be termed "currently suboptimal sites." Even after 29 to 33 years of large herbivore protection, there were no new willow recruits or individuals, and no expansion on the edges of the willow stands inside the exclosures (Singer et al. 1994).

Ungulate-use rates on suppressed willows were not lower during the 1960s, when elk populations were reduced to 25 percent those of the late 1980s (Barmore 1980, Singer at al. 1994, 1996*b*). Drastically reducing elk numbers during the 1960s did not achieve the goal of reducing browsing on willows (Barmore 1980; Singer et al. 1994, 1996*b*).

An interesting part of local folklore about northern range willows is that their condition can best be judged by comparing them with other willows outside the park. At first glance, this might seem a useful test, and in some respects it does allow for a comparison of differing management approaches. However, to point to willows in some drainage outside the park as somehow "proving" that something is "wrong" with park willows is rarely a safe comparison. For example, many willows on upper Slough Creek, outside the park to the north, are typically taller than those on the northern winter range, but this is no surprise; these willows are at higher elevations in cooler and more shaded locations, receive more annual precipitation, and are not on the elk winter range. In fact, studies have shown that these willows are subjected to more intense herbivory from local concentrations of moose that, unlike elk, browse willows for most of the year (Singer and Cates 1995). These willows, growing in a cooler, wetter area, are tall and vigorous, better defended by chemical defense compounds, and they recruit new individuals regularly, especially on new alluvial sites. These willows, like the very large willow communities south of Yellowstone Lake *in* the park, are on summer range and are less heavily browsed by elk but browsed hard by moose; in winter, snow depths exclude elk from these willows but not moose. Conversely, tall willows are abundant along the Yellowstone River 20 to 40 miles north of the park but these willows are on ranches that experience little or no elk herbivory. Domestic livestock not only do not consume willows to any extent, but they also graze grasses near the willows, thus increasing the competitive advantage of the willows.

Most willows outside the park, even those on

public lands, have been subjected to a variety of powerful human influences over the past century, influences quite different from those experienced by willows in the park. These influences have included the early (pre-1900) decimation of native ungulate populations and the introduction of large numbers of livestock, whose movements and vegetation use have been dictated by human decisions through most of this century, and whose interest in willows as food is slight. To expect these willows, growing on lands managed so differently from the park, to somehow "prove" that park willows are "too short" is to ask more of them than they can fairly provide.

The casual comparison of willow communities outside the park with those inside the park is an example of a common problem in the northern range dialogues: competing notions of how a vegetation community "should" look. Typically, when examined closely, these ideas of what "should" appear on the northern range are subjective, based on anything from local memories of some earlier decade to commercial range management standards to what willows look like somewhere in the Yukon Territory. McNaughton (1996*a*) recently elaborated on this point:

> You know, "should" is a very dangerous word in resource management. If you say it should look a certain way, you're implying that you have a basis of comparison with some presumably right appearance for the northern range. In order for me to know if their "should" is somehow the right one for Yellowstone, I have to know the context in which they define it....
>
> An ecosystem has both a state and a process. State is what you see out there on the ground at any given time. Process is what happens as the ecosystem changes from one state to another. If someone tells me that it "should" look a certain way, then they are going to have to explain to me what the processes are that lead it to that state, and why the processes must lead it to that state instead of to some other state.

The current condition of willow communities outside the park is often the result of more than a century of human activities, including agricultural irrigation, fire management, and intensive manipulation of wildlife and livestock that use those areas. Such manipulations will certainly result in differently appearing willow communities than exist in the park; but judgments about the relative superiority or health of these willow communities must be made with a full awareness of their contexts. How the park's willows "should" look is not simply a matter of comparing one land management style with another, but of understanding a complex suite of influences that shape both wild and manipulated willow communities.

Additional discussion of willow appears later in this report, under the headings of "Aspen, Willows, and Biodiversity," and "Beaver."

RESEARCH RECOMMENDATIONS: WILLOWS

Because there are so many species involved, and because the character of each species' response to browsing is not well understood, additional research will be needed to clarify willow ecology and status on the northern range and throughout the park. Among the important avenues to pursue is the historical dimension of this issue. It would be useful to reconstruct changes in hydrological systems, groundwater levels, water yields, precipitation patterns, and other influences on willow communities in the Yellowstone area since settlement began in the 1870s.

A key area of needed research is to define what environmental conditions foster seedling and vegetative establishment of new willow colonies. Little is known about the regeneration of willows and other woody riparian species by seed. Perhaps one reason for the decline of these species during the last century has been lack of suitable habitats for seedling establishment, due to a change in flood frequency and intensity related to climatic conditions. It would be useful, therefore, to study the processes of seed reproduction, dispersal, and seedling establishment in a range of habitats, for

example, point bars along rivers, drying oxbows, and near springs and seeps. New experimental exclosures such as described under the aspen research recommendations would probably be necessary for this research; such a study could greatly help to sort out the relative influences of ungulates, climate change, and geomorphic processes in the decline of woody riparian vegetation during the past century.

In the late 1980s, a group of 18 riparian scientists reviewed the state of knowledge concerning the status, condition, and trends of riparian ecosystems in Yellowstone, and made recommendations (Anderson et al. 1990). They concluded that the issue of riparian system changes has been recognized by virtually all involved, and that preliminary research has been completed by scientists from within the park and from outside institutions. Resource managers and scientists from throughout the west formulated a set of hypotheses that should be tested. In brief, they recommended that studies be directed as follows:

1. Test the hypothesis that the riparian ecosystem maintains a dynamic equilibrium with climate and geology and thus is responsive to climate changes past, present, and future.

2. Test the hypothesis that ungulates are the biotic dominants regulating the riparian system.

3. Test the hypothesis that natural disturbance events (e.g., fire, flood, etc.) profoundly affect the riparian systems.

4. Test the hypothesis that the riparian environment is an important mediator of aquatic systems.

5. Test the hypothesis that the riparian environment may mediate processes in upland areas through its effect on the movement of ungulates, nutrient loss, and plant species movement along aquatic corridors.

Each of the above hypotheses contained many subquestions too numerous to detail here. Because of cuts in research funding, little riparian research was initiated in the 1990s, but some funds were made available for work to begin with the first topic listed above, beginning in 1997, with the prospect of expanding to include the other hypotheses in the next few years. See Chapter 5.

QUAKING ASPEN

Aspen is an especially popular part of the western landscape. Because of its beauty, and because it contributes to the ecological diversity of a landscape, aspen is of great interest both to the public and to the scientific community. Aspen has been described as an "insignificant component" of the Yellowstone region for the past 20,000 years (Mullenders and Coremans 1996, Mullenders et al. 1996), but, like willows, aspen has disproportionate effects on the ecological communities of the northern range.

Barmore (1980) mapped northern range vegetation and estimated that about 2.8 percent of the vegetation was aspen. Based on remapping of the northern range and comparison with historic photos, Houston (1982) agreed:

> Compared to 2-3% of the winter range now in aspen, I estimate that 4-6% was in aspen in the original photos. A vegetation map of the winter range made in the early 1930s supported this estimate.

Kay (1993) disagreed, estimating a 95 percent decline in area occupied by aspen since the park's establishment in 1872. The spectacular disparity in estimates of this decline is some indication of the uncertainty still surrounding aspen on the northern range, and lead to calculations that suggest how far astray scientific discourse can occasionally go. Consider Kay's (1993) statement that aspen have "declined by approximately 95%" since 1872. This means that roughly 5 percent of the 1872 aspen distribution remains. But Houston's (1982) estimate that aspen currently occupy 2 to 3 percent of the northern range seems to be widely accepted. From these two figures (aspen now occupying 2 to 3 percent of the northern range, and that being 5 percent of their historic distribution), it would follow that in 1872 aspen must have occupied 40 to 60 percent of the northern range, which the photographic evidence does not support (Meagher and Houston in press.)

While there is disagreement over the extent of the decline, it is certainly true that the number of tree-sized aspen standing on the northern range has

Figure 4.5. Aspen inside a northern range exclosure grows without the effects of ungulate browsing. The most recent study of aspen/fire/ungulate history on the northern range suggests that there has only been one brief period in the past two centuries (roughly 1870-1895) when aspen was able to grow to tree height (Romme et al. 1995). NPS photo.

declined, that there has been little growth of new aspen trees since about 1900, and that aspen are now reaching "old age" and dying (Figure 4.5). In many cases the aspen clone is still viable; it is now in a shrub form, apparently unable to escape ungulate browsing and grow to tree height. The reasons for this change have been the subject of study and sometimes heated discussion for many years (Barmore 1980; Tyers 1981; Houston 1982; Despain et al. 1987; Kay 1990, 1993; St. John 1995; Wagner et al. 1995*a*). Continued decline of aspen is expected under the current combination of high ungulate use in the park, combined ungulate and livestock use outside the park, and warmer and drier climatic conditions.

In a study of aspen on the northern winter range in the Gardiner Ranger District of the Gallatin National Forest immediately north of Yellowstone National Park, St. John (1995) confirmed heavy ungulate use of aspen stands there, as well as significant impacts by livestock. Aspen stands in scree communities (which are more difficult of access for ungulates and livestock) and within 1,600 feet (500 m) of main roads (from which hunted ungulates are often displaced by human activities), recruited new stems more successfully than other stands that were accessible to ungulates.

The decline in aspen has for many years been used as proof of elk overpopulation on the northern range (Pengelly 1963, Kay 1990, Wagner et al. 1995*a*). But other investigators have suggested that the decline of aspen might be more the result of changing climatic conditions and fire suppression (Houston 1982, Despain et al. 1986) Recent research has introduced important new elements into this debate.

For most of the history of the northern range issue, most positions on aspen implicitly assumed that prior to the establishment of the park in 1872, aspen was a regular part of the setting, reproducing consistently. A variety of recent studies now challenge that assumption, and dramatically change our understanding of aspen as a member of the northern range plant community. Engstrom et al. (1991, 1996), in an analysis of pollen in pond sediments on eight northern range ponds, determined that aspen has been a marginal species on the northern range for thousands of years.

In a tree-ring study of northern range aspen, Romme et al. (1995) showed that since the early 1800s, there has been only one period during which aspen grew to adult height in large numbers; that period was from the 1870s to the 1890s, when most of the aspen that are now growing old on the northern range began their growth (Figure 4.6). Romme et al's. work was anticipated by Warren (1926), who dated aspen near present Roosevelt Lodge and found that these also dated from a short period of time, with a pronounced peak in the 1870s (Figure 4.7). These trees, then, were part of the same period of growth documented later by Romme et al. (1995). The work of Romme et al. (1995) and Warren (1926) suggests that in the early 1800s, aspen were typically unable to grow to tree height; it seems most probable that some combination of factors, including elk browsing and fire, prevented that growth.

Despain (U.S. Geol. Surv., unpubl. data) sectioned 50 dead aspen trees on the northern range, and discovered that 49 of them showed signs of annual browsing in their first three years of growth. The work of Despain, Romme et al.

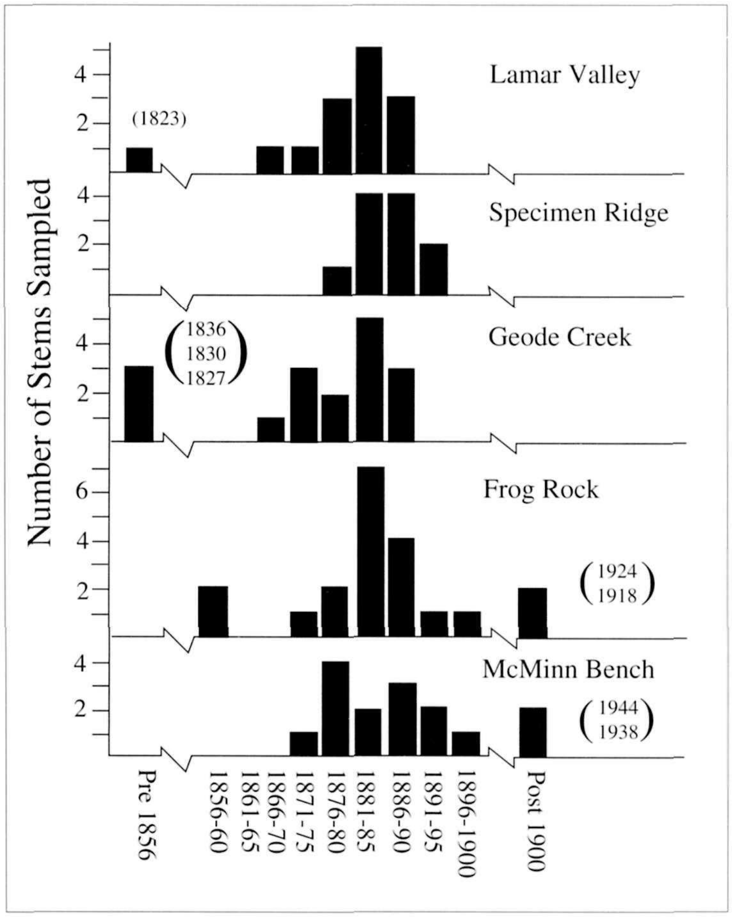


Figure 4.6. Number of aspen stems established in 5-year periods in 15 stands distributed across the northern Yellowstone National Park. A single bar is provided for the small number of stems established before 1856 and after 1900; individual dates are shown in parentheses. The relatively brief period of all aspen establishment on the northern range suggest that the set of circumstances under which aspen can grow to tree height is relatively rare. Adapted with permission from Romme et al. (1995).

(1995), and Warren (1926), suggest that for some reason or set of reasons, aspen, like willows, were better able to withstand browsing in the late 1800s than they are now.

Aspen is a relatively short-lived tree, and Yellowstone tree-ring records for this species probably do not measure aspen escapement back before about 1800 because there are no aspen that old to study. Thus the time period of local information on aspen is relatively short. Considering that there is only one major period of aspen escapement in that period, however, it may be safe to assume that aspen only rarely meet circumstances in Yellowstone that allow them to escape browsing and grow to tree-size. Pollen studies going back many thousands of years tend to support that view, suggesting that aspen have been rare on the northern range for millennia (Engstrom et al. 1991, 1996; Mullenders and Coremans 1996; Mullenders et al. 1996). It is also important to note that these aspen studies, by demonstrating that aspen were rarely able to grow to tree height prior to the 1870s, provide circumstantial support for historical analyses (Schullery and Whittlesey 1992) indicating that ungulates were abundant in the Yellowstone area before 1870. This is not to say that only ungulates were involved in suppressing aspen before 1870; as with today, it seems probable that some combination of factors was involved, especially including fire, which if very frequent may kill back the stems of small aspen and prevent them from reaching large size. If, as it now appears, aspen only occasionally are successful in reaching tree height on the northern range, they are following a pattern observed among highly preferred woody species on other ungulate ranges (DeByle 1979, Prins and Van der Jeugd 1993).

This new information leads, as it does with willows, to the question of what set of circumstances might have prevailed in the late 1800s that would allow for the growth of so many trees in such a short period. It is well known that Yellowstone elk were subjected to heavy market hunting in the 1870s, which suggests the possibility that elk were reduced to levels that would allow for aspen to escape browsing. But there is consider-

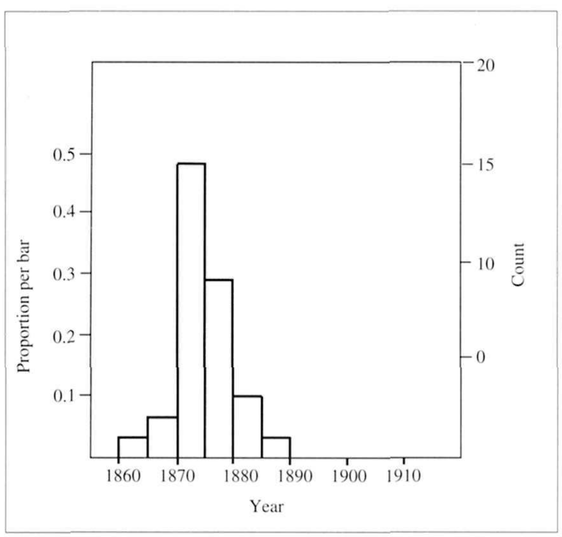


Figure 4.7. Histogram based on sample of 31 aspen trees aged near Tower Junction by Warren (1926). Though Warren's work was done roughly 60 years before that of Romme et al. (1995), his results are essentially the same, showing a surge in aspen growth in the 1870s and 1880s. Histogram by Don Despain.

able uncertainty about the extent to which elk were reduced on the northern range in the 1870s and 1880s (Schullery and Whittlesey 1992). As already noted, the market-hunting harvest was quite high in the mid-1870s, but the slaughter seemed to have dropped off by the end of that decade (Schullery and Whittlesey 1992). It also appears that if elk were markedly reduced during the 1870s, they began to recover by the early 1880s. Houston (1982) and Coughenour and Singer (1996*a*) document the quickness with which the northern elk herd recovered following the reductions of the 1960s, and there is no reason to believe elk could not do the same in the late 1800s. As already mentioned, Schullery and Whittlesey (1992) published contemporary accounts of 5,000 elk reported in mid-winter (February) on the northern range between Mammoth Hot Springs and Cooke City as early as 1883 and continuing after that year. During the most recent period of extreme elk population reduction (1963-1969), when there were usually fewer than 5,000 elk on the northern range, Barmore (1975) observed that they were still numerous enough to browse almost all aspen suckers (75 percent leader use). Some set of circumstances, almost certainly involving climate, enabled the aspen of the 1870s and 1880s to grow to tree height despite browsing, something they were unable to do during the 1960s. Houston (1982) reviewed climatic reconstructions based on tree-ring analyses, concluding that "the highest winter precipitation for the entire 161-year (1750-1910) period occurred from about 1877 to 1890."

It seems most likely that a variety of factors influenced aspen success in the 1870s and 1880s. Besides climate, other factors that may have played a part include fire history, commercial trapping of beaver in the 1870s and 1880s, and reduction of elk numbers or displacement of elk from some areas by human activities, especially hunting. It may be that all aspen clones that developed tree-size growth in that period were not successful in doing so for exactly the same reasons.

Whatever causes are eventually identified for the success of aspen in the 1870s and 1880s, it is clear now that the traditional viewpoint—that an abrupt change in elk numbers is solely responsible for the aspen decline—is incorrect. Elk prevent aspen from reaching tree size today because elk eat the young trees, but that does not mean that elk are the sole cause. Research has resulted in new hypotheses that are being investigated: 1) under proper growing conditions, aspen suckers can grow large enough in a single season and can produce enough defensive chemicals to keep elk from completely debarking and preventing young plants from attaining tree size. If proper conditions do not exist, the clone is kept in a shrub or perennial forb stage by browsing, but the clone itself—its root system—is not eliminated; and 2) aspen show an opportunistic sexual reproductive strategy following burning.

The fires of 1988 provided an excellent opportunity to test fire's role in the reproduction of northern range aspen. In the year following the fires, an unprecedented amount of aspen growth from seedlings was documented (Kay 1993, Renkin et al. 1994, Renkin and Despain 1996*b*, Romme et al. in press). However, on the northern range few if any of these seedlings have been able to escape browsing and grow to adult height, despite their tremendous numbers. Large fires alone were unable to enable aspen to escape elk and grow to tree height on the northern range (Figure 4.8).

Seedlings have been much more successful on Yellowstone's summer ranges at higher elevations. The fires of 1988 led to the widespread establishment of aspen "in extensive portions of YNP where there was no aspen before the fires" (Romme et al. in press). Establishment sites were primarily in burned lodgepole-pine forests, especially in the west-central part of the park; this event may have important implications for understanding the long-term persistence of aspen in the park. Genetic studies revealed that these new seedlings derived from some distant seed source presumably to the west of the park, not from existing aspen clones in the park. The fires of 1988 thus resulted in an apparently substantial increase in genetic diversity in the aspen populations of Yellowstone National Park. These new seedlings are persisting: "They are elongating slightly and increasing in density in at least some places despite

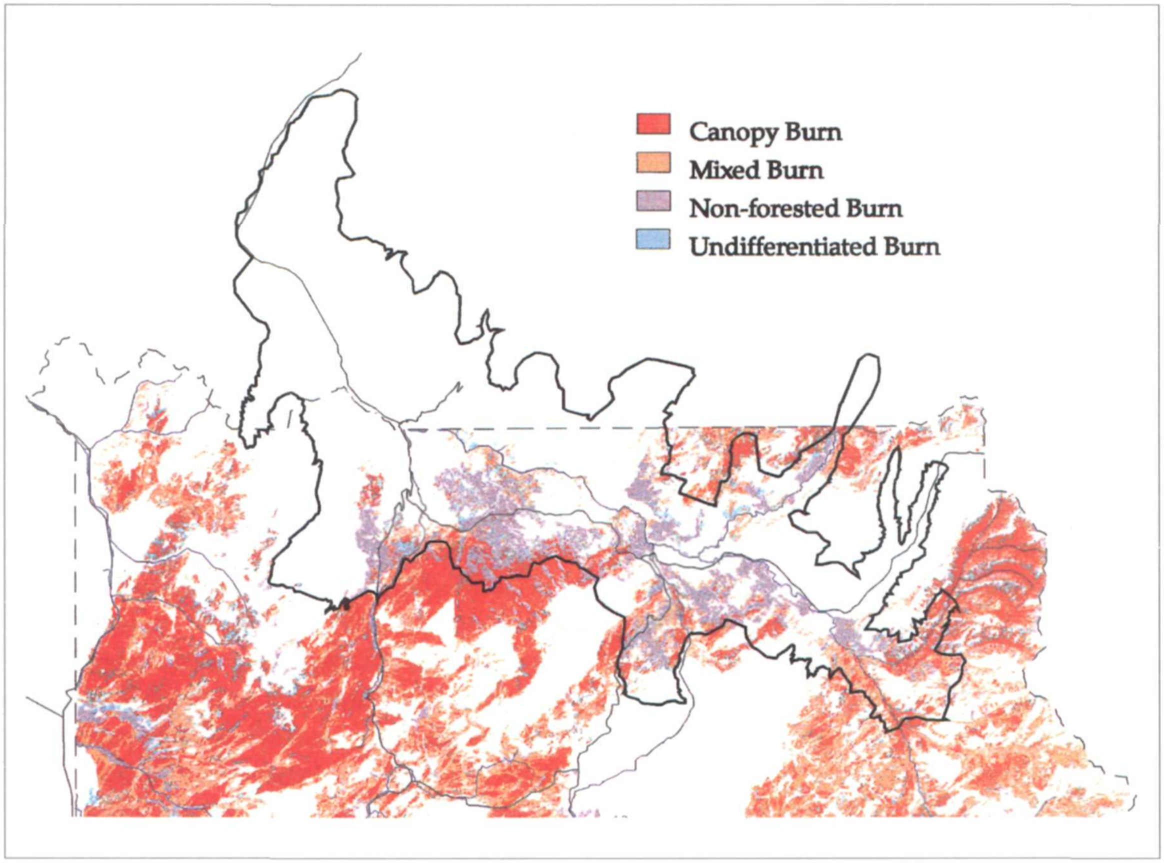


Figure 4.8. Burn map from the fires of 1988. Map by Yellowstone Spatial Analysis Center.

moderately heavy browsing pressure, and…they are establishing new clonal population structures" (Romme et al. in press). It may take several decades to determine whether these new clones can thrive in lodgepole-pine forests when the lodgepole grow tall enough to shade them out. The fate of the 1989 aspen seedlings in wet meadows may share the same long-term wait to determine if they survive, and survival may depend on whether aspen are in shrub or tree form. It is important to note that aspen do not have to grow into trees to establish and spread by root suckers. If they do persist, they may provide an instructive example of how aspen have maintained themselves in the park area's relatively inhospitable environment for thousands of years, and whether they persist or not, they are currently offering an important opportunity to further study this popular and controversial species in Yellowstone.

The ecological circumstances facing aspen on the northern range continue to change, and in recent years may have done so in favor of aspen. The initiation of wolf recovery in 1995, and a recent trend toward much wetter winters with deeper snows, may contribute to a return to the circumstances that prevailed the last time that aspen escaped browsing and grew to tree height on the northern range. Until that set of circumstances is duplicated, however, it is probable that aspen will continue to occupy the northern range at the lower levels now present in many shrub-height clones. It seems likely that other species of equally precarious status, such as cottonwoods and water birch, may share this same fate.

RESEARCH RECOMMENDATIONS: QUAKING ASPEN

It seems important to continue studying aspen on the northern range, even if it is somehow determined that their decline is entirely within the realm of natural ecological processes and is not due to elk numbers alone.

Age-structure studies on the northern range should continue, so that sufficient data is obtained

to confirm and refine the findings of Romme et al. (1996). Age-structure studies of aspen near the west and south entrances of Yellowstone National Park would provide instructive comparisons with northern range aspen from nearby areas with different ungulate and fire-history regimes. Age-structure studies from Grand Teton National Park would likewise be helpful.

Interesting avenues for experimental management exist. It may be possible, for example, through judicious "fencing" with downed trees and other devices, to create local aspen refugia: to exclude elk and other ungulates from some aspen clones and thus ensure the growth of new aspen trees in some locations on the northern range. Such a management action would be relatively nonintrusive, and would probably reassure many enthusiasts of aspen and their dependent species. Whether such an action is in keeping with current National Park Service policies, or is a justifiable divergence from that policy, is a more difficult question. However, the creation of a few such aspen refugia would be more than justifiable as a research program to test specific hypotheses about interactions among elk, aspen, fire, climatic change, and geomorphic processes. Such a study would be more useful if it also included sites with other species of interest, such as willow, cottonwood, and other riparian species.

ASPEN, WILLOWS, AND BIODIVERSITY

As with grassland studies, researchers have emphasized the importance of an integrated understanding of the many influences on woody vegetation on the northern range. And to perhaps an even greater extent than with grassland studies, the role of climate in the current condition of these species is a recurring, even overriding theme. There remains no question that ungulate browsing is the immediate cause of the decline of aspen and willows on the northern range, but there is considerable uncertainty over why that browsing has a different influence now than it has had historically.

Aspen and willows are favored though minor food items for elk in Yellowstone (Barmore 1980, Singer and Renkin 1995). Even the complete absence of these species on the northern range would not have any significant effect on the nutritional opportunities available to the northern Yellowstone elk herd. Thus it might seem puzzling at first that the decline of aspen and willows, two of the most abundant plants in North America, should play such a major role in the dialogues about northern range grazing. But these species, as well as other woody vegetation, such as cottonwood, have important cultural values for what they contribute aesthetically to the enjoyment of western landscape, and they also have important ecological values as habitat to species of animals that would not otherwise occupy the northern range in meaningful numbers, especially some species of birds. Jackson and Kadlec (1994) found that "total bird densities and total number of species were lowest in sites in which 70 percent or more of the willows were severely browsed, suggesting that birds have a threshold of tolerance for browsing-induced changes to the vegetation." They also suggested that "intense browsing does affect the assemblages of breeding birds in willows, but we also speculate that factors such as food abundance, type and gradient of adjacent plant community, and soil-water relationships are important."

The plight of neotropical migrant birds in the western hemisphere has been widely publicized in recent years; they are experiencing massive habitat degradation in wintering areas in Mexico and Central America. Though the willows of the northern range constitute less than one percent of park willows, the northern range is currently home to a more significant percentage of adult aspen clones in the park, as well as to many of the park's cottonwoods and some other woody species. Changes in the status of these species can ripple through the wildlife community in complex and significant ways, so there is some urgency to research questions relating to woody vegetation on the northern range.

But as explained in the "Willows" section, dense tall-willow habitats occur in Yellowstone in summer ranges above 7,000 feet and in many other places in the greater Yellowstone area. Vigorous aspen clones also are available, particularly in the

high precipitation western and southern edges of greater Yellowstone (such as the Jackson Hole—Hoback River areas and the Island Park foothills of Idaho). Changes in relative abundance of plant species on the northern range must be considered in this larger context; the northern range cannot be held accountable by itself to maximize all types of wildlife habitats, especially when those habitats remain abundant nearby.

In addition to their role as habitat, willows are important factors in stream processes, which they affect and often contain through their root systems. Riparian issues are considered in Chapter Five.

COTTONWOODS

Another tree whose situation in some ways parallels that of aspen is cottonwood, of which the park has three species. Though no research has yet been published in the scientific literature on Yellowstone's cottonwoods, differing interpretations have surfaced on the trend and condition of the northern range's cottonwoods (Figure 4.9). Wagner et al. (1995*a*) reported on an unpublished manuscript by Keigley (1994 in their text, 1995 in their "literature cited" list), saying that "normal trees were formed only in the early part of this century and during the elk population low of the 1960s. At other times, browsing pressure was so heavy that it hedged the young plants and prevented formation into trees. The long-range trend is a decline in cottonwoods along streams in the northern range as dying, older trees are not replaced."

Elk were abundant summer and winter residents of the northern range in the period 1900-1930, which would seem to encompass any definition of the "early part of this century." This leads to the same unanswered question now faced by northern range observers, regarding aspen and willow: why did cottonwoods thrive and reach tree height in the presence of elk then when they apparently cannot do so now?

Meagher (1997), in contrast to Wagner et al. (1995*a*) stated that in early photographs of the Lamar Valley in the late 1800s, "there weren't many cottonwoods...." Meagher concluded that:

> If anything, on a few specific sites, cottonwoods may actually have colonized since then. For reasons we may not understand, the Lamar Valley may not always be cottonwood habitat.

The condition of cottonwoods on the northern range is, then, incompletely understood. Current interpretations differ as dramatically as they do with aspen and willows.

Figure 4.9. Cottonwood grove, Lamar Valley. Cottonwood have not reproduced successfully on the northern range since early in this century, and there are disagreements over why. NPS photo.

RESEARCH RECOMMENDATIONS: COTTONWOODS

It should not be assumed that all woody species are responding to the same ecological and human influences on the northern range, or are responding to each specific influence in the same way. If, as Wagner et al. (1995*a*) maintain, cottonwood thrived and reproduced on the northern range in the early 1900s, they were flourishing after aspen experienced their only significant period (1870s-1890s) of successful growth to tree height. Why would these species thrive at different times? As with aspen and willow, further studies of historical conditions relating to hydrology and precipitation are an essential foundation to understanding cottonwood ecology. Other proposals currently under discussion, such as attempts to age the many cottonwood "driftwood" logs that survive in the upper Lamar River drainage, and building exclosures around patches of cottonwood seedlings to compare growth patterns of browsed and unbrowsed groves, should also be considered.

CHAPTER FIVE

SOIL, EROSION, SEDIMENTS, AND WATERSHEDS

RECENT EROSION RESEARCH

The idea of accelerated soil erosion on the northern range became a basic premise of much research in Yellowstone from the 1930s through the 1970s, as well as a primary reason for the elk reduction programs. In the agricultural industry, erosion has always been cause for justifiable alarm, because soil has long been considered a capital asset, and any kind of erosion has been viewed as evil. But in a wildland area being managed to allow geological and ecological processes to function without human interference, the resource is not economic; it is the integrity of the processes that counts, and erosion is an important process in wild landscapes.

Houston (1982) reviewed historical photographs of key eroded sites and determined that these sites looked essentially the same more than a century ago, prior to the supposed increase in elk-caused erosion (Figure 5.1). The major erosive sites, especially geologically sensitive areas such as Mount Everts near Mammoth Hot Springs, the Grand Canyon of the Yellowstone River, and numerous steep slopes in the upper Lamar River drainage above 8,400 feet have not significantly changed during the history of the park.

Figure 5.1 Mount Everts, photographed from the Mammoth Hot Springs Terraces by William Henry Jackson in 1871. Though erosion on this and other steep slopes in northern Yellowstone National Park has been attributed to "unnatural" concentrations of elk since the park was established, historic photographs show that the erosion patterns were the same prior to the park's creation. NPS photo.

Major erosion events, Houston observed, are an unavoidable and significant part of the Yellowstone landscape, just as they are of many other landscapes in the west. He concluded that the "available evidence does not support interpretations of widespread or accelerated erosion in the area."

Starting in 1985, an interagency team of researchers, with support from many sources (U.S. Fish & Wildlife Service, Trout Unlimited, U.S. Forest Service, Montana Department of Fish, Wildlife and Parks, Park County [Montana] Soil Conservation District, Montana Water Quality Bureau, U.S. Soil Conservation Service, U.S. Geological Survey, and the National Park Service), mapped erosive lands in the Yellowstone River drainage from the park to Livingston, Montana (Shovic et al. 1988, 1996; Ewing and Mohrman 1989; Shovic 1994, 1996; Ewing 1995, 1996). Sediment transport and turbidity in the Yellowstone River drainage was studied from 1985 through 1987. Above-normal July to September precipitation was recorded from 1982 through 1987, in the longest trend of wet summers in the preceding 21 years. High sediment transport and turbidity was associated with spring snowmelt and thunderstorm events. Major in-park sources of sediment production were found in the Grand Canyon of the Yellowstone River, Soda Butte Creek upstream of the park's Northeast Entrance, the upper Lamar River watershed, and the Mount Everts area of the lower Gardner River drainage. These sources of sediment were significant because of their geologic origin, and none but Mount Everts was in the zone of ungulate winter range. Therefore, it was concluded that the major in-park sources of sediment into the Yellowstone River were related to geologically unstable deposits, rather than to ungulate grazing.

The only one of these highly erodible slopes located on core elk winter range, the west face of Mount Everts in the lower Gardner River drainage, was intensively investigated, including aging of alluvial fan deposit debris layers using tree ring dating (J.G. Schmitt, Montana State Univ., unpubl. data). The steep escarpment visible today is the result of a Pleistocene glacier shearing off the southern flank of the mountain. The researchers found no evidence of any increased rate of development of erosive features that could be attributed to changes in elk densities or related to elk management. Erosive features on Mount Everts are, they said, "not related to grazing effects since establishment of Yellowstone National Park but [are] likely controlled by such intrinsic geomorphic

features as tectonism, climatic change, and/or changes in the Gardner River base-level."

Engstrom et al. (1991, 1996) investigated pond sediments on the northern range because such lakes are unusually sensitive indicators of erosion and other environmental changes in small drainages. Sediment cores from eight small lakes scattered across the northern range supported similar conclusions: "As a whole, our investigation of the sedimentary record does not support the hypothesis that ungulate grazing has had a strong direct or indirect influence on the vegetation and soil stability in the lake catchments or on the water quality of the lakes." Both depositional studies recognize limitations in their ability to detect only large events. However, road construction near Floating Island Lake resulted in a strong sediment signal in the core record. The question of how completely a sediment study of this sort can portray historic erosion patterns is a matter of continuing debate (Engstrom et al. 1994, Hamilton 1994), but at the very least the technique provided no evidence of additional erosion in the modern period, when some observers believe elk numbers increased.

FISHERIES AND OTHER AQUATIC RESOURCES

It has long been known that fish and aquatic invertebrates have been important indicators of environmental degradation. The U.S. Fish and Wildlife Service conducted long-term studies of the fish, habitat, water chemistry, and aquatic macroinvertebrates of the Lamar River on the northern range (Boltz et al. 1993). Their data suggest that the habitat, macroinvertebrates, and native fish populations are similar to recent past decades. Large trout are as abundant or more abundant during recent highs in elk numbers (1984-1989) as they were in the 1970s when elk numbers were lower. There were no significant trends in angler effort, mean length of fish landed, or proportional stock density and relative stock density of fish landed during the 17-year period from 1976 to 1992. There was a "slight decline" in mean-annual landing rate. In 1992, both mean angler expertise and angler satisfaction with the overall fishing experience were "among the highest reported in the park" (Boltz et al. 1993).

Anecdotal information regarding fishing in the Lamar Valley area in the last century is suggestive of similar fisheries then and now, but there are, unfortunately, no ecological studies of the Lamar River 100 or 200 years ago against which to compare modern conditions. The database described in the previous paragraphs dates only to the mid-1970s, a time when trout populations parkwide were in some cases still recovering from overfishing in earlier decades. However, the high quality of the angling experience and the robust condition of the trout population compare favorably with other park fisheries that are not on the northern range. If the aquatic ecosystem of the Lamar River is being damaged by grazing, the effects are too subtle to be recognized through an examination of the sport fishery.

Rosgen (1993) studied the morphology, channel stability, channel patterns, and channel forming processes of the Lamar River and its tributaries, and attempted to determine if it was transporting sediment loads "out of character" with its present geologic and geomorphic setting. He concluded that

> The Lamar River and it's [*sic.*] tributaries are associated with naturally high sediment supply which is primarily geologically controlled. Large volumes of sediment are delivered from steep erodible terrain and stream types in the upper watershed to the flatter gradient valleys in the mid and lower watershed position.

In his study sites he found about 26 percent of the Lamar River in "excellent condition," 30 percent in a "very unstable state," with the remainder in between the two extremes. He believed the instability observed in the middle and lower sections of the river were due to "excess bar deposition" that "led to an acceleration of natural processes" that he clearly blamed on riparian conditions. He stated that "...it is evident that natural balances are 'out of balance'..." and "To restore these systems back to natural, stable

channels in these reaches, it would be necessary to re-establish the woody species, primarily willow." Rosgen attributed these "out of balance" situations to what he regarded as historical increases in elk numbers beyond what had existed in the park area prehistorically.

Rosgen's interpretations appear to fall under the category described earlier in this report, under the Willows discussion, of presuming a full understanding of how a particular setting "should" look. The Colorado streams he used for comparison and contrast (that is, the streams he believes northern range streams "should" resemble) are managed by humans to look a certain way. Rosgen concluded that changes in climate over the past century did not cause the changes he measured in Lamar River drainage, but did not introduce any climate data to support his position. He presented no riparian data to support his interpretations, which appear to have been based on undocumented assumptions about ungulate effects on this watershed.

Rosgen also based his interpretations of current sediment conditions in the Lamar Valley on the erroneous conviction that "large herds of elk did not inhabit the greater Yellowstone ecosystem until the late 1800s." As the present volume demonstrates, large herds of elk were in fact present in the park area prior to the late 1800s. As the present volume also has explained, willow, elk, and willow thrived together in this setting in the late 1800s. This means that another explanation must be found for what Rosgen describes as the "dramatic conversion" of willows to grass communities along some Lamar Valley streams.

CONCLUSIONS

Soils normally erode in wildland settings, and often do so on a grand geological scale. The Yellowstone we see today is a relatively young landscape. Flowing water, wind, gravity, and other forces still carve the park's canyons, shift stream channels, and relocate soils. One look at the Grand Canyon of the Yellowstone River would convince most observers that this is true. As well, ungulates do move soil, and at times contribute to sediment loads in park streams. But even if there were no ungulates at all on the northern range, the rivers would become muddy, especially during the period of spring snowmelt, during high-intensity summer thunderstorms, and following fires when vegetative cover is reduced or eliminated. The sedimentation process is clearly geologically and climatically driven. Dire interpretations of erosion processes on the northern range, such as given by Rosgen (1993), are not yet persuasive because they so totally reject any factor being involved other than ungulates.

RESEARCH RECOMMENDATIONS: EROSION AND SEDIMENTATION

To date, studies of erosion and its role in northern range ecological and hydrological processes have concentrated on the grand scale of entire watersheds, starting on the highest, steepest, and most easily eroded slopes and working down the drainages to the river valleys. Research has now resolved that most of the material that muddies park streams originates in steep and geologically unstable areas where the activities of ungulates are not a significant factor in movement of material. However, as Rosgen's study suggests, important questions remain, especially involving local conditions along park streams. As already explained, grazing increases percentage of bare ground exposed to erosive processes, and in other ways may dispose soils to higher rates of erosion than would occur without grazing; ungulates unquestionably contribute to erosion.

As mentioned earlier, documented changes in willows and other riparian vegetation may affect stream processes, which in turn can have a variety of effects, including increased movement of sediment and erosion of stream banks and beds. Riparian areas occupy only a small percentage of the northern range, but ecologists have long recognized that riparian areas are disproportionately significant in the processes of large ecosystems because so much energy and activity is focused in or near them. There is a need for more information on the localized riparian areas associ-

ated with ungulate winter ranges. Though the amount of material potentially involved in erosion in these areas may be much smaller than that involved in the steep headwaters and other geologically unstable areas, winter range riparian erosion is an important topic for research emphasis.

ELK POPULATION ISSUES

IS YELLOWSTONE A COMPLETE ECOSYSTEM FOR ELK?

In 1872, when the U.S. Congress defined the park's boundaries, little thought was given to the interconnectedness of the extensive wildlands in the park area, or to the migratory habits of the diverse assemblage of wild creatures that live there. As a result, Yellowstone National Park is not a complete ecosystem for wildlife species that need great space or room to roam or migrate. This incompleteness was recognized from the park's first years, when conservationists attempted to enlarge the park to the north, east, and west in order to encompass more winter ranges (Haines 1977). It is one of the oddest features of local folklore about natural regulation management that many people believe that National Park Service policy somehow depends upon, or even promotes, the idea that Yellowstone National Park is a complete, self-contained ecosystem, when National Park Service researchers have often led the investigation of ways in which the park is incomplete. As National Park Service researcher Douglas Houston wrote in 1975, "the objective of maintaining pristine ecosystems, with modern man restricted to nonconsumptive uses, can only be partially met for the northern elk because the park does not contain the complete ecological unit for one segment of the population" (Houston 1975).

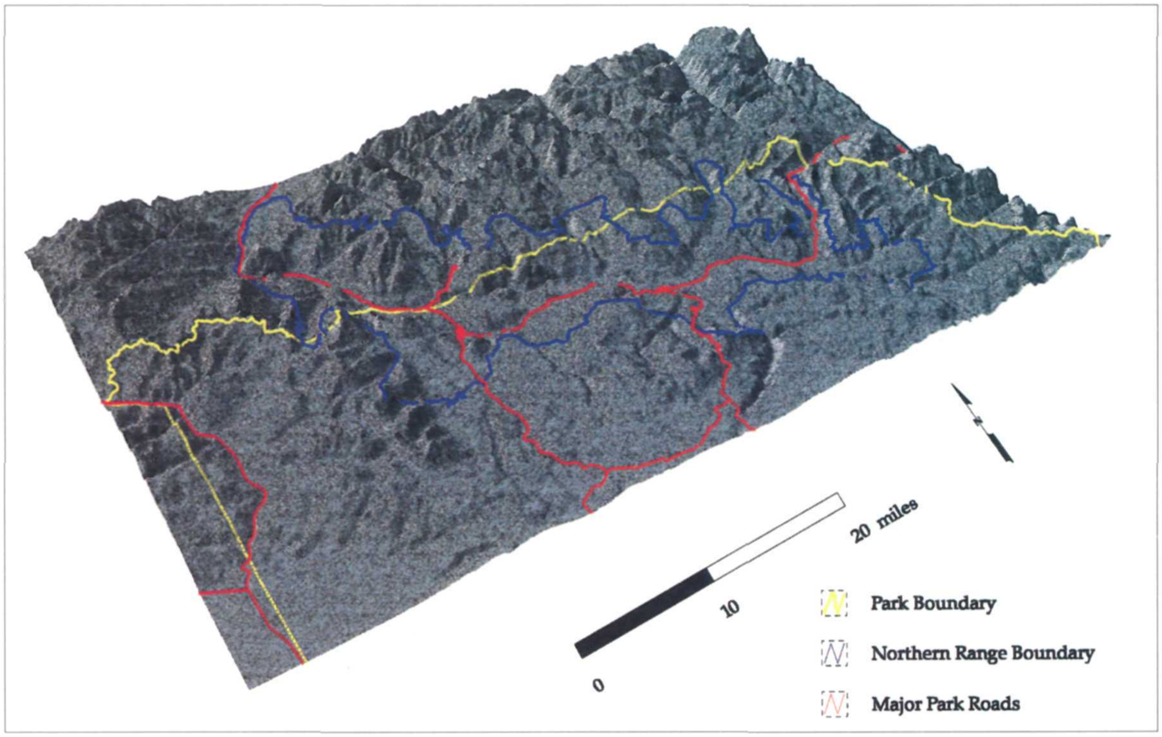


Figure 6.1. Yellowstone's northern range, outlined in blue, trends northwest-by-southeast along the drainages of the Lamar and Yellowstone rivers. Opinions vary on the historic and prehistoric northward extent of ungulate migrations during winter; as shown here, the range encompasses the south end of Paradise Valley, downstream of Yankee Jim Canyon. Map by Yellowstone Spatial Analysis Center.

The high mountains and plateaus of Yellowstone provide summer range for an estimated 38,000 ungulates of seven native species found in dozens of discrete herd units (Mack et al. 1990; Mack and Singer 1992*a*, 1992*b*). Yet, due to snowfalls that accumulate to more than 10 feet in depth on interior plateaus, only one-half to two-thirds of those ungulates winter within the park's boundaries. On the average about 20 percent (the variation is about 10-50 percent) of the northern elk herd and most of the northern mule deer herd winter north of the park boundary, where little snow accumulates (Figure 6.1).

The northern elk herd provides an important example of the human benefits that this elk herd generates in the form of sport-hunting outside park boundaries. In addition to sport-hunting being a popular pastime in Montana it is also an important economic generator. Since the implementation of Yellowstone's natural regulation policy the northern herd has become Montana's single most valuable elk herd (Duffield 1988). Of the total number of herd units analyzed statewide, the northern Yellowstone herd had the highest site or herd value and the second highest net economic value per hunting trip (Duffield 1988).

CARRYING CAPACITY OF THE NORTHERN RANGE

For more than half a century, biologists have attempted to define the carrying capacity of the northern range. Ecologists have recognized that there are at least two general types of carrying capacity (Caughley 1979, Coughenour and Singer 1991). One is the traditional type employed by livestock managers, now known as *economic carrying capacity*. That is the number of animals that is believed to provide the highest economic return on a sustainable basis. Economic carrying capacity is not concerned with native plant species composition or diversity, except to the extent that the available plants best serve the purpose of adding weight to livestock. The other is *ecological carrying capacity*. That is the varying number of animals that nature, left alone, would sustain on the range. The population numbers derived from the two concepts are often quite different, but numbers of ecological carrying capacity are always greater. Most important, ecological carrying capacity will vary greatly, even from year to year, depending upon the environmental factors that dictate food availability. For most of the history of the northern

range grazing issue, Yellowstone managers, researchers, and independent observers computed the economic carrying capacity of the northern range to the best of their abilities. When the natural regulation policy was adopted in 1968, it was in part an attempt to learn what the ecological carrying capacity of the northern range was.

Following Rush's (1932) assessment of the northern range as overgrazed, the National Park Service began monitoring the range annually, and frequently calculated carrying capacities (Tyers 1981). In 1933, for example, National Park Service staff estimated the carrying capacity as 6,565 elk; U.S. Forest Service personnel estimated it as 5,341. In 1935, it was estimated as 7,000, and because the estimated population of elk was 12,000, a reduction of 5,000 was recommended. Similar numbers were repeated later in the decade. By 1953, a winter population of 5,000 was suggested for a three- to six-year trial period to test research hypotheses, similar to estimates made by the Soil Conservation Service in 1963 (Cooper 1963). From 1954 through 1968, an average of 1,324 elk were shot in the park annually, and elk counts averaged around 5,370 through 1968, when in-park removals stopped (Houston 1982). In 1964, the National Park Service issued a report summarizing the goal of elk reductions:

> When beaver can be restored to the Lamar Valley and find ample willow, aspen and cottonwood for their dams and food, and when bighorn populations regain vigor, then some Park officials believe the desirable balance will have been achieved. It will not remain static, it will fluctuate, but Park visitors will have a richer Park experience because of wise management (quoted in Tyers 1981).

Since the end of elk herd reductions, after the natural regulation policy was adopted, carrying capacity estimates at first increased, and then stabilized. These exercises suggest the necessary imprecision of such estimates, but eventually resulted in a range of figures between 15,000 and 18,000 counted elk. Any carrying capacity estimate has pitfalls for unwary readers. For many years, estimates were based on counts of elk. Counts vary with counting conditions and methods. Recently released figures for total elk populations, based upon sightability-corrected estimates (which aim to "correct" for the number of animals not counted because they were under forest cover or were otherwise missed) are usually 10-25 percent higher than counts, so carrying capacity estimates based on counts will typically underestimate the actual number of animals. Another challenge of estimating carrying capacity is that it will vary from year to year with climatic change, drought, summer range productivity, winter severity, predator population size, large fires, and other factors. Such estimates should be expected to vary from year to year.

Cole (1969) estimated that with hunting north of the park being used as a reduction tool, the number of northern range elk counted could be held to 5,000 to 8,000. Houston (1974), after considering additional historical information on the herd's size prior to the reductions, suggested a range of 10,000 to 15,000. At the conclusion of his study during the 1970s, Houston (1982) estimated an ecological carrying capacity of 17,058 counted elk, based on winter population estimates from 1968 to 1975. Based on autumn counts of elk from 1969 to 1976, he estimated an ecological carrying capacity of 14,910 counted elk, stating that actual numbers of elk would be higher, because counts typically miss some percentage of the population. Merrill and Boyce (1991) estimated a carrying capacity of 14,000 to 15,000 counted elk for 1972 to 1987, and estimated a carrying capacity of 17,800 counted elk for the different conditions of the late 1980s. Merrill and Boyce's (1991) carrying capacity model included variations in population size depending upon snow depth and amount of winter range available; such variations, they said, were to be expected.

A significant factor in these increasing estimates was that during the period 1978-1990, elk were recolonizing winter ranges as far north as Dome Mountain, 12 miles north of the park. The size of the available winter range was increasing, so carrying capacity likewise increased. Between 1986 and 1990, 10,021 acres of elk winter range

were purchased through a cooperative effort of the Rocky Mountain Elk Foundation, the U.S. Forest Service, the Montana Department of Fish, Wildlife and Parks, and the National Park Service, that constituted a significant conversion of land use, from livestock to wildlife grazing.

From 1979 to 1988, elk counts increased from 10,768 to 19,043. The mild winters of the 1980s, a trend of increasing winter range grassland production from 1974 through 1981, and recolonization by elk of winter ranges north of the park (Dome Mountain, etc.) all effectively increased winter carrying capacity for elk, so the count of 19,043 and the calculated high of around 20,800 in January 1988 should not have been surprising. Drought, fire, and a winter of normal severity in 1988-1989 temporarily lowered the ecological carrying capacity. In the winter of 1988-1989, about 25 percent of the elk herd winter-killed and another 15 percent was harvested by hunters, so the herd was reduced by about 40 percent. In January 1990, 14,829 elk were counted on the northern range, including 2,139 on the newly-acquired Dome Mountain Wildlife Management Area. Since 1990, counts of the northern elk herd have ranged between about 16,000 and about 20,000.

The northern Yellowstone elk herd is too often viewed without reference to the other greater Yellowstone ecosystem herds, which offer further proof that nothing unseemly was happening as the northern herd increased since 1968. In fact, most of the greater Yellowstone elk and deer herds, managed under a variety of approaches and goals, increased during the 1980s, responding to the same favorable weather conditions (and perhaps other factors) that prevailed on the northern range (Figure 6.2) (Singer 1991*b*). Regionwide, mule deer doubled in number, and elk increased nearly 40 percent. The increases in the park's northern herd were reported widely as if they were something unusual or somehow "unnatural" when that one herd was only doing what all the others were also doing: growing in size as the mild winter weather conditions allowed.

The inherent variability in these ungulate herds can hardly be overemphasized. During the 1980s prior to 1988, and during years since 1988, the summers were unusually wet, with the northern range experiencing 200 percent of normal precipitation in some months. The forage produced in these years allowed the ungulates to increase their population size year after year (Merrill et al. 1988, Singer et al. 1989). The winters, on the other hand, were unusually dry, further allowing for high survival rates in populations that usually were naturally "culled" by winter mortality. Then, in 1988, not only was there the most severe drought in a century, resulting in a lower food crop, but also the fires burned a portion of the ranges, further reducing forage.

The winter following the fires further compounded the challenge for the animals, as it was the first in many years with normal snowfall. In February, three Arctic cold fronts fatally stressed many animals that had previously benefited from a series of mild, easy winters (Singer et al. 1989, Singer and Schullery 1989, Coughenour and Singer 1996*b*, Singer and Harter 1996). Many animals died as a result of this "triple whammy" (forage reduced by summer drought and further reduced by burning, and a severe winter). Following the mortality of elk in 1988-1989, population recovery was rapid, facilitated by the return of the wet summers, dry winters, and probably also by the superior quality and quantity of post-fire forage.

There is a long-standing paradox in the notion that the northern elk herd is far too numerous for the range's carrying capacity. Since 1968, when the elk herd was no longer controlled by shooting in the park and was allowed to grow to whatever size it could, the northern range was somehow able to fuel an increase in the elk population from less than 5,000 to as high as 20,000, and to maintain that higher level of elk population for more than 10 years. All the time this was happening, alarm was expressed about the condition of the range with "too many elk" on it. But these alarms beg a fundamental question: How could a range that had been characterized as overgrazed for more than half a century produce so many elk, year after year? Even if the many research projects of the past 20 years had not called into question traditional views of an overgrazed

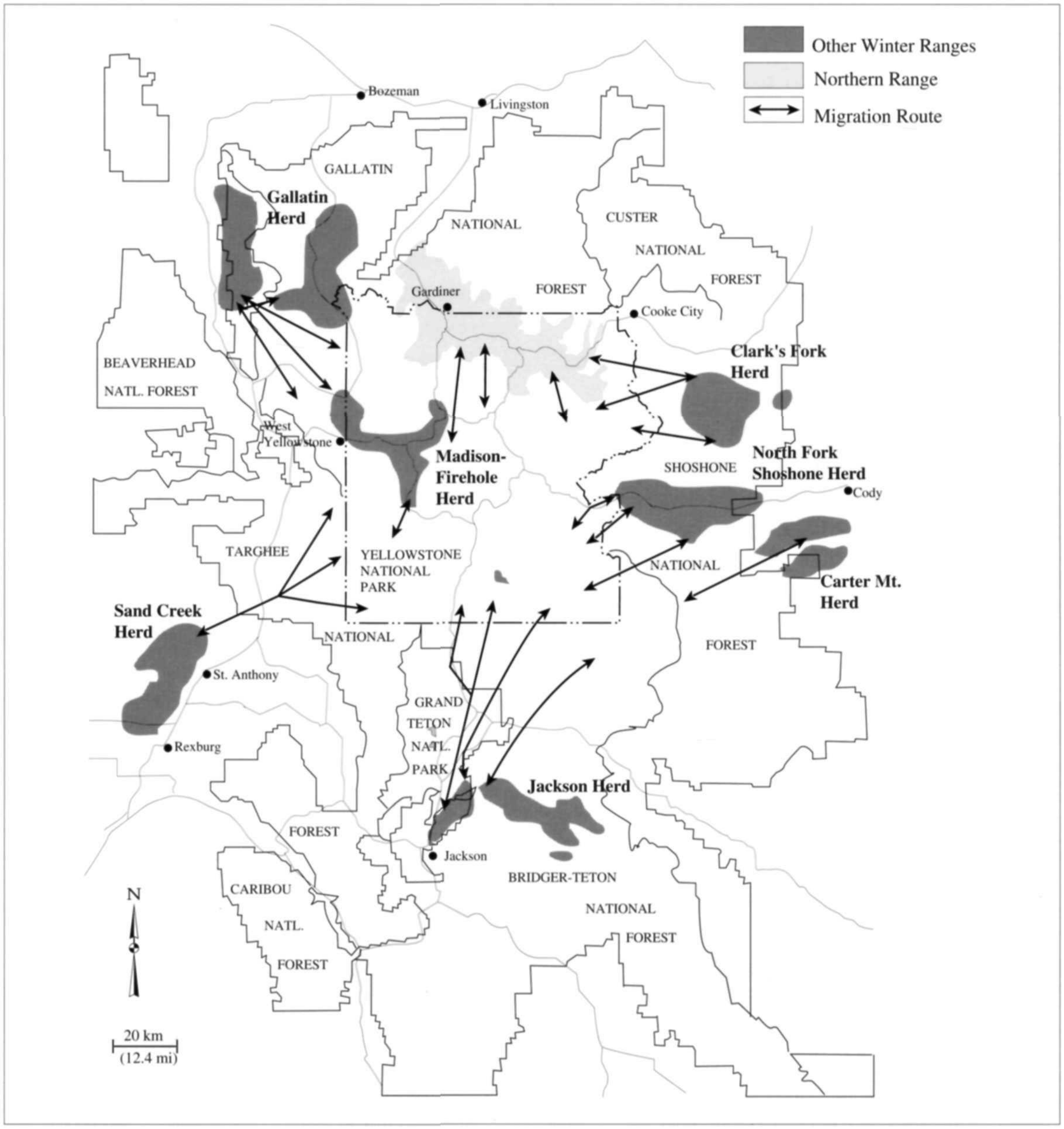


Figure 6.2. Winter ranges of greater Yellowstone elk herds, with migration routes. Map by Yellowstone Center for Resources.

range, the elk were presenting us with important evidence that was being ignored. Each year, the elk calf crop grows up healthy and large. Each year, the adult elk are fit, and the park population produces many trophy bulls and fat cows that are hunted in the winter when they migrate to lower ranges north of the park. These things could not happen without a robust source of nutrition. As Coughenour and Singer (1996*a*) have said, "Forage biomass measured from 1986 to 1988, when 16,000 to 19,000 elk were counted, was similar to forage biomass from 1935 to 1950, when 10,000 to 13,000 elk were counted." The range's remarkable ability to provide forage to upwards of 20,000 elk year after year is practical proof that the range is not "overgrazed," and that the ecological carrying capacity of the northern range is far greater than the traditional range and wildlife managers suspected.

IS THE NORTHERN YELLOWSTONE ELK HERD NATURALLY REGULATED?

A variety of forces act to control the size of the northern elk herd. There are two categories of

these forces. The first includes all those innate factors within the elk population, such as physiology, behavior, and genetics. For example, at higher population densities, cows carry less fat and produce fewer calves, which have lighter birth weights and thus poorer survival. This is known as a "density-dependent" effect of the population's size. In a review article on population regulation, Sinclair (1989) said that population regulation is almost necessarily density dependent.

The second category includes environmental factors, such as predation, winter severity, and climatic effects on forage production. For example, Merrill and Boyce (1991) showed that a high winter snowpack produced superior summer range forage than a low snowpack. This is known as a "density independent" effect, because it is an external force acting on the elk population.

Many such factors, both density dependent and density independent, have been demonstrated for the northern Yellowstone elk herd. Barmore (1980) and Houston (1982) both estimated that first-year mortality of elk calves varied between about 50 percent and 75 percent. Both investigators discovered a correlation between elk calf survival in their first year and the size of the elk population. When the northern Yellowstone elk population was larger, calf mortality was higher, an indication of "density dependence" in the northern herd, a key element in natural regulation. Causes of mortality were not entirely known to these researchers, but were clarified by a later study (Singer et al. 1993) of predation on newborn elk calves from 1987 to 1990. Grizzly bears, black bears, coyotes, and golden eagles killed approximately one-third of newborn elk calves before they reached one month of age (Singer et al. 1993, Singer et al. 1997). Singer et al. (1997) found that another 20 percent or more elk calves died from a variety of causes including predation before reaching a year in age, and that overwinter mortality of calves increased at higher population densities. Several species of predators also kill adult elk. Bulls are especially susceptible to predation by grizzly bears during the fall rut (Mattson et al. 1991), mountain lions kill adult elk (Murphy et al. 1993), and coyotes take elk that are in poor condition or whose movements are hampered by snow (Gese and Grothe 1995).

Figure 6.3. Numerous factors, including predation, winter severity, and elk population size affect successful production of new calves each year. Typically more than 50 percent of new calves will not survive their first year. NPS photo.

The restoration of wolves to Yellowstone National Park beginning in 1995 adds another dimension to population regulating factors facing the northern herd. Computer models predict a wolf-caused reduction of the herd from 8 to 20 percent (Boyce 1990, 1993, 1995*a*; Garton 1990; Mack and Singer 1992*b*, 1993*b*). Human hunting of elk north of Yellowstone National Park has also long been recognized as an important additional element contributing to regulation of the northern herd (Houston 1982).

The amount of forage available to elk is a limiting factor on population size (Coughenour and Singer

1996*d*), so, perhaps not surprisingly, "population recruitment appeared to be strongly influenced by precipitation" (Coughenour and Singer 1996*d*). Evidence of food limitation was observed (Merrill and Boyce 1991). "Population growth rates decline as elk numbers increase towards a fluctuating upper limit set by total available forage." Undernutrition at higher elk densities, density-dependent population responses, increased over-winter mortality of elk at higher densities, and population modeling (Barmore 1980; Houston 1982; DelGiudice et al. 1991*a*, 1991*b*, 1994, 1996; Dennis and Taper 1994; Coughenour and Singer 1996*d*; DelGiudice and Singer 1996; M. Taper, Mont. State Univ., pers. commun.) all indicate natural regulation processes are working on the northern Yellowstone elk herd. Farnes (1996*b*) showed that winter severity was the major factor limiting elk survival.

There are other population-regulating mechanisms acting on northern range elk. Elk-calf winter survival was inversely related to elk population size (Singer et al. 1997). Both yearling and adult cow elk pregnancy rates declined at higher densities (Houston 1982). Yearling elk recruitment (that is, the number of yearling elk added to the population each year) declined at higher population densities (Houston 1982). Population growth rates were also strongly density dependent (Merrill and Boyce 1991; Coughenour and Singer 1996*a*, *d;* M. Taper, Montana State Univ., pers. commun.).

Following the fires of 1988, concern was expressed that forage growth enhancement due to burning might cause a large increase in elk numbers, but Pearson et al. (1995) concluded that, though ungulates did preferentially feed in burned areas, fire effects on ungulates would be "relatively short-lived," and ultimately would be less important to ungulate population dynamics than winter conditions. Conversely, Turner et al. (1994) theorized that the number of postfire seedlings and propagules varied considerably due to fire intensity and other factors, and that a longer view of the effects of fires on ungulates might be warranted. Because the drought of 1988 and the harsh the winter of 1988-1989 saw such a dramatic mortality

Figure 6.4. Mountain lions were eradicated from Yellowstone National Park by about 1930, but have since reestablished a viable population around the northern range. NPS photo.

of elk, Turner et al. (1994) developed a simulation model that Wu et al. (1996) then used "to explore how elk mortality that winter might have been different under alternative weather conditions, spatial patterning of the burn, and initial elk numbers." Confirming Farnes (1996*b*), as well as what Merrill and Boyce (1991, 1996) projected in their extensive modelling work in the 1980s, Wu et al. found that winter weather was by far the most important factor in determining elk overwinter survival:

> Ironically, the single most important determinant of elk winter survival appears to be the weather, over which managers have no control. Those factors that can be controlled to some degree—fire pattern and initial elk numbers—are important, but their effects interact with the effects of winter weather conditions and may be completely overshadowed by the influence of snow depth and snow water equivalent (Wu et al. 1996).

Others have disagreed with Wu et al. (1996) of the importance of weather. Dennis and Taper (1994) applied a statistical test that they call a parametric bootstrap ratio (PBLR) test to the northern elk population data from the end of the elk reduction era (1969) through 1979, and concluded that "the population appears to have subsequently attained a stochastic equilibrium." Later and additional work by Taper and Gogan (M. Taper,

Montana State Univ., pers. commun.) on population data from 1969 through 1995 shows strong natural regulation dimensions, but minimize the notion that weather is a significant factor.

IS NATURAL REGULATION A THREAT TO BIODIVERSITY?

National Park Service policy contains a potential internal tension because it directs park managers both to protect native species and to protect ecological processes. But even without human influences, native species come and go from a landscape. Virtually all of the Yellowstone Plateau was covered by ice only 20,000 years ago (Good and Pierce 1996); all of that land, once relieved of its ice cover, had to be recolonized by the many species of plants and animals that now reside and are considered native there. The tension in park policy, then, involves what to do if ecological processes pose a threat to a native species; which part of the policy mandate is given preference?

In some cases, were such a situation to develop, other laws would override policy. If ecological processes threaten grizzly bears, for example, the Endangered Species Act would presumably require the National Park Service to find ways to protect and sustain the grizzly bear population. But in most cases, which would involve species that are probably abundant elsewhere and need no special local protection, it is more likely that the species would not receive special protection. No such case has arisen in Yellowstone, or to our knowledge in any other national park; native species are routinely threatened by the introduction or invasion of non-native species, or by other causes, but not by the ongoing ecological functioning of the ecosystem.

Biological diversity, commonly referred to as biodiversity, has become a central concern of conservation biologists because human activities around the globe have drastically accelerated the rate of extinctions of species (Grumbine 1992, Soulé 1996), and national parks have become recognized as reservoirs of native species diversity. Biodiversity has several levels of meaning in a landscape. At a basic level, it may involve the genetic diversity within an individual species (for example a rare predator whose genetic diversity is facing a "bottleneck" as its numbers decline). At another level, it may involve the diversity of species that inhabit a landscape, and is often referred to Alpha diversity. At a more complex level, it may involve the diversity of communities of species (Beta diversity), communities that occupy different parts of a landscape.

As explained earlier, in the history of the northern range issue, the first concerns over species diversity involved the herbivores that some people believed were being pushed out by the elk. Recent studies have demonstrated that the history and real status of two of these species—beaver and white-tailed deer—were badly misunderstood (see Chapter Seven, under "White-tailed deer" and "Beaver" for more details). White-tailed deer were quite rare in the park except for a slight increase in numbers around the turn of the last century, and elk seem to have had a secondary effect on beaver numbers following the collapse of the beaver population because of a beaver-caused food shortage (Jonas 1955, Houston 1982).

More important, elk are not threatening the more common northern range ungulates. No significant relationship has been found between elk and pronghorn numbers, and bison and mule deer numbers have increased along with elk numbers during the past three decades. Moose and bighorn sheep offer more complicated scenarios, but even if significant head-to-head competition for resources should be conclusively demonstrated in the future, neither species is believed to be in danger of disappearing from the northern range.

Numerous investigators, cited earlier, have demonstrated that grazing and browsing of northern range plant species by ungulates does not decrease native plant species diversity. Singer (1996*a*) found that the number of grass, forb, and shrub species in grassland-steppe communities was the same in grazed and ungrazed plots. On the other hand, community diversity has experienced some reduction, as aspen and willow stands have declined. No communities have disappeared, but they are relatively less abundant than they were on

the northern range. Yet on the other hand, as mentioned earlier, species diversity in the understories of browsed willow stands has increased, probably because browsing opened the willow canopy and increased the amount of light reaching the ground layer.

It is important to point out, however, that National Park Service policy mandates do not place a value judgment on this process. In other words, the policy does not judge management as somehow more successful because it *increases* species diversity. The primary goal is not the most possible species stockpiled in each park; the goal is the protection of the ecological processes that determine species diversity.

In some areas, then, there is ample reason to consider the natural regulation policy as a benign force for or against species diversity. On the other hand, the intensive research of the past decade has posed important questions about other kinds of diversity. However, as northern range willows have declined, and as the aspen groves that started in the late 1800s grow old and fall, certain habitats are reduced. In the case of aspen, and eventually some other deciduous species such as cottonwoods, it is entirely possible that they will largely disappear from the northern winter range, affecting a variety of vertebrate and invertebrate species that use them for habitat. In recent years, it is these changes in the northern range that have caused the most alarms to be raised about biodiversity and natural regulation, so they merit more consideration here. Conversely, all of these water-loving woody plants could return to the northern range with a change to a cooler, wetter climate.

During the past century, willows declined on the northern range during periods of drought rather than during periods of exceptionally high elk numbers. Elk are, quite obviously, the immediate reason that winter range willows do not grow taller, because they browse them. But under a different environmental regime a century ago those same willows did grow tall in the presence of large numbers of wintering elk. It appears that the investigators who believe that much more is going on here than a mere "overpopulation" of elk are right, and it is to be hoped that continued research will clarify this situation. In the meantime, and as mentioned earlier, northern range willows constitute only about half of one percent of park's willow communities. Their decline does not presage the disappearance of willow communities and their habitats from the park, because they are robust elsewhere in the park and in the greater Yellowstone ecosystem. If, as appears likely, the decline in northern range willow is the result of climatic changes, then it may be necessary to accept that decline as an aesthetically regrettable but ecologically inevitable part of the system's adaptation to a changing environment. But it is also possible that the return of a cooler, wetter climate to the northern range, if it persists, might result in the return of tall willows.

Aspen, on the other hand, owe their present abundance on the northern range to one demonstrably brief period of success in escaping browsing in the late 1800s. It may be necessary for all of us who enjoy aspen for their great beauty to admit that aspen are only an occasional occupant of the northern range, and that the park's first century was one period when we were fortunate enough to enjoy them here. It is to be hoped that further study will improve our understanding of aspen on the northern range, but in the meantime, they will not disappear entirely, either in or outside the park.

National parks are enjoyed by people for a wide variety of subjective reasons. Just as there are people for whom the sight of large herds of elk are an important part of the Yellowstone experience, there are other people who like aspen more than they like elk, and they will argue on that subjective basis that aspen should be protected and preserved because they are such a lovely, even spectacular part of the historic Yellowstone landscape. Eventually, National Park Service management may wish to address that question, perhaps by considering the establishment of discreetly protected "refugia" in which aspen can thrive without ungulate browsing. That esthetic issue should, however, be kept separate from the reality that under the current set of environmental

conditions on the northern range, aspen cannot make it on their own, except as widely distributed shrub forms.

Recent research on invertebrates in the northern range has shown how interwoven ungulates are with biological diversity. For example, bison dung in Yellowstone is a common host to a species of fly, *Hypodermodes solitaria*, that is currently very rare in North America. Up until the turn of the last century it was commonly collected in many high altitude and high latitude places on the continent. In this case, Yellowstone's bison reserve may act as the last refugia for a species of animal that was apparently once widespread throughout historic bison ranges of North America (M. Ivie, Montana State Univ., pers. commun.). For another example, studies in 1978 and 1993 showed that many of the 445 species of carrion beetles known to inhabit the northern range are heavily dependent upon ungulate carcasses (Sikes 1994). According to this work, "while a carcass is present, beetle abundance and species richness in a habitat greatly increases" (Sikes 1994). In these highly specialized carrion beetle communities, bison and elk carcasses host significantly different sets of species.

The northern range under natural regulation has undergone a number of significant shifts in the relative abundance of species, but has not experienced the loss of diversity that critics of the policy predicted. The success of the various ungulate species in the face of the dreaded increase in elk numbers, and the demonstrated increases in plant species diversity in both grasslands and riparian communities, disprove such predictions.

If research over the past 30 years has proven anything beyond a doubt, it is that Yellowstone National Park is in no sense ecologically disconnected from the world. The migratory habits of the ungulates, predators, neotropical passerine birds and waterfowl, and the subterranean geothermal aquifers that run in several directions from the park to surrounding lands, the movement of both native and non-native plant species, and many other ecological processes demonstrate the extent to which Yellowstone is part of a global ecosystem. Much if not most of that global ecosystem is in the midst of a more severe biodiversity crisis than is the greater Yellowstone ecosystem. There is growing sentiment among conservation biologists that traditional definitions of nature reserves, which stress their isolation and administrative independence, are no longer relevant in this global crisis (Botkin 1990, Grumbine 1992). The mandate of the national parks has undergone continuous evolution since the creation of Yellowstone National Park, and will no doubt continue to evolve in the future. Perhaps if at some future time the biodiversity crisis is judged severe enough, the shifts in species abundance that have occurred on the northern range may regarded as unacceptable because of conditions beyond the park's boundary. For example, the plight of neotropical migrant birds, whose wintering areas in Mexico and Central America are suffering from intensive alteration by human activities, may be judged grave enough that summering areas such as northern range willow communities will be regarded as worthy of special protection. National Park Service managers, and the scientific and conservation communities that assist and watchdog them, must be attentive to such opportunities and trends. In the meantime, there is nothing better that Yellowstone and its human community can do for these broader issues than learn as much as possible about the northern range, to be prepared should such opportunities present themselves.

CONCLUSIONS

Though the northern Yellowstone elk herd's winter range in Yellowstone National Park is not a complete ecosystem and depends upon cooperative management of public and private lands to the north of the park, it appears that the cooperation developed in the past 20 years allows for a large, thriving elk herd of great interest both to park visitors and to hunters and other recreationists north of the park. In fact, the interagency initiatives in which a nongovernmental group, the Rocky Mountain Elk Foundation, has provided inspired leadership, have vastly improved the management options and recreational opportunities associated with the northern Yellowstone elk herd.

It has evolved in the past 20 years to become Montana's most economically valuable elk herd (Duffield 1989). Historic developments like this improvement in cooperation and long-range habitat protection are models that should be useful for many other cross-boundary initiatives near Yellowstone National Park and elsewhere.

Longstanding preconceptions about the abundance or perceived overabundance of some wildlife species, and resultant population reduction programs, have been questioned in the United States and elsewhere (Houston 1982, Macnab 1991). Wildlife managers now face difficult questions about "appropriate" levels of abundance for many popular wildlife species (Garrott et al. 1993). Due to confusion with commercial livestock standards, the ecological carrying capacity of the northern range was underestimated for many years prior to the early 1970s, and as additional winter range was made available to the elk in the 1980s, that carrying capacity increased. Since the reoccupation of that additional winter range, the elk population has not increased further, nor has the density of elk on the park's winter range increased. Instead it has fluctuated in response to varying climatic conditions.

The northern Yellowstone elk herd is not now, and has never been, growing "out of control." The factors limiting that growth include quality and quantity of available forage, winter severity, predation by a variety of large carnivores, and human hunting north of the park. During the 1970s and 1980s, as the herd responded to release from the extreme suppression of the 1960s, it may have appeared to many observers that it was in fact growing without any sign of stabilizing, but many other greater Yellowstone ungulate herds were also increasing, especially during the easy years of 1980 to 1986, when wet summers and mild winters fostered population increases.

The natural regulation policy, now almost 30 years in place, has provided Yellowstone National Park with its foremost opportunity to learn about the northern range grazing system, but the vast amount of new information has not led to a resolution of many of the debates over the northern range. Natural regulation policy has been criticized for lacking the rigid hypothesis-testing criteria required of many such experiments. Such criticisms are easy to make but difficult to back up with a fundable alternative research approach. The northern range is a huge, complex wildland ecosystem still potentially subject to the full range of climatic, geophysical, and ecological variables it has experienced since the glaciers retreated more than 12,000 years ago, as well as to the still poorly understood influences of humans for almost as long. Short of an epic science-fiction treatment, it is impossible to imagine an experimental test approach broad, comprehensive, and massively funded enough to fully address all of the hypotheses either stated or implied in the natural regulation policy. Indeed, there is considerable disagreement over what those hypotheses were in the first place, or should be now. Changes in scientific understanding of ecosystems have come so fast in the past 30 years that any such complete set of hypotheses developed at the initiation of the natural regulation policy (and dealing not merely with ungulate-vegetation interactions but with everything else) would in fact be either inadequate or even obstructive today. This report shows that a tremendous amount of productive research on the northern range has successfully addressed many aspects of natural regulation, and has made great progress in clarifying the workings of the northern range. This report also shows that much more needs to be done.

For most of this century, the foremost recommendation regarding the northern range has been to reduce the number of elk living there. Similar recommendations have prevailed in other national parks, most involving elk or white-tailed deer (Wright 1992, Wagner et. al 1995*a*). The most recent generation of science in Yellowstone has provided abundant cause to question the wisdom of such reductions. There is ample reason to believe that ungulates were common in the park area prehistorically, there are varied carnivore species whose wellbeing is tied closely to the large herds of ungulates, and there is now a considerable regional economic stake in the existence of a large migratory northern Yellowstone elk herd.

Porter (1992) is the latest of several authors

to point out that "the debate about natural regulation and ecosystem stability currently cannot be resolved by science. In many parks, the decision about whether or not to intrude must be made before we have sufficient scientific understanding of ungulate-vegetation interactions." As strong as this statement is, it probably understates the complexity of the scientific situation. Barbee (1995) took the consideration of scientific uncertainty to another level, well beyond simple lack of knowledge, into scientific contention:

> We must have good science [in the National Parks]. That said, I can't overemphasize the complications of dealing with the scientific community. First, on an issue of any substance at all, the scientists will almost certainly disagree. Sometimes they will gather conflicting data, sometimes they'll just disagree over what the data means, but as an issue matures, you can be sure that they will agree less and less. The more complex the subject, the less agreement you get.

The scientific and public debates over the northern range are, regrettably, as bitter as modern political races. Indeed, Porter (1992) has proven correct in his assertion that, because science cannot settle the debate over the northern range, it "will have to be addressed in the political arena." After all, policy is a political product to achieve social goals. It is our hope, however, that at every stage the best possible science will be employed to inform the decisions that are made.

The preponderance of evidence suggests that the northern Yellowstone elk herd is naturally regulated. The changes in northern range vegetation that have caused observers to raise alarms for decades are either not the result of elk "overpopulation" or are part of long-term processes we do not fully understand. For these reasons, there is no compelling reason to intervene at this point with some drastic return to the unsuccessful policies of elk reduction. There are still many unanswered questions about the northern range, and the natural regulation policy seems no less great a learning opportunity now than it did when it was instituted in 1968.

RESEARCH RECOMMENDATIONS: ELK POPULATION ISSUES

It is essential that annual monitoring of this herd continues, as now conducted by the efforts of the Northern Yellowstone Cooperative Wildlife Working Group—Yellowstone National Park, the Montana Department of Fish, Wildlife and Parks, the Gardiner District of the Gallatin National Forest, and the Biological Resources Division of the U.S. Geological Survey. They record total elk count, age/sex composition, and other basic population information. This information is important for its own sake in understanding elk population dynamics, but it is also very important because the addition of wolves to the ecological equation, as mentioned previously, is likely the most important event since the curtailment of in-park elk culling in the 1960s. A research and monitoring program on the effects of wolves on elk, especially in concert with the other elk predators including human hunting north of the park, is clearly warranted in future years.

Other research recommendations associated with the effects of elk on grasslands, shrubs, riparian, and other woody species are dealt with in those specific sections.

ELK AND OTHER WILDLIFE SPECIES

ELK AND OTHER HERBIVORES: RESEARCH SUMMARY

The northern Yellowstone elk herd more than quadrupled in numbers between 1968, the time of their release from in-park reductions, and 1988 (Appendix B). This increase has given rise to concerns in the popular press (Chase 1986) and in scientific circles (Kay 1990, Wagner et al. 1995*a*) that elk are pushing other ungulate species off the northern range.

As mentioned earlier, competition between species is a fact of life in nature. The existence of competition in itself should not be regarded as proof that something is wrong. Dozens of birds species and thousands of insect species compete for common resources on the northern range, but the varying fortunes of these competing species are not commonly thought of as something in need of repair. Thus, though it is true that the ungulates of the northern range do to varying extents specialize in food selection, they also overlap, some greatly. This leaves the difficult question of how much overlap and competition can be tolerated under the National Park Service's mandates to preserve native species. As discussed in chapters Four and Six this is a complex question. In this section, research findings on this subject are reviewed.

Competition theory suggests that diet and habitat overlaps between species should decline, that is, the usable niche of each species should diverge and be more restricted, if they are competing. This is the opposite of what was observed on the northern range (Singer and Norland 1994, 1996). Two lines of evidence for direct competition between elk and the less abundant ungulates were investigated: 1) if they were in serious competition, elk numbers should depress the population growth rates of other ungulate populations, and 2) if they were competing for a food item or habitat, the diet and/or habitat overlaps between pairs of ungulate species should decline.

Neither Barmore's (1980) study from 1962 to 1970 nor Houston's (1982) study from 1970 to 1979 suggested direct competition between elk and mule deer, pronghorn, or moose. However, Houston (1982) found significant association between elk and bison numbers, and both Houston and Barmore considered elk-bighorn sheep competition at least a possibility. Houston pointed out that Keating (1982) found competition between elk and bighorn sheep. Total ungulate numbers on the northern range nearly tripled between 1969 and 1988, so the differences in ungulate population growth rates, diet overlaps, and habitat overlaps were compared between the 1960s data and the period between 1986 and 1988 for possible evidence of increasing competition between ungulate species (Singer and Norland 1994, 1996). Singer and Norland found no evidence that the population size of elk had a major depressing influence either upon population growth rates or on productivity rates of other ungulates. These are important findings, but it must be stated that the possibility that elk numbers slowed the population growth rates of the other species can not completely be ruled out, particularly with bighorn sheep, mule deer in the Boundary Line Area, and moose throughout the northern range, because no control situations existed for the studies.

Singer and Norland (1994, 1996) found that elk and pronghorn diets did not change significantly between the 1960s and the 1980s. Bison, mule deer, and bighorn sheep diets did change. Bison ate 19 percent more grasses and 24 percent less sedges, while mule deer ate 14 percent less grasses and 7 percent more shrubs. Bighorn sheep diet changes were more subtle. They ate 7 percent more grasses, 3 percent more shrubs, and 10 percent less forbs. Apparently, bison changed their diets due to range expansion to include winter range areas with more rolling terrain, more grasses, and fewer sedges. None of the diet changes suggested any decline in the number of forage species. None of the diet changes were consistent among the ungulate species. For example, two ungulate species ate more grasses, but three species ate fewer grasses; three ungulates ate more shrubs, but two ate less; and three ungulates ate more conifers, but two species ate less. None of the diet changes were interpreted as evidence that forages were limited, or that the northern range was overgrazed.

Only 3 of 10 possible diet overlaps between species of ungulates, and only 2 of 30 possible habitat overlaps, changed between the 1960s and the 1980s. All the diet and habitat overlaps increased. These changes do not suggest that ungulates were competing for resources in short supply.

BISON

The bison of Yellowstone National Park were almost extirpated from the park by market hunters prior to 1900 (Appendix B) (Meagher 1973). A few dozen animals survived in the wild in 1902, when additional animals from domesticated herds elsewhere in the country were introduced to Yellowstone. For almost a half century, a small wild herd roamed Yellowstone and a larger, intensively managed semi-domesticated herd was established on the northern range, where it was subjected to a variety of ranching and husbandry practices until the 1950s (Figure 7.1) (Meagher 1973). Roughly concurrent with elk reductions, the park bison population was reduced from 1,477 in 1954 to 397 in 1967 (Figure 7.2). When reductions ceased, the entire park population grew steadily to more than 3,900 the mid-1990s (Meagher, U.S. Geol. Surv., unpubl. data). For centuries bison have survived winters in the Yellowstone area by

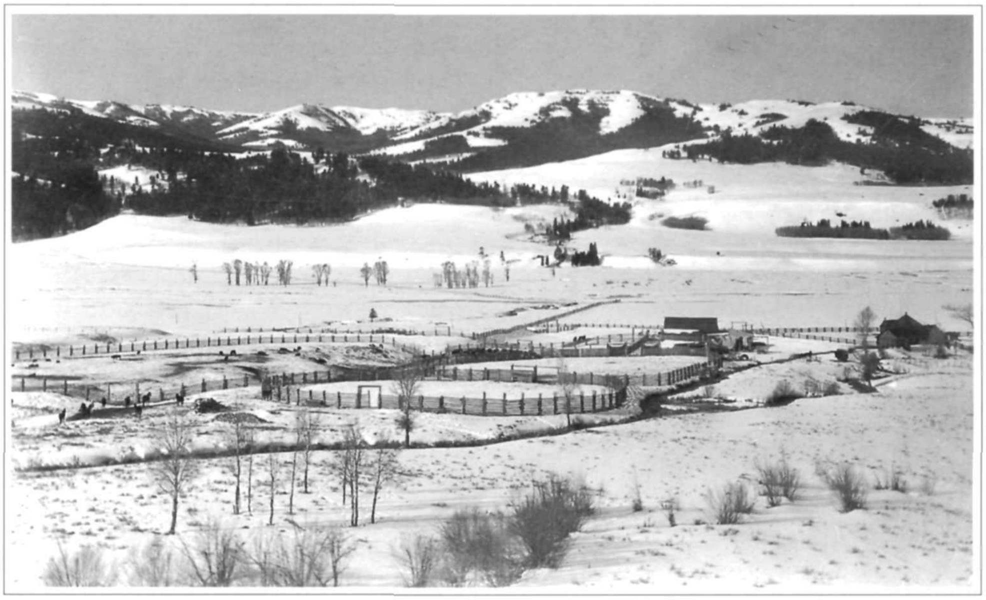


Figure 7.1. At its most extensive period, prior to the 1950s, the "Buffalo Ranch" operation in the Lamar Valley involved not only the ranch facilities, but introduction of exotic feed grasses in the valley, manipulation of animal movements in the valley (note the fence reaching clear across the valley), and other husbandry of the valley's plants and animals. NPS photo.

migrating to low-snowpack geothermal areas inside the park, and to lower elevation ranges found within and outside present park boundaries (Figure 7.3). Bison have wandered outside park boundaries periodically for the past century but disease concerns by state and other federal agencies in the late 1960s and early 1970s forced the park into signing "boundary control agreements" with each of the adjacent three states. These agreements began the "official" policy of excluding bison outside park boundaries, even when they roamed on publicly-owned wildlands such as the national forests. By the winter of 1988-1989, the northern bison herd numbered about 900, most of whom migrated to or beyond the northern boundary that winter, resulting in the killing of 569 by sport hunters and state management agencies. In the winter of 1996-1997, unprecedented snowfall and icing conditions forced an even greater number of bison to seek lower elevation ranges outside park boundaries and over 1,000 were killed in Montana by state and federal officers.

The presence of brucellosis in Yellowstone bison has been controversial for many years (Meagher 1989*a*, 1989*b*; Price and Schullery 1993), and has greatly complicated bison conservation in Yellowstone, originally seen as one of the great early successes of the conservation movement (Haines 1977). The increase in numbers of bison leaving the park, especially to the north and west, in the late 1980s and early 1990s has also caused concerns related to overpopulation. These migrations are seen by some people as somehow

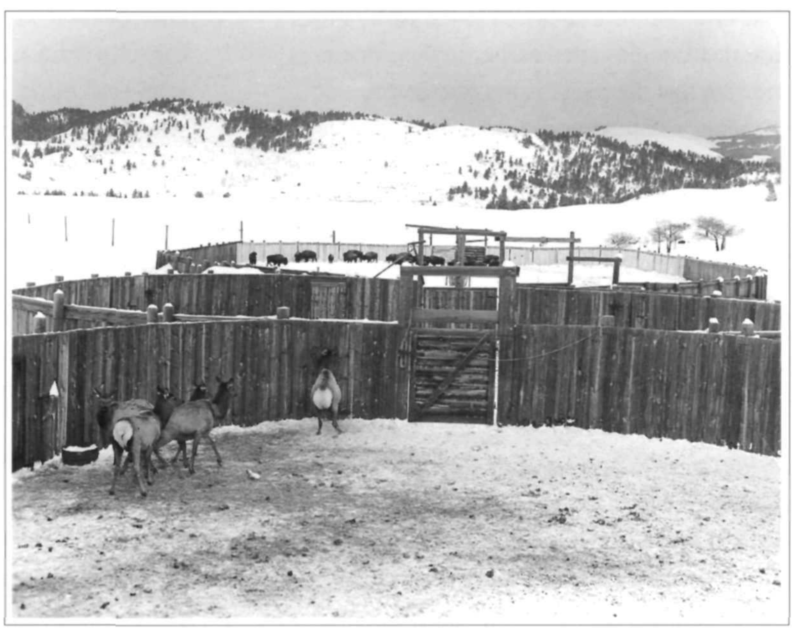


Figure 7.2. Elk and bison in holding corrals, 1961. Bison as well as elk were reduced to very low numbers during the 1960s. NPS photo.

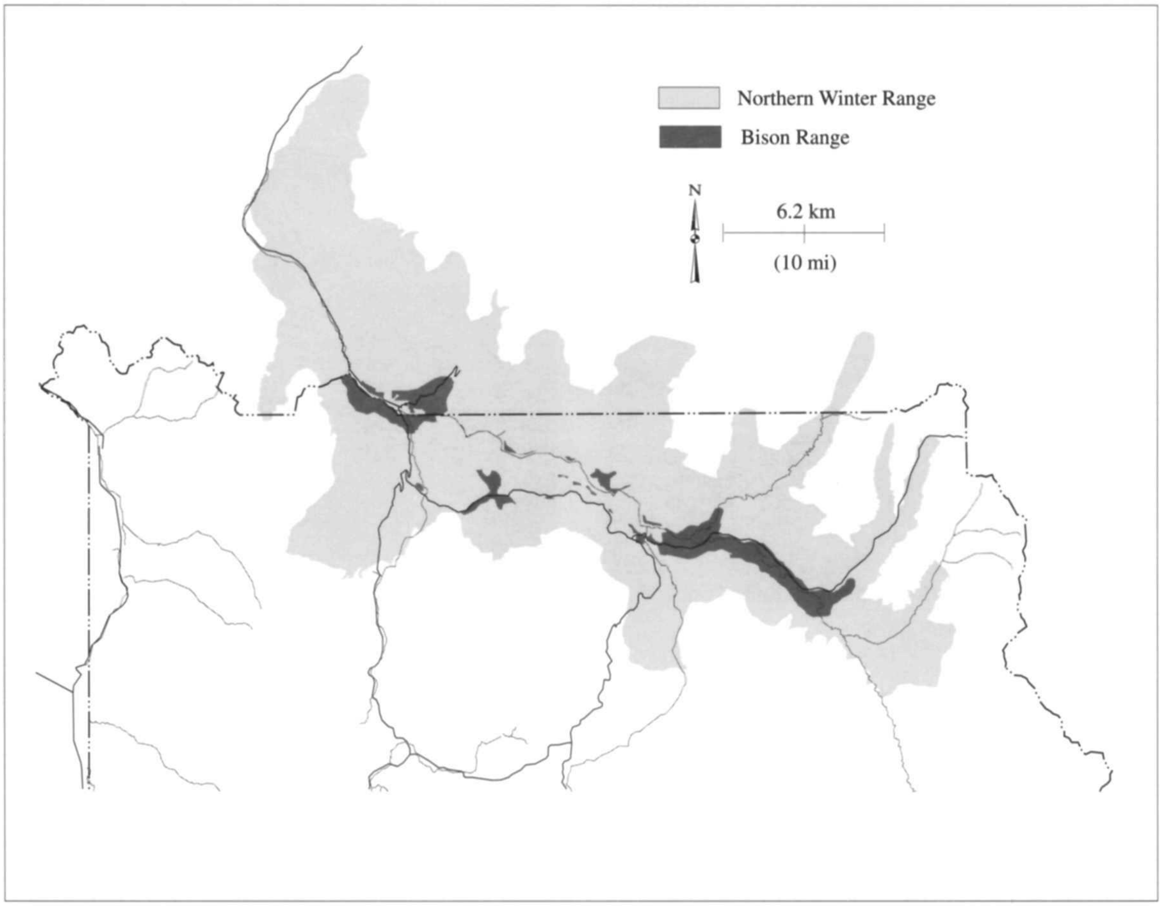


Figure 7.3. Bison winter range. Since the early 1980s, bison have learned of potential winter ranges north of the park boundary, leading to a variety of controversial management actions, including public hunting in the 1980s and capture, test, and slaughter operations more recently. Map by Yellowstone Spatial Analysis Center and Yellowstone Center for Resources.

evidence of food shortages caused by overgrazing in the park. Meagher (1989*a*, 1989*b*, 1996) evaluated these movements and concluded that much of the movements, if not all, are associated with bison learning to use hard-packed snowmobile roads for ingress and egress to the park. The grassland studies cited earlier in this document indicate that the range is not overgrazed. Meagher's observations further indicate that bison "roam" regardless of snow depth or forage availability. Once the migratory habit is learned, as it now is in the northern range bison herd and near the west boundary, the bison will quite naturally be inclined to move to lower elevations in the winter, just as the elk do. The animals shot by hunters or by management agencies after leaving the park in recent years were in good to even excellent condition as judged by body fat; they were not starving for lack of food in the park (K. Aune, Mont. Dept. Fish, Wildl. and Parks., unpubl. data; M. Meagher, U.S. Geol. Surv., pers. commun.) They were moving, as bison moved for millennia prior to the settlement of the west by Europeans.

Kirkpatrick et al. (1996) compared bison pregnancy rates of the smaller northern herd with those of the more robust Mary Mountain herd. They concluded that the northern herd, which was considered to be below its ecological carrying capacity (ECC), had higher pregnancy and birth rates than bison in the Mary Mountain area, which was considered to be near or at ECC. This was broadly considered to be physiological evidence of density dependence and natural regulation in Yellowstone bison. DelGuidice et al. (1994), while not directly addressing the natural regulation question, provided physiological evidence also suggestive of the northern bison herd being below ECC and the Mary Mountain herd being at or near ECC.

Bison, unlike elk, deer, moose, bighorn sheep, and pronghorn, have few constituencies to champion their cause on public or private lands outside of Yellowstone Park. As noted above, their population has increased and they have learned

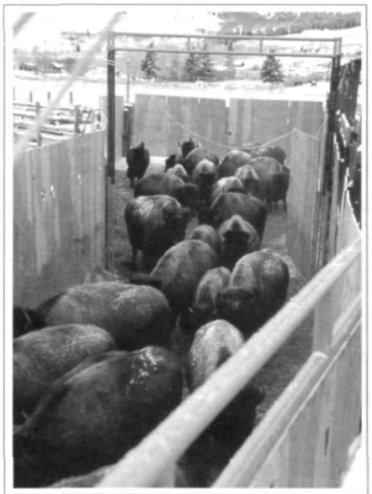


Figure 7.4. Park rangers herding bison toward Stephens Creek holding pen inside Yellowstone's north boundary, January 1997. NPS photo.

Figure 7.5 (Far left.) Bison in the holding pens at Stephens Creek, January 1997. NPS photo.

new migratory routes in the process. As a consequence, and with the further complication that some of the animals carry the livestock disease bacteria, *Brucella*, the management agencies have been compelled to confine bison to the park for most of this century (Figure 7.4 and 7.5).

In the current contention over bison management, a public desire for bison presence in and outside the park (especially on public lands already dedicated to wildlife conservation), is pitted against the purported risk to livestock producers of bison infecting cattle with brucellosis. The Department of the Interior agencies are strongly committed to current research to increase our knowledge about the disease organism in wildlife and its eventual elimination; a task that cannot be done reasonably until an effective vaccine is developed. At the same time, the management agencies and their various constituencies are involved in a number of dialogues, planning processes, and lawsuits in an attempt to find mutually agreeable solutions.

MOOSE

Monitoring and research on elk, mule deer, pronghorn, bighorns, and moose has been a cooperative interagency effort under the auspices of the Northern Yellowstone Cooperative Wildlife Working Group (formerly the Northern Yellowstone Elk Working Group) since 1985.

Though Schullery and Whittlesey (1992) found tantalizing evidence of moose presence on or near the northern range prior to 1882, Houston believed moose immigrated naturally to the northern range in greater numbers starting about 1913 (Appendix B) (Houston 1982). Moose are heavy users of willows and other riparian vegetation, and if that historical scenario is accurate, then moose entered the northern range picture about the same time riparian vegetation began to decline (Figure 7.6). Northern range moose numbers may have declined somewhat since the fires of 1988 because of their suggested dependence on old

Figure 7.6. Moose colonized the northern range in numbers beginning early in the twentieth century. NPS photo.

growth forests (1995). Recent estimates were of about 200 on the northern range but counts are often inconclusive because moose are solitary animals that spend much time in forested areas. In winter, northern range elk ate about 80 percent grasses, 17 percent browse, and 3 percent forbs (Houston 1982). By contrast, moose are primarily browsers. From 1986 to 1990, Tyers (U.S. Forest Service, Gardiner Dist., unpubl. data) studied moose on Yellowstone's northern range in a slightly expanded area that included adjacent, higher elevation areas not studied by Houston. Tyers found that moose ate 39.6 percent subalpine fir, 25.5 percent willows, 10.6 percent lodgepole pine, 4.6 percent gooseberry, and 4 percent buffaloberry. Most of their browsing occurred in 300+ year-old lodgepole forests, the oldest spruce-fir forests, and the 100- to 300-year-old lodgepole forests. Moose are able to winter in snow 150 percent as deep as can elk, and tend to winter at higher elevations than elk.

Moose population data on the northern range is meager compared to the other ungulate species, which is a function of their solitary habits in forested habitats. The Northern Yellowstone Cooperative Wildlife Working Group stopped conducting aerial censuses for moose after 1992, believing them to be inaccurate but lacking a better method. Still, there is evidence of a decline of moose on the northern range since the 1960s, and particularly since the fires of 1988. While competitive exclusion by elk cannot be ruled out as a reason for the suggested decline, the fires and overhunting may be factors as well.

MULE DEER

Mule deer winter in the Gardiner Basin from the vicinity of Mammoth Hot Springs, Wyoming, to the south end of Yankee Jim Canyon (Figure 7.7). The herd's winter distribution is contiguous with that of other mule deer herds north of Yankee Jim Canyon. The bulk of the herd winters beyond the northern border of Yellowstone National Park because of shallower snow depths at those lower elevations (Figure 7.8).

Northern range mule deer numbers, like those of many greater Yellowstone ungulate herds, increased during the 1980s when the northern Yellowstone elk also were increasing (Appendix B). Even if several research projects had found evidence of elk outcompeting mule deer for food or other resources, the doubling of the mule deer herd is circumstantial evidence that competition is not causing the mule deer herds significant problems.

In the winter of 1993, P. Gogan (U.S. Geol. Surv., pers. commun.) began a research project designed to identify the summer range of the northern Yellowstone mule deer herd, and determine the extent to which it had been affected by the 1988 fires. Sixty adult female mule deer were captured in the Gardiner Basin and fitted with radio collars in March 1993. These does were relocated by aircraft to determine their seasonal movement patterns and location of summer ranges. An additional 25 adult females were captured and radiocollared in the same area in March 1995. Results of radiotracking showed that some 30 percent of the deer were year-round residents of the Gardiner Basin, simply moving to higher elevations in the same drainage in which they winter. The remaining 70 percent of the deer moved seasonally. Those deer wintering on the east side of the Yellowstone River generally moved to the east, to summer ranges in all the drainages between Crevice Creek and Cooke City, as well as the Mirror Plateau and to the northeast to Mill Creek in

Figure 7.7. Environmental factors that favored increases in elk numbers in the 1970s and 1980s also favored increases in mule deer. NPS photo.

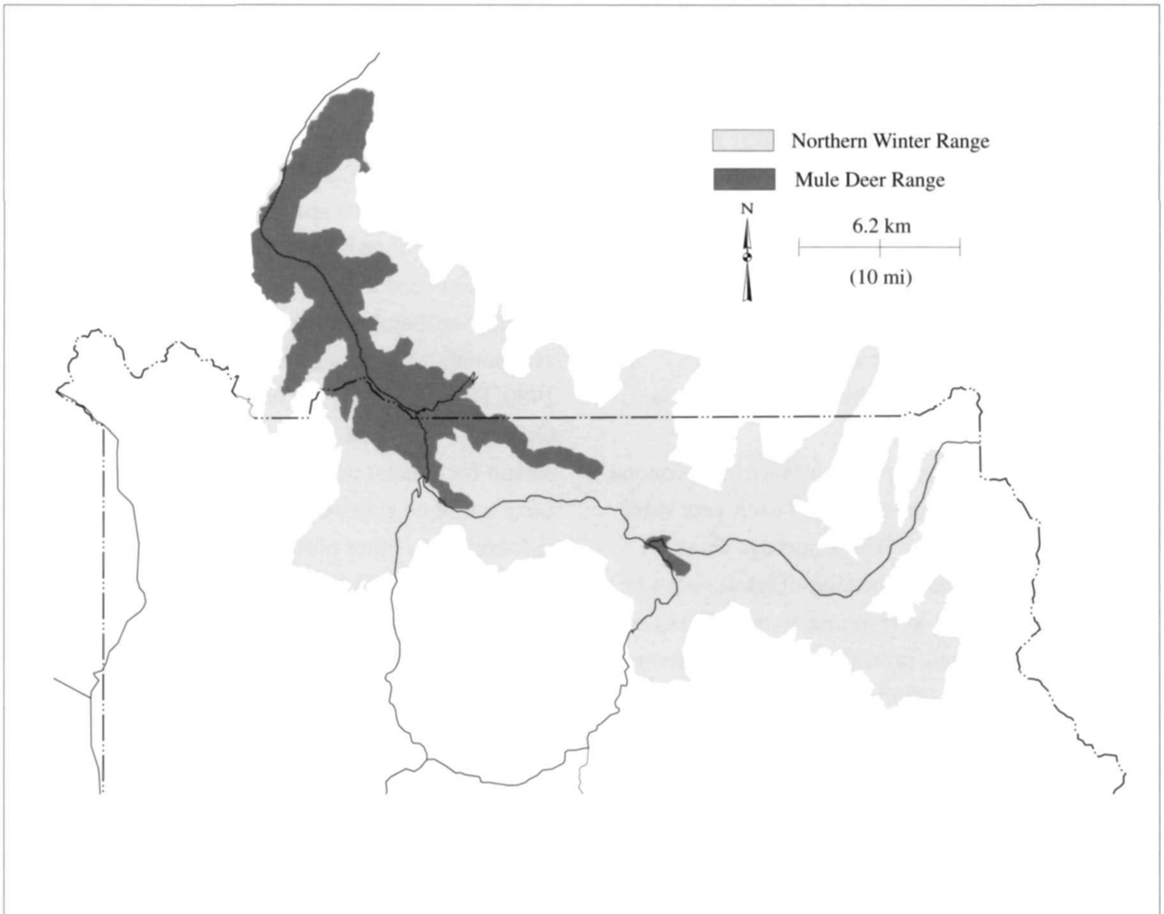


Figure 7.8. Mule deer winter range is primarily north of the park boundary. Map by Yellowstone Spatial Analysis Center and the Yellowstone Center for Resources.

Paradise Valley. Deer from one drainage on the east side of the Yellowstone River crossed the river and the Gallatin Mountain range to summer near Big Sky, Montana. Those deer wintering on the west side of the Yellowstone River moved to summer ranges along the western park boundary from the vicinity of Monument Mountain to West Yellowstone and south to Bechler Meadows. Other deer wintering on the west side of the Yellowstone River used summer ranges from Norris Geyser Basin south to Shoshone and Lewis lakes. An analysis of the nature of the deer summer ranges and the extent to which they were altered by the 1988 fires is currently under way in cooperation with Montana State University.

Our interpretation of the mule deer population data follows two lines. In one scenario based on recent counts, the entire population of mule deer has more than doubled in the last two decades. Counting techniques, however, were not standardized until 1986. In the second scenario mule deer have increased less, but have still grown at least 40 percent, based on the standardized regular counts from 1986 to 1996. Numbers of mule deer counted have increased from approximately 1,800 in 1986 to about 2,500 in 1996. In either scenario, it would appear that the environmental factors contributing to an increase in numbers of elk on the northern range were also favorable to an increase in mule deer numbers in the herd.

Despite the increase in the entire herd, the mule deer that winter in the Boundary Line Area (again recognizing that two different counting techniques were used) have declined from about 230 in the 1960s to about 100 in the 1980s (Barmore 1980, Singer 1991*b*). The question, then, that can be asked is: how we can observe an increase on the entire mule deer herd but have a decline in a subunit on about five percent of the deer's winter range? The answer probably lies in a slow decline of big sagebrush, a key winter deer food, in the Boundary Line Area. Because we are

not aware of a decline in big sagebrush anywhere else on the mule deer winter range, and lacking any other lines of evidence, we can speculate that the sagebrush decline may be due to heavy, year-round use by pronghorn. To further complicate this question, the sagebrush decline seems to be restricted to the Wyoming subspecies, and mostly to high ground such as ridges, upland slopes, and rolling terrain with a high soil clay component. In the lower areas and swales where the basin subspecies dominates, sagebrush is tall, abundant, and apparently vigorous.

The composition of the northern Yellowstone mule deer herd has been estimated each year since 1990 using a helicopter. These surveys show a steady increase in the proportion of adult males in the herd, presumably in response to modifications of hunting regulations promulgated by the Montana Department of Fish, Wildlife and Parks.

PRONGHORN

Early accounts of the greater Yellowstone ecosystem report large numbers of pronghorn in all the major river valleys radiating out from the present park area (Figure 7.9). Agriculture, settlement, and market hunting were probably responsible for the demise of these large, continuous populations. Many accounts of the northern range prior to 1882 also mention frequent sightings of pronghorn, but these are reports of summering animals (Schullery and Whittlesey 1992). It does not appear that the park contains significant winter range for pronghorn; their winter range is at lower elevations downstream of the north park boundary, where they are competing with a growing amount of human activity and development (Figure 7.10).

Pronghorn is a species of special interest on the northern range because their numbers have at times been very low, causing concerns over their genetic wellbeing and even their long-term survival as a population entity (Appendix B) (Barmore 1980, Houston 1982, O'Gara 1990, Scott and Geisser 1996). Lee et al. (1994) added a further reason for special interest: Yellowstone pronghorn carry a unique genetic element (mtDNA haplotype J) found in no other pronghorn herd in the west. Surprisingly, the Yellowstone pronghorn contains more genetic diversity than any other North American herd studied, yet has never received stocked pronghorn from elsewhere. The authors stated:

> The pronghorn herd of Yellowstone National Park is one of the few remaining undisturbed populations. The most parsimonious explanation for the great amount of mtDNA variation in the Yellowstone herd is that Yellowstone was a refuge when other herds were exterminated or greatly reduced. This genetic resource should be conserved.

Yellowstone pronghorn populations of 550 to 700 were reported in the 1930s, and these increased to 600 to 800 in the 1940s following the addition of

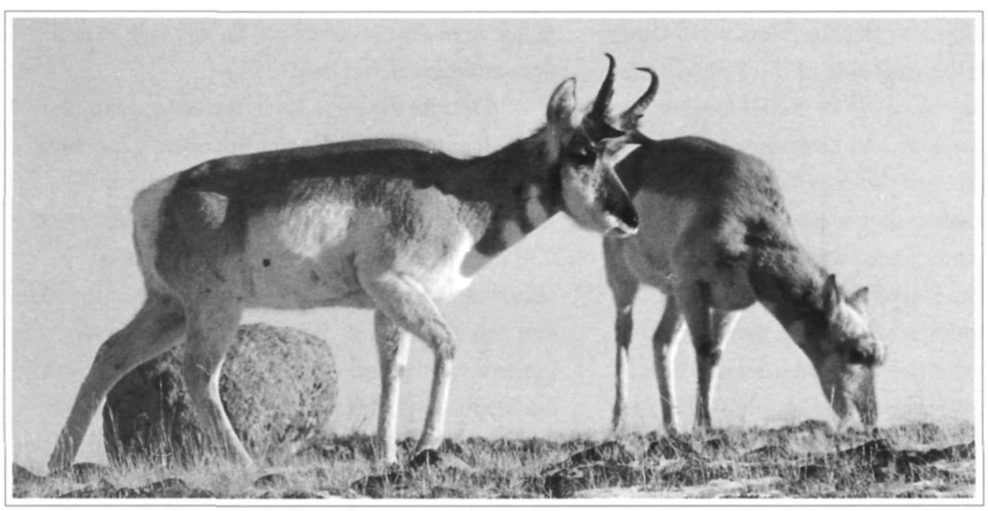


Figure 7.9. Pronghorn were extremely abundant in the lower river valleys of greater Yellowstone prior to the creation of the park in 1872. Because of its small size and isolation, the northern Yellowstone pronghorn population is at some risk of extinction. NPS photo.

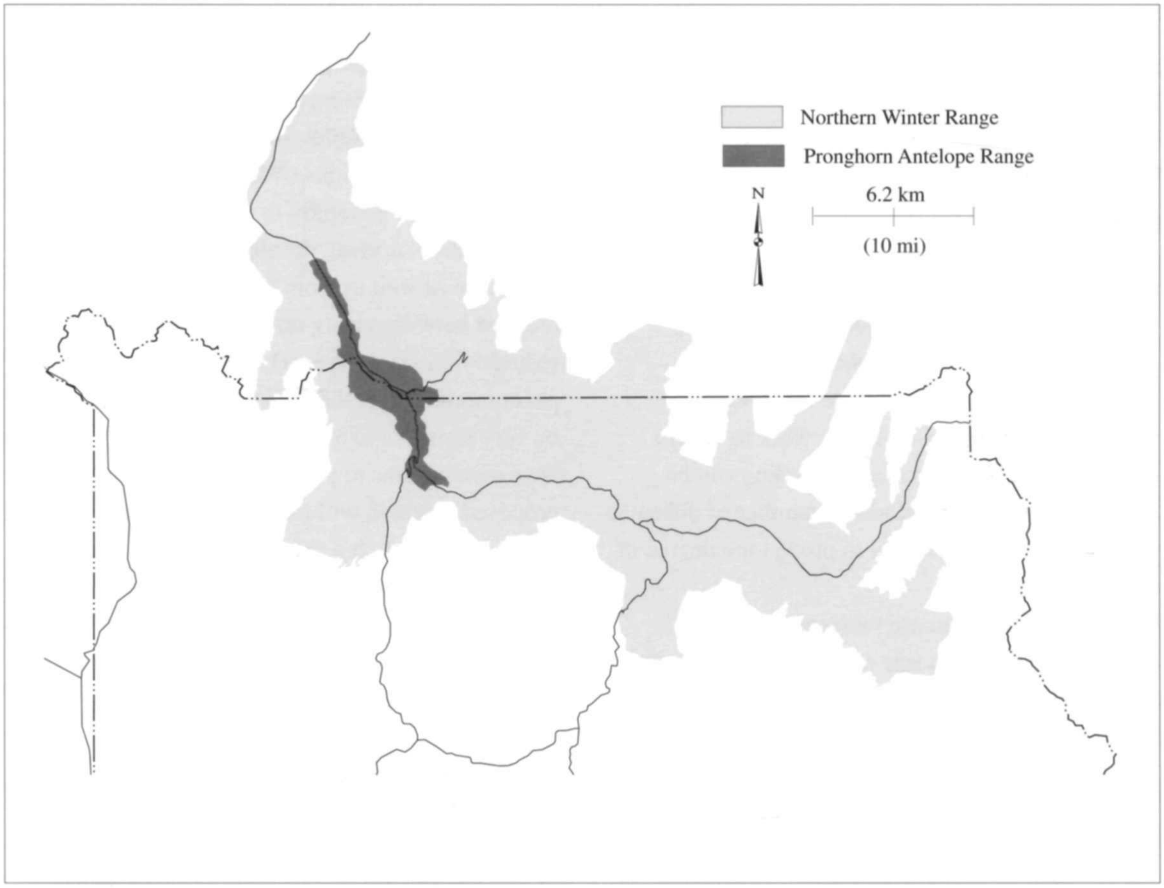


Figure 7.10. Pronghorn winter range is restricted primarily to lower elevation areas in the BLA and north of the park. Map by Yellowstone Spatial Analysis Center and the Yellowstone Center for Resources.

winter ranges north of the park and the removal of a boundary fence. Pronghorn populations were reduced in conjunction with elk and bison control after this period, so that by 1967 there were only about 188 (Barmore 1980, Houston 1982). During the 1970s, counts averaged about 140, but increased to a peak of 594 in 1991 and dropped to 229 in 1996 (see Table, Appendix B).

Goodman (1996) estimated the prospects for the Yellowstone pronghorns through population viability analysis. He concluded that "this antelope population is extremely vulnerable to wide swings in numbers, and the risk of extinction is high…A run of 'bad luck,' such as a few consecutive years where coyote predation prevents successful recruitment of young, coupled with a disease or weather event causing high adult mortality, could eliminate the herd." Goodman added, "the [limited special damage] hunt [reinstituted in the late 1980s at the request of a private landowner] could in fact contribute to the dynamical variability that poses a threat to the long term prospects for survival of the population.

Goodman estimated that the probability of extinction within 100 years was 18 percent and noted:

> It is conventional…to consider a population…severely endangered when its probability of extinction within 100 years is above 5 percent…

RESEARCH RECOMMENDATIONS: PRONGHORN

In 1989, the park convened a group of western pronghorn experts to review the state of knowledge on Yellowstone's pronghorns and make recommendations for future research. In synopsized form the group recommended the park:

1. Continue annual counts and recording of age group distributions as has been done for many years, augmented through radiomarking a subgroup to determine sightability and thus the total popula-

tion size, and ascertain if there are discrete subpopulations. They felt the historical data was of good enough quality to warrant correlations with vegetation, climate, or other environmental factors. Crucial habitats, such as for kidding and wintering, should be identified.

2. Improve the database on habitat quantity and quality, including vegetation production, on summer, winter, and migratory ranges.

3. Preserve the Yellowstone pronghorn population as a genetically pure resource in perpetuity, and continue genetic work to ensure that negative effects such as inbreeding can be avoided. They recommended a number of different methods that could be used to predict the degree of risk of extinction.

4. Conduct disease monitoring in the pronghorn population (the herd is known to have been exposed to livestock diseases such as bluetongue, leptospirosis, ParaInfluenza-3, and Bovine Virus Diarrhea).

One researcher (D. Scott, formerly Natl. Park Serv., pers. commun.) feels that the avoidance of private lands in recent years, due to a crop damage hunt on adjacent private lands, has hurt the population due to loss of a rich food source in the farm fields plus interspersed tall sagebrush patches. Also of concern is the decline of two subspecies of sagebrush in the upland portions of the Boundary Line Area. However, these shrubs were utilized at the same high rate in the 1960s when pronghorns were controlled and kept within a population of 100 to 200 animals (Barmore 1980, Singer and Renkin 1995).

Based on the proximity of the herd to humans in the Gardiner, Montana area, many suggestions have been made to reduce the impact of humans on this population, especially in agricultural areas and in places where they need security, such as kidding fields. Control of the pronghorn population to potentially reverse the decline in several subspecies of sagebrush is unacceptable because it could place the pronghorns at an even higher risk of extinction than the high rate that already exists due to their small herd size and isolation.

Yellowstone pronghorn are in crucial need of additional research. New research proposed to begin in 1997 would measure heterozygosity in the Yellowstone pronghorn population and compare it to descendants of Yellowstone pronghorn now living in other locations. While small, isolated populations are generally in danger due to reduced growth rates, survival, developmental stability, and/or disease as well as from inbreeding depression, reduced heterozygosity does not always result in reduced *fitness*. J. Byers (Univ. of Idaho, per.commun.) hypothesizes that pronghorn may not be very sensitive to inbreeding, or that they may have mechanisms to prevent inbreeding. The proposed research will increase our understanding about whether such a small ungulate population will or will not suffer with a loss of genetic diversity.

Other research suggested by the experts consulted in 1989 is still needed as well.

BIGHORN SHEEP

Early accounts of the Yellowstone area reported large numbers of bighorn sheep, especially in the Absaroka Mountains along the eastern side of the park, leading to the suggestion that bighorn sheep were more numerous before the park's establishment than they are now (Figure 7.11) (Schullery and Whittlesey 1992). Possible reasons for decline in bighorn numbers include overhunting, the introduction of domestic livestock diseases, and the known difficulty that bighorn sheep have in recolonizing ranges from which they have been extirpated (Appendix B) (Schullery and Whittlesey 1992).

Interpretation of elk-bighorn sheep relationships during the natural regulation era (1968-present) is complicated by the *Chlamydia* epidemic and associated mortality among bighorns in the winter of 1981-1982 (Meagher 1981, Meagher et al. 1992). Keating (1982) concluded that "elk numbers negatively impacted bighorn [sheep] numbers on the Mount Everts winter range." A more recent study (Singer and Norland 1994, 1996) reported that bighorn sheep population growth rates did not differ significantly between 1968 and 1981 or 1982 and 1990, but the sample sizes

(number of years) are small. Diet overlaps are large between elk and bighorns on the northern range (Houston 1982, Keating 1982, Singer and Norland 1994, 1996). The data on elk-bighorn relations are as inconclusive now (Singer and Norland 1994, 1996) as they were from earlier periods reported by Houston (1982), whose regressions of bighorn sheep numbers for 1955-1978 showed no significant association with winter severity or elk numbers. Competitive interactions between the two species remain a real possibility, but have not yet been demonstrated at the population level.

Figure 7.11. Bighorn sheep numbers in and near Yellowstone National Park may be lower than they were before the park's creation, because of human hunting, introduced livestock diseases, and the slowness with which bighorns recolonize areas from which they have been extirpated. NPS photo.

While the importance of diet overlap between elk and bighorn sheep is well known in the literature, their actual on-the-ground habitat separation is less clear and should be further studied. Varley (1994, 1996) noted substantial niche separation between elk, non-native mountain goats, and bighorn sheep on summer ranges in the Absaroka-Beartooth Mountains north of the northern winter range but little work has been done on the competitive interactions between these species on winter ranges.

Findings by Smith (1991) that most bighorn

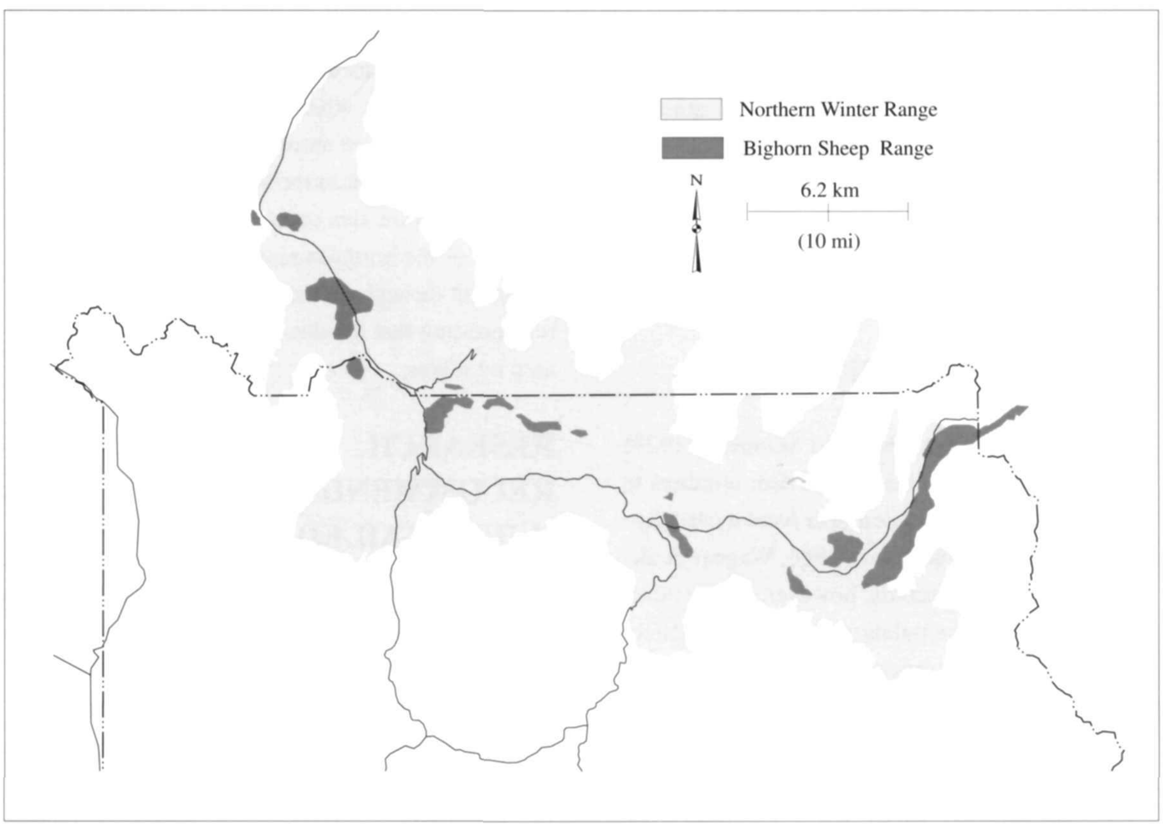


Figure 7.12. Bighorn sheep winter range, like their summer range, is confined to areas on or near "escape terrain": steep cliffs where sheep are able to outmaneuver and elude predators. Map by Yellowstone Spatial Analysis Center and Yellowstone Center for Resources.

activity (95 percent) occurs in confined escape terrain (steep cliffs) or areas within 1,000 feet of that terrain confirms observations of others (Figure 7.12) (Oldemeyer et al. 1971, Van Dyke et al. 1983). Elk or bison are rarely found in the kind of escape terrain defined by Smith (1991). Interspecific diet data, then, has limited usefulness in interpreting competition unless the terrain that the diet items were obtained from in has been factored into the equation.

RESEARCH RECOMMENDATIONS: BIGHORN SHEEP

Even with previous studies of Yellowstone's bighorns, and with information made available from other populations in the west, we lack basic information on bighorn sheep: 1) the seasonal movements and habitat use of wild sheep, factors limiting their population growth, and interchange with other sheep populations in the Gallatin-Absaroka-Beartooth Mountains; 2) as docile as bighorns appear to the public in the park, we still have no definitive data on the effects of people, trails, and roads on their well-being; and finally 3) it is vital that we determine the effects of introduced domestic cattle and sheep diseases they are frequently exposed to on their winter and summer ranges to determine if that factor is significant in the well-being of the bighorn sheep. A new study beginning in 1997 will contribute to our understanding of the first two items (L. Irby, Montana State Univ., pers. commun.)

WHITE-TAILED DEER

Many observers have used Skinner's (1929) report of a decline in white-tailed deer numbers to suggest that the white-tailed deer were a casualty of elk overpopulation (Chase 1986, Wagner et al. 1995*a*). Historical records, however, suggest that Skinner's reported population of 100 white-tailed deer on the northern range around 1890 was a short-term increase in the presence of that species (Houston 1982). Schullery and Whittlesey (1992), in their analysis of 168 pre-1882 accounts of Yellowstone National Park-area wildlife, found ten statements about the presence (unspecified location) of white-tailed deer (in the entire park and surrounding area), but only one actual sighting of white-tailed deer in the park, and concluded that white-tailed deer appeared "not to have been common in the park area during the period we studied." Murie (1940), Barmore (1980), and Houston (1982) agreed that the park was "the extreme upper limit of marginal winter range" for white-tailed deer. Houston (1982), noting that this increase in white-tailed deer presence in and near the park around 1900 occurred "in the presence of very high elk numbers" and in a human-altered habitat, thought it "unlikely that interspecific competition with elk for food was the primary cause of the decline" in their numbers. He suggested that "a combination of land clearing, livestock grazing, and human predation outside the park," along with "fire suppression and artificial concentrations of elk in the boundary area of the park," caused the disappearance of this small group. Others have noted that white-tailed deer increased around the turn of the century when hay was being set out for elk and other ungulates. For these reasons, it does not seem that past alarms raised about a "decline" in white-tailed deer in the park were either accurate or justified. Finally it must be noted that white-tailed deer are not absent from the park. Rare animal sighting reports collated by the park in the 1980s and 1990s continue to show this species as an uncommon resident of the northern range and an occasional inhabitant throughout the remainder of the park. It is interesting that the does are frequently accompanied by fawns.

RESEARCH RECOMMENDATIONS: WHITE-TAILED DEER

It is recommended the park continue to monitor white-tailed deer as it has for many years using the "Rare Animal Observation Monitoring System." Given the low numbers of the species in the park, yet the robust populations in other parts of the greater Yellowstone ecosystem, especially its

lowlands and farmland periphery, it would seem expensive and somewhat futile to study this animal within the park when it is so abundant elsewhere in greater Yellowstone, and because the park is likely marginal white-tailed deer habitat.

MOUNTAIN GOATS

Mountain goats do not appear in the paleontological, archeological, or historical records of Yellowstone National Park. Recognizing even the incompleteness of the paleontological and archeological records, and the spottiness of the historical record, it still seems unlikely that goats lived in the present park area for several thousand years (Laundré 1990).

Goats were introduced in Montana north of Yellowstone National Park between 1947 and 1959, and in the Absaroka-Beartooth Mountain area between 1942 and 1958, by the Montana Department of Fish, Wildlife and Parks (Laundré 1990). The state of Idaho Department of Fish and Game introduced goats near Swan Valley between 1969 and 1971 (Laundré 1990).

Animals from the Montana populations have thrived and now are common north of the park boundary in the North Absaroka and Beartooth Ranges and Gallatin Mountains (Laundré 1990, Varley 1996), and since the 1980s have colonized in Yellowstone Park in those adjacent drainages. A population now appears established in Yellowstone's Pebble and Slough Creek drainages and perhaps Sepulcher Mountain as well (Varley 1996). The Absaroka and Gallatin mountains seem to be the only areas that will likely support substantial, long-term populations in the park (Laundré 1990), but the Absaroka Range, which forms the Wyoming—Yellowstone boundary east of the park appears to be good habitat as well (Varley 1996.)

While goats are not a major element of the Yellowstone National Park fauna, there is cause for concern over their imminent increase. Houston et al. (1991) noted that goats colonizing Yellowstone and Grand Teton National Parks "may eventually pose problems to park managers that could prove embarrassingly similar to those experienced at Olympic [National] Park." Exotic goats in Olympic have seriously degraded rare, endemic alpine plants found nowhere else on the continent. While there are no known unique alpine flora in Yellowstone, the alpine area is relatively unstudied, and concerns over potential competition between goats and sheep remain.

Goats are spectacular mammals with many romantic associations among the public; problems with exotic goats in Olympic National Park have been vastly complicated by the animal's public popularity (Houston et al. 1991). It would be well to deal with this situation before the animals become well enough established to have a large constituency among park wildlife-watchers, for whom the sight of goat may be a higher value than the National Park Service's legislative mandates to prevent the spread of exotic species.

RESEARCH RECOMMENDATIONS: MOUNTAIN GOATS

In reviewing the Olympic National Park plight between exotic mountain goats and rare native alpine plant species, the obvious omission from the Yellowstone database is the lack of a serious inventory of alpine plants that may be affected by goats; either by the consumption of those plants or by their wallowing in them. In addition, studies of potential competition between bighorn sheep, mountain goats, elk (or other herbivores) on winter ranges are necessary.

BEAVER

Next to the elk and other ungulates, the animal most often spoken of in relation to the reported overgrazing of the northern range has been the beaver. Interpretations of beaver history in Yellowstone National Park have been employed to argue that the park's northern range is overpopulated and overgrazed by elk, that aspen have declined unnaturally, and that other misfortunes have befallen the park (Kay 1990, Wagner et al. 1995*a*). No detailed analysis has been published of the historical and scientific record of beaver on the northern range, however, so it is important to

pursue the subject at some length here. Recent studies shed light on the history of beaver in the park, and suggest that beaver were not simply the victims of elk overpopulation.

There appears to be no question that beaver are native to the Yellowstone National Park area. Hadly (1995), in the only vertebrate-oriented paleontological study on the northern range, reported a total of seven beaver bones found in 4 of 16 strata at Lamar Cave on the northern range.

Accounts of the Yellowstone National Park area written prior to the establishment of the park suggest that beaver were abundant in the park and drainages downstream from the park (Schullery and Whittlesey 1992). Human-beaver relationships may have been quite complex prior to the establishment of Yellowstone National Park. Trapper Osborne Russell's 1835 report of Indians eliminating beaver from some drainages in the Lamar Valley (Haines 1965) is a fascinating glimpse at a possible instance of localized heavy harvest of wildlife by Native Americans. Euramericans repeatedly trapped Yellowstone streams as well, from the 1830s on into the early years of the park. Whittlesey (1988) reported that "Father Pierre DeSmet's map in 1851 showed this stream [the Lamar River] as 'Beaver Creek.'" At the time of formal exploration and early development of the park, between 1869 and 1880, beaver were reported as common (Schullery and Whittlesey 1992).

Though it is impossible to derive precise population estimates from these anecdotal accounts, it appears certain that commercial trapping intensified in the park's first decade. In 1880, Superintendent Philetus Norris regarded the park as such favorable habitat for beaver that without trapping "soon they would construct dams upon so many of the cold-water streams as literally to flood the narrow valleys, terraced slopes, and passes, and thus render the Park uninhabitable for men as well as for many of the animals now within its confines" (quoted in Schullery and Whittlesey 1992). This was obviously an unrealistic view, as most of the park is not suitable beaver habitat in the first place, and even if it were, it is not topographically susceptible to such inundation. But because he held this extreme view of the landscape-altering power of beaver, Norris allowed trappers to take "hundreds, if not thousands" of beaver from the park in the late 1870s (Schullery and Whittlesey 1992). Trapping of beaver and other furbearers was officially prohibited in 1883, but even allowing for some hyperbole in Norris's account, it seems probable that the beaver population was reduced significantly.

The earliest historical record, then, provides an unclear picture of beaver numbers in Yellowstone National Park. It is safe to assume that beaver were distributed in appropriate habitats in Yellowstone National Park in the middle and late 1800s.

As discussed earlier, preferred beaver foods, especially aspen, have persisted but have been only marginally common in Yellowstone National Park for thousands of years (Whitlock et al. 1991, Whitlock 1993, Mullenders and Coremans 1996, Mullenders et al. 1996). As a consequence of the park's limited supply of preferred beaver foods, Jonas (1955) summarized the park's potential as beaver habitat as likewise marginal:

> Actually, the environment indigenous to Yellowstone Park has never been conducive to heavy beaver habitation and most activity was on a marginal basis. Therefore, any slight deviation of the factors affecting the beaver's surroundings has had a comparatively great effect upon the population (Jonas 1955).

Such a deviation occurred in the first decade after the establishment of Yellowstone National Park. Norris' report of intensive beaver trapping roughly coincided with a number of other events, including a widespread slaughter of ungulates, a concurrent and widespread poisoning of predators, the early development of a road system in Yellowstone National Park (Haines 1977), and, as already discussed, an abrupt increase in successful aspen growth.

Based on contemporary accounts, including early published interviews with poachers active in the late 1880s and early 1890s, Schullery and Whittlesey (1992) have suggested that beaver,

whose numbers were suppressed in the 1870s and early 1880s, were still illegally harvested for some years following the 1883 regulation prohibiting their harvest. By the 1890s, however, military managers of Yellowstone National Park were more consistently successful in capturing poachers, and wildlife protection improved (Haines 1977, Schullery 1995*a*). If, as seems probable, beaver numbers continued to be suppressed through the 1880s, that suppression probably helped facilitate the growth of some aspen groves in Yellowstone National Park. Schullery and Whittlesey (1992) assumed that this sudden success in aspen growth in the 1870s and 1880s was followed by a sudden growth of beaver numbers beginning about the turn of the century, as the beaver population responded to improved protection and the increase in available food.

Later writers both in and out of the scientific literature (Chase 1986, Glick et al. 1991, Wagner et al. 1995*b*) have pointed to a study by Warren (1926) in the early 1920s as providing today's managers with a population size of beavers that "should" occupy the park, but the historical realities are quite different. The reason that Warren was invited to conduct his study was that park managers and naturalists were alarmed over the population irruption of beaver, and were fearful that the beaver were going to kill all the park's aspen (Warren 1926). The high beaver numbers of the 1920s seem to have been a response to a historically unusual quantity of preferred food (aspen), a supply that contemporary accounts suggest the beaver population may have been in the process of "overshooting." The 1920s, then, seems the least likely of times to get a reasonable idea of how many beaver the park might normally support. Use of the 1920s as a baseline for judging modern beaver abundance is further complicated by the fact that Warren (1926) looked at beaver in only a small portion of the park (Yancey's Hole) on the northern range.

Warren's data on the age of the aspen trees killed by beaver (Warren 1926) suggest that he could have been aware of the aspen "birth storm" that occurred in the 1870s and 1880s. The 31 aspen that he cored and dated near Roosevelt Lodge began their growth at the beginning of that period, and the many stumps that he measured were of similar sizes and so may also have dated from the same period (D. Despain, U.S. Geol. Surv., pers. commun.). But Warren seems not to have grasped the significance of this aspen escapement to the beaver population irruption. He attributed the "great increase in the number of beaver" only to their protection from trapping and the predator-control program then underway in Yellowstone National Park.

Warren did not estimate the parkwide beaver population in the 1920s, but Wagner et al. (1995*b*) note that Skinner (1927) reported a very large beaver population in Yellowstone in the 1920s. Skinner's actual words were "I have estimated the beaver population of Yellowstone National Park at about 10,000, but believe that figure to be very conservative." This was during the peak of the beaver irruption studied by Warren, but Skinner gave no information on data or methods for his estimate; the only formal study of beaver in this period was Warren's, limited to the area near present Tower Junction. More important, and in fairness to the historical record, Wagner et al. (1995*b*) should also have cited Park Naturalist Sawyer, who reported at about the same time as Skinner that "800 would be a reasonable estimate of the present Beaver population"(Seton 1929). Sawyer's sources or methods for arriving at this number are likewise not known. Thus, our only two contemporary authorities for beaver numbers during this presumably peak period differ by a factor in excess of 1,000 percent. We simply do not know anything specific about the size of the park beaver population in the 1920s beyond the small area studied by Warren, so it seems incautious to rely too heavily on either of the estimates.

Thirty years after Warren's study, Jonas (1955) reported scattered pockets of beaver activity in the park following a general decline of beaver from the 1920s. Jonas concluded that the "primary factor limiting beaver activity in Yellowstone was the lack of preferred food species of vegetation." Though sometimes erroneously represented as attributing this lack of food solely to an overpopulation of elk (Chase 1986), Jonas believed several

factors were involved. The first factor he listed was that "the inherent vegetation of the park was primarily coniferous," reinforcing his remark, quoted earlier, that Yellowstone was only marginal beaver habitat. The second factor he listed was the one reported by Warren (1926), that the "overpopulation" of beaver in the 1920s resulted in a depletion of beaver food sources. This was to say that the beaver declined because *they* ate all their food. The third factor Jonas listed was the then-widely believed "overpopulation" of elk on the northern range, which kept aspen in a low, shrub stage, thus reducing or eliminating its availability to beaver. The fourth factor Jonas listed was "intensive forest fire control" by park managers, which he believed reduced beaver habitat.

Jonas thought that other factors besides food shortage affected beaver abundance, including "poor water conditions" because of an extended drought period from 1919 to 1938, and silting in of beaver dams (caused in part by the steep gradients of local streams and "overbrowsing" by elk). He regarded predator control, diseases, and visitor pressures near beaver colonies to be "minor factors" in limiting beaver numbers.

The relationship between beaver numbers and elk numbers is interesting throughout the period of beaver increase (roughly 1895 to 1930) and decline (roughly 1930 to 1950). Houston (1982) pointed out that the beaver increase of 1900-1920 occurred in the presence of large numbers of elk, which would hardly suggest direct competition for a limited food source. In fact, hunter harvests north of the park, management removals, and other factors may have kept elk numbers *lower* during the period of beaver decline than during the period of beaver increase (Houston 1982). A host of factors, including the extended drought through the 1930s, changing elk management practices inside and outside the park, and the exhaustion of the aspen supply by the beavers, challenge simplistic interpretations of this period.

The historical overview allows this proposed sequence of events: northern range beaver populations were subject to unquantified levels of human harvest before the park was established, by both native Americans and, during the early 1800s, by white trappers. During the park's first decade, beaver were heavily harvested by trappers with the encouragement of the superintendent, and beaver numbers may have been kept low by continued poaching well after sanctioned trapping terminated in about 1883. Beaver may not have been free of this trapping until the early 1890s. In the early 1890s, at about the time that more effective law enforcement provided beaver with better protection, a 20- to 25-year surge in aspen escapement (roughly 1870 to 1890) was concluding, and the newly protected beaver exploited this food source so successfully that, by 1920, an ecologist was invited to study the beaver population irruption which was seen as a threat to park aspen. Once the beaver had used up this abundant food source, probably by about 1930, their numbers began to decline. From then on, probably aided by a drying climate that made the plants more vulnerable, elk browsed new aspen growth each year, preventing significant aspen escapement to tree height. Beaver decline coincided with the beginning of the severe drought of the 1930s. It seems likely that beaver, seeking replacement foods once they had exhausted the supply of accessible aspen, may have contributed to the decline of willows that occurred during the 1930s.

Though there is a public perception that beaver have been extirpated from Yellowstone National Park, Consolo Murphy and Tatum (1995) reported that "at least 28 lakes, streams, or stream segments had signs of current beaver activity in 1994." Similar levels of activity were found in a 1988-1989 survey (Consolo Murphy and Hanson 1993). They reported that beaver persist in the park with no apparent risk of disappearance, though these animals exist in very low levels on the northern range. As already mentioned, elk browsing of aspen and willows is regarded as the overriding immediate cause of suppressed willows and aspen in the park (Houston 1982, Kay 1990, Singer et al. 1994). The extent to which this situation, and present beaver numbers, can be considered a departure from some normal or desirable range of conditions, is still open to debate.

In an aerial survey in the autumn of 1996, Smith et al. (1997) found beaver active in at least 49 colonies parkwide, one of which was on the northern range. Consolo Murphy (Natl. Park Serv. pers. commun.) commented that, based on visual observations of animals and upon ground surveys, aerial surveys appear to underestimate beaver living in bank dens along rivers such as the Lamar and Gardner. While beavers were not widely distributed in Yellowstone, they were not rare, and in appropriate habitats they were common; "parkwide beavers are probably not common because there are too many high-gradient streams...and because so much of Yellowstone is dominated by conifers..." (Smith et al. 1997).

RESEARCH RECOMMENDATIONS: BEAVER

Human influences on beaver and their habitats, both before and since the establishment of the park in 1872, have been complex and are not yet adequately understood. Further research could focus on paleontological evidence of beaver; archeological, anthropological, and ethnographic studies of human-beaver interactions in the area, especially prior to the creation of the park; excavation and dendrochronology of old beaver lodges, dams, and other workings; the ecology and populations estimates of present beaver populations; and on continued overall refinement of our understanding of the Yellowstone landscape prior to the creation of the park.

Beaver populations have the ability to significantly influence ecosystems (Naiman et al. 1988); the extent and effect of their habitat alteration deserves further study, especially considering that there is already a considerable body of research on elk, aspen, fire, predators, and the long-term climatic regime available or underway. This should be done not only on the northern range, where beaver exist in very low levels, but in a comparative study area where beaver persist at higher levels, such as the Madison, upper Yellowstone, or Gallatin river drainages.

Also, Yellowstone National Park sits at the headwaters of five major river systems and is generally referred to as a "source" and refugia for wildlife populations. This may not be applicable to beaver, as the headwaters may be the lowest quality beaver habitat; thus, beaver populations in the park may be more highly influenced by external factors than are many other wildlife species. An interesting research question would be to examine the beavers' role in areas more likely to be sources—such as the Hebgen Lake-lower Madison River and Jackson Hole-Snake River areas—and compare their role in these areas with external influences (water diversions, dams, trapping, residential development, sport fishery management) to the role of beaver in the relatively unmanipulated Yellowstone Lake and River system.

The park hopes to continue using aerial surveys following the methods of Smith et al. (1997) every two to three years to develop a solid long-term database to increase our knowledge of beaver occupancy throughout Yellowstone National Park.

PREDATORS

Yellowstone National Park has one of the highest large-mammal prey bases of any large North American wildland ecosystem, and numerous studies have indicated the importance of this prey base for native predators and scavengers (Houston 1982; Knight et al. 1983; Servheen et al. 1986; French and French 1990; Gunther and Renkin 1990; Singer 1990*a*, 1991*b*; Boyce 1991, 1993, 1995*a*; Mattson et al. 1991; Mack and Singer 1992*a*, 1993*a*). To these scientists, a large elk population has generally been perceived as being to the advantage of these predator and scavenger species (Figure 7.13). It has been suggested that overbrowsing of woody vegetation by elk could harm grizzly bears by reducing some preferred habitat types (Chadde and Kay 1991), but no quantification has been provided, and the elk themselves provide more than adequate nutritional compensation to the grizzly bears for any lost habitat qualities caused by elk abundance (Figure 7.14) (Servheen et al. 1986, Mattson et al. 1991).

Figure 7.13. Numerous scavengers quickly consume the carcasses of elk and other ungulates on the northern range. NPS photo.

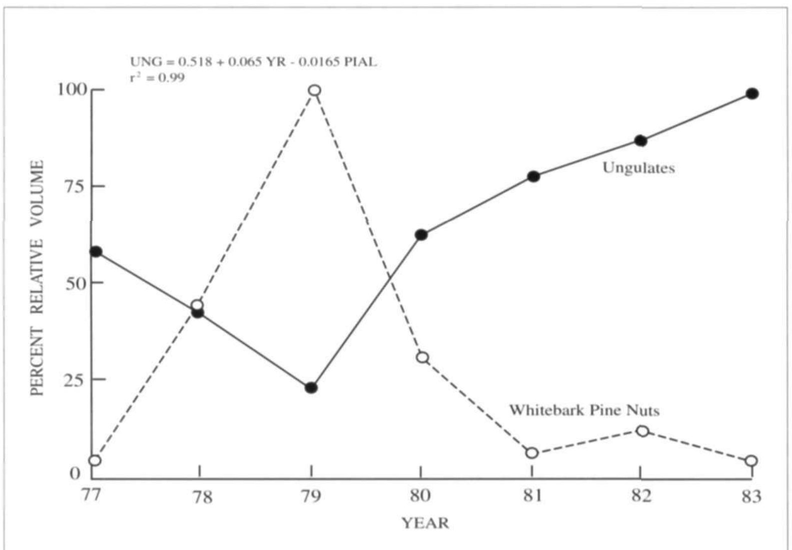


Figure 7.14. Yellowstone grizzly bears are adaptable omnivores, adjusting to the varying supplies of preferred foods. Scat analysis has shown that in years of poor whitebark pine nut crops, bears compensated by increasing their consumption of ungulates. The northern Yellowstone elk herd is an important component of the diet of the threatened grizzly bear. Interagency Grizzly Bear Study Team.

Recent calculations by Singer et al. (1997) suggest each grizzly bear within the calving range of the northern elk herd kills and consumes, on the average, about 15 elk calves per year. Of course, this rate would vary from bear to bear since some animals specialize more in the hunting of elk calves than others, and the rate would also vary from year to year (Singer et al. 1997). Based on close observations of a small number of bears for short time periods, French and French (1990) calculated that some bears killed at least one calf per day, on average, during the four to six weeks each year that calves are vulnerable to bear predation.

With the reintroduction of wolves to the northern range in 1995, the entire northern range ecological and ungulate management issue has entered an important new phase (Phillips and Smith 1996, Schullery 1996). This addition to the suite of predator/scavengers (grizzly and black bears, mountain lions, wolverines, coyotes, foxes, plus numerous bird species) is significant (Figure 7.15). Several writers have pointed out the incompleteness of the natural regulation experiment as long as the full complement of native mammalian predators was not in place (Peek 1980, Houston 1982, Mech 1991). The arrival of the wolf is perhaps the single most important event in the evolution of northern range management since the 1967 Senate hearings that led to the cessation of traditional elk, bison, and pronghorn control.

Prior to wolf reintroduction, North American wolf experts, while expressing a majority opinion about the probable effects of Yellowstone wolves, also had minority views that expressed a wide range of opinion in the probable effects (Vales and Peek 1990, Boyce and Gaillard 1992, Singer 1991, Lyme et al. 1993). All predicted some decline in elk numbers and some predicted declines or increases in other ungulates. Singer (U.S. Geol. Surv., unpubl. data) predicted a decline in coyotes and an increase in foxes, and no effects on grizzly and black bears, mountain lions, and wolverines. They predicted an increase in pronghorns, moose, bighorns, and beaver, and noted that mule deer should be monitored closely. They also concluded that the moderate wolf densities they expect in future, and their effects on the large herbivore populations would not likely result in any significant effects on the northern range's vegetation. In

the end, however, virtually all of these speculators mentioned that the only way to know what the effects of wolves would be is to reintroduce them, wait, and watch.

Figure 7.15. Yellowstone's recently reintroduced wolf packs are relying almost solely on elk as prey. The restoration of wolves has long been seen as essential to testing natural regulation on the northern range. NPS photo.

RESEARCH RECOMMENDATIONS: PREDATORS

Given the already large but growing complement of predators on the northern range, and the relatively slow rate of growth of many predator/scavenger populations, it is possible that some predator populations are still recovering from the combined effects of predator control programs earlier in the century, plus the ungulate herd control practiced through the 1960s. This possibility, plus the recent reintroduction of wolves (while not fully established) seem to warrant further investigations of predator-prey relationships including the complex interactions. In addition, the status of several predators and scavengers, (e.g., wolverines, lynxes, and fishers), remains virtually unknown in our knowledge and are deserving of study (S. Consolo Murphy and M. Meagher, Natl. Park Serv. and U.S. Geol. Surv, unpubl. data).

CONCLUSIONS

Wildlife management policy and practice have undergone almost continuous evolution in Yellowstone National Park (Haines 1977, Houston 1982, Schullery 1992, Wright 1992). Following the initial decade of uncontrolled wildlife slaughter, civilian and military administrators adopted intensive husbandry practices, including protection, culling, the killing of predators, winter feeding of ungulates, and semi-domestication or other manipulation of a variety of species. A gradual shift away from human intervention in the ecological setting led to a less intrusive approach, governed by policies protecting native species and the ecological processes generated by the interaction of all elements of the landscape.

There has been an additional shift in the past 30 years, from viewing park landscapes as "primitive vignettes," (Leopold et al. 1963) being managed to preserve settings as they were when first encountered by whites, to viewing parks as places where ecological processes (indeed, all processes, whether geological, hydrothermal, or other) function as unhindered as possible by humankind. The national park has evolved, then, from its original goal of conserving distinct wonders (in Yellowstone's case, these were originally geological: geysers, lakes, canyons, waterfalls, and other scenery), to preserving distinct wonders and favored wildlife species, to preserving all wildlife species, to preserving the

complex set of processes that drive a wild ecosystem and shape its various components.

Numerous commentators have considered the challenges of managing for ecological processes in the national parks (Darling and Eichhorn 1969; Cole 1971; Houston 1971, 1982; Chase 1986; Despain et al. 1986; Schullery 1989*c*; Rolston 1990; Kay 1990; Boyce 1991; Whitlock et al. 1991; Wright 1992; Christensen 1994; Wagner et al. 1995*a*; McNaughton 1996*a*, *b*). The policy statements that guide management are typically generalized enough that they are susceptible to countless rhetorical exercises, depending upon the interpretation each reader chooses to give them. Some observers have very sharply criticized natural regulation and National Park Service policies, most often for a perceived lack of definition or direction. Wagner et al. (1995*a*), for example, regarded the goal of achieving "naturalness" or replicating the ecological setting of some past time as "both unknowable and unattainable." This seems surprising considering that Wagner et al. and others (Kay 1995*a*) display extraordinary confidence in their ability to know how the prehistoric practices of the first Americans affected Yellowstone wildlife. Wagner et al. (1995*a*) insisted that "if the parks are to have seriously attainable, wildlife-management goals, they will have to be more realistic and less idealistic." They proposed, among other things, "management protocols" and a "menu of parameters" that would give managers a clear idea of when the ecological setting was misbehaving.

On the other hand, all such prescriptions that have yet been proposed for making the goal "more realistic and less idealistic" are in fact *pro*scriptions, that, by outlawing variation beyond some precisely defined point, pass judgment on what an ecosystem is or is not allowed to do. Considering the frequency with which these proscriptions are published, it is easy to propose such criteria, but has so far proven impossible to justify any of them to the satisfaction of science or the park's management professions.

On the other hand, other observers have found "ecological process management" a satisfactory or at least promising approach (Boyce 1991). Boyce (1991), in discussing the entire greater Yellowstone ecosystem, maintained that "although humans have altered the ecology of the GYE, the ecosystem is nevertheless functioning and worthy of perpetuation." He then elaborated on the challenge facing present and future researchers here, not only in Yellowstone National Park and throughout the greater Yellowstone ecosystem:

> At some level, all environments in the world have been affected by human development and agriculture. But it is not always clear that these influences are great enough to require management intervention. Although ecologists tend to emphasize the interconnectedness of nature, perturbations at one link in the ecosystem do not necessarily cascade into all its dimensions. The issue is one of embeddedness, that is, how complexly a species is embedded within the ecosystem. In greater Yellowstone there has been little research on this issue. Thus in many cases we unfortunately have no concrete basis for establishing ecosystem management policy.
>
> Indeed, the conviction of the National Parks and Conservation Association (Gordon et al. 1989) is that the National Park Service does not understand well enough the resources it seeks to manage. Future management must depend on our developing research programs to ensure that we understand, as well as possible, the complex GYE ecosystem.
> Until we do, however, we should not interfere with its function while doing whatever we can to ensure that ecosystem components remain intact (Boyce 1991).

As Yellowstone's northern range has repeatedly demonstrated over the past 120 years, landscapes are full of surprises, and ecology is an especially imperfect science. It has taken several generations of research to reveal the many flaws in earlier interpretations of the range's condition. Considering the well-intended but overconfident

efforts of previous generations of northern range observers and managers to control the northern range's behavior, recent proposals for how to "fix" or "control" the range seem almost embarrassingly naive. Thus, Boyce's recommendations for research programs, and his admonition to keep interference to a minimum, seem especially well-aimed at the northern range and its management issues. Indeed, there is a direct link between research and a range whose ecological processes are as little manipulated by humans as possible. Were it not for a natural regulation policy that gave ecological processes such free range over the past 30 years, research would have had far less opportunity to examine the true ecological character of the northern range.

That said, the formulators of the original natural regulation policy 30 years ago would have benefitted much from the recent research initiative. Hindsight allows us to recognize shortcomings in their approach. Recent research in other areas shows that they may have underestimated the potential effects that predators may have on ungulates. Gasaway et al. (1992) and others showed that predators can hold some ungulate populations at less than one half of ecological carrying capacity. Working with equilibrium models available at the time, the formulators of natural regulation policy may have predicted too much of a steady state in northern range ecological processes. The recent discovery that aspen recruit only episodically on the northern range is a strong indication of the great variability of this system. Furthermore, natural regulation's formulators could not have foreseen the public acquisition of thousands of acres of additional winter range north of the park in the 1980s, and thus could not have predicted the tremendous recolonization of that range by elk, and attempted recolonization of it by bison.

Much has been learned in the past 30 years about natural regulation and the very real limitations such a policy must face in a multijurisdictional situation like the northern range. No doubt much more will be learned in the next 30 years. It therefore seems appropriate that the management model devised in the early 1970s be periodically revisited. It is time for the managers of Yellowstone, in cooperation with the scientific community, to restate the management model in accord with current knowledge. As ecological understanding advances, so must ecological process management.

If the northern range has one overriding lesson to offer, it may be this: each generation of Yellowstone's caretakers (including managers, scientists, and advocacy groups) has assumed that they knew enough about this ecosystem to manage it aggressively and intensively, and each generation was viewed by the next generation as having gotten it wrong. Many position-holders in today's debates over the northern range have adopted this same confident position. This is not to say we lack faith in the science of the northern range. Quite to the contrary, it is the science of the last 35 years that has led us to where we are today. Science has given us a sound theoretical basis and a solid empirical foundation for the park's current management direction.

In the past three decades most of the foundation concepts and certainties held by earlier generations have been reconsidered, revised, or entirely rejected. Many longstanding interpretations of soil erosion, grassland condition, aspen/willow history, elk carrying capacity, effects of predators, and many other topics are now regarded as uninformed, naive, or simply wrong. The rate of conceptual change has also accelerated; new interpretations and hypotheses are challenged and reconsidered in the space of only a few years. Thus, while the current generation of scientists and managers is wealthy with knowledge compared to the previous ones, we must assume that the next generation will know much more.

It seems therefore shortsighted to suggest that National Park Service management of the northern range should be less idealistic. In fact, there is a great deal to be said for honoring the idealism that seems to make critics of the current management policy so nervous. This hardly seems the time to abandon a very promising idealism in favor of yet another recipe-book, intrusive, and manipulative approach to management. The northern range's ecological processes are making

practically all of the decisions that determine the condition, trend, and fate of the plant and animal communities. To attempt to replace that native decision-making process with the value-judgment-driven opinions of any alternative position in the northern range debates—that is, to once again try as our predecessors did to overrule a system that has 10,000 years' experience at managing itself—would be to announce that we haven't learned a great deal from our own history.

On the other hand, commitment to the ideal of a naturally regulated northern range does not mean that future management of the northern range cannot be practical. Indeed, the growing understanding of the complexity of the northern range, and of the compromises already made with its "purity" as a native grazing system, have led some observers to: 1) accept the imperfections of the present arrangement (acknowledging that there is no perfect restoration of prehistoric systems); and 2) suspect that the existing ecological processes are quite able to sustain the system in a productive and educational way (Macnab 1983, Rolston 1990, Boyce 1991). These latter observers are in effect saying that this ecosystem may not be perfect, but it shows every sign of functional integrity, so rather than wring our hands over possible flaws or tinker without sufficient cause, let's get on with it, learn from it, and see how it goes.

This is not a recommendation to avoid intervention on the northern range at all costs. Such intervention, whether to restore wolves or fight fire or not fight fire or suppress exotic plant invasions, or poison exotic fish and restore native fish, or cull bison, in fact, occurs on a routine basis. National Park Service policy and a shelf of legislation require managers to intervene in national park settings for many reasons, including the protection of endangered species, the restoration of exterminated species, and so on.

The challenge for the manager, then, is to pay aggressive attention to the changes and consequences of the ecological processes while resisting the temptation to overmanage by stepping in too soon to "fix" a situation that is always more complex than it at first appears. The national parks provide their ecological settings with the opportunity to exercise a variability and freedom somewhat akin (though probably never identical) to their prehistoric states. Given this freedom, all the operative factors in landscape evolution, including climate, earthquakes, volcanism, erosion, predation, herbivory, fire, and many others, interact and provide many opportunities for enrichment of human knowledge and for human appreciation of a wildland setting.

This, as was stated earlier, is a difficult and complex undertaking on the northern range, because so many North American grassland communities have been altered extensively by contemporary human uses, especially those associated with agriculture and livestock grazing, that we are without local comparisons (and have only a few such comparisons available globally) by which to judge how the range is doing. The disciplines associated with wildland ecology have taught us a rather shocking fact: there are relatively few places left where we can even see a setting that is relatively undisturbed, operating as it did in prehistoric times, with its native complement of predators, scavengers, grazers and plant species (Frank 1990). It is also difficult because the human activities of the ancient past have been replaced by remarkably dissimilar human activities of the industrial present.

Despite a well-catalogued list of imperfections or changes from its pre-establishment condition, Yellowstone National Park has been identified by scholars as one of the best remaining opportunities to examine wildland ecological processes on a large scale (Houston 1971, Frank 1990, McNaughton 1996*a*, Soulé 1996). The research summarized in this book amounts to the broadest, most comprehensive examination of an ecological issue in any North American national park, and it provides ample evidence that there is no urgent need to intervene on any large scale on the northern range at this time. In fact, there appear to be excellent reasons for not intervening, the best of which includes the opportunities that the northern range provides us for learning about wildland ecosystems.

In summary, current understanding of the northern range is based on the following general

observations.

1. The current herbivore-carnivore wildlife community of the northern range has inhabited that range for thousands of years. It is not possible with current data to compare the relative abundance of these animals at any prehistoric date with today, but changing environmental conditions demonstrate that northern range wildlife and vegetation communities were always dynamic rather than static; it is neither desirable nor possible nor appropriate to set any single historic or prehistoric date as the "appropriate" scenario by which to judge today's northern range.

2. Longstanding geological and climatic processes, not ungulates, have been the primary factor in erosion on the major river drainages of the northern range, and on associated summer ranges, in Yellowstone National Park. Sediments in park rivers are within the normal range observed in western streams, and ecological conditions, including the quality of sport fisheries, are as good or better than found in most western streams. Additional research is necessary to clarify the roles of ungulates and other species in riparian zone and stream-bed and bank erosion.

3. Northern range grasslands are not deteriorating. They are highly productive. The variability in grasslands observed from year to year appears to be primarily influenced by climate. The conversion of forests to grasses caused by the fires of 1988 increased the ecological carrying capacity of elk and bison by about 20 percent. Ungulates are an important element in nutrient cycling and plant production in the perpetuation of the grasslands. Native ungulate grazing of these grassland communities preserves native plant species diversity when compared to ungrazed experimental plots.

4. Northern range willow communities have declined from their size and extent in the 1890s in the mid- and low-elevation portions of the winter range and little new recruitment is evident. This decline occurred primarily in the 1920-1940 period during severe drought, and no significant additional decline has occurred since 1959, despite the cessation of elk control in the late 1960s and a resultant 400 percent increase in elk numbers. Willows continue to successfully replace themselves on the upper elevation one-third of the winter range. Thus, we estimate a continued slow decline in willow communities on the northern range until such time as the climate becomes cooler and wetter, possibly in conjunction with lower elk densities. While willow communities prehistorically have never constituted a large component of Yellowstone, large fluctuations in their abundance occurred in the distant past and can be expected in the future. Northern range willow communities as they existed a century ago constituted less than 1 percent of willow communities in Yellowstone National Park. Robust tall willow communities persist and thrive in many locations in the park above about 7,000 feet or where annual precipitation is above 20 inches per year.

5. Aspen has been a comparatively minor plant community on the northern range for thousands of years, but provides important habitat for some vertebrate and invertebrate species. Contrary to popular perception, aspen did not continuously thrive on the northern range prior to the establishment of the park in 1872. Since about 1800, the only period of major growth of aspen trees was between about 1870 and 1890. During at least the 50 years prior to that period, some combination of factors, probably including ungulate browsing and fire, apparently suppressed aspen. Some combination of factors then allowed aspen to overcome browsing during the period 1870-1895. The fires of 1988 showed that large fires alone are not sufficient to enable aspen to overcome browsing on winter ranges, at least under the current warmer and drier climate conditions and high densities of elk. Aspen continue to do well in the park, and in other parts of the greater Yellowstone, on ungulate summer ranges and in those areas that are unusually wet due to surface groundwater discharge, where annual precipitation is more than 25 inches per year.

6. Current numbers of elk and bison on the northern range do not appear to be negatively affecting the numbers of other ungulate species with the potential exception of moose. Under the current climate regime, seven species of the hundreds of native plants on the winter range

appear suppressed by high densities of elk. Where competition is suspected or proven between ungulate species, it does not seem outside the realm of normal sharing of a common range, and does not seem to threaten the survival of any species. The elk and bison are a crucial source of nutrition for numerous predators and scavengers, including federally listed rare species such as grizzly bears, wolves, and bald eagles, all protected under the Endangered Species Act.

7. Despite more than 60 years of dire predictions of overgrazing and imminent disaster, the northern range continues to produce large, healthy ungulate herds year after year in harmony with a productive range. The northern range elk herd is regulated by a variety of natural and modern human forces, including predation by a full suite of native animals and variations in climate. Hunting by humans north of the park may have also influenced both the population's dynamics (age and sex ratio, population numbers), and certainly its migratory and diurnal behavior. Since intensive scientific study began on the northern herd in the 1960s, the herd has shown several strong density-dependent, or naturally regulating responses.

8. Large ungulate herds and intensive grazing on the northern range do not appear to be negatively affecting native species biodiversity. The evidence indicates the number of grass, forb and shrub species on the northern range was the same in grazed and ungrazed sampling plots. Community plant diversity on the northern range, however, may have experienced a slow decline in the past century due to the decline in aspen and willow stands, but this is somewhat unclear due to the greater native species diversity outside of exclosures versus inside exclosures. While some species of native vertebrates (e.g., tall willow-obligate breeding birds) are selected against on the northern range, there are appropriate similar habitats available in other parts of the park and the ecosystem, and there are other vertebrate species that are favored in short willow and other riparian habitats. Native invertebrate diversity appears to be enhanced by the high levels of ungulates.

9. Yellowstone's northern range, one of the few places remaining in the world with all of its "component parts and processes," continues to provide ecologists with one of the world's most exciting and challenging "natural laboratories" for studying the complexities of landscape ecology, and clearly has much more to teach us about the processes that shape wildlands and native grazing systems.

10. The northern Yellowstone elk herd has long had great social value, as demonstrated by consistently high public interest in northern range controversies. These elk have intrinsic value as part of the Yellowstone experience, for visitors from around the world. With the cessation of artificial population control on the northern herd, this herd has also taken on great regional economic value as the basis of one of North America's premier recreational hunts and wildlife viewing attractions. Communities near the park have experienced significant economic gains because of recreational interest in the northern herd, and the negative economic impacts on those communities must be considered in any deliberations over future artificial manipulation of this elk herd.

11. In the past, the National Park Service and others have referred to the natural regulation policy on the northern range as an "experiment." In the strict sense of the scientific method it is not because it has no scientific controls and no replication. It is instead, a management model in the sense of Walters' (1986) and Macnab's (1983) "adaptive management" of renewable resources, where the management model is updated or revised on a periodic basis as new information is obtained. Such an update is warranted now in light of the enormous amount of information becoming available as a result of the recent research initiative.

ACKNOWLEDGMENTS

The text was written by Norm Bishop (NPS, Yellowstone), Paul Schullery (NPS, Yellowstone), Francis Singer [U.S. Geol. Surv.—Biol. Res. Div. (BRD)], Fort Collins, Colorado, and John Varley (NPS, Yellowstone). The manuscript was reviewed by Mark Boyce (Univ. of Wisconsin, Stevens Point), Wayne Brewster (NPS, Yellowstone), Don Despain (BRD), Bozeman, Montana), Doug Frank (Syracuse University), Doug Houston (BRD), (Olympic National Park), Sue Consolo Murphy (NPS, Yellowstone), Dan Huff (NPS, Denver), William Romme (Fort Lewis Coll., Colorado). Additional technical assistance was provided by Irving Friedman (U.S. Geol. Surv.—Geol. Res. Div., emeritus, Denver), John Mack (NPS, Yellowstone) and Jennifer Whipple (NPS, Yellowstone). Assistance with figure research was provided by Susan Kraft and Vanessa Christopher (NPS, Yellowstone).

This book was produced by the Yellowstone Center for Resources, Yellowstone National Park. Copyediting and proofreading was by Sarah Broadbent, Sue Consolo Murphy, and Renée Evanoff, with text styles by Sarah Broadbent. Tables and figures were adapted or created by Sarah Broadbent, Lori Compas, Sue Consolo Murphy, Renée Evanoff, Linda Phillips, and John Varley. Maps created by the Yellowstone Spatial Analysis Center, Sarah Broadbent, and Renée Evanoff. The ornamental figures and sketches throughout the book by Renée Evanoff.

We express our deep appreciation to Canon USA Inc., who generously donated the costs of printing this document through their "Expedition into Yellowstone" program.

Appendix A. Conferences, Meetings, and Workshops Relating to the Northern Range

Meetings, workshops, sessions, and conferences held relating to northern range research since Congressionally funded research initiative began in 1986.

First annual meeting of research and monitoring on Yellowstone's northern range, January 28-29, 1988, Mammoth Hot Springs, Yellowstone National Park (abstracts bound and distributed).

Second annual meeting of research and monitoring on Yellowstone's northern range, March 22-23, 1989, Mammoth Hot Springs, Yellowstone National Park (abstracts bound and distributed).

Yellowstone riparian work group, meeting, spring, 1989 (final report submitted to Yellowstone Superintendent Robert Barbee, July 9, 1990).

Third annual meeting, research and monitoring on Yellowstone's northern range, April 5-7, 1990, Mammoth Hot Springs, Yellowstone National Park (abstracts bound and distributed).

Riparian investigation meeting, February 19, 1991, Mammoth Hot Springs, Yellowstone National Park (report produced with recommendations).

Plants and their environments: the first biennial scientific conference on the Greater Yellowstone Ecosystem, September 16-17, 1991, Mammoth Hot Springs, Yellowstone National Park (proceedings published, April 1994).

The ecological implications of fire in Greater Yellowstone: second biennial scientific conference on the Greater Yellowstone Ecosystem, September 19-21, 1993, Mammoth Hot Springs, Yellowstone National Park (proceedings published, 1996).

Greater Yellowstone predators: ecology and conservation in a changing landscape, third biennial scientific conference on the Greater Yellowstone Ecosystem, September 24-27, 1995, Mammoth Hot Springs, Yellowstone National Park (abstracts published and distributed at conference, proceedings (Northern Rockies Conservation Cooperative, publisher) in press, and book of invited papers in preparation).

Ecological Society of America, Wildlife management in the U.S. National Park system: the self-regulation theory revisited, August 13, 1996, Providence, Rhode Island (papers submitted for future ESA publication).

Appendix B. Ungulate Counts and Estimates

Estimates of elk numbers in Yellowstone, 1890-1920. Detailed treatment of each is given in Houston 1982.

Year	Estimate	Comment	Source
1890	2,000-3,000	"in the neighborhood of Soda Butte last winter."	Supt. Boutelle.
1891	25,000	Houston indicates this is a *summer* estimate for multiple herds throughout the park.	Supt. Anderson
1892	25,000	Also believed a summer estimate.. "The very severe winter was hard on them, and I judge that from 2,000-5,000 perished."	Supt. Anderson
1893		"In winter...That there are several thousand elk in the Park and adjoining country is quite certain..."	Geologist Hague
1894		"A party sent out to Yancey's to investigate.. in March saw at least 3,000 if them at one time from a single point of view."	Acting Supt. Anderson
1895		"The elk have quite held their own or increased their numbers..."	Acting Supt. Anderson
1896		"During the spring months the elk are found in their several winter ranges in herds of thousands."	Acting Supt. Anderson
1897		"I believe that more than 5,000 winter in the park, and that at least 15,000 leave the park in autumn to winter in the lower country... Of those that winter in the park, the largest herd ranges north of the Yellowstone River..."	Cavalry Lt. Lindsley *in* Young 1897
1898		"Elk—Numerous, and are increasing...Immense herds can be seen in nearly any direction in winter..."	Acting Supt. Erwin
1899	35,000-60,000	Apparently a parkwide summer estimate. "Some of the scouts...estimate that as many as 5,000 died during the past winter."	Acting Supt. Brown
1900		"I have the assurance of the scouts, who have seen the game at all seasons, that, with the exception of the bison..all varieties, including..elk..are increasing..."	Acting Supt. Goode
1901		"The elk are very numerous, but unless something is done to prevent the encroachment of settlers on their winter range south of the park and the slaughter of them...it is possible they will soon be reduced to the number that can live entirely within the...park and this number I believe to be about 25,000."	Acting Supt. Pitcher
1907	25,000	"Seems to be a safe estimate."	Supt. Young
1908	25,000-30,000	"They seem to do fairly well in the ordinary winter but when the snow falls to an unusual depth—say one winter in four—many perish."	Supt. Young
1909	30,000-40,000	Apparently a parkwide summer estimate.	Supt. Benson
1910	30,000-40,000	Apparently a parkwide summer estimate. "Many of these elk wander out of the park into the adjoining states and a few of them are there killed during the hunting season."	Supt. Benson
1911		"Elk in certain portions of the park are very numerous, and are numbered by thousands both in winter and summer."	Supt. Brett
1912	30,101	Houston reports that this and the following two censuses apparently included elk wintering along the Gallatin and Madison rivers and their tributaries. Review of methods and procedures cast serious doubt on their accuracy. "During last April an approximate census was taken...along the northern border of the park. Twenty-seven thousand eight hundred and one animals were counted inside the park and 2,300 were observed outside and therefore belonging to the same herd..."	Supt. Brett

Year	Estimate	Comment	Source
1913	32,967	"A census of elk in and along the north line of the park was taken between April 9 and May 1...The elk were in excellent condition all winter, and but few dead ones were found..."	Supt. Brett
1914	35,209	"A census was made again of the elk, comprising the northern herd in the park, between April 11 and May 2..."	Supt. Brett
1915	27,800	Quoting Supt. YNP for winter herd in Lamar and Yellowstone River Valleys. "At best these estimates are inaccurate and in many cases it is impossible to tell just how many belong to one herd or if the animals are included in estimates of different herds."	Simpson and Bailey, U.S. Forest Service and U.S. Biological Survey
	37,192	Estimated total. "The weather was so mild and there was so little snow in March and April that the elk went up to higher ground earlier than usual, and it was impractical to take an accurate census of them."	Supt. Brett
1916	11,515-11,564	The former reported as a count including elk in the Madison, Gallatin, and Yellowstone River valleys; the latter was an estimate for the total herd. Additional reports of censuses exist in 1916 and contribute to controversy discussed in depth by Houston.	Bailey, and U.S. Forest Service and U.S. Biological Surv. unpubl. rept.
1917	10,769-17,422	The former reported as a census occurring between May 26 and June 9; the latter estimate comes from adding nearly 7,000 elk not seen.	Supt. Lindsley and Gallatin NF Supv. Nelson rept.
		"The northern group comprises slightly more than 19,000, the number having been determined by actual count conducted in the spring of 1917..."	Graves and Nelson
1918	20,700	"Game animals were reported during the month [of January] as follows" (Numbers approximate)..."	Supt. Lindsley
1919	18,694	"In connection with their patrols, the rangers in the most important districts during March made a count of the elk. The total...not including those in Gallatin and Riverside districts nor those now ranging outside of the park, amounted to 18,694."	Acting Supt. Hill
1920	No census	Houston discusses in detail "the epitome of confusion [that] occurred during the winter of 1919-1920", which resulted in many "patently incorrect" reports of a disastrous winter and population crash.	Numerous, cited in Houston

Elk counts, population estimates, and numbers of animals removed by hunting and/or management reduction programs, 1922-1996. (Data for 1922-1976 is from Houston 1982; data for 1975-1996 from T. Lemke et al., Montana Dept. Fish, Wildlife and Parks, unpubl. data.)

Year	Date	Actual Count	Estimated Population[a]	# of Elk Removed	Comments
1922-23				82	
1923-24				55	
1924-25				425	
1925-26				168	
1926-27				826	
1927-28				1,716	
1928-29				15	
1929-30		8,257		422	
1930-31		7,696		318	Considered to be a very poor census.
1931-32		10,624		327	
1932-33		11,521		179	
1933-34		10,042		147	
1934-35		10,112		3,265	Combined ground and aerial counts; other census data are ground counts unless otherwise indicated.
1935-36		10,281		2,844	
1936-37		8,794		831	
1937-38		10,976		3,823	
1938-39				3,278	
1939-40				138	
1940-41				287	
1941-42				2,216	
1942-43		8,235		7,230	
1943-44				135	
1944-45				403	
1945-46		8,513		2,167	
1946-47				3,145	
1947-48		7,815		1,009	
1948-49		9,496		2,286	
1949-50				874	
1950-51				2,083	
1951-52				3,800	
1952-53				282	
1953-54				809	
1954-55				1,361	
1955-56		6,963		6,535	Helicopter count.
1956-57				1,289	
1957-58				586	
1958-59		4,884		1,706	Considered to be a very poor census; done by fixed-wing aircraft.
1959-60				859	
1960-61		8,150		1,459	Done by helicopter and fixed-wing aircraft.
1961-62		5,725		4,744	Helicopter count.

Year	Date	Actual Count	Estimated Population[a]	# of Elk Removed	Comments
1962-63				1,820	
1963-64				1,151	
1964-65		4,865		1,904	Helicopter count.
1965-66				1,270	
1966-67		3,842		2,648	Helicopter count.
1967-68		3,172		1,100	Done by fixed-wing aircraft. Elk reductions stopped.
1968-69		4,305		50	Done by fixed-wing aircraft.
1969-70		5,543[b]		50	Done by fixed-wing aircraft.;
1970-71		7,281		45	Helicopter count.
1971-72		8,215		75	Helicopter count.
1972-73		9,981		154	Helicopter count.
1973-74		10,529		210	Helicopter count.
1974-75		12,607		147	Helicopter count.
1975-76	12/17-18/75	12,014	12,354	1,529	Beginning of late-season elk hunts.
1976-77	1/23-24/77	8,980	9,199	219	Survey conditions exceptionally poor resulting in inaccurate count.
1977-78	12/20-21/77	12,680	12,941	1,067	
1978-79	12/29-30/78	10,838	11,149	341	
1979-80		No count		661	
1980-81		No count		376	
1981-82	1/6-7/82	16,019	16,473	1,359	
1982-83		No count		1,881	
1983-84		No count		2,061	
1984-85		No count		1,571	
1985-86	12/19-20/85	16,286	16,885	1,498	
1986-87	12/10/86	17,007	17,901	1,739	
1987-88	1/19/88	18,913	19,316	579	
1988-89	1/26;2/9/89	10,265	11,148	2,896	
1989-90	1/18-19/90	14,829	15,805	1,299	
1990-91	2/6/91	9,456	10,287	1,005	Survey conditions exceptionally poor resulting in inaccurate count.
1991-92	12/16/92	12,859	15,587	4,515	
1992-93	11/21;12/3/92	17,585	18,066	2,055	
1993-94	1/20-24/94	19,045	19,359	527	
1994-95	12/21/94	16,791	17,290	2,538	
1995-96		No count			
1996-97		No count			Limited aircraft availability and poor flying conditions resulted in no count.

[a] Minimum fall population estimate = maximum survey count + estimated fall harvest + late hunt removals that occurred prior to survey date, if any.

[b] Maximum counts obtained in December or January from 1970 to 1979.

Bison winter numbers, 1901-1997.

Winter	Total Count
1901-02	44
1902-03	47
1903-04	51
1904-05	74
1905-06	
1906-07	84
1907-08	95
1908-09	118
1909-10	149
1910-11	168
1911-12	192
1912-13	215
1913-14	
1914-15	270
1915-16	348
1916-17	397
1917-18	
1918-19	504
1919-20	501
1920-21	602
1921-22	647
1922-23	748
1923-24	
1924-25	830
1925-26	931
1926-27	1008
1927-28	1057
1928-29	1109
1929-30	1124
1930-31	1192
1931-32	
1932-33	
1933-34	

Winter	Total Count
1934-35	
1935-36	847
1936-37	674
1937-38	755
1938-39	811
1939-40	868
1940-41	809
1941-42	869
1942-43	964
1943-44	747
1944-45	932
1945-46	791
1946-47	
1947-48	960
1948-49	1126
1949-50	1094
1950-51	
1951-52	976
1952-53	
1953-54	1477
1954-55	
1955-56	1258
1956-57	543
1957-58	
1958-59	
1959-60	
1960-61	869
1961-62	
1962-63	
1963-64	
1964-65	
1965-66	388
1966-67	226

Winter	Total Count
1967-68	397
1968-69	418
1969-70	556*
1970-71	592*
1971-72	565
1972-73	713
1973-74	837
1974-75	873
1975-76	1068
1976-77	1125
1977-78	1252
1978-79	1626
1979-80	1727
1980-81	1803
1981-82	2396
1982-83	2239
1983-84	2160
1984-85	2229
1985-86	2456
1986-87	2470
1987-88	2861
1988-89	3159
1989-90	2606
1990-91	3178
1991-92	3426
1992-93	3304
1993-94	3551
1994-95	3956
1995-96	3600
1996-97	3400

Data source 1901-1969, Meager 1973, numbers are total actual count; 1970-1997, M. Meagher, U.S. Geol. Surv., unpubl. data, numbers are total early winter counts, * are total mid-winter counts.

Counts and estimates of moose in Yellowstone National Park, 1912-1970.

Year	Date of Count	Parkwide count[a]	Parkwide estimate	Comments from source	Data source[b]
1912	Summer		550	Estimate by Scout McBride.	1
1920			500 800		2
1923				"Moose are scattered in nearly every section of the park."	3
1924	Winter	121	385	Reported from all sections of the park.	3
1925	Winter 170	170	525	"Moose are widely distributed. No losses reported during the year."	3
1926	Winter	103	575	"Number not considered to represent a decline from previous year. Conditions were not as favorable for making a count as the previous 2 years. Four lost to natural causes during the year. Six unlawfully killed by Idaho hunters near the park boundary."	3
1927	Nov.	73	600	"Although there has been an apparent decrease the past 2 years, total in the park are believed to have increased moderately. Moose conditions in the park are excellent. Losses during the year: natural causes-1, accident-1; legal kill-25, illegal kill-13 near park boundary in bordering states."	3
1928	Summer	111	650	"Roadside counts. Known losses: legal kill-11; illegal kill-2 near park boundary in bordering states, winter kill-1. Moose conditions are excellent."	3
1929			675		4
1930	Feb.	198	700	"Population is increasing."	4
1931	Apr.	54	700	"Counting conditions and accuracy were low. Nine illegal kills."	5
1932	Jan.	90	700	"Counts were much better than last year."	6
1933		71	700	"A thorough count wasn't made. It is safe to assume the number is the same as last year."	7
1934			700	"Increasing. No winter losses."	7
1935		100	700	"Steadily increasing."	7
1936		270	702		8
1937			700	"Counts and estimates include summer observations. Moose are thought to be increasing."	9
1938			700	Status unchanged.	10
1939			700	Status unchanged.	11
1940			700		12
1941			700	Status unchanged.	13
1944			700	Status unchanged.	7
1945			600	During the summer of 1945 rangers made intensive observations. Figure given represents the total of their counts and estimates. Status unchanged from previous years. Estimate is based on more recent field work.	14
1946			600		15
1947			600		16
1949			600		17
1950			400	Estimate is based on continued observations by park rangers during the summer of 1950.	7
1951			400	Fall estimate. No important change in status.	18
1953			Common	Status unchanged.	7

Year	Date of Count	Parkwide count[a]	Parkwide estimate	Comments from source	Data source[b]
1955				Trend counts = 63.	7
1956			Common	Trend counts = 73; 3 were incidentally counted on a March 20-22 helicopter census of the Northern Yellowstone elk herd. Insufficient time to count moose as accurately as elk.	19
1958			Common	Trend counts = 54.	20
1961				Five were incidentally counted on a March 20-26 helicopter census of the North Yellowstone elk herd.	21
1962			400	Ten were incidentally counted on an April 3-4 helicopter census of the North Yellowstone elk herd.	22
1963			400		23
1964			450		24
1965			450	Sixteen were incidentally counted on a April 6-9 helicopter census of the North Yellowstone elk herd.	25
1966			450		26
1967			450	Sixteen were incidentally counted during a March 27-28 helicopter census of the Northern Yellowstone elk herd. Eleven were counted during a January 12-18 Piper Supercub survey of elk distribution on the Northern Yellowstone winter range.	27
1968			450	Counts during 3 Piper Supercub surveys of elk distribution on the Northern Yellowstone winter range between February 29 and June 14 were: 6, 8, 25.	28
1969			450	Counts during 9 Piper Supercub surveys of elk distribution on the North Yellowstone winter range between November 14, 1968 and May 28, 1969 were: 10, 24, 8, 10, 3, 6, 6, 23, 25.	29
1970			450	Counts during 8 Piper Supercub surveys of elk distribution on the North Yellowstone winter range were: 2, 23, 13, 12, 8, 5, 18, 20.	30

[a] Ground counts unless otherwise specified.

[b] DATA SOURCES: (1) Acting Superintendent, 1912; (2) Denniston, 1956; Superintendent's Annual Report, 1920; (3) Superintendent's Annual Reports for the respective years; (4) Baggley, n.d.; (5) Baggley, 1931; (6) Edwards, 1932; (7) Anonymous for the respective years; (8) Barrows, 1936; (9) Barrows, 1937a; (10) Barrows, 1938a, (11) Barrows, 1939a; (12) Skinner, 1940; (13) Skinner, 1941b; (14) Anonymous, 1945a; (15) Rogers, 1946; (16) Kittams, 1947; (17) Anonymous, 1949a; (18) Evans, 1951; (19) Kittams, 1956; (20) Kittams, 1958a; (21) Kittams, 1961a; (22) Howe, 1962a,b; (23) Howe, 1963b; (24) Howe, 1964; (25) Howe, 1965a,c; (26) Barmore, 1966; (27) Barmore. 1980; Barmore, 1967b; (28) Barmore, 1980; Barmore, 1968a; (29) Barmore, 1980; Bucknall, 1969; (30) Barmore, 1980; Bucknall, 1970.

Counts of moose observed by aerial flights, northern Yellowstone winter range, 1968-1996. (Data from Barmore, Houston, and Tyers *in* Tyers 1995[a].)

Year	Date	Moose Counted	Comment
1968-69		37	Areas observed were: Lamar Valley, Upper and Lower Slough Creek, Tower, Blacktail Plateau, Gardner's Hole, Gardner River/Mt. Everts, and Below Mammoth.
1969-70		41	"
1970-71		52	"
1971-72		100	"
1972-73		52	"
1973-74		75	"
1974-75		33	"
1975-76		50	"
1976-77		38	"
1977-78		38	"
1978-86			No counts attempted.
1985-86		4	Only moose recorded were in Upper Slough Creek.
1986-87		14	"
1987-88		28	"
1988-89	December 6,8, 1988	55	Areas surveyed were: Gardner's Hole, Blacktail Plateau, Soda Butte, Slough Creek, Buffalo Fork, Hellroaring, and Bear Creek.
1989	May 18, 1989	47	Areas surveyed were: Gardner's Hole, Blacktail Plateau, Soda Butte, Slough Creek, Buffalo Fork, and Hellroaring. Bear Creek was not surveyed.
1989-90	November 30, 1989	59	Areas surveyed were: Soda Butte, Slough Creek, Buffalo Fork, Hellroaring, and Bear Creek. Gardner's Hole and Blacktail Plateau were not surveyed.
1990	May 2, 1990	25	Areas surveyed were: Soda Butte, Slough Creek, Buffalo Fork, Hellroaring, and Bear Creek. Gardner's Hole and Blacktail Plateau were not surveyed.
1990-91	December 12, 1990	24	Areas surveyed were: Gardner's Hole, Blacktail Plateau, Soda Butte, Slough Creek, Buffalo Fork, Hellroaring, and Bear Creek.
1991	May 17, 1991	19	Areas surveyed were: Gardner's Hole, Blacktail Plateau, Soda Butte, Slough Creek, Buffalo Fork, Hellroaring, and Bear Creek.
1992	May 7, 1992	13	Areas surveyed were: Gardner's Hole, Blacktail Plateau, Soda Butte, Slough Creek, Buffalo Fork, Hellroaring, and Bear Creek.
1992	May 12, 1992	12	Areas surveyed were: Gardner's Hole, Blacktail Plateau, Soda Butte, Slough Creek, Buffalo Fork, Hellroaring, and Bear Creek.
1992-96			No counts attempted. Aerial surveys not believed to be effective technique.

[a] DATA SOURCE: Tyers, D. 1995. Winter ecology of moose on the northern Yellowstone winter range. Unpubl. rept. on file at YNP. 630pp.

Counts and estimates of mule deer for Yellowstone National Park, 1904-1970[a]. (Source: Barmore 1980.)

Year	Parkwide			Northern Yellowstone winter range					
				Count					
	Count	Estimate	Date of count	Inside park	Outside park	Total	Estimate	Comments from sources	Data source[g]
1904						120		Partial count.	1
1907		1,000							1
1908						300-400		Count on feed grounds in Mammoth-Gardiner area.	1
1909						500		Count on feed grounds in Mammoth-Gardiner area.	1
1910						800		Count on feed grounds in Mammoth-Gardiner area.	1
1911						1,000		Partial count.	1
1912		400						Based on actual counts or close observations.	2
1914	892		Apr. 9-May 1					Count was made during elk census. Pains were taken to count deer. Either scarce or scattered for 2-3 years. Gratifying increase over any counts in recent years.	
1915		2,000[b]							4
1916		2,000[b]							4
1917		2,000[b]							4
1922		1,000[b]							1
1923		1,000[b]							1
1924	314	1,800[b]	winter					Count probably represented less than 1/2 total in park. Count date not given.	1, 4
1925	602		?						1
1926	798	1,850[b]	?						1, 4
1927	683		?						1
1928	822	1,000[b]	?						1, 4
1929	835		?						5
1930		800	April	688	90	778		Deer scattered and correct check hard to submit. Count is as correct as can be had. No increase from previous year. Numerous losses from bot flies, not forage conditions.	5
1931	706	800	Feb.					Light winter. Very few losses of any kind.	6
1932	885	885	April					Very successful count. Considerably better than for several years. Doesn't reflect increase just better counting methods. Losses not excessive considering past few light winters haven't disclosed many winter kills.	7
1933	396	850	?					Count very low, doesn't reflect true number. Estimate is conservative. No increase from previous year.	8
1934	363	850	Mar. 14-16					Count not complete due to mild winter.	8

Year	Parkwide			Northern Yellowstone winter range				Comments from sources	Data source[g]
				Count					
	Count	Estimate	Date of count	Inside park	Outside park	Total	Estimate		
1935	610	850	?					No increase. Mild winters for 3 years caused abnormal increase.	8
1936	673	787	Mar. 18-19 and Apr. 2	622	Not counted	622	736	Count not fully successful. Deer counted separately on lower range but with elk on higher range. No noticeable increase last year. Status rather precarious. Depredations by predators reported in a number of instances.	9
1937	843	907	Mar. 2-5	801	Not counted	801	848	Thought to be one of the most complete and accurate counts ever made.	10
1938	964	1,000	Feb. 24-26	817	104	921		Through coverage was obtained. Count is quite accurate. No change in status over previous year.	11
1939	935	1,000	Mar. 22-24	649	267	916		Excellent weather but deer scattered due to light snow. No change in status from previous year. Losses were between January 1 and May 1 due to malnutrition and bot flies. All were coming yearlings or old.	12
1940	1,114	1,200	Mar. 19-20	748	342	1,090		Separate deer count. Higher count partly due to better methods. Losses were hunter kill and <half of last year. Favorable weather decreased losses.	13
1941		1,200						Deer remained widely scattered. Status same as in 1940.	14
1944							700	Heavy losses during severe winter of 1942-43.	8
1945		700						Status generally satisfactory.	15
1946		700		516		516		Count probably doesn't accurately represent actual number. Estimate based on previous year.	8
1947		600						Estimate in 1946 appears to have been conservative--perhaps considerably too low. Many deer taken in fall 1946 hunting season.	16
1948		800[c]	Feb. 17-19	236	442	678	678	Counted during elk census. Results not entirely successful due to counting both species at once. Count was only a fair appraisal of present numbers. Abnormal increase from 1939-42 followed by substantial winter losses in 1942-43. Population increase next 2 years was balanced by heavy hunting.	17
1949		600						Status satisfactory. Most migrate out of park during winter. Not possible to determine actual numbers (probably refers to summer population in the park).	18
1950		600							8
1951		600						Numbers in north part of park have increased in recent years, but the number wintering in the park are considerably smaller than prior to 1943.	19

Year	Parkwide		Northern Yellowstone winter range					Comments from sources	Data source[g]
				Count					
	Count	Estimate	Date of count	Inside park	Outside park	Total	Estimate		
1953		Common						Appear to be increasing possibly due to relatively mild winters. Losses rather high in early 1952.	8
1955		Common						Status unchanged even though hunting has been liberalized.	8
1956		Mar. 20-22	192[c]					Helicopter count incidental to counting elk. Insufficient time to count deer as accurately as elk.	20
1957		Common						Population appears static even though hunter bag north of the park is 2 deer.	21
1961				161[c]				Helicopter count incidental to the elk census.	32
1962		Common							23
1963		Common							24
1964		Common							25
1965		Common							26
1966		Common							27
1967		Common	Mar. 5	265[c]				Helicopter census of pronghorn winter range only. Less effort made to count deer. Deer hard to see on bare slopes or in sagebrush. Many probably were missed in forested areas.	28
1968		500[d]	Mar. 5	252[c]	27	279		Same comments as above except an effort was made to count all deer.	29
1969		500[d]	Mar. 20-21	172[f]				Fixed-wing check of elk distribution and intensive pronghorn census. Special effort was made to count deer on pronghorn winter range. Deer were hard to see.	30
1970		500[d]							31

[a] Ground count unless otherwise noted.
[b] Probably for summer.
[c] Helicopter count.
[d] Winter.
[e] Fall.
[f] Piper Supercub.
[g] DATA SOURCES: (1) Superintendent's Annual Reports for respective years; (2) Acting Superintendent, 1912a; (3) Acting Superintendent, 1914; (4) Bailey, 1930; (5) Baggley, n.d.; (6) Baggley, 1931; (7) Anonymous, 1932; Acting Superintendent, 1932; (8) Anonymous for the respective years; (9) Barrows, 1936; Skinner, 1936b; (10) Barrows, 1937b; (11) Barrows, 1938a,b; (12) Barrows, 1939a,b; (13) Barrows, 1940; Skinner, 1940; (14) Skinner, 1914b; (15) Anonymous, 1945a; (16) Rogers, 1947; Kittams, 1947; (17) Rogers, 1948; (18) Anonymous, 1949a; (19) Evans, 1951; (20) Kittams, 1956; (21) Kittams, 1958a; (22) Howe, 1961a; (23) Howe, 1962a; (24) Howe, 1963b; (25) Howe, 1964; (26) Howe, 1965c; (27) Barmore, 1966; (28) Barmore, 1967b,c; (29) Barmore, 1968a,b; (30) This study; Bucknall, 1969; (31) Bucknall, 1970.

Counts of mule deer on Yellowstone's northern range, 1971-1996.

Year	Date	Deer Counted	Comments	Source[a]
1971-78		No counts		
1978-79	April 3	1,108	Helicopter classification count. Observer: G. Erickson.	1
1986	March 14-15	1,863	Helicopter survey. Observer: F.J. Singer.	2
1987	March 31- April 1	2,134	Helicopter survey. Observers: K. Alt, F.J. Singer.	2,3
1988	April 11-12	2,217	Helicopter survey. Observers: F.J. Singer, C. McClure. Source 2 shows a count total of 2,274.	2,3
1989	April 30- May 2	1,796	Helicopter survey. Observers: T. Lemke, F.J. Singer.	3
1990	April 18-20	1,616	Helicopter survey. Observers: T. Lemke, F.J. Singer.	3
1991	May 16-17	2,082	Helicopter survey. Observer: T. Lemke.	3
1992	April 20	2,544	Helicopter survey. Observer: T. Lemke.	3
1993		No count		
1994	May 3-4	1,985	Helicopter survey. Observer: T. Lemke.	3
1995	May 2-4	2,411	Helicopter survey. Observer: T. Lemke.	3
1996		1,620	Helicopter survey. Observer: T. Lemke.	3

[a] DATA SOURCES: (1) Foss and Taylor 1980 *in* Wolves for Yellowstone? Vol. IV; (2) Singer 1986-88, unpubl. repts. in YNP files; (3) Lemke 1989-96, unpubl. repts in YNP files.

Population estimates and reductions for pronghorn, northern Yellowstone winter range, 1877-1970. (Source: Barmore 1980.)

Date	Actual count			Estimated population[a]	Artificial reduction	Comments from sources	Data source[c]
	Total	Inside park	Outside park				
1877						"Thousands of antelope."	1
1880						"Abundance of antelope."	1
1885						"Several bands of antelope."	1
1886						"Antelope are here in large numbers."	1
1887						"Large numbers of antelope."	1
1891						"Numerous and on the increase."	1
1892						"Thriving and increasing."	1
1893						"One herd of four to five hundred wintered on Mt. Everts and one or two smaller herds elsewhere."	1
1894						"500 wintered on Mt. Everts."	1
1895						"800 wintered on flat near Gardiner."	1
1896						"A great increase in number."	1
1897						"500 wintered in valley and on Mt. Everts."	1
1898						"Are yet numerous."	1
1899				700-800			1
1900						"Increasing."	1
1902						"Number of bands from 50 to 100 wintered on slopes of Mt. Everts."	1
1903				1,000			1
1904				1,150			1
1905				1,500			1
1906				1,500			1
1907				1,500			1
1908 Summer				2,000		"All but 25 left the park in winter and many didn't return."	2
1909						"Increasing."	1
1910				600-700		The balance were reported to have escaped from the park.	1
1911 ?	450						1
1912 July				500	12	Estimate based on actual counts or very close observations and are pretty nearly correct.	3, 4
1913						"Increased slightly."	1
1914 ?	600						1
1916 ?				500			2
1917 Spring[b]				200		Most of the 1916 herd left the park and the 200 were what were driven back.	2
1918 ?	350					This was the number seen in one day. "... no special pains were taken to make a complete count of the herd."	5
1920 ?				300			6

Date	Actual count: Total	Inside park	Outside park	Estimated population[a]	Artificial reduction	Comments from sources	Data source[c]
1922 Late Nov.	234	234	None	300		One day count by 7 men of Blacktail, Turkey Pen Trail, Mt. Everts, and Gardiner areas. Woodring thought that Skinner's count was high. Had reason to believe there were a few others in Geode Cr.-Oxbow Cr. area.	7
1922 Dec. 12	248	198	50			One day count by 3 men. Those outside park were just below Stoll's Ranch but not yet down to Hoppe's Place. Thought the count was not complete.	8
1923 Spring[b] Fall	253			300			9
1924 Jan. Fall	325			395		Five died during the winter leaving 320. About 65% of the herd are males. Census was a "full count."	10
1925 Late Apr.	417						11
1926 Winter Fall	497			600			12
1927 Winter Fall	641			700			13
1929 ?	638						14
1930 Feb. Spring[b]	510	510		650		Other counts: January-416, March-384, April-498.	14
1931 Feb. Spring[b]	646			646		Other counts: January-544, April-363.	15
1932 Apr. Spring[b]	668			646			16
1933 Spring[b]	599			700		Low count, by no means representative of the actual numbers.	17
1934 Mar.	321			700		Incomplete count.	17
1935 ?	419			750			17
1936 Apr. 2	406	406	Not covered	603		Count by 7 men considered not fully successful. Unsuccessful count also tried March 19. Mammoth area-4, Mt. Everts-84, Gardiner-Reese Cr.-415 (for total of 503).	18
1937 Mar. 2-3	600	600	Not covered	627		Count by 10 men was one of the most accurate and complete ever taken. Increase over last year reflects better count rather than actual increase. Count by areas was: Reese Cr.-Gardiner-446, Mt. Everts-51, Mammoth-0.	19
1938 Feb. 24	786	786	0	800		Six men, excellent weather, thorough coverage of counting units. Outside count by Forest Service. Antelope are increasing. Count by area: Reese-Cr.-Gardiner-504, Gardiner-130, Mt. Everts-152, Mammoth-0.	20
1939 Mar. 22-24	741	653	88	800		Park count by 12 men, excellent weather, but animals widely scattered which might account for lower count than year before. Outside count by Forest Service. Count by area: Reese Cr.-Gardiner-347, Gardiner- 210, Mt. Everts-103, Mammoth-2, Beattie Gulch-88.	21
1940 Feb. 7	811	566	245	900		Pronghorn, deer, sheep counted separately for first time and may have increased count accuracy. Normal to mild winter. Includes 70 reported by Forest Service and ranches near Corwin Springs which wasn't covered.	22

Date	Actual count Total	Inside park	Outside park	Estimated population[a]	Artificial reduction	Comments from sources	Data source[c]
1941 Mar. 24	784	776	8	900		Though weather and snow not favorable for easy and thorough count, it was considered reasonably successful. Less accurate than 1940. Count by 9 men. Herd size same as in 1940. Count by area: Reese Cr.-Gardiner-446, Gardiner-Mammoth-58, Gardiner-Mt. Everts-272, 8 outside were at Cinnabar Mt.	23
1942 ?				900			24
1943 ?						"Some losses occurred during the winter and 58 carcasses were found during the dead animal count."	25
1944 Fall				800			26
1945 Feb. 21-22	773	726	47	800	See comments	Eleven men; probably missed very few. Count by areas: Reese Cr.-Gardiner-624, Mt. Everts-68, Mammoth-34, north of park to Mol Heron Cr.-47. In fall, 1945, Montana F. and G. Dept. tried unsuccessfully to trap just north of park boundary.	27
1946 Mar. 26	698	698	Not covered		See comments	Favorable counting conditions. Count by 10 men in park was reasonably accurate. Lower count than in 1945 probably due to wider distribution out of park (not covered) rather than reduced numbers. Authority to reduce herd to 400 granted in summer, 1946. Trapping in fall, 1945, caused unusual disturbance. Count by areas: Reese Cr. and boundary-72, Gardiner-Reese Cr.-538, Mt. Everts-88.	28
1947 April Fall	545			625	294	236 trapped in Jan. 1947, 58 on Dec. 16, 1947. During Dec. 16 trapping 12" of heavy crusted snow at the tree nursery. After January trapping most pronghorn remained out of park as far as Carbella but returned by March 1.	29
1948 Jan. 6	409	162-337	72-147		?	Poor weather; favorable counting conditions; count a fair appraisal of current numbers. Aerial checks during trapping prior to ground count indicated not many more than 400. Count by areas: Mt. Everts-85, Stephens Cr.-Mammoth-77, Stephens Cr.-Cinnabar Mtn.-175, Cinnabar Mtn.-Carbella-72.	30
1948 Feb. 10	342		Some			Poor weather handicapped 13 counters and caused pronghorn to seek shelter. This count plus one in Jan. indicates about 400 pronghorn after 1947 reduction. Count by areas: Mt. Everts-O, Mammoth-Stephen's Cr.-146, Stephens Cr.-Devils Slide-196, Devils Slide-Carbella-0.	31
1949 Feb. 1	410	23	387	400		Highly successful count. Weather and other conditions unusually favorable. All known pronghorn range covered. Boundary-Cinnabar Mtn.-387, Stephens Cr.-Reese Cr.-23.	32
1950 ?				400		Studies show that not over 200 pronghorn should be retained until seriously over-used winter range improves.	33
1951 Feb. 21-22 Fall	215			270	258	Livetrapping done in Jan. and Feb. Winter range almost snow-free and animals were widely scattered with many much higher than usual. Recent airplane herding partly responsible.	34
1953 Feb. 12 Fall	382	367	15	460		Mild, little snow, pronghorn in small bands and scattered, but counters felt they saw nearly all animals and avoided duplication. Count by area: Mt. Everts-71, Reese Cr. to Chinaman's Garden-296, Beattie Gulch-8, bench north of Cinnabar Mtn.-7. Approval granted to reduce herd to 100-125 animals.	36
1953 Dec. 15	485					All range to Corwin Springs was covered by 10 men. Count believed to be fairly accurate. Count by area: Stephens Cr. north-125, Stephens Cr.- Mammoth-219, N. end Mt. Everts-141.	35

Date	Actual count			Estimated population[a]	Artificial reduction	Comments from sources	Data source[c]
	Total	Inside park	Outside park				
1954 Dec.	334				207	Livetrapping was in early 1954.	37
1955 Fall				400	207	Trapping tried in early 1955, but unsuccessful.	37
1956 March	356-431	356-431				Helicopter census. Good conditions. Total seen was 356 with possibly 75 more on North end Mt. Everts where separation of bands was questionable.	38
1956 Dec.	395	385	10			Ideal counting conditions.	38
1957				330	120	Livetrapping was in February.	39
1958 Feb. 20	158	158	Not covered			Seven men, poor counting conditions. "I seriously question the completeness of the recent count, as antelope very probably were dispersed over more area than that...covered..."	40
1959 ?				400			41
1961 Mar. 17	299	299	Not covered			Helicoptered census specifically for pronghorn.	42
1962 Apr. 4	278			300		Helicopter census specifically for pronghorn; 35 min. flying time; coverage to about 1 mile north of park boundary.	43
1963 Spring[b]				350			44
1964 Spring[b]				350	25	Livetrapping Dec. 16, 1964.	45
1965 Jan. 5 Spring[b]	182-210			300	7	Partial helicopter census in conjunction with livetrapping of pronghorn. Livetrapping Jan. 6, 1965.	46
1966 Spring[b]				200	94	Reduction by shooting between summer 1965 and April 1966.	47
1967 March Spring[b]	188	188	0	200	6	Reduction by shooting in October 1967. Helicopter census; good to excellent condition; partial coverage outside park; probably included 95% of pronghorn on winter range inside the park.	48
1968 Dec. Spring[b]	149			200		Special pronghorn census from Piper Supercub.	49
1968 Mar.	85	43	42			Helicopter census specifically for pronghorn. Area outside of park covered to Carbella but not as intensively as inside park. Severe winter had caused many to leave the park; hard to get complete count.	50
1969 Mar Spring[b]	133	133		150		Special antelope count by Piper Supercub. Partial coverage outside park, but not as intensive as inside.	51
1970 Jan. Spring[b]	158			170		Comments as above.	52

[a] Date for which estimate applies unknown unless otherwise indicated.
[b] Spring before fawns are born.
[c] DATA SOURCES: (1) Skinner, 1922; (2) Bailey, 1930; (3) Superintendent's Annual Report, 1912; (4) Halloran and Glass, 1959; (5) Superintendent's Annual Report, 1918; (6) Superintendent's Annual Report, 1920; (7) Woodring, 1922 for count, Superintendent's Annual Report for 1921-22 for estimate; (8) Loyster, 1922; (9) Superintendent's Annual Report, 1923; (10) Woodring, 1924; (11) Superintendent's annual report, 1925; (12) Superintendent's Annual Report, 1926; (13) Superintendent's Annual Report, 1927; (14) Baggley, n.d.; (15) Baggley, 1931; (16) Anonymous, 1933; (17) Anonymous, 1936; (18) Skinner, 1936b; (19) Barrows, 1937b; (20) Barrows, 1938b; (21) Barrows, 1939b; (22) Barrows, 1940; (23) Skinner, 1941a; (24) Superintendent's Annual Report, 1942; (25) Superintendent's Annual Report, 1943; (26) Anonymous, 1944; (27) Anonymous 1945a,b; (28) Anonymous, 1946; (29) Rogers, 1948 for the count, Kittams, 1947 for the estimate, LaNoue, 1948a for the reduction; (30) Grimm, 1948; (31) LaNoue, 1948b; (32) Joffe, 1949 for count, Anonymous, 1949a for estimate; (33) Anonymous, 1950; (34) Johnston, 1951 for count, Evans, 1951 for estimate; (35) Chapman, 1953; (36) Kittams, 1953b for count, Kittams, 1953b for estimate, Superintendent's annual report, 1953; (37) Anonymous, 1955; (38) Kittams, 1956; (39) Kittams, 1957a; (40) Kittams, 1958b; (41) Chapman, 1960; (42) Howe, 1961b; (43) Howe, 1962a for count, Howe, 1962b for estimate, Management Assistant for Yellowstone National Park, 1962 for coverage; (44) Howe, 1963b; (45) Howe, 1964; (46) Barmore, 1965b for count; Howe, 1965c for estimate, (47) Barmore, 1966; (48) Barmore 1967b for count, Barmore, 1967c for estimate; (49) this study for count, Barmore, 1968a for estimate; (50) Barmore, 1968b; (51) this study; (52) this study for count, Bucknall, 1970 for estimate.

Pronghorn counted during spring surveys on Yellowstone's northern range, 1971-1996.

Date	Pronghorn Counted	Comments	Source[a]
1971 (April 1)	13[illegible]	(Max.)	1
1972 (January 28)	134	(Max.)	1
1973 (March 9)	129		2
1974 (April 23-24)	103	Highest of 5 counts listed for season.	1
1975 (February 18)	165	Highest of 5 counts listed for season.	1
1976 (April 8)	130	Highest of 5 counts listed for season.	1
1977 (March 15)	121	Highest of 5 counts listed for season.	1
1978 (March 21)	146	Highest of 5 counts listed for season.	1
1979	146	Helicopter survey by MDFWP.	3
1979 (23 April)	152		4
1980 (April 8)	157		4
1981 (March 21)	102		4
1982 (April 17)	131		4
1983 (March 8)	310		4
1984 (March 23)	365		4
1985 (April 9)	364		4
1986 (February 28)	363		4
1987 (March 17)	478	Highest of 3 counts listed for season.	1
1988 (April 14)	495	Reported as "best count" of season.	1
1989 (April 9)	372	Reported as "best count" of season.	1
1990 (March 20)	472	Reported as "best count" of season.	
1991 (April 2)	588?	Various file references refer to a total of 522, 588, 591, and 594 on this date. Caslick indicates observation forms total 588 counted.	1
1992 (March 24)	536	450 adults, 86 yearlings.	5
1993 (April 8)	416	416 adults, 23 yearlings	6
1994		No count conducted	
1995	235	"Poor count".	6
1996 (March 25)	229	"Counting conditions were excellent".	6

[a] DATA SOURCES: (1) Data compiled by M.D. Scott *in* Caslick, J. 1995. Unpubl. YNP Rept. on status of pronghorn information, on file at YNP; (2) Houston ltr to Superintendent, Mar. 19, 1973, *in* YCR file 1427, YNP. (3) Unpubl. Rept *in* YNP file N1427, Antelope; (4) Unpubl. rept. on Northern Yellowstone antelope count, F.J. Singer, obs., 1986, YNP files; (5) Memo dated Nov. 19, 1993 on file at YCR, YNP; (6) Unpubl. rept. of aerial count by J. Mack, YNP files.

Counts and estimates of bighorn sheep in Yellowstone National Park, 1880-1970. (Source: Barmore 1980.)

Year	Date of count	Actual count[a] Parkwide	Actual count[a] Northern Range	Estimate Parkwide	Estimate Northern Range	Comments[e]	Data source[f]
1880						Sheep were abundant.	1
1887						Found on all mountain ranges.	1
1897				200			1
1912				210		Estimate based on counts or close observation and are very nearly correct.	2
1919						Mountain sheep were seen in about the usual numbers.	3
1920				200		"...it is evident that our estimated number of 200 in the park is too low if anything."	4
1922				250		"Sheep scab, the disease that threatened for a time to exterminate our mountain sheep, has practically disappeared and we have a large, thriving herd of about 250..."	5
1923		233		300+			6
1924	Winter	200	217	300		(Most or all of count was probably on North Yellowstone winter range.)	7
1925	Winter & Spring	195		600		(Most or all of count was probably on North Yellowstone winter range.)	8
1926	Winter & Spring	217		600		(Most or all of count was probably on North Yellowstone winter range.)	9
1927	Winter & Spring	346		650		(Most or all of count was probably on North Yellowstone winter range.)	10
1928	Feb.	170		500		Known losses of 9 to hunters and 31 to scabies mites and lungworm infections. "...as determined by laboratory examination." Known losses were believed far short of actual losses during the year.	11
1929		120	120[b]				12
1930	March	125	125[c]	150	150	Increasing.	12
1931	April	101	101[c]	150	150	Status much better than a few years ago.	13
1932	April	79	79[b]	150	150	Sheep on some inaccessible peaks not counted. (Probably those in the NE corner of the park.) No change in status.	14
1933	?	82	82[b]	150	150	Counted along with all other ungulates.	15
1934	March 14-16	125	125[b]	150	150	Status more favorable than last year.	16
1935	?	126	126	200	200	Count thought to be more accurate than others for a number of years.	17
1936	Dec.	118	118	200	200	Count didn't cover all the sheep winter range.	18
1937	Mar. 2-5	175	175[c]	195	195	One of the most accurate and complete counts ever taken.	19
1938	Feb. 24-26	181	181[b]	200	200	No change in population status. Includes 6 on North Yellowstone winter range outside the park.	20

		Actual count[a]		Estimate			
Year	Date of count	Parkwide	Northern Range	Parkwide	Northern Range	Comments[e]	Data source[f]
1939	Mar. 22-24	228	228[d]	250	250	Excellent weather, but sheep were scattered due to mild winter. Includes 9 on North Yellowstone winter range outside the park.	21
1940	Mar. 7-14	272	272[d]	300	300	Sheep were counted separately from other ungulates. None on North Yellowstone winter range outside the park.	22
1941	Mar. 24-26	200	200[d]	300	300		23
1942	Mar. 9-12	139	139			Unfavorable weather, incomplete coverage.	24
1943	Mar. 22-29	138	132[b]			Mild late winter permitted sheep to scatter making a count difficult. Includes 16 on North Yellowstone winter range outside the park.	25
1944				300			26
1945	Mar. 5-8	182	182[d]	280	249		27
1946	Mar.	176		280		(Count was probably mostly or entirely for the North Yellowstone winter range.)	28
1947	Mar. & Apr.	140	140[b]	280		A number of areas where bighorn were regularly found weren't counted.	29
1948	Feb. 17-19	176	176[d]	250	250	Sheep were counted in conjunction with the North Yellowstone elk census. Some areas where sheep were occasionally found weren't covered. Two were on North Yellowstone winter range outside the park. Population status essentially static for many years.	30
1949	Feb. 28-Mar. 7	144	144[d]	200	200	Count was intensive. Ideal conditions. All well-known wintering areas were covered by good observers, very good to excellent coverage. Population status not satisfactory. Fifteen counted on North Yellowstone winter range outside the park.	31
1950	Mar.	101	101[b]	170	170	Count only covered accessible parts of the North Yellowstone winter range. It appears that an actual population decrease has occurred.	32
1951				170	170	The population may be decreasing. Status is unsatisfactory.	33
1953				Uncommon		Population probably static or decreasing.	34
1955	Feb. 10	192	189	200		Count by fixed-wing aircraft.	35
1956	Mar. 20-22		121			Helicopter count in conjunction with census of North Yellowstone elk herd. Other ungulates not counted as accurately as elk.	36
1957				Rare			37
1961	Mar. 20-26		118			Helicopter count in conjunction with census of North Yellowstone elk herd. Special attention given to counting bighorn sheep.	38
1962	Apr. 3-4		148	200		Helicopter count in conjunction with census of North Yellowstone elk herd. Special attention given to counting bighorn sheep. Continuously good flying weather.	39

Year	Date of count	Actual count[a] Parkwide	Actual count[a] Northern Range	Estimate Parkwide	Estimate Northern Range	Comments[e]	Data source[f]
1963				200			40
1964				200			41
1965	Apr. 6-9		227[d]	300		Helicopter census, partly during a special flight to count sheep, but mostly done in conjunction with the helicopter census of the North Yellowstone elk herd.	42
1966			229[d]	300		Count was based on frequent winter counts by researcher John Oldemeyer.	43
1967	Mar. 22-27		231[d]		300	Helicopter count in conjunction with the census of the North Yellowstone elk herd. Probably not as accurate as the 1965 census. Eleven additional sheep were counted on Cinnabar Mtn. on the North Yellowstone winter range outside the park.	44
1968			178 (257)[d]	560		Counts by Piper Supercub in conjunction with flights to check elk distribution. 160 = highest single count. 257 = highest counts on major terrain features over several late winter flights.	45
1969			247 (295)[d]	560		Counts as described for 1968. 247 = highest single count. 295 = highest counts on major terrain features over several late winter flights.	46
1970			323 (392)[d]	600		Counts as described for 1968. 332 = highest single count. 392 = highest count on major terrain features over several late winter flights. Includes 8 at Golden Gate.	47

[a] Ground counts unless otherwise specified.

[b] Probably didn't include sheep that winter on higher peaks in the NE corner of the park (Mt. Norris, Thunderer, Abiathar Pk., Barronette Pk., and possibly Druid Pk.).

[c] Census didn't include the peaks mentioned above.

[d] Census specifically did include most or all peaks mentioned in b above.

[e] Comments in parentheses are mine and not from data sources.

[f] DATA SOURCES: (1) Mills, 1937; (2) Acting Superintendent, 1912a; (3) Superintendent's Annual Report, 1919; (4) Superintendent's Annual Report, 1920; (5) Superintendent's Annual Report for 1921-22; (6) Superintendent's Annual Report, 1923; (7) Superintendent's Annual Report, 1924 for parkwide count and estimate, Superintendent's Monthly Report for January, 1924 for northern Yellowstone count; (8) Superintendent's Annual Report, 1925; (9) Superintendent's Annual Report, 1926; (10) Superintendent's Annual Report, 1927; (11) Superintendent's Annual Report, 1928; (12) Baggley, n.d.; (13) Baggley, 1931; (14) Edward's, 1932 and Anonymous, 1932; (15) Anonymous, 1933; (16) Anonymous, 1934; (17) Anonymous, 1936; (18) Barrows, 1936 and Parsons, 1936; (19) Barrows, 1937b; (20) Barrows, 1938b; (21) Barrows, 1939b; (22) Barrows, 1940; (23) Skinner, 1941a; (24) Superintendent's Annual Report, 1942; (25) Coleman, 1943; (26) Anonymous, 1944; (27) Anonymous, 1945a,c; (28) Anonymous, 1946; Rogers, 1946; Superintendent's Annual Report, 1946; (29) Rogers, 1947; Kittams, 1947; (30) Rogers, 1948; (31) Anonymous, 1949a,b; Coleman, 1949; (32) Anonymous, 1950; (33) Evans, 1951; (34) Anonymous, 1953; (35) Anonymous, 1955; Buechner, 1960; (36) Kittams, 1956; (37) Kittams, 1957a; (38) Howe, 1961a; (39) Howe, 1962a,b; (40) Howe, 1963b; (41) Howe, 1964; (42) Barmore, 1965a; Howe, 1965c; (43) Oldemeyer, 1966; Barmore, 1966; (44) Barmore 1967b,c; (45) This study; Barmore, 1968a; Woolf, 1968; (46) This study; Bucknall. 1969; (47) This study; Bucknall, 1970.

Ground and aerial counts of bighorn sheep on northern winter range, 1971-1996. (Source: Houston 1982:439; YNP Files.)

Year	Aerial Count	Ground Count	Comments	Data Source[a]
1971	227		Maximum on 4/3 and /4 of five counts from 12/31-5/1 (see text); range, 128-227 sheep. Abiathar Peak and other areas in extreme NE corner of the park were not covered on these flights unless otherwise mentioned.	1
1972	373		Maximum on 4/3 and /4 of five flights from 12/2-5/3; range, 169-373. One flight per year aimed to coincide with particular environmental conditions from this year through 1978 (see text).	1
1973	332		Maximum on 4/26 and /27 of four flights from 12/9-4/27; range 225-332.	1
1974	446		Maximum on 4/22 and 23 of four flights from 1/3-4/23; range, 141-466.	1
1975[b]	404		Maximum on 5/13 and 14 of four flights from 12/29-5/14; range, 152-404.	1
1976	426		Maximum on 5/7 and 8 of four flights from 12/17-5/8; range, 110-426.	1
1977	430		Maximum on 4/21 and 22 of three flights from 1/23-4/22; range, 130-430. An additional 10 sheep counted on Abiathar Peak on 3/16.	1
1978	471		Maximum on 4/28 and 5/4 of four flights from 12/20-5/4. An additional 20 sheep counted on Abiathar Peak on 5/4.	1
1979		89	Ground count of sheep between Mt. Everts, YNP and Point of Rocks, Montana	2
1980		265	Ground count of sheep between Mt. Everts, YNP and Point of Rocks, Montana	2
1981		156	Ground count of sheep between Mt. Everts, YNP and Point of Rocks, Montana	2
1982		72		2
1983		38		2
1984		46		2
1985		59		2
1986		93		2
1987		108		2
1988		117		2
1989		121		2
1990		151		2
1991		69		2
1992	222	105	Ground count done in December as usual; aerial count was done by helicopter later in spring and covered more area inside YNP toward Soda Butte.	3

Year	Aerial Count	Ground Count	Comments	Data Source[a]
1993		79		3
1994	141	115	Helicopter count done in spring; ground count done in winter and covered less area.	3
1995	152	116	Helicopter count done in spring; ground count done in winter and covered less area.	3
1996	182	103	Helicopter count done in spring; ground count done in winter and covered less area.	3

[a] DATA SOURCES: (1) Houston, 1982; (2) YNP Files; (3) YNP Files; aerial count information provided to YNP by T. Lemke, MDFWP in unpubl. repts.
[b] In addition, the Absaroka Mountains were searched inside the east boundary of Yellowstone Park for sheep on 2/24, 3/14, and 4/17, 18, 21/75. None were observed.

REFERENCE LIST

NOTES ON THIS REFERENCE LIST

This list is more than a compilation of references cited in the text. It includes all technical publications and many popular publications produced by researchers on Yellowstone's northern range since 1970. It is by no means a complete bibliography of all earlier northern range research. Except in a few special circumstances where it was necessary to cite peripheral material, this list does not include publications relating to the northern range by writers who have not engaged in professional research there.

The careful reader will notice that in several cases, two or even three variants of similar titles may appear under one author's name or group of authors' names. This is because of the complicated process by which this material was prepared for final publication. All of these variants are included in this list so that there is at least one complete bibliographical "biography" of this period of northern range research. Likewise in the interest of thoroughness, when an author's work is cited in the text, the parenthetical citation will typically include the redundant citations. If authors or others notice that a paper or publication is missing that ought to be included, please notify the Yellowstone Center for Resources, so that as complete and accurate as possible a reference list can be maintained.

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The publication of this study was made possible by Canon U.S.A., Inc.
through its program *"Expedition Into Yellowstone."*

Yellowstone National Park is a beneficiary of Canon's farsighted support
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Yellowstone's northern range has inspired one of this century's most far-reaching dialogues on the management of a wildland. *Yellowstone's Northern Range: Complexity and Change in a Wildland Ecosystem,* provides all participants in this dialogue with a vast amount of new information that has previously been available only in highly specialized technical journals. More scientific research on the northern range has been published in the past 15 years than in the previous century. This book summarizes these exciting and often surprising findings, and provides a clear direction for future research and management.

The northern range, especially its controversial elk herd, is a fascinating case study in the complexity of ecological systems and the equally complex process by which generations of scientists, managers, and the public have sought to care for one of North America's most extraordinary and best-loved wildlife resources. Provocative, informed, and urgently important, *Yellowstone's Northern Range* will occupy a central role in deliberations over Yellowstone for many years to come.