Interim Report
Yellowstone National Park
Northern Range Research

Research Division
Yellowstone National Park

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Introduction

The condition of the Northern Winter Range (referred to here as the Northern Range) of Yellowstone National Park has been of concern to the public, managers, and scientists for more than 60 years (32). 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. Overgrazing was almost always attributed to high elk numbers.

Changing perspectives in management and in the ecological sciences in the past thirty years have resulted in an intensive reconsideration of past views, and have also resulted in renewed controversy over the range and its management. Evidence of changing perspectives in the ecological sciences appeared in two extended studies of the Northern Range, by National Park Service ecologists William Barmore (from 1962-1970) and Douglas Houston (1970-1979). These studies agreed that the range showed no appreciable deterioration due to overgrazing by ungulates (2,32).

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. 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 process of selection of the university researchers to receive Congressional funding was turned over to the University of Wyoming. Yellowstone National Park did not vote in, or influence, the selection process. This research initiative, one of the largest in the history of the National Park Service, has involved scientists from many universities, institutions, and agencies, and has once again challenged traditional views of the range (57,59).

Some of the findings of this research initiative have now been published, and many more are still in press or preparation. The two most significant forthcoming publications relating to Northern Range issues are R. Evanoff and F. Singer, eds., Effects of grazing by native ungulates in Yellowstone; a report to Congress (scheduled publication date, summer 1992), and D. Despain, ed., Plants and their environments; papers from the first biennial scientific conference on the Greater Yellowstone Ecosystem (projected publication, late 1993).

In the following narrative, some of the titles from these forthcoming volumes are cited, but much of the information presented here is based on material already available, having been published in scientific journals and other publications.

The numbers given in parentheses in this text are keyed to the bibliography at the conclusion of the narrative. In many cases, the actual publications are also appended. In the case of most

long papers, only the abstract or conclusions of each are provided. In the case of papers still in press, only the abstract is provided, as appropriate. To protect the professional rights, and in some cases the copyrights, of the many researchers involved, only those findings that have either been published or summarized in a public forum (such as a scientific conference or other meeting) are mentioned here. This means that most of the papers in the forthcoming report to Congress are not represented here; they must first be presented to Congress prior to distribution.

This is not an attempt to provide a review of the entire scientific history of the Northern Range issue; we concentrate primarily on material published recently, because that is the material that is least known to some participants in the dialogues. Numerous publications and reports predating the recent Congressionally mandated research are also cited; most of these are not appended, but are readily available at libraries. The Yellowstone National Park Research Library, in the basement of the Albright Museum at Mammoth Hot Springs, contains a large collection of past and recent research publications relating to the Northern Range.

The Prehistoric and Historical Contexts

Since the turn of the century, a number of naturalists, ecologists, and other observers have interpreted and reinterpreted the historical record of early Yellowstone to determine how common the large animals were prior to the establishment of the park. Two viewpoints have emerged. One is that large mammals were rare or absent prior to the arrival of European humans in the greater Yellowstone area. According to this view, elk and other ungulates became more abundant about 1890, due to human influences and loss of preferred ranges outside the park. The other view is that large mammals were always, for many centuries at least, abundant in the present park area, using the habitat as climate would allow.

The paleontological, archeological, and historical record of early Yellowstone wildlife must be used cautiously. It is rarely safe to lift single statements out of a specific publication or source, especially a historical account, to "prove" some viewpoint. Though the Greater Yellowstone Ecosystem is not fully explored either in its paleontology or its archeology, enough work has been done so that a general idea of animal presence and distribution has emerged.

Perhaps the most important of all recent studies, Elizabeth Hadly's (University of Northern Arizona) study of Lamar Cave, revealed that elk, bison, and other ungulates have been common on the Northern Range for at least the past 2,000 years (27). Hadly, in commenting on the argument that elk were not abundant in the Yellowstone area prehistorically, wrote the following:

> This argument is refuted by evidence from Lamar Cave. Elk occur in 7 of 10 levels from the cave, both above and below a level date 960 + or - 60 yr. B.P. Elk is also the most common ungulate in the Lamar Cave faunal assemblage. The occurrence of elk in the Lamar Cave establishes its presence in Yellowstone prior to historic disturbances, and is thus significant to park management and to the diachronic study of ecosystem dynamics. The elk remains from Lamar Cave are primarily juvenile, suggesting further

that the area was used by elk in the past much as it is today.

The presence of juvenile remains indicates that elk were present in early spring, and that the area around the cave site was an elk calving area, as it is today. A second paleontological study is now nearing completion, as is a review of all archeological evidence of the prehistoric fauna of the Greater Yellowstone Ecosystem.

A common part of traditional understanding of western landscapes was the belief that large mammals lived primarily on the plains and were uncommon in mountainous areas. This general belief has been applied to Greater Yellowstone, but there is no reason these animals would leave perfectly usable ranges vacant for thousands of years. As already mentioned, paleontological and archeological work in recent years has established that ungulates did use appropriate habitats in and near Yellowstone Park for millenia prior to the arrival of European humans, and probably used them much as they do today.

The historical record is very persuasive on this point when it is used fully. Past reviews of the historical record never involved more than about 25 of the early accounts between 1830 and 1880. A much more comprehensive review has just been completed by Paul Schullery and Lee Whittlesey of the National Park Service, and is now in press (54). This is the first time that this subject has been examined formally by historians, and their use of more than six times as many sources as any previous analysis is an important contribution to the historical scholarship of the Northern Range. Their review makes use of about 150 accounts from between 1806 and 1882, and provides overwhelming evidence of abundant large mammals throughout Greater Yellowstone.

However, unlike some previous investigators, Schullery and Whittlesey do not believe that even this much larger body of historical material is sufficient to allow a precise estimate of animal numbers. Instead, they maintain only that the evidence provided by these sources indicates general abundance. The evidence does not, for example, allow for accurate comparisons of pre-1872 numbers of elk with modern numbers, beyond demonstrating that elk were reported, often in large numbers, distributed in all the areas of the park where they appear today.

It should be pointed out that this paleontological and historical evidence merely supports what seems to at least some ecologists to be intuitive. There is no ecological reason these ranges and habitats would have remained vacant for the 10,000 years since the retreat of the glaciers.

Because a few historical sources have been used to "prove" that these animals were not abundant, we present here a few of the most commonly cited examples, providing the historical context that is usually missing when they are used selectively.

The Lewis and Clark Expedition has been cited as proving that large mammals were not common in the mountainous regions of the west. The record of the expedition, however, suggests the opposite about greater Yellowstone. On their way east, in 1806, Captain Clark and his party traveled along the northern edge of the Greater Yellowstone Ecosystem, coming within

50 miles of the present park area, crossing the Gallatin Range near Bozeman, and following the Yellowstone River past the sites of present Livingston, Big Timber, and Billings. While in the Greater Yellowstone Ecosystem, at the very foot of the mountain ranges, they reported numerous species of large mammals in great abundance (63).

Approaching from the west, in the area of the Gallatin Valley, about 20 miles from the Bridger Mountains, Clark reported that he saw, "several Antelope, common Deer, wolves, beaver, otter, Eagles, hawks, crows, wild gees [sic] both old and young, does, &c., &c." Near the present site of Bozeman, Montana, he "saw Elk, deer & Antelopes, and a great deel [sic] of old signs of buffalow" [sic]. He reported a variety of mammals along the Yellowstone River near Livingston, including beaver and black bears, and near the mouth of the Shields River, he reported, "Several gangs of Elk from 100 to 200 in a gangue [sic.] on the river, great numbers of Antelopes. one Elk only killed today." Upstream from Big Timber, he "Saw a large gangue [sic.] of about 200 Elk and nearly as many Antilope [sic.] also two white or Grey Bear in the plains..." Below Big Timber he reported "not so many Elk & more deer" (63).

This is in fact a description of a valley immediately adjacent to the mountains that comprise much of the Greater Yellowstone Ecosystem, and this valley could be considered "the plains" according to traditional definitions of where ungulates lived. But again, it must be emphasized that there is no ecological rationale to justify believing that the animals would be this abundant on the Yellowstone River in this area and would not also be using appropriate habitats in the present park area. There are no barriers between the two, only continuous hospitable range. There are, however, large amounts of historical evidence that the animals were in the park area throughout this period. There are numerous statements from the early historical period to support it, including many firsthand accounts.

We provide a few examples of these accounts here, but remember that the real value of the historical record is in using it all, not in selective quoting. We only offer these as examples, not as conclusive proof in and of themselves. Much more material on these sources is provided in the full analysis by Schullery and Whittlesey.

In 1830, according to the famous trapper Joe Meek, quoted in F.F. Victor's River of the West (1870), "The whole country lying upon the Yellowstone and its tributaries, and about the headwaters of the Missouri, at the time of which we are writing, abounded not only in beaver, but in buffalo, bear, elk, antelope, and many smaller kinds of game" (64).

Osborne Russell was a literate trapper and journalist who visited the Yellowstone area several times in the 1830s. On a visit to the Yellowstone Lake area in August of 1837, he reported the "whole country swarming with Elk we killed a fat Buck for supper and encamped for the night the next day Allen shot a Grizzly Bear..." (52). It might be noted that bear sightings were extremely common among early travelers in this period of Yellowstone history; the park area obviously had both its present ungulates and its predators.

An example of the misuse of historical material to prove animals were not abundant is provided

by a famous Jim Bridger remark. Bridger has been quoted as describing the Yellowstone region when he said that, "A bird can't fly over that without taking a supply of grub along." This use of Jim Bridger's statement, in fact, rivals the prevarications for which the mountain man himself was famous.

The quotation of Bridger appeared in the official report of Captain W.F. Raynolds, published in Washington by the U.S. Government Printing Office in 1868 (48). In the spring of 1860, Raynolds was leading an expedition toward the Yellowstone Park area (the park was not established until 1872) from the southeast, and Bridger was his guide. On May 30, the party was near Union Pass and the headwaters of the Wind River, at least 20 miles south of the present Yellowstone National Park boundary.

Raynolds' goal was to cross over the high mountain pass between his party and the headwaters of the Yellowstone River, and then follow the Yellowstone River downstream into the present park area and travel north. As might be expected in late May, they encountered deep snow near Union Pass; this would be expected even today.

It was on May 30 that Jim Bridger was quoted by Raynolds as making his famous remark that "a bird could not fly over that without taking a supply of grub along." It is clear from the context of Raynolds' report, however, that Bridger was talking about the high mountain country between the party and the headwaters of the Yellowstone River. The headwaters of the Yellowstone River are, of course, at a high-elevation south of Yellowstone National Park. That is, Bridger was talking about an area entirely to the south of the present park. As important, he was talking about country that even today, at that season, would be snowed in and have little game available.

Raynolds himself provided evidence of game abundance that same day, when he noted that even this close to the snowbound and impassable mountains, game was "abundant." He specifically mentioned abundant sign of bison, "numerous" antelope, and at least one grizzly bear, all apparently observed the day Bridger made his statement about the high passes (48).

Incidentally, Jim Bridger made only one published remark about the wildlife conditions in the present park area. The remark appeared in J.W. Gunnison's book The Mormons, or Latter-day Saints (1852), which quoted Bridger as saying that "Bear, elk, deer, wolf, and fox are among the game" in the Yellowstone area (26).

A number of writers have cited various early survey parties' reports on the park in the 1870s as proving that animals were rare in the park. The forthcoming analysis by Schullery and Whittlesey deals with all these sources in great detail, and so an example or two should suffice here to demonstrate the complexity of the information being used.

The challenge facing historians in using this material is to use it all. The mentions of animals are often quite incidental to the real reasons for the published reports, and so many writers were not consistent in mentioning animals they saw. For example, consider the Washburn-Langford-

Doane expedition of 1870. Nathaniel Langford was one of the diarists on this trip, and his account is often cited as proof of scarcity of game (39). But the party left a total of twelve written accounts. When these are all consulted, it becomes clear that they saw many animals, and evidence of many more.

For example, Lt. Gustavus Doane, leader of the military escort for the party, reported that near Mt. Washburn, "The ground was everywhere tracked by the passage of herds of elk and mountain sheep. Bear signs were everywhere visible" (4). In the same area, Cornelius Hedges reported that "bear and elk [were] very plenty" (29). In Hayden Valley, Doane reported that "elk were feeding in small bands on the other side of the valley." South of Yellowstone Lake, Doane reported that "The ground was trodden by thousands of elk and sheep" (4). Also south of the Lake, Warren Gillette reported that, "Occasionally where the trees are sparse, you see verdure suitable for the game that abound in this region" (10). Doane also noted that near Heart Lake, two of his privates "found game plentiful and tame, and had no difficulty in obtaining an abundant game supply" (4). These are only a few of the many accounts of animals left by this party.

This is not to say they always found animals; they didn't, and sometimes ran short of meat because animals were not successfully hunted for several days in a row. Like any group of travelers, some days they found game and some days they didn't, but they left much evidence of abundant game in the park area.

The Hayden Survey of 1871 provides an even more instructive example of the need to find all the historical sources and then use them carefully. Reading Hayden's published report alone may give the impression that little game was present, because Hayden reported seeing little (28). But remember that Hayden was there to survey geological and topographical features; game was not of scientific importance to his work. In fact, Hayden himself concluded, based on his observations, that game was abundant in the park, but that during the time of their visit it was scattered in the high country.

But using only Hayden's account again reveals the error of using too few sources. A full review of the many published and unpublished firsthand accounts of their visits make it clear they agreed that large mammals were abundant. For example, the Hayden party was accompanied by the now-famous western photographer William Henry Jackson, and several of his photographs show elk or elk antlers in park views, including a photograph of the party hunters with several dead bull elk near the Canyon, and two of the hunters with a load of elk meat on a packhorse (because of the slow exposure time necessary for photographs then, he was not able to photograph free-ranging animals). In Jackson's published catalog of his photographs on this survey, he noted that elk were "very abundant about the lake" (35). Jackson also photographed the Bottler ranch, north of the park near present Emigrant, Montana, showing a large shed with hundreds of large animals skins hung or stacked, evidence of the extensive skin-hunting then occurring in the park area.

It is important to know that these early accounts sometimes do not agree, even among members

of the same party. For example, Hayden reported little success at hunting for game in the park to feed the party, but other accounts, such as Jackson's and the unpublished diaries of Party member A.C. Peale (47), indicate that elk were killed regularly for food. The best hope for gaining reliable historical information from this kind of material is to use as much of it as possible, rather than rely on a few easily found items. The cumulative evidence makes it clear, in any event, that Hayden was justified in claiming that the park area contained a "good supply of game of all kinds" (28).

In 1873, Captain William Jones of the U.S. Army Corps of Engineers led a troubled expedition through the park, and reported animals abundant but difficult to hunt successfully. His report is sometimes even amusing as he sarcastically expressed his exasperation with his hunters for their incompetence. Near the east border of the park, along the upper Shoshone, he reported that "Elk, deer, and trout are abundant." In the mountainous terrain near the eastern park border, he found "fresh tracks of mountain sheep exceedingly numerous," and also saw two bears. He reported that three of his men, lost from the main party, killed an elk near Yellowstone Lake. Near the south boundary of the park, close to the Yellowstone River, he reported that "All through this basin game-tracks have been very abundant, but our party from its size makes a good deal of noise, which will account for the fact that we did not see a great deal" (33).

Theodore Comstock, a geologist on the Jones expedition, proved that Jones was right in assuming the party was too large to see much game. Comstock spent a few days alone or with one companion, on one occasion traveling from the Lake up Pelican Valley and then down to the Lamar Valley, hiking much of the way on well-worn game trails, several times seeing "numbers of elk," once seeing "a large drove of elk and some deer," and hearing a wolf howl (11).

This pattern of information is consistent for all of the early survey parties; It is not safe to use one account from a given visit, as the use of multiple accounts invariably reveals a greater number of sightings. In fact, it might be said as a general rule that the more accounts a party left, the more evidence of wildlife sightings they left.

More important than an objective consideration of a few accounts is analysis of the dozens of other accounts from the same period. For example, Senator John Sherman, in the park in 1881, said that "Elk, deer, antelope and bear were plentiful, and we had no difficulty getting all the fresh meat we wanted" (55). That these animals were still easily obtainable in 1881, after a decade of hide-hunting and casual shooting by tourists, is some indication of their great abundance. Numerous writers referred to the abundance of game, calling the park a hunter's paradise. In fact, of the many accounts that discuss game abundance one way or the other, only one or two actually believed that animals were not abundant. Virtually all of them believed, based on sightings or indirect evidence, that there were plenty of large animals in the park area in the period before 1882.

Another kind of evidence that has led some writers astray has been the official reports of park

managers, which have often been used in ignorance of their context. For example, early superintendent's reports are taken out of context to prove things they did not intend to prove. When Acting Superintendent Capt. George Anderson reported in 1891 that "the elk have increased enormously" he was referring in part to a perceived restoration of elk numbers following their artificial reduction by the hide-hunting that occurred in the 1870s and 1880s prior to the army's arrival in 1886.

Other factors that may have contributed to a perceived or real increase include the greater visibility of the elk that were no longer legally hunted in the park, the destruction of many of the park wolves and other predators by poison in the 1870s, and the cessation of elk hunting in Montana, which Anderson believed allowed the elk in the northern Yellowstone area to flourish.

Douglas Houston, in The Northern Yellowstone Elk: Ecology and Management (1982), has reviewed this army period very carefully, and found many inconsistencies in these early reports (32). Because it is the most complete review of the history of the elk population, Houston's entire chapter on this subject is appended to this report. It reveals the many complexities of using these early records.

We might summarize Houston's historical review by saying that it is often not clear when early administrative reports included only the northern herd, the northern herd and one or two others, or even all nine park elk herds. In short, isolated quotations are nearly meaningless in a scholarly dialogue of elk numbers because their context is so important. For example, some early reports appeared to include the Yellowstone Timber Land Reserve, an area of hundreds of thousands of acres created in 1891, immediately to the east of the park, in their tallies. Thus it is that between 1891 and 1910 estimates for park elk varied between 25,000 and 60,000. Picking a couple of numbers out of that complex context adds nothing but confusion to the dialogue.

Light overviews of this complex historical story rarely can do justice to it. Only scholarly examinations will yield the information necessary to judge the situation accurately, and even then the details may remain unclear. The most current paleontological and archeological research indicates large ungulates were abundant in Greater Yellowstone. The most exhaustive review of the historical literature agrees.

The Biological Context

There are several general areas of interest in Northern Range ecology: erosion, grasslands, aspen and willow, and carrying capacity of the Northern Range. Part of the issue of carrying capacity concerns the interactions between different species of ungulates, as well as between ungulates and other animals.

It is important to note at the outset, however, that the issue of Yellowstone's range conditions is not simply a scientific argument. There are fundamental philosophical issues here as well. The most central is that the park, like all national parks, is not being managed to achieve the

objectives of commercial livestock ranges. By law and policy, the parks are managed to preserve, to whatever extent possible, native North American settings (5,30,32). A century of management experience and an accumulation of legislation has led the national parks to the point where management is aimed at preserving not merely scenery and favored assemblages of animals, but the processes that maintain these features of the landscape. This means that what has been called "ecological process management" is aimed at maintaining something more dynamic than a giant outdoor garden or zoo (5). Instead, the parks, to whatever extent practical, are providing the ecological setting with the opportunity to exercise its prehistoric variability, in which all the factors, including climate, erosion, predation, herbivory, fire, and many others interact. The interaction of these forces provides, in turn, many opportunities for enrichment of human knowledge and for recreation in a wildland setting.

This is a difficult and complex undertaking, because virtually all North American grassland communities have been altered extensively by contemporary human uses, especially those associated with agriculture and livestock. 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 undisturbed, operating as it did in prehistoric times, with its native complement of grazers and plant species (22).

Yellowstone National Park has been identified by scholars as one such place (22,23,24,30,40,41), and even Yellowstone has suffered from localized overgrazing due to human manipulation of wild animals (at and near feeding grounds, for example) and from early livestock-grazing practices on lands later added to the park. The accidental or intentional introduction of dozens of species of non-native plant species in some parts of the park further complicates its status as a window to the prehistoric past. The incompleteness of the park itself as an ecosystem further complicates this situation. 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" (31).

It is odd that, despite widely-published statements such as Houston's, supported by a massive scientific research effort, there is still a surprisingly common belief among the regional public that the National Park Service has as a policy goal the preservation of some idealized ecosystem entirely within the park boundaries. "Common knowledge" on this subject, much like common knowledge about the "overgrazing" of the Northern Range, will probably persist indefinitely in the minds of some portion of the public, a misfortune that could probably be reduced by a greater agency effort to communicate research findings to the public.

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 (25). Much of this confusion results from our changing understanding of how range ecosystems function. In the 1920s, and into the 1950s, it was widely believed that most vegetation systems--range or forest--tended to reach a stable state, a sort of ideal equilibrium, that was easy enough to manage. In recent decades,

however, instability has become more apparent, and has become especially important to students of wild ranges that are grazed only by native ungulates.

Research into these questions has more and more focused on sites like Yellowstone's Northern Range--areas that, for all their localized imperfections, are the closest we can come to seeing truly wild ranges. The researchers are telling us many interesting things, some of which will be reviewed below. Perhaps most important of all, they are telling us that a wild range, grazed only by native ungulates that are allowed to reach whatever population levels nature will sustain, will not look the same as a commercial livestock range. Wild ungulates will not use the range in the same way that livestock do; they will use the plants differently, they will move as the seasons dictate rather than when humans decide to move them, their numbers will vary with environmental conditions, and the range's appearance will depend upon many natural factors rather than upon close supervision by a human manager whose primary goal is to maintain a high economic carrying capacity on the range.

This is not to say that either type of range is necessarily better looking, or better managed; both management approaches have critics today. It is, however, to say that for a livestock specialist to come into Yellowstone Park and judge it by the standards of livestock management is as inappropriate as going to a livestock range and expecting it to resemble a primitive ecosystem. 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, we can expect grim pronouncements from the livestock industry about Yellowstone to continue, just as we can expect a host of wildland ecologists to 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. In the following paragraphs, we summarize some of the recent research findings regarding the Northern Range. Keep in mind, however, that, as mentioned earlier, much work is still underway; there is still much to be learned about this complex ecosystem. Thus, what follows is only a summary of some of the recent work on the Northern Range. Publication of major reports will be announced as they are completed, and many investigators will also pursue publication of their findings in technical journals.

Erosion

Many observers from both government agencies and other institutions have expressed the belief

that elk accelerated erosion at key sites on the Northern Range. This was a matter of great alarm, because soil has long been considered a capital asset, and any kind of erosion has been viewed as evil. The idea of accelerated 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. However, a recent review of numerous historical photographs dating as far back as 1871, compiled and interpreted by Drs. Douglas Houston and Mary Meagher (National Park Service), revealed that these sites looked essentially the same more than a century ago, prior to the supposed increase in elk-caused erosion (32). This analysis and interpretation has not been challenged by subsequent investigators; the major erosive sites, especially geologically sensitive areas such as Mount Everts near Mammoth Hot Springs and numerous steep slopes in the upper Lamar River drainage, have not significantly changed during the history of the park. Major erosion events, they concluded, are an unavoidable and significant part of the Yellowstone landscape, just as they are of many other landscapes in the west.

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 Soil Conservation District, Montana Water Quality Bureau, U.S. Soil Conservation Service, U.S. Geological Service, and the National Park Service), mapped erosive lands in the Yellowstone River drainage from the park to Livingston, Montana. The study identified a number of key areas, including those geologically sensitive ones mentioned above, as by far the most important sediment producers. These sites are, generally, either on slopes too steep to be used by ungulates, or are not even on the winter range (21,56).

More recently, a team of researchers from the University of Minnesota and the Carnegie Museum of Natural History analyzed pond sediments of eight lakes on the Northern Range; lakes are unusually sensitive indicators of erosion and other environmental changes in small drainages. They found no evidence to suggest that elk numbers changed dramatically during the past 150 years, as has been proposed, and they found no evidence that ungulate grazing is affecting vegetation or soil stability (20,66).

It is important to understand that erosion is not seen, either by researchers or managers, as a simple issue. They are not saying erosion does not occur. It does occur, and on a grand geological scale. Yellowstone is a relatively young landscape, and it is still carving its canyons and in other ways moving sediment; one view of the Grand Canyon of the Yellowstone River would convince most observers that this is true.

As well, no one is claiming that ungulates do not move soil, or do not at times contribute to sediment loads in park streams. At several valley locations such effects are apparent. But the wholesale movement of sediment by ungulates across the Northern Range (in what is known as sheet erosion), or a sudden increase in erosion caused by a sudden increase in the intensity of elk grazing, as presupposed by many earlier observers and researchers, have been disproved. Even if there were no ungulates at all on the Northern Range, the rivers would become muddy. The sedimentation process is geologically and climatically driven, and is most noticeable during

spring runoff and during intense summer thunderstorms.

The question that remains is not whether ungulates do move some soil; they do. The question is this: does that movement represent a departure from the conditions that prevailed prior to the establishment of the park? Keep in mind how complex soil processes are. Just in terms of soil movement, there are important issues not addressed in traditional evaluations of the range. Pocket gophers, for example, move tons of soil, and "plow" acres of soil in activities perhaps more influential than ungulates on soil processes. Grasshoppers and nematodes appear to consume much more vegetation than do ungulates. Until all these other aspects of the soil and its vegetation on the Northern Range are fully sorted out, it would be incautious, if not foolhardy, to pronounce too confidently upon just how this ecosystem is functioning (32,46).

Studies of erosion and its role in Northern Range ecological and hydrological processes have proceeded from the grandest scale to the most local, starting on the highest, steepest, and most easily eroded slopes and working down the drainages to the river valleys. Research has now resolved that the gross movements of material originate in steep and geologically sensitive areas where ungulate activities are not a significant factor. Research has also resolved that these erosive processes have been underway since prehistoric times (20,66).

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. Now the need is for additional information on the localized riparian areas associated with ungulate winter ranges; though the amount of material potentially involved in erosion in these areas is much smaller than that involved in the steep headwaters, winter range riparian erosion is nonetheless an important topic for research emphasis (38). A number of research initiatives involving riparian areas are either in the planning stages or underway; it is possible to greatly improve and refine present understanding of the role ungulates play in these extremely sensitive ecosystems.

Grasslands

Perhaps of greatest concern in the long history of the Northern Range issue has been grasslands. The winter range has been at the center of this subject; the much larger summer ranges have not been judged unhealthy in these dialogues. Many investigators and observers described the winter range as overgrazed, especially since the drought of the 1930s (history of this research reviewed in 32). As mentioned above, the concept of overgrazing has undergone rapid evolution, so that what a wildland ecologist might consider normal grazing, a livestock manager might consider unacceptable, and vice versa. Thus, recent scientific investigators have approached the subject of overgrazing from a broader and more ecosystem-related perspective.

Michael Coughenour (Colorado State University) and Francis Singer (National Park Service) have conducted a new and especially broad analysis of the overgrazing concept as it can be applied to Yellowstone (15). They 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." Of these various schools of thought on overgrazing, it was determined that by any of the modern standards, the Northern Range grasslands are not overgrazed. This comparative review is essential to an understanding of the differences between various concepts of overgrazing, partly because it reveals that, by any of these definitions, it is difficult to judge the Northern Range as overgrazed.

Grassland studies have been more or less continuous in Yellowstone since the 1950s, and the park's flora has been catalogued (17). The intensity of this work increased following the 1986 Congressional mandate to investigate the grazing issue, as work was initiated by even more researchers, from numerous universities and several agencies. These grassland researchers have agreed that the Northern Range is not overgrazed. It is worth reviewing these findings here, to show the breadth of the disciplines applied to this question, and the complexity of the ecological processes that the research has revealed.

Douglas Frank of Syracuse University studied the interactive ecology of plants, large mammals, and drought on the Northern Range. He concluded that ungulate grazers "stimulate plant aboveground growth by causing plants to allocate to aboveground parts, while making all resources, light, water, and nutrients, more available." (22,24). In this, he found that Yellowstone was similar to another great wildland ecosystem, the African Serengeti.

This is a milestone scientific finding; it dramatically reverses traditional views by demonstrating that not only do 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 (22).

Another important point provided by Frank concerned the timing of ungulate use of the winter range. Like National Park Service Plant Ecologist Don Despain (unpubl. data), Frank 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 to higher elevations and summer ranges. Unlike fenced or penned livestock, they do not remain on any given range for long, but move as the mood strikes them or as environmental conditions dictate. This means that they are never grazing winter range forbs and grasses during the critical and most vulnerable growing period of those plants. By the time the elk return to the winter ranges,

the plants have stored their essential energy reserves in their root system, and the elk eat the aboveground plant matter without affecting the plants' ability to regrow the following year (22). 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.

Linda Wallace (University of Oklahoma) studied the effects of drought, fire, and grazing on Northern Range grasslands as well (59,65). Among her conclusions was that grazing increased plant species diversity, a finding as significant as the above-mentioned demonstration that grazing enhanced plant growth. Wallace also noted what has been observed by many previous scientists, that "climate has a stronger control on system structure than does grazing."

An important aspect of these studies is their attention to many environmental factors at once. Rather than focus on the immediate effects of ungulate grazing alone in a given year, they instead measure other important factors, especially climate, that appear now to be fundamental in controlling ungulate grazing and population levels. This approach allows for a more ecosystem-based analysis than past studies. In 1982, Houston 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" (32). Wallace, Frank, and other studies are providing that look, and the results are proving to be fascinating and important.

Coughenour, Singer, and James Reardon (National Park Service) revisited the Parker Transects, a set of measurement sites established in 1958 to assess long-term trends in distribution and composition of grassland plant species on the Northern Range. In the 1960s, elk numbers were artificially reduced to less than 4,000 on the northern range, before manipulation of the population in the park ceased in the late 1960s. Since then, the Northern herds of elk and bison have increased substantially, to as many as 20,000 elk (and currently about 16,000), and 3,000 bison, their numbers varying depending upon a variety of environmental conditions. Coughenour found that "dominant perennial grasses either maintained their relative abundance or increased. Forbs decreased in relative abundance, and increased after 1986 both in and out of exclosures in response to drought. On the basis of these trends, we conclude that elk grazing has not degraded the Yellowstone Northern Winter Range" (16).

Coughenour also 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" (13). Like several other investigators, Coughenour emphasized the importance of climatic conditions in affecting grazing responses of plants (13,14).

Singer and Mary Harter (National Park Service) 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...Morphological characteristics were not influenced by grazing, with the exception that vegetative culms of grasses were shorter on grazed sites (60).

The use of exclosures (that is, ungulate-proof fences) to study vegetative 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 growth is higher; if the exclosure includes shrubby vegetation, the difference is even more dramatic. These exclosures are easily seen at several locations on the Northern Range. The implication of the publishers of the photographs, however, 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 <u>if it had no large animals on it at all</u>. It is assumed, by all researchers, that vegetation that is not eaten will grow taller. That proves nothing in itself, however effective it may be in dramatizing perceived problems.

Though there is always room for more study, the grassland studies conducted the past two decades, in which the range was evaluated not for its similarity to a commercial livestock range but for its ecological well-being as a wild herbivore-rangelands system, show that the Northern Range is in no danger. When compared to the few remaining wild herbivore-rangeland systems elsewhere on the earth, Yellowstone looks fine (40,41). These projects place much higher emphasis on climate than earlier studies did, and suggest that most of the variation observed in the condition of the vegetation from year to year is linked more to climate than to grazing.

What is occurring on the Northern Range is actually a very exciting process; it might be said that the grasslands and the grazers coevolved over the past several thousand years to live with one another on the range. The vegetation we see today on the Northern Range is the product of that long process. The entire life cycle of the ungulates--cropping of the standing vegetation, tillering of the soil, promotion of dense, short vegetation stands of high diversity, deposition of feces and urine with their chemical contribution to soil condition, and the eventual contribution of the dead ungulates to the whole biological system--are essential parts of the maintenance of these wild grasslands. If this interaction of animals and vegetation is judged now to be somehow wrong, then it has been wrong for thousands of years.

These grassland researchers are telling us, in effect, that at least 90 percent of the Northern Range--the grasslands that provide most of the food for the ungulates is in good health. In the remaining percent, especially in the riparian areas, there are still many unanswered questions.

Willow and Aspen

Changes in willow and aspen were noted long ago on the Northern Range. In fact, it is always a little puzzling when a sudden flurry of attention is focused on these issues, because the National Park Service has published widely on the changes for several decades. Indeed, most of the attention traditionally drawn to the two issues has been done so by National Park Service researchers (reviewed in 32).

The history of the status of willow is well-published, and a variety of recent research is now complete, nearing completion, or underway (reviewed in 32, additional studies include 7,8,9,36,37,59,61). Willows occupied perhaps 1 percent of the Northern Range a century ago, and have reportedly declined to about half that today; early historical photographs show dense, high stands of willow in some locations where the plants are now gone or in a shorter form.

There are different schools of thought on the willow. One view is that willow were common in Yellowstone before 1890 because ungulates were scarce (36,37). This view, though still very popular in many circles, now goes against the accumulating prehistoric and historical evidence mentioned above, that suggests that these animals were quite common in the park prior to 1890 (27,54). Thus, there are a number of theories regarding the declines of willow, and the question is still open (18).

One recent study concluded that unnaturally high levels of ungulate use were solely responsible for willow decline (36). Other studies suggest that though ungulate browsing is the immediate cause of the willows being shorter, there may be other factors involved that allow ungulates to browse willow shorter than at other times in the past. These include the possible effects of fire suppression since 1900 on willow condition or on fluvial processes conducive to willow growth (32), possible changes in biochemical factors that make the various willow species more or less susceptible to browsing (6,18,61) and, perhaps most important, ongoing long-term climate changes (32).

The subject of climate change brings us to a recent misunderstanding that has developed over the nature of these climate changes. At least a few people apparently have the mistaken idea that ecologists are claiming that human-caused global warming, or greenhouse warming as it is sometimes called, has affected shrubs and trees on the Northern Range. We are not aware of any such statement, though a number of researchers, both within and outside of the NPS, believe that in the future global climate change may play a role in defining Greater Yellowstone ecological processes (1,51).

However, long-term natural changes in climate, over the course of the past several thousand years, are well documented in the ecological literature, and certainly have played a key role in the distribution and abundance of various plant species. Keep in mind that only a little more than 10,000 years ago, the entire Yellowstone region was largely covered by glaciers, and that 6,000 years ago, it was so much drier than it is today that Yellowstone Lake did not even have an outlet. More recently, about 1,500 years ago the Lamar Valley underwent a transition from a wetter tall-grass prairie to a drier, semi-arid bunchgrass plant community (3). We assume that these changes would continue today as they have in the very recent past, even were global climate change not to occur. The variations in regional climate are sometimes dramatic, and in ecological terms they are frequent. Scientific monitoring of these variations has gone on for little more than a century, hardly long enough to reflect the full variability that the ecosystem experiences.

It is also important to keep in mind that these climate changes, at least from an ecological

perspective, were neither good nor bad. As mentioned earlier, environmental variability is a hallmark of natural ecosystems, and there is ample evidence of such changes in Yellowstone both historically and prehistorically (3,20,66). The long-term drought of the 1930s is only one example. The well-documented "Little Ice Age" that cooled much of the northern hemisphere for at least two centuries prior to 1850 is another. One of the many scenarios that must be considered in analyzing the very complex issue of vegetation change is the possibility that this long colder period deepened snow on the Northern Range and made it less accessible to ungulates during the winter season, thus reducing their impact on willows and other plants, and resulting in the more robust appearance of the willows and aspen in early photographs of the park. Until questions like this are more fully investigated, it is premature to conclude exactly what the relationship of vegetation, climate, and ungulates is.

Long-time residents of the Yellowstone region know how little it takes to affect the vegetation. A timely period of warm Chinook winds--just a few days--can break a hard winter, and a timely spring rain can cause major increases in grassland production. The single summer of 1988, during which precipitation was extremely low (when judged by the short perspective of our century of records) provided ample evidence of the effect one such year can have on the system. The environment of the region around Yellowstone is sensitive to what, in other parts of the country, might seem minor changes in climatic conditions.

In any case, the willows and other riparian vegetation certainly require further attention. The willow of the Northern Range have not changed appreciably since about 1959, when the declines ceased (61). There are more than 20 willow species on the Northern Range, and one of the questions that must be asked in greater detail is how and why different species thrive or do not thrive. Incautious comparisons of these species are "apples and oranges" exercises that may be quite misleading, or simply wrong.

Another traditional approach to analyzing park willows is the comparison of park willow communities with willow communities outside the park. There are a number of problems with this. One is the possible differences in species between the sites considered "unhealthy" and those that are not. Another is that the willow communities that are pointed out as being less browsed are typically in areas of deeper winter snows; they are, by virtue of their locations, not exposed to winter browsing pressures as are the ones at lower elevations on the Northern Range, and thus are bound to be less browsed. Willow communities <u>in</u> the park that have greater snow depth are often quite tall, too. Willows on heavily used winter ranges throughout the Greater Yellowstone Ecosystem tend to be shorter, as would be expected.

But the most fundamental issue is the one that too often gets lost in such discussions. No one denies that willow that are not eaten will usually grow taller. The mere fact that some park willow are shorter than non-park willow means little. In areas where the snow is deeper or the number of ungulates is limited by humans (as it is in many non-park willow communities), the willow will quite naturally grow taller. That is obvious.

There is a presumption in many of the criticisms of the Northern Range, that more or taller

vegetation is necessarily more healthy or more appropriate. If you fence or otherwise protect vegetation, it will grow taller, and may look more aesthetically pleasing. But you have not necessarily proven anything about the well-being of the willow community, much less about its being somehow "overbrowsed." It is clear to us that the Northern Range has for a long time been inhabited by many ungulates. These animals will always have some effect on the vegetation; indeed, often their effects are quite visible and significant. But what does that effect prove? Remember that the goal of the park is not to produce a garden-like setting in keeping with some predetermined notion of what size plants look nicest. The goal is to preserve the ecological processes and the landscapes they maintain. The questions we now face are, are ungulate effects on the landscape within the realm of variability one could expect in a healthy wild system, and if not, why not?

Much the same questions must be applied to the study of park aspen. Aspen occupy about 2 percent of the Northern Range, and there has been a decline of perhaps 50 percent in the number of tree-sized aspen clones during the past 80 years (32). In many cases the aspen clone is still there; it is now in a shrub form, apparently unable to escape elk browsing and grow to tree height. The reasons for this change have been the subject of study and heated discussion for many years.

Aspen is an especially popular part of the western landscape. Because of its beauty, as well as because of what it contributes to the ecological diversity of a landscape, aspen, like willow and other comparatively minor plant communities on the Northern Range, is of great interest both to the public and to the scientific community. Aspen have been especially interesting to scientists for their responses to the fires of 1988 (36,49,50).

It appears that occasionally, perhaps only rarely, aspen meet circumstances in Yellowstone that allow them to escape browsing and grow to tree-size. Exactly what that set of circumstances is remains unclear. One such period occurred in the 1880s and 1890s, when elk were, according to the historical accounts, abundant on the Northern Range, and when many of the adult aspen trees that are now growing old got their start. A recent tree-sectioning study revealed that 98 percent of the old aspen trees on the Northern Range showed clear evidence of annual browsing in their first two years of life. Some set of circumstances, almost certainly involving climate, allowed them to escape browsing at that time; only a few have grown to tree size since then (19).

Because of the numerous variables in aspen ecology, and because we know that elk were abundant in the park area prior to 1890, we are hesitant to accept the simplistic traditional view that an abrupt change in elk numbers is solely responsible for the aspen decline. Elk are the immediate cause of their present inability to reach tree size, because elk eat the young trees, but that does not mean that elk are the sole cause. The harder we look at this question the more complex it becomes, and the less persuasive we find the simplistic answers being offered by many casual observers, and even some scientists.

For example, a little-appreciated aspect of aspen ecology in Yellowstone is that the park is

marginal aspen habitat, several hundred miles north of optimum aspen habitat in the Rocky Mountains. A recent study of lake sediment pollen accumulations over the past 10,000 years showed that aspen have always been a minor part of the plant community here (66). That suggests that it takes only slight environmental changes to affect their success. Climatic records, as found in tree-ring studies and other sources, indicate that Yellowstone's climate is anything but stable, and so aspen must occasionally be subjected to changes here. We are left with more questions than answers about aspen, but we have hopes that continued research will help us understand the relationship aspen has with the other elements of its environment.

Carrying Capacity

For more than half a century, biologists have attempted to define the carrying capacity of the Northern Range. Past estimates ranged as low as 5,000 and as high as the 20,000 or more that was made possible in part by the recolonization of habitats north of the park during the 1980s (reviewed in 32).

When artificial control of the elk and bison populations was terminated in the 1960s, both animals increased in numbers. Some careless journalists have reported these increases as proof of overpopulation, when in fact the animals were merely responding to their release from extremely tight control. The more recent increases, in the 1980s, when the elk population grew from around 12,000 to as much 20,000, were apparently the result of several factors, including the reoccupation of large amounts of winter range north of the park and mild environmental conditions, especially open winters.

The northern Yellowstone elk herd is too often viewed without reference to the other greater Yellowstone herds, which offer further proof that nothing unseemly was happening as the northern herd increased. In fact, most of the greater Yellowstone elk and deer herds, managed under a variety of approaches and goals, experienced large increases during the 1980s, responding to favorable conditions throughout the region (58). 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 conditions allowed.

An intriguing related issue has been that of beaver on the Northern Range. At times beaver have been quite common on the Northern Range, but by the 1880s their numbers may have been greatly reduced by commercial trapping (54). But even after that, the history of the beaver is quite difficult to sort out, and opinions differ on what has happened to them. For example, because beaver numbers are apparently much lower today than in the park's early days, it has often been proposed that elk outcompeted beaver on the Northern Range, destroying their habitat and food. However, the beaver experienced a pronounced population irruption between 1900 and 1920, in the face of a very large elk population (32), hardly suggesting that they could not compete with the elk. Ironically, in the 1920s it was believed that an overpopulation of beaver, rather than of elk, would soon lead to the destruction of the aspen on the Northern Range (54). Beaver still occupy numerous locations in the park, including sites on the Northern Range, and

appear to be in no danger of disappearing (12). Continued study of their habitat may yield helpful information about their changing population status.

As with the grazing issue, philosophical differences have gotten in the way in the dialogues over carrying capacity. Recently, ecologists have recognized that there are at least two general types of carrying capacity (15). One is the traditional type, now known as economic carrying capacity. That is the number of animals that is believed to make the best sense for a livestock range. The other is ecological carrying capacity. That is the number of animals that nature, left alone, would put on the range. The two are often quite different. Perhaps most important, ecological carrying capacity will vary greatly, even from year to year, depending upon the environmental factors that dictate food availability.

Variability is a very important aspect of this. Modern commercial livestock managers recognize that their standing crop of feed will be much poorer in a very dry year, and a series of wet years, in which the rains come at just the right time to enhance plant growth, will allow for much more livestock to be grazed. But commercial livestock managers work toward a general goal of stability in their vegetation management, while wildland range managers expect, indeed respect, variability.

Yellowstone provides a vivid example of just this variability. In the six years prior to 1988, the summers were unusually wet, with some months experiencing 200 percent of normal precipitation, allowing the ungulates to increase their population size year after year (45,53,62). The winters, on the other hand, were unusually dry, 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 grazing potential.

The winter following the fires further compounded the challenge for the animals, as it was the first in many years with even normal snowfall, thus increasing winter stress on animals that had experienced a number of mild, easy winters (62). Many animals died as a result of this "triple whammy" delivered by nature, and no doubt similarly dramatic events have occurred in the thousands of years elk have been here. Elk population recovery was fast, facilitated by the return of the wet summers, dry winters, and possibly the superior quality of post-fire forage.

Such variability seems to be central to many ecosystems. Often it is the extreme years that really test and control populations. While such variations are the last thing that a commercial range manager may want, they are the very soul of a wild system, and their functionings are one of the things that keep the Yellowstone ecosystem vital and dynamic.

This background is necessary to understand the issue of the size of Yellowstone elk and bison populations. The traditional view, espoused for many years by scientists in the state and federal agencies and in the university community, was that the park was overpopulated with elk (reviewed in 32). However, that view is now questioned for many reasons.

For one, all of the grassland studies, mentioned above, do not suggest that there are too many elk eating the grasses. For another, a study of summer ranges conducted by a team of University of Wyoming researchers, concluded that the current populations of elk in the park are well within the capacity of the summer ranges, and if they are currently larger than anticipated, it is the result of climatic mildness (44,45).

For another, there is a long-standing paradox in the notion of overpopulation of elk. As late as the 1960s, professional researchers reported that the park was badly overgrazed and that elk and bison population numbers should be kept low. Since then, as park management changed direction, this reportedly "overgrazed" range was somehow able to fuel an increase in the northern elk herd from less than 5,000 to as high as 20,000, and then was able to maintain that higher level for nearly a decade. We are left to wonder: How could a badly overgrazed range do that? 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 that are hunted in the fall when they migrate to lower ranges north of the park. These things could not happen without a robust source of nutrition.

The increase in numbers of bison leaving the park, especially to the north, in the late 1980s and early 1990s has also caused concerns related to overpopulation. These migrations are seen as somehow proving food shortages, caused by overgrazing, in the park. Mary Meagher (National Park Service) has evaluated these movements (42,43), and an interagency bison management plan is now in preparation. The grassland studies cited above indicate that the range is not overgrazed. Meagher's observations further indicate that the migrations sometimes occur regardless of snow depth or forage availability. Once the migratory habit is learned, as it now is in the Northern Range bison herd, 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 or even excellent condition; they were not starving for lack of food in the park. They were moving, the way bison moved for millenia prior to the settlement of the west by Europeans.

The Northern Range continues to produce a large number of elk, bison, and other animals year after year. As elk numbers increased in the 1980s, so did bison, mule deer, and pronghorn. Recent studies of several carnivores revealed that these ungulate populations are an important nutritional source for coyotes, mountain lions, grizzly bears, black bears, and a number of smaller predators and scavengers. The increases in Northern Range herds were parallelled by increases in the ungulates of other Greater Yellowstone Ecosystem herds. The grasslands of the Northern Range, according to numerous scientists from both management agencies and other institutions, are not suffering, the willow stopped declining more than thirty years ago, and the animals do not show any signs of undernutrition beyond those naturally expected among the older animals or when suddenly the environment shocks the herd with a hard winter. The range's continued high production of ungulates seems like the best proof it is not overgrazed.

There is still much to be learned, and many questions to be asked. One of the foremost lessons of the recent Congressionally mandated research initiative is that a large, wild ecosystem

experiences many changes, and is subjected to great variability, over time, so that even decades of observation and study will not prepare managers for all eventualities.

Conclusions

With proper communication channels open, there is much to be gained by different land managers understanding how the others think and work. What we are hearing in Yellowstone, especially from some of the most foresightful and prominent ecologists working here, is that the park has important lessons to offer other land managers. They are telling us that the park, with its representative native fauna and vegetation still largely intact, could serve as a baseline, a valuable measuring stick by which others can assess the changes that have occurred on more intensively managed lands.

Very few lands are managed with the goals of national parks; we are not making a value judgment about one management approach being somehow better than another. However, it is the very rarity of the kinds of landscapes that occur in national parks that make them seem so different to most observers. It is unfortunate that "different" is too hastily equated with "wrong." In fact, it is because they are different that national parks can contribute important knowledge about other land management practices. The more any land manager knows about the inherent tendencies of a landscape, the better that manager can get what is needed from the land. Yellowstone provides a rare opportunity to ask questions about such natural tendencies.

With that background, we offer a few general conclusions based on the research summarized above.

1. The Yellowstone Park area, including the park itself, was inhabited by large numbers of ungulates prior to the establishment of the park in 1872.

2. Longstanding geological processes, not ungulates, have been the primary factor in erosion on sensitive erosive lands on the Northern Range, and on associated summer ranges, in Yellowstone Park.

3. Even in the face of what are widely perceived as high numbers of ungulates, the Northern Range grasslands are not deteriorating, and appear to be primarily under the influence of climate.

4. Even in the face of what are widely perceived as high numbers of ungulates, the Northern Range willow communities are not deteriorating beyond their condition in 1959, when it was mistakenly believed that reductions in ungulate numbers would allow willow and aspen to prosper.

5. Aspen and willow have been comparatively minor plant communities on the Northern Range for 10,000 years, and have undergone substantial variations in their success during that time.

6. Ungulate grazing not only causes no decrease in biological diversity among native plant species, on the Northern Range, it enhances that diversity.

7. High numbers of elk and bison on the Northern Range do not appear to be negatively affecting the numbers of other ungulate species, and are a crucial source of nutrition for several predators and scavengers, including the threatened grizzly bear.

8. None of the traditional measures of animal fitness, including winter fat, winter mortality of prime-age animals, birth weights, or antler size, indicate any nutritional problem in the Northern Yellowstone ungulate herds. They are thriving, which should not be possible if the range has been chronically overgrazed for thirty years.

9. Yellowstone's Northern Range continues to provide ecologists with one of the 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 wild grazing systems.

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Appendices

Note: Papers listed in bold in the bibliography are appended here, either entirely, in part, or in abstract. Papers appear in alphabetical order by author's name.

Abstract from
Plants and Their Environments: First Biennial Scientific Conference on the Greater Yellowstone Ecosystem
September 16-17, 1991
Mammoth Hot Springs
Yellowstone National Park, Wyoming

GRASSLAND CHANGE OVER 2000 YEARS IN NORTHERN YELLOWSTONE PARK

Barnosky, E.A. (Department of Integrative Biology, University of California, Berkeley, CA 94707)

Plant communities of the Northern Range in Yellowstone National Park are composed of a patchwork of microhabitats locally governed by a variety of environmental factors including slope, aspect, substrate, effective moisture, and soil type, to name a few. Along the Lamar River upstream of its confluence with the Yellowstone River, microhabitat ecotones are especially pronounced along moisture gradients. The majority of the large till-covered surface above the river is sparsely vegetated with grassy patches and sagebrush (*Artemisia*). Mesic sites with denser grass are found in small swales and drainages. North-facing slopes are covered with Douglas-fir (*Pseudotsuga menziesii*) forest.

Evidence from a paleontological site, Lamar Cave, suggests that the spatial coverage of these and other microhabitats has changed during the past 1700 years. At least 1500 years ago, the prairie vole (*Pitymys ochrogaster*) occupied the study area, as did the western jumping mouse (*Zapus princeps*). Neither now occupy the study area and both are tall-grass inhabitants today. Also at 1500 years ago, relative percentages of small mammals [voles (Microtus)] that dwell in mesic microhabitats today were prevalent over those that favor open, xeric grasslands [ground squirrels (*Spermophilus*)]. By 1000 years ago, this condition was reversed with ground squirrels dominating the faunal assemblage at the cave and the prairie vole and jumping mouse absent from the record. Slightly more mesic conditions have returned since 1000 years ago, evidenced by a slight rise in vole percentages relative to ground squirrels; however, the present is still drier than the mesic conditions of 1500 years ago.

This evidence from the small mammal fossils of Lamar Cave indicates that grass density has changed over 2000 years and suggests that microhabitats expand and contract with changing environmental conditions, in this case probably effective moisture.

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WATER STRESS AND SECONDARY METABOLITE PRODUCTION IN SUPPRESSED, GRAZED AND INTERMEDIATE, UNGRAZED WILLOWS

Cates, R.G. (Department of Botany and Range Science, 495 WIDB, Brigham Young University, Provo, UT 84602), F.J. Singer, and L. Mack

A significant decline in willow (*Salix* spp.) abundance on Yellowstone's Northern Range was observed between 1919 and 1938. This decline appears to have continued at a slower rate in some areas and has stabilized in other areas. Consequently, many willow individuals or clones have persisted for at least 30 years as short (0.3 m), suppressed, non-seed producing members of the plant community. At other sites, willows of intermediate and tall height classes that possess good access to surface water show adequate growth, productivity, little dead woody material, and some reproduction. In general, the former group is heavily utilized by ungulates and the latter group less so.

Little is known about water stress and secondary metabolite or defensive compound production between these two groups of willows, nor how these differences may vary among species and sites. Presented in this paper are a comparison of the level of water stress and secondary metabolite production between suppressed and intermediate or tall willows from different sites, species differences in water stress and secondary metabolite production, and the effect of the 1988 fires on water stress and secondary metabolite production of willows. Pre-dawn water potentials taken from ungrazed tall willows showed significantly greater water stress than the suppressed, grazed group. Burned willows were found to exhibit greater water stress as compared to unburned willows. Species differences due to burning when compared to the unburned controls were less frequent as compared to differences found among grazed and ungrazed species. Water potential data indicate that *Salix wolfii* was experiencing in 1989 a high degree of water stress at the Upper Slough site. This stress may result in greater ungulate utilization of this species. Finally, highly productive willows of intermediate height showed greater water stress than did the suppressed, grazed willows.

The tannin content in *Salix bebbiana* twigs and leaves was found to be 42% lower in suppressed, grazed willows as compared to the tall, ungrazed willows. Also, 8 of the 11 phenolic - flavonoid glycosides decreased in suppressed, grazed willows as compared to the tall, ungrazed controls. Alternatively, twig and leaf samples from suppressed, grazed *Salix pseudomonticola* showed significantly higher tannin levels and only 3 of 11 glycosides decreased in concentration as compared to the ungrazed tall willows. This willow also showed less water stress than did *S. bebbiana*. For both *S. boothii* and *S. geyeriana*, burned plants were significantly lower in tannin content in twigs and leaves, and more phenolic - flavonoid glycoside compounds decreased in concentration. It appears that grazing and burning do not have the same effects on water stress, and tannin and phenolic - flavonoid glycoside production.

INFORMATION PAPER NO. RM-1
Yellowstone National Park
National Park Service
U.S. Department of the Interior

S. L. Consolo
Management Biologist
February 28, 1990

BEAVER IN YELLOWSTONE NATIONAL PARK

Beaver have lived in Yellowstone Park since its inception, although the riparian areas in the park vary widely in their ability to support persistent colonies. In much of Yellowstone, beaver colonies are widespread and ephemeral (Houston 1982). However, a survey completed in 1988-89 found beaver present and active in at least 43 stream segments or lakes in the park (Consolo and Hansen in prep.)

In 1988, resource management staff began a parkwide survey to document presence and distribution of beaver. Based on previous observations and surveys, 84 lakes or stream segments were prioritized for ground survey. Two aerial surveys were also completed to help identify potential beaver sites. Between May and October of 1988 and 1989, ground survey was completed for 88% of the targeted routes, representing approximately 460 km of riparian habitat. Beaver activity was characterized as present or recent, based on animal observations or finding green leaves or mud on beaver dams or lodges, recently flooded vegetation, fresh cuttings, wood chips, and/or caches. Old sites were characterized by the absence of any recent sign and evidence of abandonment, such as collapsed lodges, grayed tree stumps or cut logs, and barely evident or long-breached dams.

Current activity was evident on 43 lakes or stream segments 5 km or longer; 82 sites or areas showed signs of previous activity, and 15 locations had signs of both present and previous activity. A total of 140 lodges were located, of which half (71) appeared active, 8 appeared recently abandoned, and 61 looked old. Signs of numerous, persistent beaver colonies were found in the upper Yellowstone River/Thorofare region, the Bechler region, the lower elevation reaches of the Gallatin River drainage, and portions of the Madison River drainage. Evidence of moderately persistent activity was found on Yellowstone Lake, the Yellowstone River downstream from the Lake, Slough Creek, the Gardner River, the Beaver Ponds and Slide Lake north of Mammoth Hot Springs, Obsidian Creek in Willow Park, and along the Snake and Lewis Rivers. While the amount of beaver sign observed is not indicative of beaver numbers (Easter-Pilcher 1987, Swenson et. al. 1983, Hay 1958, Townsend 1953), it does reflect current animal presence and distribution.

In 1988 and 1989, 42 reliable beaver sightings were collected throughout the park, representing a minimum of 27 individual beaver. Observations of beaver and signs of fresh activity continue to be recorded, and should be reported to the Resource Management Office (307-344-7381, x2252).

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INTERACTIONS BETWEEN HERBACEOUS PLANTS AND LARGE HERBIVORES ON THE NORTHERN YELLOWSTONE ELK WINTER RANGE - INTEGRATING LANDSCAPE, CLIMATE, PLANT GROWTH, ELK NUTRITIONAL REQUIREMENTS AND POPULATION RESPONSES

Coughenour, M.B. (Natural Resource Ecology Laboratory, Colorado State University, Ft. Collins, CO 80523)

Interactions between large herbivores and plants on the Northern Yellowstone Winter Range are variable over time and over the landscape. Plant growth processes are affected by climate and by landscape structure. In this paper I calculate the extent to which plant productivity may limit elk population growth, and assess the levels of elk herbivory on herbaceous plants, accounting for these spatial and temporal variations. Evidence for nutritional limitation of the Northern Yellowstone Elk Herd derives from a synthesis of observed elk population dynamics 1970- 1990 and results of several different herbaceous plant growth studies. I present a model that uses climate and landscape data to calculate available forage for elk on their winter range. Available forage is related to metabolically-based calculations of the nutritional requirements of the elk. The model is used to determine forage limitation of elk numbers and the fraction of plant growth that has been utilized by elk. These results are an essential part of any assessment of whether elk populations become limited by herbaceous forage before they impose detrimental impacts on the process of herbaceous plant growth.

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THE PARKER TRANSECTS REVISITED: LONG-TERM HERBACEOUS VEGETATION TRENDS ON THE NORTHERN WINTER RANGE, 1954-1989

Coughenour, M.B. (Natural Resource Ecology Laboratory, Colorado State University, Ft. Collins, CO 80523), F.J. Singer, and J. Reardon

A method to rapidly assess range condition and trend from line transect measurements of basal area and species composition was first applied in Yellowstone in 1958 in association with grazing exclosures on the Northern Winter Range. Transects in and out of the exclosures were resampled in 1962, 1967, 1974, 1981, 1986, and 1989. Total live plant frequencies increased significantly, both in and out of exclosures between 1967 and 1981, and decreased from 1981 to 1986. Changes in plant frequencies between 1958-1989 were much more significant than changes due to exclosure from grazing. Precipitation variability was the most probable cause of these temporal changes. Exclosure had no impact on total live plant frequencies. There was more grass outside exclosures on the upper winter range. A greater proportion of *Koeleria cristata* outside exclosures was due to greater absolute abundance rather than to reduced absolute abundances of other species. A relative decrease in *A. spicatum* outside lower winter range exclosures was suggested 1986-1989, but was not statistically significant. This decrease occurred during a period of drought and unusually heavy elk use. The increase in total plant frequency until 1981 implied a converse decrease in bare ground. The decrease in plant frequency after 1981 was climatically driven, as evidenced by parallel changes within exclosures. Dominant perennial grasses either maintained their relative abundance or increased. Forbs decreased in relative abundance until 1986, and increased after 1986 both in and out of exclosures in response to drought. On the basis of these trends, we conclude that elk grazing has not degraded the Yellowstone Northern Winter Range.

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AN ALTERNATE HYPOTHESIS TO EXPLAIN THE COEXISTENCE OF ASPEN AND ELK

Despain, D.G. (Division of Research, P.O. Box 168, Yellowstone National Park, WY 82190)

It has long been noted that aspen clones in the Northern Elk Winter Range in Yellowstone National Park have no intermediate sized stems and that all the smaller stems are heavily hedged by browsers. The lower two meters of the boles of aspen trees are heavily scarred; evidence of earlier animal feeding. These conditions have been attributed to browsing by the large number of elk. It has been hypothesized that 1) the large numbers of elk present today were not a part of the Yellowstone ecosystem prior to the advent of European settlers, thus aspen stems were free to develop into trees, 2) elk were present but periodically dropped to very low numbers and aspen were able to escape browsing long enough to get above their reach, 3) predators were able to keep elk at very low numbers allowing aspen to escape browsing, or 4) past fires were large enough to stimulate enough aspen root suckers that elk could not browse them all before they were too tall. Evidence of browsing preserved in the pith traces of the lower two meters of aspen tree boles and observations of complete consumption of unscarred bark on fallen trees or trees from which protection is removed indicates that these hypotheses are false. Another hypothesis is proposed to explain the existence of aspen trees in Yellowstone National Park. It is proposed that 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 the young trees. The scars resulting from exploratory nibbling grow as the diameter increases and protect the tree for the remainder of its life. If proper conditions do not exist at the time the suckers are produced, the clone is kept in a shrub or perennial forb stage by browsing but is not extirpated from the site.

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PLANT-UNGULATE ECOLOGY OF GRASSLANDS ON THE NORTHERN RANGE OF YELLOWSTONE NATIONAL PARK

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Although Yellowstone's Northern Range grasslands and their large herds of native ungulates have been a favorite topic of study for both botanists and zoologists alike, no study has investigated how these herbivores influence energy and nutrient flows in Yellowstone. The objectives of this study were 1) to determine what effect ungulates have on aboveground production of Northern Range grasslands, and 2) to measure consumption at diverse sites on winter, transitional, and summer ranges, and associate rates of consumption with productivity on the Northern Range.

The effect of ungulates, primarily elk and bison in this study, on aboveground primary production was determined by comparing productivity of grazed vegetation with that of ungrazed, permanently fenced vegetation at four sites. Temporary exclosures (1.5 x 1.5 m, n = 5-7 per site) moved every four weeks from snowmelt to snowfall were used to measure production under grazing, and productivity of ungrazed vegetation was taken as peak biomass in permanent exclosures (10 x 10 m or 15 x 15 m, 3 per site). Productivity of grazed vegetation was higher than ungrazed vegetation from 36 to 85% above ungrazed levels at three sites, indicating ungulates stimulated aboveground production. One exception was a summer range grassland where grazers had no effect on aboveground production. We believe the lack of ungulate stimulation of production at this site was likely a consequence of the severe drought conditions the summer range experienced in 1988, which effectively eliminated the indirect positive feedback by ungulates on their forage both the year of and the year after the drought.

Aboveground production of grazed vegetation and ungulate consumption were measured at 13 sites. An average of 45% of the aboveground productivity was consumed among grazed sites. Aboveground production was positively and linearly related with the amount consumed by herbivores. This indicates that across the Northern Range landscape, as patch productivity increases, so too does consumption at a constant rate per unit productivity. In addition, an analysis of when the sites were grazed indicated that consumption occurred while plants were growing. Young vegetation was found to have higher nitrogen content compared to phenologically older tissue. These results indicate that elk and bison in Yellowstone track young vegetation across the landscape, which in the Northern Range proceeds as a wave up an elevational gradient from low elevation winter range to high elevation summer range. This migratory behavior results in ungulates increasing the duration of a high quality diet. Furthermore, the temporal coupling of grazing and plant growth across the Northern Range may be an important factor underpinning large herbivore stimulation of grassland productivity.

LATE HOLOCENE MAMMALIAN FAUNA OF LAMAR CAVE AND ITS IMPLICATIONS FOR ECOSYSTEM DYNAMICS IN YELLOWSTONE NATIONAL PARK, WYOMING

by

Elizabeth Anne Hadly

A Thesis

Submitted in Partial Fulfillment

of the Requirements for the Degree of

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May 1990

Approved:

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ABSTRACT

LATE HOLOCENE MAMMALIAN FAUNA OF LAMAR CAVE
AND ITS IMPLICATIONS FOR ECOSYSTEM DYNAMICS
IN YELLOWSTONE NATIONAL PARK, WYOMING

ELIZABETH ANNE HADLY

This thesis describes and interprets the mammalian fauna contained in late Holocene deposits of Lamar Cave, a paleontological site in northern Yellowstone National Park. Mammals from Lamar Cave represent 6 orders, 14 families, 27 genera, and 36 species. More than 3 m^3 of cave fill has been removed and the deposits excavated thus far represent ~1700 years of record. Approximately 10,000 bones, including fish, amphibians, reptiles, birds, and mammals have been recovered and ~1600 mammalian specimens have been identified at least to genus. Only the mammals will be discussed. The mammal remains recovered from Lamar Cave are analogous to the biota in the park today.

Based on physical modification of bones and identification and diversity of fauna, the taphonomic agents of the Lamar Cave fauna were packrats, carnivores, and avian predators. Episodic alluvial events sealed organic deposits and indicate minimal mixing of bone-bearing deposits in the cave.

Environmental interpretations are based on the small mammal fauna found in the cave. Microtine rodents dominate the small mammal assemblage of the oldest excavation levels, about 1695±60 yr B.P. Sometime prior to 960±60 yr B.P., microtine rodent percentages began to decline gradually relative to sciurid rodent percentages. This trend continues until sciurid rodents dominate the small mammal assemblage by 960±60 yr B.P. The occurrence of *Microtus ochrogaster*, an extralimital species today, is limited to deposits in the cave older than

960$\pm$60 yr B.P. The presence of this species and the trend in small mammal percentages are interpreted as evidence of a decline in grass cover in the habitats near Lamar Cave over the past 1700+ years. Support for this hypothesis is found in a pollen record from a nearby lake in northern Yellowstone.

Elk and wolves are both present in the Lamar Cave faunal record prior to 1000 years ago, which provides evidence supporting the presence of these species prior to the influence of Europeans.

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RELATIONSHIPS AMONG BREEDING SONGBIRDS, WILLOWS, AND BROWSING BY ELK AND MOOSE IN AND AROUND NORTHERN YELLOWSTONE NATIONAL PARK

Jackson, S.G. (Department of Fisheries and Wildlife, Utah State University, Logan, UT 84322-5210), and J.A. Kadlec

Although the impacts of cattle on riparian zones and associated wildlife have been well-documented, little is known about the impacts that browsing by large native ungulates such as elk and moose may have. In the northern Yellowstone area, some willow stands experience intense browsing by elk and moose, whereas others experience medium or very low amounts of browsing. In 1989 and 1990, we measured densities of nesting songbirds and aspects of habitat structure in eight large willow stands that have experienced different intensities of browsing. The densities of five focal species (Common Yellowthroat, Lincoln's Sparrow, Warbling Vireo, Wilson's Warbler, and Yellow Warbler) varied considerably among sites in which more than half of the willows were severely browsed, suggesting a threshold of tolerance. Principal Components Analysis indicates that the study sites vary in terms of distances between shrubs, shrub heights, height heterogeneity, foliage density at various height intervals, and frequency of severely browsed willows. We believe that browsing does affect the assemblage of breeding birds in these sites, but we speculate that site- and landscape-level factors such as food abundance, willow species composition, hydrology, type and gradient of adjacent community, and riparian zone width and elevation also play important roles.

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HISTORICAL CONDITION OF WOODY VEGETATION ON YELLOWSTONE'S NORTHERN RANGE: A CRITICAL EVALUATION OF THE "NATURAL REGULATION" PARADIGM

Kay, C.E. (Department of Fisheries and Wildlife, Utah State University Logan, UT 84322-5210), and F.H. Wagner

The Park Service's "natural regulation experiment" is predicated on the assumption that large numbers of elk (12-15,000) wintered on Yellowstone's Northern Range for the last several thousand years. Agency biologists believe that the park's vegetation coevolved with these herbivores and reached equilibrium conditions which they term ecological carrying capacity. According to this model, elk influences on the vegetation are "natural" and represent the "pristine" condition of the park. If this paradigm is correct, then early historic photographs of woody vegetation in the park should show that 1) aspen, willows, and conifers were as heavily browsed or high-lined by ungulates in the early years of the park's existence as they are today, and 2) aspen stem damage by elk was the norm then as it is now.

To evaluate these predictions and to test the "natural regulation" paradigm, we reviewed approximately 50,000 early images taken in the park. Photos of aspen stands on the park's Northern Range taken during the 1880s-1890s do not show any evidence of elk-induced bark damage. Photos of aspen, willows, and conifers taken from 1872 to the 1890s do not show evidence of ungulate browsing or high-lining. Some early photos do show occasional conifers which lacked their lower branches, but that was due to light ground fires burning or killing the lower branches or human high-lining, not ungulate browsing. Previous authors apparently confused fire and human high-lining with that caused by ungulates.

Since conifers and other woody vegetation in these 1870-1890 images were approximately 70-100 years old or older when they were photographed and since they show no evidence of ungulate use, this would indicate that few, if any, elk wintered in Yellowstone from the late 1700s through the 1870s. Thus, ungulate high-lining of conifers and repeated browsing of other woody vegetation is not "natural" and represent a departure from conditions which existed prior to the establishment of Yellowstone National Park. These photographs do not support the Park Service's contention that Yellowstone was always a major elk wintering area and that the northern herd did not increase and alter the vegetation. Since these data falsify one of the key assumptions upon which "natural regulation" is based, the paradigm must be rejected.

Abstract from
Plants and Their Environments: First Biennial Scientific Conference on the Greater Yellowstone Ecosystem
September 16-17, 1991
Mammoth Hot Springs
Yellowstone National Park, Wyoming

INTERACTIONS BETWEEN SEDIMENTOLOGY AND VEGETATION ON RECENT FLUVIAL LANDFORMS

Keigley, R.B. (Division of Research, P.O. Box 168, Yellowstone National Park, WY 82190)

The riparian ecosystem contains a mosaic of plant communities that are developed on a variety of fluvial landforms such as point bars, channel islands, and relic chutes. Within a given riparian system, these landforms may be represented by examples ranging in age from those newly created to features that were developed long ago and situated some distance from the current fluvial system. A river's characteristics such as discharge, sediment load, and gradient control the spatial distribution of a landform's sediment grain size, mineralogical composition, local topographic relief, and distance to water table. These differences in microenvironment, in turn, control the colonization of the landform by vegetation. Upon establishment, vegetation may significantly alter the local hydrologic regime, thus imposing another influence on microenvironment. The objective of this study is to describe the sedimentology and vegetation of selected landforms having young plant communities. Subsequent study will examine how those kinds of communities change over time.

Abstract from
Plants and Their Environments: First Biennial Scientific Conference on the Greater Yellowstone Ecosystem
September 16-17, 1991
Mammoth Hot Springs
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SUCKERING IN BURNED ASPEN AS RELATED TO ABOVE- AND BELOWGROUND BIOMASS

Renkin, R.A. (P.O. Box 168, Yellowstone National Park, WY 82190), and D.G. Despain

A planar-intercept technique was developed to sample root biomass, which was then correlated to aboveground standing crop biomass. Select sites were burned, and portions of aspen clones were trenched and exclosed. Aspen sucker production, in terms of biomass per unit area and average height, was positively correlated with total root biomass. The data demonstrates the above- and belowground relationship of aspen response to burning, rather than the standard practice of equating response to fire intensity.

Abstract from
Plants and Their Environments: First Biennial Scientific Conference on the Greater Yellowstone Ecosystem
September 16-17, 1991
Mammoth Hot Springs
Yellowstone National Park, Wyoming

ASPEN SEEDLING FOLLOWING THE 1988 YELLOWSTONE FIRES

Renkin, R.A. (P.O. Box 168, Yellowstone National Park, WY 82190), D.G. Despain, and D.L. Clark

Aspen (*Populus tremuloides*) seed germination and early seedling growth is reported exclusively within burned areas of Yellowstone National Park. Survey results revealed establishment across a broad range of burned sites and in varying densities. The presence of paired cotyledons, a fibrous root system, and leaf characters differing from the adult form were used as seedling identifiers. Nine permanent transects (three forested, six nonforested) and two fenced exclosures showed that seedling survival was negatively influenced by the presence of ungulates, spring flooding, and intraspecific competition. Aspen seedlings in burned forests had a significantly higher percentage of survival than in burned nonforested sites. Percent survival of aspen and lodgepole pine (*Pinus contorta*) seedlings in burned forests was not significantly different although aspen were 3.4 times taller after 2 years. The data reported here suggests aspen exhibit an opportunistic sexual reproductive strategy, and contributes to the scant life history information on aspen in the Rocky Mountain west.

Yellowstone's Northern Range Revisited

By Francis J. Singer

Management of elk and bison on the northern winter range of Yellowstone NP has remained a controversial subject through most of this century. Elk were artificially controlled particularly from 1935-68, and bison were fenced and cropped in the park. However, beginning in 1969 these reductions were terminated, and by 1971 a hypothesis of self- or natural-regulation of Yellowstone's ungulates was formulated by Glen Cole and Douglas Houston. Houston reported the experiment to be largely successful through 1979 in his book *The Northern Yellowstone Elk – Ecology and Management* (1982 Macmillan).

However, a series of events in the 1980s prompted renewed concern over the success of the experiment. Bison, elk, mule deer, and pronghorn antelope numbers increased dramatically. Elk counts rose from 10,500-12,000 in the 1970s to 16,000 by 1982 and then to 19,000 by 1988. Pronghorn antelope counts roughly tripled in the 1980s from 152 to 495, while the mule deer counts increased from 1,007 to 2,217. Elk largely reoccupied the portion of the northern range outside the park, effectively increasing the size of the winter range by about one-fifth. Seven of the first eight winters in the 1980s were less severe than normal. In August 1986, the NPS Washington office provided special funding through its Natural Resource Preservation Program to investigate the status of the northern range. In October 1987, Congress directed the NPS to "start a study on Yellowstone to see whether there is evidence of overgrazing."

A multidisciplinary approach was taken to studying the effects of elk grazing upon the northern winter range, and to date, 40 separate research projects involving 5 park scientists, 4 other agency scientists and 34 scientists from 18 different universities have been initiated. A series of five problem analyses has been conducted by outside scientists on key problem areas (elk population dynamics, grassland herbivory, riparian area concerns, willow ecology, and pronghorn conservation biology). Each panel has consisted of two to eight outside scientists, and their recommendations have helped shape the park's research programs.

The initial round of studies emphasized the grassland, meadow and sagebrush-bunchgrass communities, since elk derive most of their forages from them. Comparisons between ungrazed sites (within exclosures) and grazed sites were made for soil nutrients, soil compaction, soil infiltration rates, plant species abundance and production, and plant root biomass. Consumption rates by ungulates, grazing tolerances of key forage, and long-term grassland trends from LANDSAT imagery were investigated in separate university-based projects.

The paleoecological history of the northern range for the past several thousand years has been investigated through studies of pond sediment pollen histories, and for the past one thousand years cave deposits. Elk ecology studies have included radiotelemetry-assisted studies of migrations, habitat preferences, the ecological separation of mature bulls from cows and young bulls, and rate and causes of elk calf mortality.

The data suggest no statistically significant changes this century (the period of proposed elk overpopulation) in the nutrient inputs, sediment accumulation, or pollen profiles of eight northern range ponds when compared to pre-park levels. Winter range grasslands apparently are influenced very little by elk grazing.

RESEARCH ON YELLOWSTONE'S NORTHERN RANGE

Funded by the National Park Service

Project Title	Principal Investigator	Institution
Collect population statistics and monitor population size and mortality rates of elk, mule deer, and pronghorns.	F. Singer	NPS
Document sources and rates of elk calf mortality.		
The response of aspen to burning and ungulate browsing.	D. Despain	NPS
Range relations of five ungulate species.	F. Singer	NPS
An analysis of elk summer habitat.	F. Singer	NPS
Collect population statistics, and monitor population size and mortality rates of bighorn sheep.	M. Meagher	NPS
Bison ecology studies in Yellowstone National Park.	M. Meagher	NPS
Rehabilitate abandoned ranchlands dominated by exotic plants.	C. McClure, D. Despain	NPS
Evaluate condition and determine trends in elk winter range through exclosure comparisons.	F. Singer C. Montagne	NPS Mont. St. U.
Moose numbers, movements, habitat and forage use, and effects upon riparian areas.	F. Singer T. Puchlerz D. Tyers	NPS U.S.F.S. U.S.F.S.
Determining the sources of Yellowstone River sediment and turbidity.	Numerous individuals	Several Agencies
Comparative study of winter nutrition of Yellowstone elk using snow-urine analysis.	G. Del Giudice F. Singer	U. of Minn. NPS
Debris flow-dominated alluvial fans on Mt. Everts in northern Yellowstone National Park: depositional frequency and chronology of fan development.	C. Craig J. Schmitt	NPS Mont. St. U.
Food habits of the Yellowstone grizzly bear.	R. Knight	I.G.B.S.T.
A study of the range use and movements of elk in the upper Yellowstone area, in and out of Yellowstone Park.	J. Swenson J. Vore, H. Picton	Mont. Fish, Wildl. Parks Mont. St. U.
A study of the relationships between prehistoric humans and wildlife in the northern range of Yellowstone Park.	E. Hadly L. Agenbroad	NPS N. Ariz. U.
Forage production and utilization patterns by elk and bison on all four seasonal ranges.	S. McNaughton, D. Frank	Syracuse U.
LANDSAT interpretation of grassland standing crops.	M. Boyce, E. Merrill, Marrs	U. of Wyom.
Ecology of mature bull elk.	J. Peek, D. Vales	U. of Idaho
Human disturbance of wintering elk.	E. Ables, F. Cassirer	U. of Idaho
Hunter and recreationist disturbances of elk near Gardiner, Montana.	H. Picton J. Vore	Mont. St. U. Mont. Fish, Wildl. Parks
Herbivory on the northern Yellowstone winter range.	M. Coughenour, J. Detling	Col. St. U.
The status of willows: distributions and browsing impacts on the northern range.	F. Singer	NPS
Behavioral and activity comparisons of Madison-Firehole, Lamar Valley, and Mammoth Hot Springs elk.	E. Ables	U. of Idaho
Riparian vegetation of the northern range, Yellowstone National Park: classification, succession, and environmental relationships.	R. Pfister, S. Cooper	U. of Mont.
The relationships of climate to sedimentation rates in lakes and ponds on the northern range in Yellowstone National Park.	H. Wright C. Barnowsky	U. of Minn. Carnegie Instit.
Factors that limit elk populations in the greater Yellowstone ecosystem.	C. Kay, F. Wagner	Utah St. U.
An intensive study of mountain lions in Yellowstone National Park and in the Yellowstone River drainage outside the park.	M. Hornocker	Wildl. Res. Instit.
Responses of major forage species to grazing by bison and elk.	L. Wallace	U. of Okla.

There were no differences in 12 soil nutrients or in runoff or sediment yield (as determined by a rainfall simulator), between grazed and ungrazed areas. However, there were higher surface bulk densities and lower soil infiltration rates in grazed areas. Several grasses that can increase when grazed, including junegrass, bluegrasses, and thickspiked wheatgrass, were more abundant in grazed areas. However, annual production of grazing-sensitive grasses – bluebunch wheatgrass and Idaho fescue – were not influenced by grazing, as were 19 other grasses, 87 forbs, and 22 shrub species found on the study sites. Root biomass and total plant cover were uninfluenced by grazing, although there was less dead litter and more bare ground on grazed sites.

The studies indicate only subtle differences between grazed sites on winter ranges and sites protected within exclosures for 27-31 years. None of the differences suggest departures from natural conditions. The park recognizes that total protection from grazing as in exclosures does not represent natural conditions. The 27-31 year old exclosures only serve to emphasize how little elk grazing affected the drier, winter range sites. This evidence further supports D. Houston's contention (1982) that precipitation patterns influenced the grasslands more than elk grazing. From 1958 to 1981, total plant cover more than doubled on grazed and ungrazed study sites apparently due to a pattern of wetter summers, at the same time elk numbers more than quadrupled following termination of the artificial reductions.

Few conclusions may be made about the effects of elk and bison grazing upon the summer range, because most of those studies are still in progress. Perhaps a greater influence from grazing summer range may be documented because ungulates graze the plants on summer range while they are growing, in contrast to grazing cured, dormant forages on winter range after these plants have transported their nutrients to their root systems in the fall. The frozen ground and protective snow cover further minimize grazing effects on winter range plants. One study, however, suggests that summer range grassland standing crops, as determined from LANDSAT imagery, are significantly correlated to optimal winter snowpack and not to elk numbers. Summer range grassland production, however, was directly correlated to elk calf crops.

Another study has found fewer plant species inside exclosures on summer ranges. Short-statured plants were less abundant inside exclosures, probably because grazing did not trim taller plants. Research on willows and aspen has just been initiated, and will include studies of grazing intensities, annual production, and the effects of drought and fire upon ungulate preferences of plants and the production of plant secondary defense compounds.

The severe drought and the fires of 1988 may help to answer several questions about the northern range. A large number of willow and aspen stands burned in 1988, for the first time this century. The opportunity has been presented to document fire responses of these species. Park biologists are predicting enhanced growth, new seedling establishment, and greater abundance of willow and aspen. Although palatability may also be enhanced by the burning, many aspen and willow stands may escape to above the height of ungulate browsing after the fires.

As a combined result of the drought, burning of winter ranges, and a severe winter in 1988-89, mule deer numbers declined 19 percent, pronghorns 27 percent, and elk 38-43 percent (of which 14-15 percent was harvest and 24-27 percent was winterkill). The opportunity now exists to document the ungulate recovery from the winterkill and response to large scale burns of both winter and summer ranges. Currently, one group of biologists is predicting fire-related enhancement of elk carrying capacity due to greater nutrient content and greater forage production in burned areas. Another group of scientists is predicting only moderately enhanced carrying capacity and only minor or no increase in elk numbers as a result of the fires. This group maintains that fire-related enhancement of forage quality is often minor (only a few percentage points) and the effects may be short-lived, lasting perhaps only 1-3 years. Additionally, elk are so efficient at selecting a consistently high level of nutritious forages, especially on summer ranges, that even though fires enhance forages, the net benefit to elk is relatively minor. The fires of 1988 have provided a unique opportunity to investigate these conflicting hypotheses on a large scale.

Abstracts from the First and Second Annual Meetings of Research and Monitoring on Yellowstone's Northern Range (January 28-29, 1988 and March 22-23, 1989) are available from J. Varley, Chief of Research, Box 168, Yellowstone NP, WY 82190. Also available from the same address is a Summary of Significant Findings dated July 15, 1989, and copies of final reports on the winter range exclosure studies (soil, grasslands) and the pond sediment studies.

Singer is a Research Biologist at Yellowstone NP.

PARK SCIENCE
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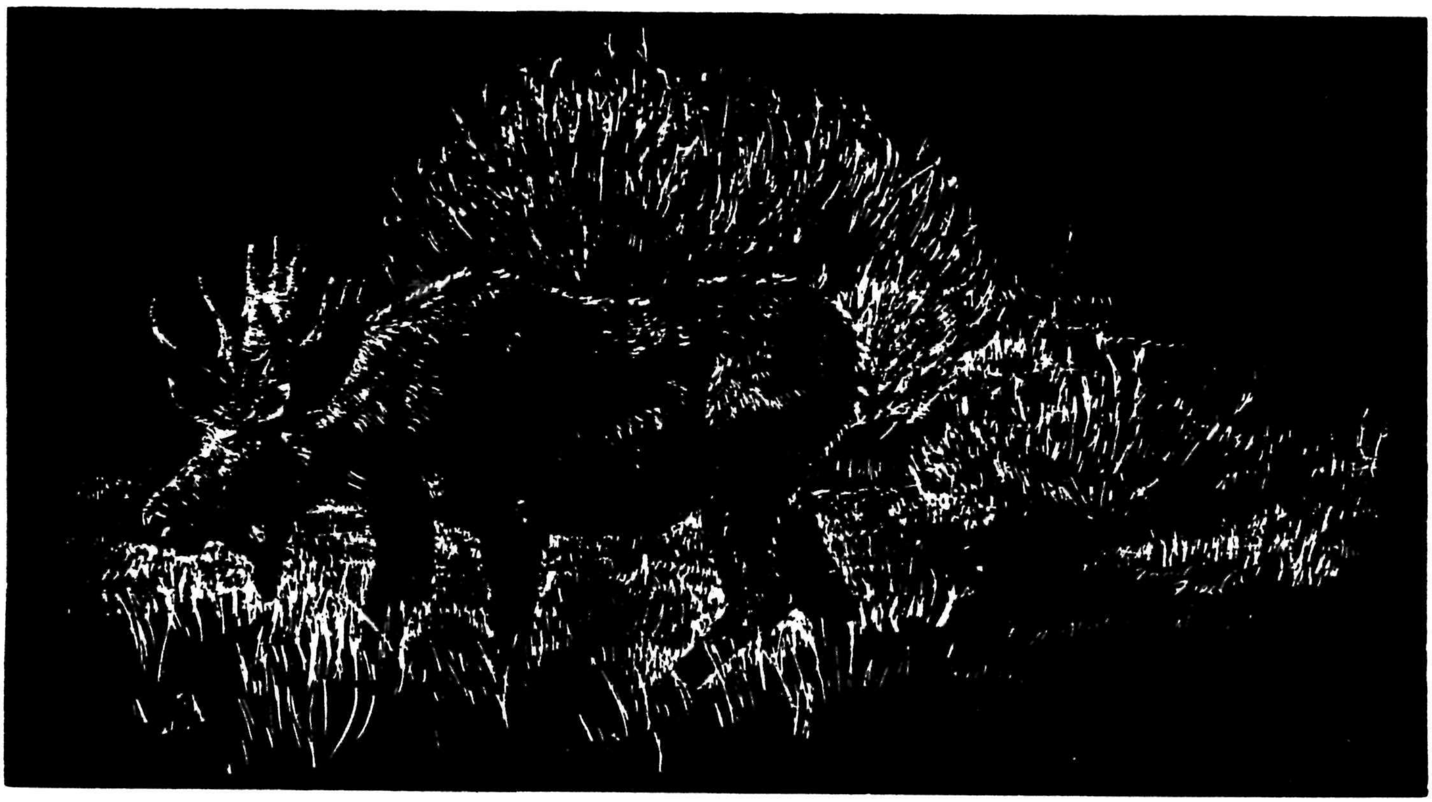
GRAZING INFLUENCES ON YELLOWSTONE'S NORTHERN RANGE II

Research Summaries August 15, 1990



Compiled by

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GRAZING INFLUENCES ON
YELLOWSTONE'S NORTHERN RANGE
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INTRODUCTION

This is the second annual report of project summaries on the ecology of Yellowstone's northern ungulate winter range. It is intended primarily as an interim briefing statement for the park Superintendent until such a time as final reports and publications become available. Copies of the first report, printed in July 1989, are still available from the Research Division, P.O. Box 168, Yellowstone National Park, Wyoming 82190. In addition, the highlights of both the 1989 and 1990 reports have been condensed into a companion report entitled "A Digest of Research into Grazing Influences by Native Ungulates on Yellowstone's Northern Winter Range." It is also available from the Research Division.

This report summarizes studies funded through a large National Park Service (NPS) research initiative of the Natural Resources Preservation Program, 1985-1988. The report also includes northern range research funded by other NPS sources, especially postfire and wolf study funds, as well as studies partially or wholly funded by sources outside the NPS.

This report is the second response to the October 1987 Congressional Directive to the National Park Service to: "start a study on Yellowstone to see whether there is evidence of overgrazing."

TITLE: Effects of the 1988 fires on the northern range: 1989 forage productivity, winter elk habitat use, and snow relations

AUTHORS: Jack E. Norland and Francis J. Singer, Yellowstone National Park

PUBLICATION REPORT STATUS:
1. Annual reports.
2. Publication in Journal Wildlife Management, Summer 1991.

OTHER PROJECTED PUBLICATIONS:
Data will contribute to nutritionally-based model of elk carrying capacity slated for J. Applied Ecology.

PROJECTED PUBLICATION DATE: Summer 1991.

INTRODUCTION:

The fires of 1988 burned extensive portions of the winter range on the northern range. Fires in previous studies (Christensen et al 1989) have shown that fires increase forage production and change ungulate habitat use patterns to where more use is in the burned areas. The fires in Yellowstone are hypothesized to increase forage production in all major habitats resulting in more elk use in the burned areas. With the increase in production we also hypothesized an increase in forage quality and an increase in elk use of the burned areas. Snow relations in the burned areas may mediate the change in use of burned areas by elk. Snow relations are hypothesized not to change in forested areas only influenced by surface burns. In canopy burned areas greater depth and harder snow structure due to the lack of tree canopy could result in a decrease in elk use. In sagebrush areas the snow relations may result in less use because sagebrush is thought to facilitate elk foraging in the snow.

METHODS:

1. Forage production under 40 cm was measured in both Douglas fir habitats and sagebrush habitats. The Douglas fir habitat had production stratified by soil heating properties, those soils which were heated to a depth of 5 cm were classified as moderate and those which only had the surface organic material charred classified as light. In each habitat four sites were chosen where similar conditions occurred in the burned and unburned areas. At each site 15 .5 meter sq. plots were chosen along a 60 meter transect. Transect ends were marked so the exact plots can be resampled in the future. At each plot the production of each species was measured with the canopy intercept method of Frank and McNaughton (1990). The sagebrush production was measured in September and early October of 1989, and the Douglas fir from early October

to early November 1989. Production was analyzed utilizing a blocked ANOVA design and only forage classes were examined.

2. Habitat use by elk was estimated for sagebrush and Douglas Fir habitats. Habitat use was indexed by estimating the density of feeding craters in habitats in burned and unburned portions. Ten pairs of burned to unburned comparisons were chosen in each habitat. In addition four transects were placed in a canopy burned Douglas Fir habitat to compare against similar surfaced burned only Douglas Fir habitats. Belt transects 4 meters in width and approximately .75 km long were randomly placed in each site. Transects estimated approximately 5% of the total area of the site. Transects were run in December and January, for early winter estimate of use, and in February for late winter estimate. Data was analyzed in a blocked ANOVA design where each paired comparison was a block.

3. Snow relations were measured in both sagebrush and Douglas Fir habitats. Snow depths and densities were measured with the standard SCS snow sampler tube. Within each habitat four sites were chosen with burned and unburned areas which had similar conditions. At each site 10 feeding craters were randomly chosen and the depth and density of snow was measured. In addition 10 sites were measured in a canopy burned Douglas Fir area to be compared with the other Douglas fir sites. To see how different snow depths and density was from idealized snow depths without any influence from wind, tree canopy, or other disturbance snow courses following the SCS guidelines for site selection of these were followed. The comparison of these with the depths will show how different the feeding sites are from the idealized depths and densities. Data was collected in January 1990 for early winter and late February and March for late winter. Depths and densities were analyzed using a blocked ANOVA design. Multiple comparisons used Tukeys HSD.

4. All significant differences were at the $P<.05$ level.

SUMMARY OF PROGRESS AND FINDINGS:

1. Forage production the first growing season after the fires decreased about 23% on the Northern range in the sagebrush habitats (Table 1). The decrease was attributed to small patches in the burned sagebrush areas which had plants killed by moderate soil heating.

2. Forage production in the Douglas Fir forest was decreased in those areas that had moderate soil heating, but was not different on those areas only lightly heated. The drop in production in the moderately heated soil was due to the

plants being killed by the fire. The lightly heated soil had few plants killed by the fire. In the future species composition will be compared between treatments looking at differences and changes as both treatments evolve.

3. The habitat use of burned areas by elk was not significantly different from the use of unburned areas for both sagebrush and Douglas fir habitats. Even the canopy burned area in the Douglas fir did not differ in the amount of use.

4. Depths of snow at feeding sites were significantly different between burned and unburned sites in both sagebrush and Douglas fir habitats. Canopy burned Douglas fir habitats had significantly deeper snow than the burned and unburned treatments. Snow course snow depths were significantly deeper than all of the treatments in both habitats. Greater snow course depths were not unexpected since elk will select lower snow cover when available. Deeper snows in canopy burned sites was expected since previous studies (personnel communication Phil Farnes, SCS) had found that the removal of tree canopy results in higher snow depths.

5. Snow densities were significantly different for several treatments in both habitats. The interpretation of the densities has not been worked out. Further work will be conducted on how snow densities influence on elk foraging behavior.

6. There was no change in in the habitat use of the elk due to the changes brought about by the fires. Future changes in the various resource parameters measured may eventually alter elk foraging behavior, but the changes in resource parameters the first year post fire did not alter elk habitat use.

Several other aspects are being studied which will have a bearing on the interpretation of these results, these being: 1. forage quality in both habitats, 2. winter diets of elk. In the future these will be incorporated into the interpretation of these data.

Literature Cited:

Christensen, N.L. et al. 1989. Ecological consequences of the 1988 fires in the Greater Yellowstone area. National Park Service, Yellowstone National Park, WY.

Frank, D.A. and S.J. McNaughton. 1990. Aboveground biomass estimation with the canopy intercept method: a plant growth form caveat. Oikis: in press.

Table 1. Mean forage production, grams/meter sq., on the northern range (SE in parenthesis).

Forage	Sagebrush Burned	Unburned
Graminoid	84.5 (9.2)A	117.5 (9.4)B
Forb	15.4 (1.7)A	11.5 (1.3)B
Total	99.9 (9.3)A	129.1 (9) B

Forage	Douglas Fir Moderate Burned	Light Burned	Unburned
Graminoid	1.5 (0.5)A	52.4 (6.6)B	63.3 (5.5)B
Forbs	0.9 (0.4)A	5.3 (0.8)B	6.1 (0.8)B
Shrubs	0.7 (0.4)A	7.2 (1.1)B	9.4 (1.7)B
Total	3.1 (0.9)A	64.9 (7.2)B	78.8 (5.7)B

means not followed by a common letter were significantly different p<0.05

Table 2. Mean snow depths in inches and mean percent densities of snow for early and late winter (SE in parentheses).

	Lodgepole Forest Burned	Unburned	Snow Course	Canopy Burned
Depth-Early	10.5(0.4)C	9.3(0.4)C	17.3(0.2)A	13.3(0.6)B
Depth-Late	14.7(0.5)C	14.6(0.4)C	24.6(0.4)A	20.7(0.6)B
Density-Early	16.3(0.5)AB	14.6(0.6)A	16.3(0.4)B	15.4(0.6)AB
Density-Late	19.9(0.7)AB	19.3(0.6)A	21.8(0.3)B	20.9(0.3)AB

	Sagebrush Burned	Unburned	Snow Course
Depth-Early	14.3(0.4)A	14.5(0.3)A	17.3(0.2)B
Depth-Late	17.7(0.6)A	17.2(0.4)A	24.6(0.4)B
Density-Early	16.7(0.5)A	17.7(0.5)A	16.4(0.4)A
Density-Late	22.6(0.5)B	20.6(0.5)A	21.8(0.3)AB

means not followed by a common letter were significantly different P<0.05.

PROGRESS REPORT - COOPERATIVE MOOSE PROJECT

TITLE

Ecology of moose on the Northern Winter Range of Yellowstone National Park and the Gallatin National Forest.

AUTHORS

Daniel Tyers for: Frank Singer, Tom Lemke, Dr. Lynn Irby.

AFFILIATION

U.S. Forest Service; National Park Service; Montana Department of Fish, Wildlife and Parks; and Montana State University. (The Safari Club International - Montana Chapter is an additional cooperator but is not an author of this report.)

PUBLICATION REPORT STATUS

Project still in progress. Completion date for fieldwork is fall 1990. Data analyses and report writing are scheduled for winter 1990-1991.

A dissertation will also result from the project.

OTHER PROJECTED PUBLICATIONS

It is anticipated that a variety of papers will be written cooperatively by the agencies involved. This will occur where this project overlaps with other projects and where certain specific agency interests need to be expressed. These areas have yet to be identified.

PROJECTED PUBLICATION DATE FOR WORK IN PREPARATION

1991 or 1992.

DATE OF PROGRESS REPORT

July 1990.

SUMMARY OF OBJECTIVES

1. Determine the effect of 1988 fires on the Shiras moose on the Northern Winter Range of Yellowstone National Park and the Gallatin National Forest.

2. Describe the winter ecology of the Shiras moose on the Northern Winter Range.

3. Provide management recommendations to the participating agencies relevant to such issues as hunting quotas and vegetation manipulation (i.e. silvicultural practices and prescribed burning).

4. Provide baseline data on population size and trends, and determine the validity of different census techniques.

5. Obtain information on the relationship between moose and the willow communities on the Northern Winter Range.

SUMMARY OF MOST SIGNIFICANT FINDINGS

1. Effect of the 1988 fires: Two years of data were collected on moose habitat and dietary preferences, home range size, and population dynamics before the fires of 1988. The same methodology used before the fires was continued for 2 years after the fire. A comparison of pre- and post-fire data for moose in areas that burned indicates important changes in diet, home range size, cow/calf ratios, and distribution.

The moose used several strategies for foraging in areas where their habitat was changed by the fires. After the fires, lodgepole pine and, to a lesser degree, willow increased in the diet of moose in burned drainages. The first year after the fire, the burned twigs of lodgepole were prominent in the diet of moose in one of the study units (Slough Creek) that burned extensively. In some cases, moose moved to a higher elevation to get above the perimeter of burned areas to forage. This often resulted in the moose foraging in snow depths in excess of previous years' averages. In general, moose demonstrated a pronounced avoidance of burned areas during the winter for the 2 years following the fires of 1988.

2. Winter ecology: Collecting data for 4 years has brought a good understanding of moose habitat and dietary preferences from four different study units within the study area. This is for the time frame of November to April. The main browse species are: subalpine fir, willow, gooseberry, lodgepole pine, and buffalo berry. The relative proportions of these browse species in the diet of the moose vary significantly from month to month and from study unit to study unit through the winter. However, there is a lot of consistency from year to year. The distance traveled for the equivalent number of "bites" in each feeding effort also varies a great deal by month, study unit, and cover type. In areas that have burned or have more wintering elk, the moose tend to travel further when browsing. Also, there is a strong relationship between moose and late successional stage lodgepole and spruce-fir forests. They will spend much of the winter in these cover types.

3. Management recommendations: No decisions have been made based on the data collected through this project as to whether the hunting quotas for moose are commensurate with the population size. However, the State expects to use information from this project to assist in making these decisions and to monitor the appropriateness of the harvest levels.

The best moose winter range appears to be between 7000-8000 feet, in late successional lodgepole and spruce-fir forests, and where snow depths average between 70-110 cm. In addition, in preferred sites the understory of subalpine fir and gooseberry appears to be comparatively very high. Timber harvest in these areas has the biggest impact on moose. A disparity in snow accumulation and consistency between older forests and clearcuts make clearcuts less desirable to moose. Harvest units have greater snow depths and more heavily crusted snow conditions than adjacent uncut forests. These factors make the retention and location of intact forests important as travel corridors. Timber harvest has enhanced moose habitat in some locations. This has occurred where the forest canopy has been opened next to decadent willow communities allowing them to increase, and where selective cutting has partially opened the forest canopy allowing an increase in understory shrub production while still maintaining hiding and thermal cover.

4. Population size and trend/census techniques: A survey was conducted from horseback for 4 years in the 1940s and then repeated for 5 years in the 1980s to classify the moose population. It will be repeated for 4 more years. It seems to indicate a decline in the number of moose seen per day from the 1940s to the 1980s and a decline in the number of calves per cows after the fires of 1988.

Attempts to count moose from fixed-wing aircraft have identifed two brief and predictable windows of observability for seeing moose. These occur during about the first of December and the end of April when the moose congregate in several large willow communities. The reason why the moose congregate at these specific times is not entirely known. Efforts to count moose at all other times of the year are very unproductive.

A sightability model is still in the developmental stages.

5. Relationship between moose and willow communities: Moose winter range in the study area extends from about 6800 feet to 8800 feet. Willow communities are found at all elevations within this zone. Elk are also found in the study area but usually winter lower in elevation than the moose, although there is some overlap. Snow depth and consistency impact when both elk and moose use willow communities for browsing. Track transects reveal that snow precludes the availablity of willow communites located at the highest end of moose winter range from late December to early June. Very little elk activity occurs here through any part of the winter. Consistent with this, browse utilization measurements taken in the spring reflect a very low level of use in these areas. Moose abandon willow communities between 6800 and 7400 feet in elevation around the end of January and do not return until the end of April. Utilization at these sites is higher. Elk seem to be forced to leave the willow communities in "moose habitat" several weeks earlier than moose and do not seem to return in the spring. In the "best moose habitat," elk numbers are less than moose numbers. Similar work conducted in Yellowstone Park at an elevation of about 6500 feet provides the opportunity for comparisons. In these areas, the willow is available to ungulates much of the winter and elk numbers are much higher.

TITLE: Effects of disturbance by cross-country skiers on elk in northern Yellowstone National Park.

AUTHORS: E. Frances Cassirer and Ernest D. Ables

AFFILIATION: Dept. of Fish and Wildlife Resources, University of Idaho, Moscow.

DATE OF REPORT: May 1990.

SUMMARY OF OBJECTIVES:

Movement and heart rate responses of elk to disturbance by people on foot and skis were examined in 3 areas of northern Yellowstone National Park. Objectives were to determine at what distances skiers disturbed elk, how far elk moved in response to disturbance, what factors influenced elk responses, and how long elk were displaced following skier disturbances. Energetic costs of movements and effects on energy balance over the course of the winter were estimated. Baseline heart rates of elk were documented, and the magnitude and duration of heart rate increases were assessed as an index to the degree of human disturbance in Mammoth Hot Springs and the Lamar River drainage.

SUMMARY OF MOST SIGNIFICANT FINDINGS:

1. Elk in the Lamar Valley and Stephen's Creek areas were disturbed when people were at average distances of 573 m. These elk moved an average of 1.88 km when disturbed. They temporarily left the drainage and their home range core areas and moved to higher elevations, steeper slopes, and into forested areas when disturbed. Average return time to the drainage was 2 days. Skier numbers did not affect elk flight distances or distance moved.

2. Elk in Mammoth Hot Springs were less disturbed by human activity than those at Lamar and Stephen's Creek, but increased responses when disturbed outside areas consistently used by people.

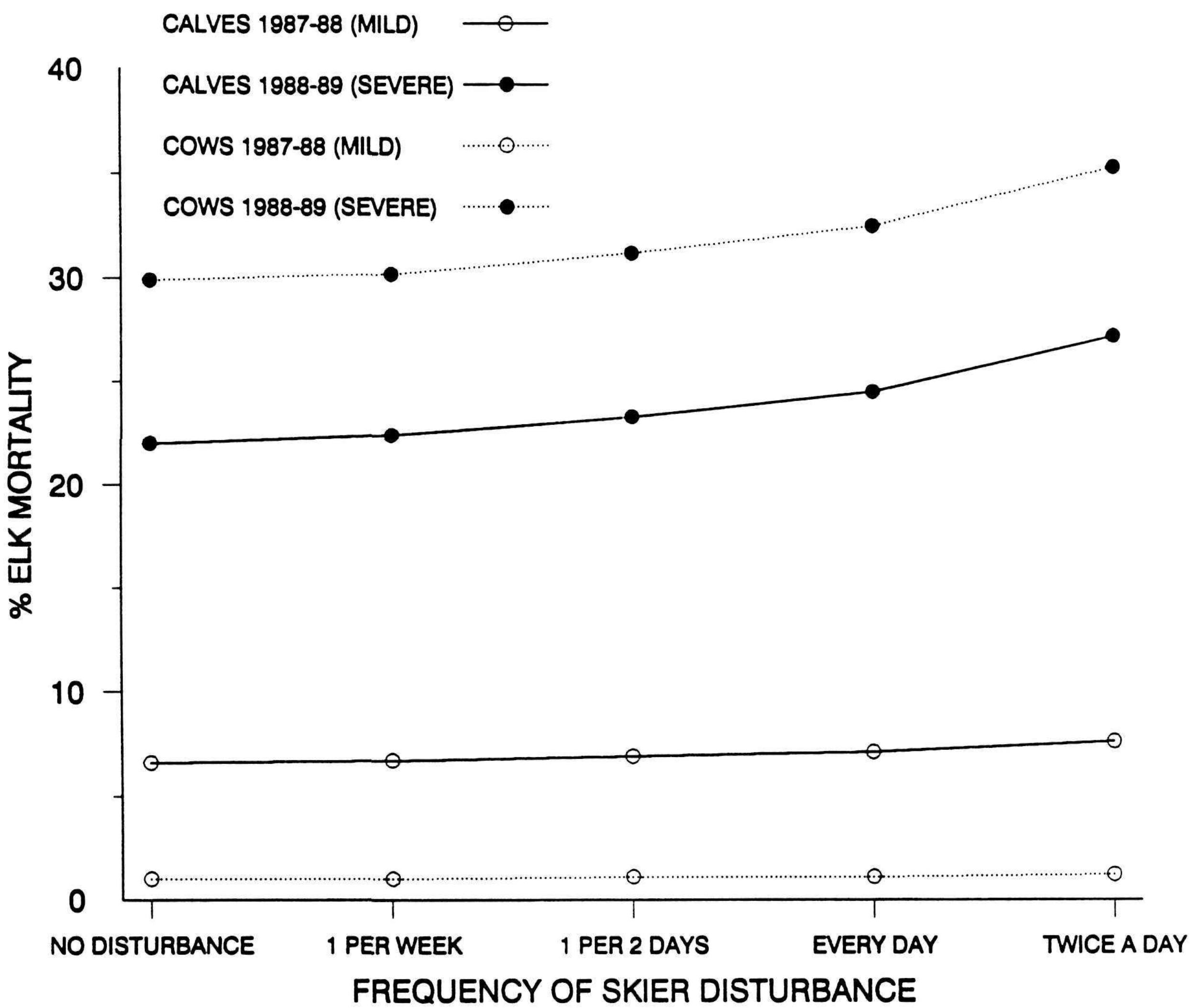
3. Elk in Lamar and Stephen's Creek expended an estimated 365 kcal for locomotion per disturbance. Potential negative effects of these additional energy costs on mortality and reproduction would be greatest when elk were in poor physical condition going into the winter, or when forage availability and quality on the winter range were low.

4. Heart rate responses to disturbance were greatest when elk were disturbed by people on foot or skis. Heart rate responses confirmed observations of

behavioral responses to disturbance and heart rates generally returned to normal before maintenance behavior was resumed. Undisturbed heart rates of elk in Lamar were lower than those of elk in Mammoth Hot Springs during February and March. Baseline heart rates of elk in Mammoth Hot Springs were lowest in February, and increased 76% between February and May.

5. Skier activity should be located at least 600 m from elk wintering areas.

6. Displacement of elk by skiers on the winter range would be minimized by concentrating skiers in forested areas with abundant topographic relief.



Predicted mortality rates of cow and calf elk in Lamar and Stephen's Creek with and without skier disturbances based on an average of 1.88 km moved per disturbance. This model, based on Hobbs (1989) publication <u>Linking energy balance to survival in mule deer: development and test of a simulation model</u>[1] incorporated data from Yellowstone and published research on elk and deer in other areas to simulate mortality rates during a mild winter (1987-88) and a normal winter preceded by a drought summer (1988-89). It does not address energy costs incurred if elk are displaced to lower quality habitat by skiers, or sublethal effects of reduced fat reserves such as lower reproductive rates or calf survival. Skier disturbances were more likely to affect mortality rates if elk were disturbed every other day or more, and would potentially have the greatest affect when accompanied by severe environmental conditions.

[1] Wildlife Monograph No. 101.

TITLE: Population characteristics of mountain lions in the Northern Yellowstone Ecosystem

AUTHORS: Kerry M. Murphy and Maurice G. Hornocker

AFFILIATIONS: The Wildlife Research Institute at the University of Idaho, Moscow

PUBLICATION REPORT STATUS: Continuing work. Manuscripts to be submitted to The Journal of Wildlife Management or Wildlife Monographs

PROJECTED PUBLICATION DATE: Unknown

DATE OF REPORT: April, 1990

SUMMARY OF OBJECTIVES:

The objective is a thorough documentation of population parameters of mountain lions on the northern winter range

SUMMARY OF MOST SIGNIFICANT FINDINGS:

Mountain lion densities on the northern range during winter 1989-90 was 13-23 mi^2/lion. Sex ratios among adults were 2 females: 1 male. Winter home ranges of 8 females and 3 males averaged 19 mi^2 and 27 mi^2, respectively, calculated using the convex polygon method. Home ranges of female lions overlapped up to 70%, but ranges of males were nearly unique. Size among 10 litters born to study area females since the beginning of study was 2.8 kittens. The mortality rate among 28 kittens from birth to independence was 75%. Among 9 mortalities to adult lions, sport harvest, fighting with other lions, and disease accounted for 6 (66%), 2 (22%), and 1 (11%) losses, respectively.

TITLE: Development of a Scaled Index of Winter Severity for Animal Studies in Yellowstone National Park.

AUTHORS: Phillip E. Farnes, Water Supply Specialist

AFFILIATIONS: Soil Conservation Service, Bozeman, Montana

PUBLICATION REPORT STATUS: Will be submitted to 1991 Western Snow Conference and possibly other symposiums.

PROJECTED PUBLICATION: Proceedings of Western Snow Conference.

PROJECTED PUBLICATION DATE: Mid-1991

DATE OF REPORT: May 1990

SUMMARY OF OBJECTIVE: Develop an index of wintering conditions that is flexible, easily interpreted by both professionals and lay persons and based on readily available data.

SUMMARY OF THE FINDINGS:

1. This scaled index of winter severity (SIWS) involves calculation of a probability analysis of minimum daily temperatures, snow water equivalent (SWE), snow depth, snow density and precipitation or SWE accumulation above a threshold level. Data is obtained from existing National Weather Service (NWS) Climatic Stations and Soil Conservation Service (SCS) snow courses and SNOTEL sites.

   Most of the Data and Statistical procedures are available through the Centralized Forecast System (CFS) on the SCS snow survey computer in Portland, Oregon. Access to CFS is available via modem and terminal.

2. The weighting of each parameter can be adjusted to represent the effect on different species.

3. Two or more stations can be combined to represent conditions on the larger wintering ranges.

4. The index rating is scaled from +4.0 for the mildest winter to -4.0 for the most severe winter with 0.0 being average. The scaling of this index makes it easy for wildlife managers and the general public to evaluate the mildness or severity of a given winter. Also, the procedure can be used to accumulate months as the season progresses and to assess conditions each month.

<u>**Rating Scale**</u>

+4.0 very mild	+1.0 slightly mild	-2.0 moderately severe
+3.0 mild	0.0 average (normal)	-3.0 severe
+2.0 moderately mild	-1.0 slightly severe	-4.0 very severe

5. A spring severity index can also be calculated to represent young mortality due to weather conditions and combined with the winter index to relate population trends to weather conditions.

6. An example of scaled index of winter severity for the Mammoth area is shown in figure 1.

The SIWS is the combined weighting of 0.4 X TMIN + 0.4 SWE +0.2 PRECIP for 1948-1990. TMIN is the accumulation of daily minimum temperatures below 0 F at Yellowstone Park climatic station (Mammoth), and presents the severity due to cold temperatures. SWE is the sum of April 1 SWE at Crevice Mountain and Lupine Creek snow courses and represents severity due to snow accumulation. PRECIP is the June plus July precipitation for the summer preceding the winter and represents the severity due to reduced forage production on the winter range. These weights and indexes can be adjusted to represent any specific condition that may have a bearing on the severity of a winter for any specific area, for any specific species or any specific area (where there are available data) or can be used as a general index.

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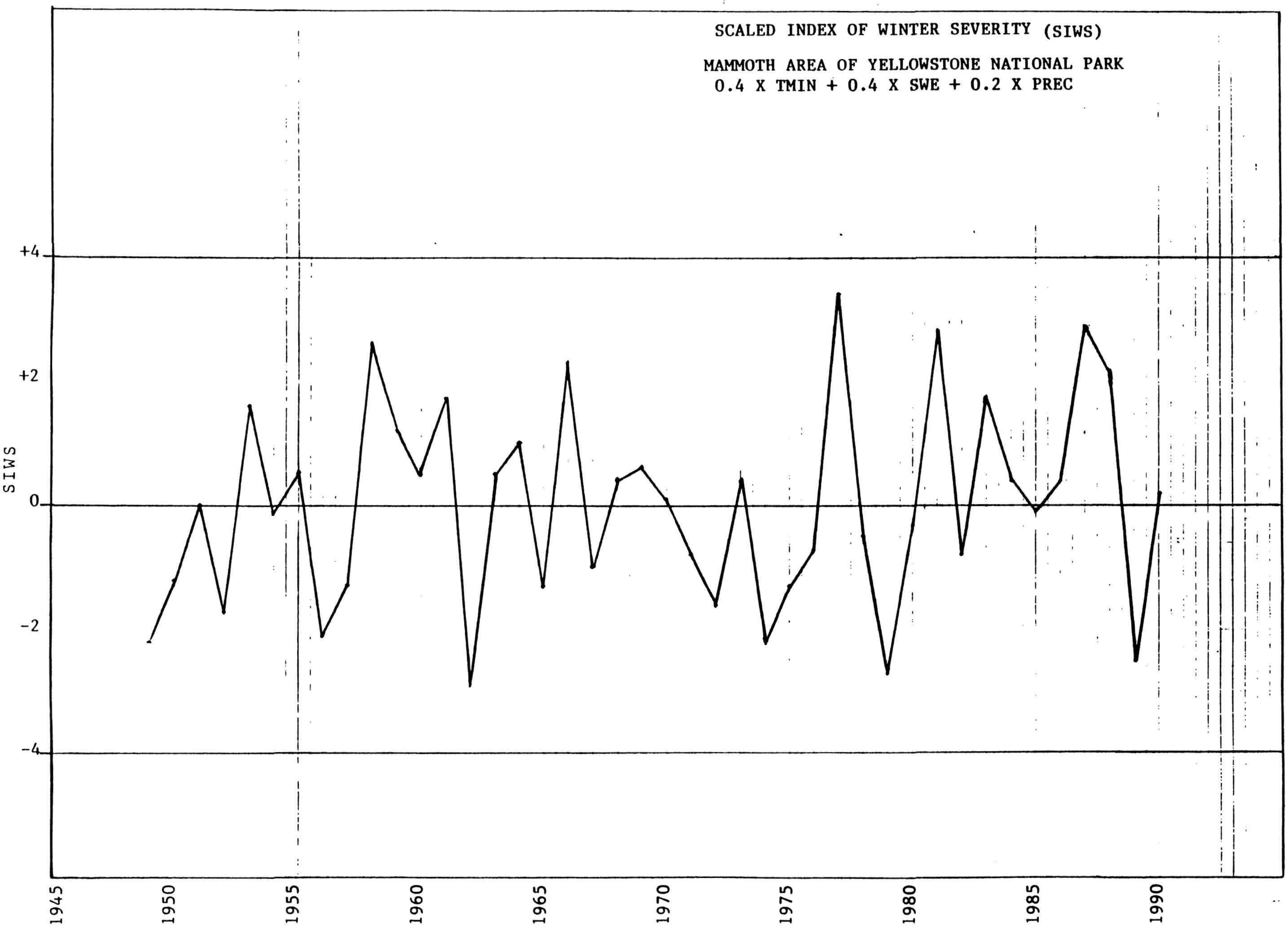

SCALED INDEX OF WINTER SEVERITY (SIWS)
MAMMOTH AREA OF YELLOWSTONE NATIONAL PARK
0.4 X TMIN + 0.4 X SWE + 0.2 X PREC
SIWS
+4
+2
0
-2
-4
1945
1950
1955
1960
1965
1970
1975
1980
1985
1990

TITLE: Physiological assessment of winter undernutrition in elk of Yellowstone National Park.

AUTHORS: Glenn D. DelGiudice, Francis J. Singer, and Ulysses S. Seal.

AFFILIATIONS: Research Service, U.S. Veterans Affairs Medical Center and Yellowstone National Park.

PUBLICATION REPORT STATUS: Submitted to The Journal of Wildlife Management.

PROJECTED PUBLICATION: The Journal of Wildlife Management.

PROJECTED PUBLICATION DATE: ?

DATE OF REPORT:

SUMMARY OF OBJECTIVES:

This study physiologically assessed and compared the extent of undernutrition in elk (cow:calf groups) on the lower, middle, and upper portions of the Northern range, and on the Madison-Firehole range during winter 1987-88. Physiological assessments were accomplished by chemical analysis of elk urine excreted in snow. This technique permitted direct assessment of the physiological status of elk with minimal disturbance. Findings were related to differences in snow cover, herd composition, and elk distribution.

SUMMARY OF MOST SIGNIFICANT FINDINGS:

1. Urinary excretion of urea (the end-product of dietary and body protein metabolism), sodium, potassium, and phosphorous varied within the four sampling areas as winter progressed and differed among the areas during each of four sequential sample collections (early January to late March).
2. Association of increased renal excretion by elk of urea

nitrogen with diminished excretion of potassium and sodium by early March, reflected progressive undernourishment. Data suggested accelerated net catabolism of body protein in elk across the Northern range and on the Madison-Firehole range that continued through at least late March.

3. Elk on the upper Northern range were in the poorest condition during early winter. Approximately 10% of the Upper elk were exhibiting metabolite data indicative of prolonged undernutrition and were relying heavily upon body protein as an alternate energy source. At this time elk density was greatest on the upper Northern range (44 elk/km^2), and snow cover was deeper than on the lower and middle portions of the range. Calf:cow ratios were lowest among Upper elk than middle and lower elk.
4. By early March, a portion of the Upper elk subpopulation had migrated to lower elevations. Elk density decreased to 14 elk/km^2 on the upper Northern range and the calf:cow ratio decreased by 50%. Elk density remained stable on the middle (28 elk/km^2) and lower (34-37 elk/km^2) Northern range during the same interval, but calf:cow ratios decreased by 48 and 35%, respectively. By early March, urinary metabolite data indicated prolonged undernutrition in approximately 13.5 and 10% of the Middle and Lower elk, respectively. None of the remaining Upper elk exhibited data suggesting prolonged undernutrition.

5. By late March, the proportion of Middle and Lower elk experiencing prolonged undernutrition declined dramatically; however, three times as many Middle elk compared to Lower and Upper elk, exhibited this nutritional status.

6. Physiological data suggested that Madison-Firehole elk, occurring at much lower densities, but in an area of notably greater snow cover than on the Northern range, benefited nutritionally by using the snow-free thermal areas. At Madison-Firehole, prolonged undernutrition peaked during late March (6.7%), about two weeks later than on the Northern range (7.1%).

7. During sample collections 1-4, 3.8, 0.6, 7.1, and 2.9% of elk throughout the Northern range exhibited urinary data indicative of prolonged undernutrition. This seemed to agree with an estimated mortality rate of less than 5.0%.

6. Our data tended to support Houston's (1982) contention that population density and winter severity (e.g., snow depth) were critical factors affecting natural regulation of the elk population via nutrition. However, in contrast to past studies, the data yielded by sequential collection and chemical analysis of urine in snow, additionally facilitated assessment of the nutritional status of elk that survived winter.

7. Furthermore, our data suggest that prolonged deep snow (84 cm during April) and restriction of Madison-Firehole elk to thermal areas might result in a proportional winterkill that

is ultimately greater than on the Northern range.

Winter Foraging Behavior of Elk and Bison in Yellowstone National Park, Wyoming.

Gillian Bowser

National Park Service, Yellowstone National Park, Wyoming.

April, 1990

Summary of Objectives:

Foraging behavior is one way to quantify the impacts of environmental parameters on animals. These parameters include snow depth, elevation, and winter severity (precipitation, temperature, and snow density). Mechanisms affecting herd movement and wintering locations can be identified by quantifying the influence of weather parameters on foraging behaviors such as bites, translocations, and rates of movement within or between craters.

This study examined the following hypotheses:

- There should be a functional relationship between environmental parameters such as snow depth or density, and foraging behaviors.
- Foraging data correlates with animal physiological condition and food habits.
- Environmental factors are measurable and influence observable behaviors in foraging animals.

Methods:

- Animals were observed using zoom spotting scopes for fixed intervals (observation bouts) following Altmann (1972) focal animal techniques.
- Behaviors were classified as head movements (swings, bites, chews, pulls, etc.) or as body movements (steps, paws, interactions with other individuals, etc.).
- Behaviors were analysed as behavior observations--the occurence of a particular behavior per observation bout; translocations--frequencies of body movement behaviors per number of bites during an observation bout; snow movement behaviors--frequencies of bites per swings, paws, nose pushing during an observation bout.
- Statistical analyses were performed on behavior occurrences (bites per unit time), or behavior frequencies (bites per swing, bites per step, etc.) for each

location. Locations were compared by snowdepth and water equilivalent using Soil Conservation Service data.

Summary of Most Significant Findings:

- There were significant differences between locations for all foraging behavior classes in bison.
- Northern range sites were significantly higher in all behavior frequencies than interior sites for bison. Movements between craters occurred more frequently for northern range sites than interior ones.
- Interior sites had fewer within- or between-crater behaviors than northern range sites. Animals appeared to re-use craters or stay within a particular crater for a longer period of time.
- Behavior ratios as indicators of snow movement and translocation (movements between craters, expressed as frequencies per step) were significantly different between sites for bison.
- Behavior ratios showed no significant functional relationship with snowdepth parameters, suggesting that the observed differences were due to otehr variables.
- Elk behaviors were highly variable between sites with no significant differences between locations.
- Snow density and water equilivalent did not vary between sites. Other parameters in the snowpack such as crystal types, and ice layers amy have a greater impact on foraging behaviors.

Recommendations and Conclusions

- Locations differ significantly in behavior ratios for bison, but not for elk. Future studies should concentrate on the effects of habituation and distributances on elk.
- Elk behavior ratios showed no significant differences. This result is in agreement with the lack of significance difference between snow density and water equilivant for each locations.
- Bison behavior ratios were significant in snow movement behaviors such as head-swings or pawing per bite, suggesting that these behaviors were more variable than translocation--steps per bite--behaviors. The variations in translocation behaviors may be governed by the amount of previous crater activity, and the size of the herd.
- Habituation effects may be subtle. The elk reduced bite rates in the presence of humans and vehicles while under observation.

- Snow characteristics within the snow column like ice layers and crystal sizes were not measured in this study. Snow characteristics potentially influence snow movement behaviors in ungulates by reducing food availability and increasing the energy required for foraging.
- Forage quality and quantity were not directly measured during this study. Future studies could examine forage aspects and ungulate food habits in greater detail.

The implications for foraging behavior projects for park research and management are wide-spread. Tourist influences on the winter survival of ungulates may be more subtle than measured by herd movements and range use. Reductions in ungulate bite rates in the presence of visitors suggests a hidden cost in the habitual human use of winter range areas by reducing food intake rates (frequency of bites per unit of movement).

The impact on ungulate survival during the winter may be snow quality (density, ice layers or crystal structure) and not quantity. The insignificant affect of varying snow depths on foraging frequencies suggests that other factors in the snow column may contribute to the different foraging rates. These factors include hoar frost concentrations near the ground surface, ice layers within the snow column, and snow pack shear conditions such as crystal-bonding and -strength.

In sum, foraging behavior studies provide detailed information on the effects of winter parameters on ungulates. This information, when combined with physiological data and food habits work, can provide a complete picture on the winter effects of ungulate populations.

TITLE: Collared elk response to the 1988 drought and fires in Yellowstone National Park.

AUTHORS: David J. Vales and Albert L. Harting.

AFFILIATIONS: Department of Fish and Wildlife Resources, University of Idaho and Research Division, Yellowstone National Park.

PUBLICATION REPORT STATUS: Rejected by the *Journal of Wildlife Management.* Resubmission to the *Wildlife Society Bulletin* is planned.

PROJECTED PUBLICATION: *Wildlife Society Bulletin.*

PROJECTED PUBLICATION DATE: Early 1991.

DATE OF REPORT: 21 May 1990.

SUMMARY OF OBJECTIVES:

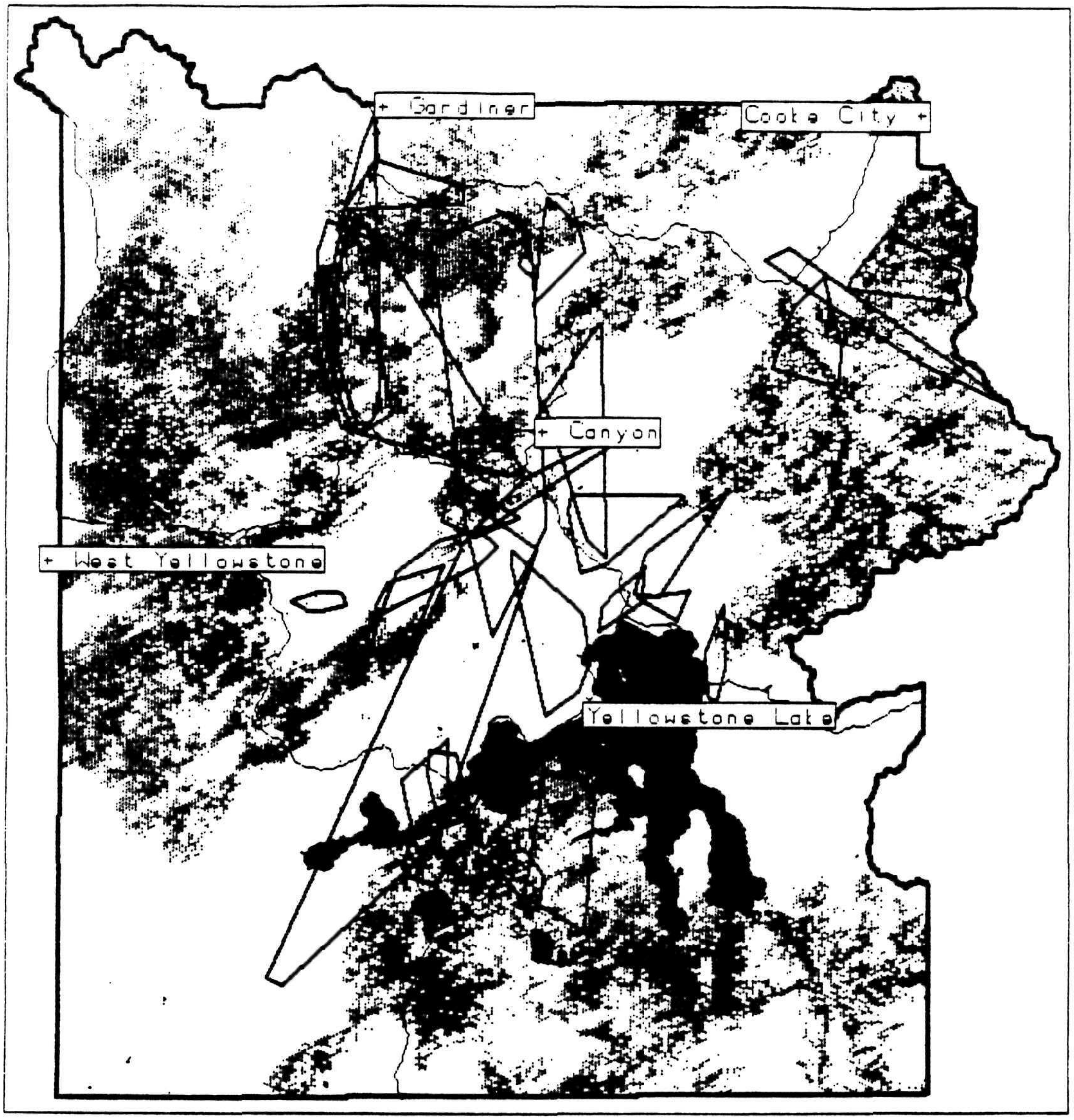
Thirty-two radio-collared adult elk from Yellowstone's northern winter range had been collared and monitored prior to the fires in 1988. For 27 of these animals we had summer 1987 home ranges; the other five were collared winter 1987-88. In this paper we evaluated the potential short-term impacts of the fires and drought on our collared elk. Data were presented on post-fire locations outside of pre-fire home ranges, changes in home range size between 1987 and 1988, and differences in timing of migration between 1987 and 1988. We examined relationships between these three potential response variables and percent of home range burned.

SUMMARY OF MOST SIGNIFICANT FINDINGS:

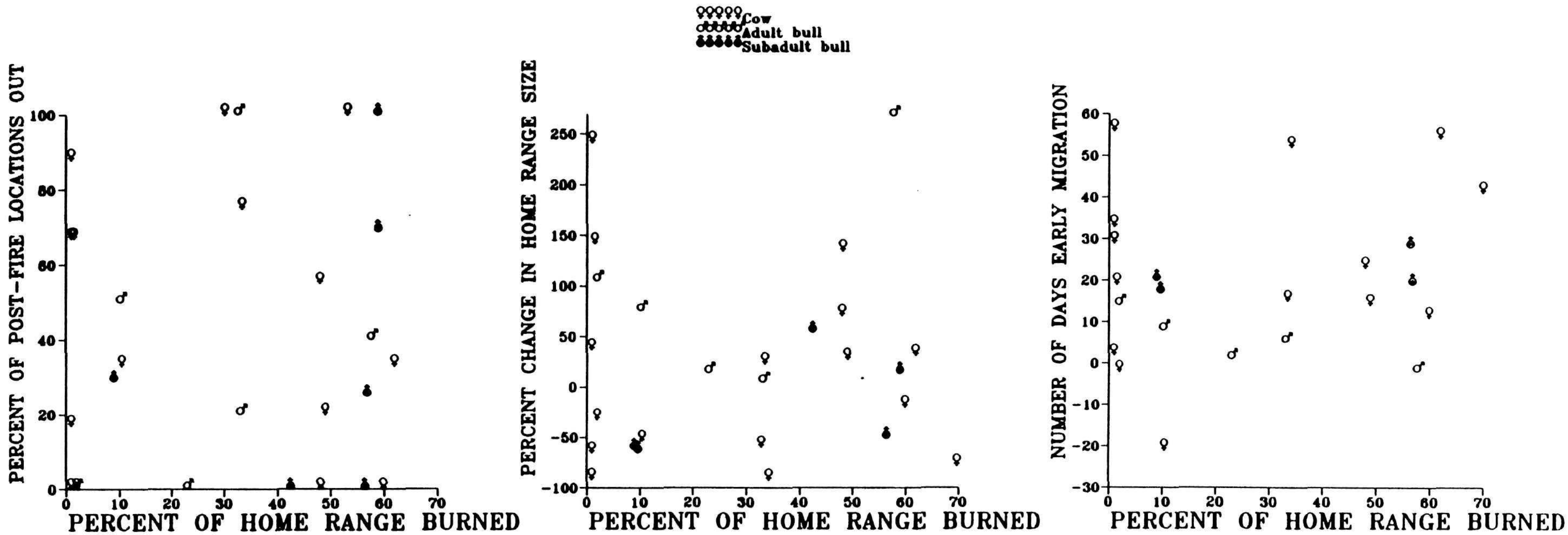
1. No collared elk died in the fires. Eight elk had 1% or less of their pre-fire summer home ranges burned, 4 had 2-10% burned, and 20 had more than 10% burned.

2. No relationships were found with (1) percent of post-fire locations outside of the pre-fire home range, (2) change in size of home range between 1987 and 1988, or (3) early migration to percent of home range burned. Lack of significant correlations indicated that there was no increased movement by elk on summer range that could be attributed to the fires.

3. Migrations averaged 19 days earlier in 1988 than in 1987. Because 6 cow elk least affected by fires migrated as many days earlier as 8 cows with more burning within their home ranges, we concluded that the drought of 1988 rather than the large-scale fires and associated activities influenced elk movements. Early desiccation of plants due to the prolonged summer drought was the most likely factor stimulating early elk migrations in fall 1988.



Burned areas and 100% minimum convex polygon pre-fire summer home ranges of elk in Yellowstone National Park. Dark tones represent lakes, light tones are burned areas.



Relationships of percent of post-fire locations outside of the pre-fire home range, percent change in summer home range size between 1987 and 1988, and number of days elk migrated earlier in 1988 compared to 1987, to percent of the pre-fire home range burned.

TITLE: Antler characteristics of northern Yellowstone elk: 1988.

AUTHORS: David J. Vales.

AFFILIATIONS: Department of Fish and Wildlife Resources, University of Idaho.

PUBLICATION REPORT STATUS: One paper on antler allometric relationships (predicting weight from dimensions) for *Wildlife Society Bulletin* co-authored with John Woods that includes data from Banff National Park. A second on population comparisons, also with John Woods, for *Journal of Wildlife Management*. A third on antler density, spongy tissue, and mineral characteristics and how they relate to age and habitat use by bull elk for *Journal of Mammalogy*. All are currently in preparation.

PROJECTED PUBLICATION: *Wildlife Society Bulletin*, *Journal of Wildlife Management*, and *Journal of Mammalogy*.

PROJECTED PUBLICATION DATE: 1991 and 1992.

DATE OF REPORT: 21 May 1990.

SUMMARY OF OBJECTIVES:

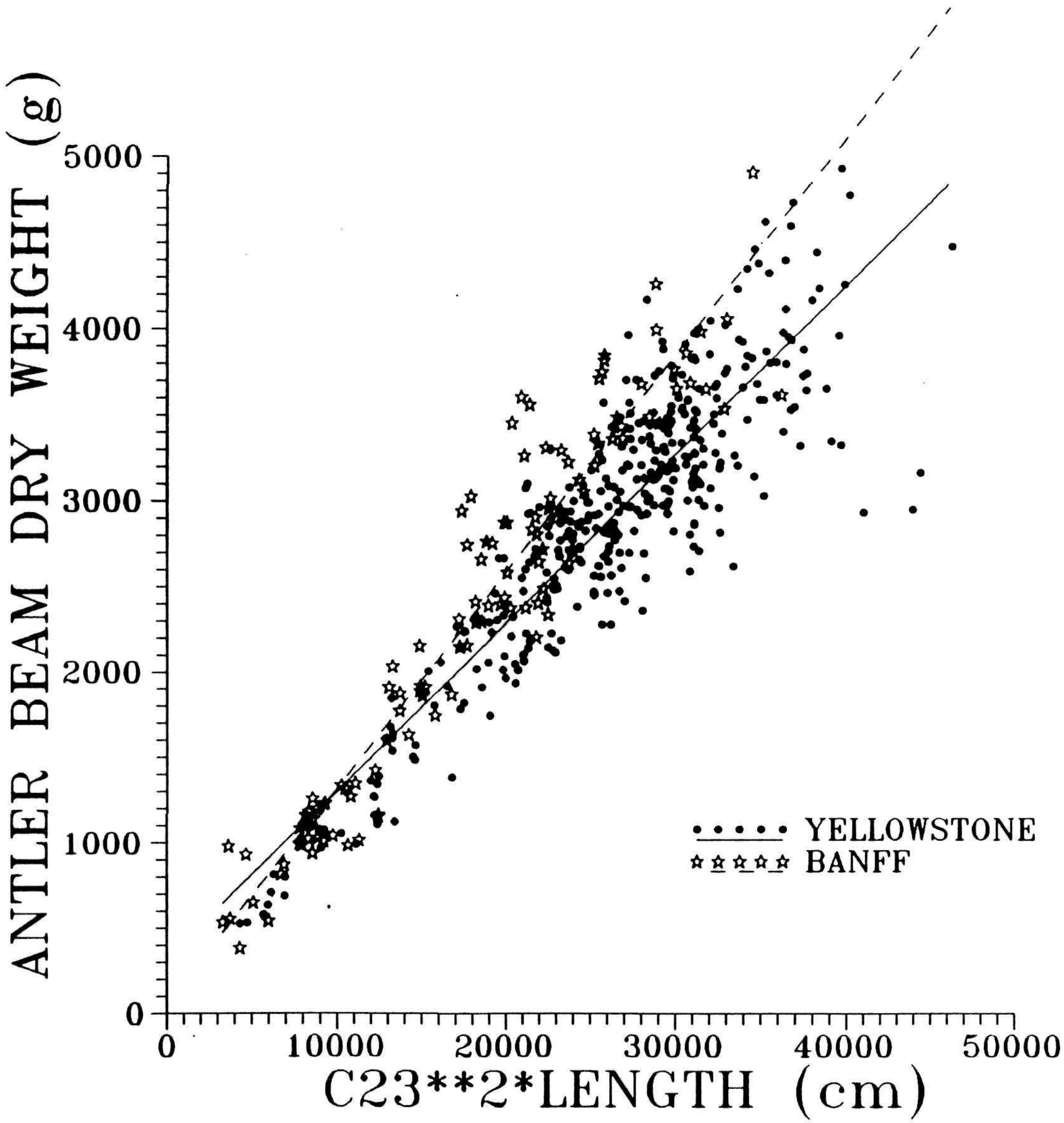
Antlers were cut off, weighed, and measured from bull elk dying naturally during the winter 1988-1989. Objectives were to: 1) predict antler weight from dimensions, compare allometrics among populations, and develop generalized equations if possible; 2) compare characteristics (weight, length) among populations, relate these to population levels, and infer potential nutritional effects on antler growth; and 3) relate antler density and mineral content to animal age, and tie in results with bull elk forage and habitat use data. The data can be used for future comparisons in Yellowstone as population size or nutritional conditions change.

SUMMARY OF MOST SIGNIFICANT FINDINGS:

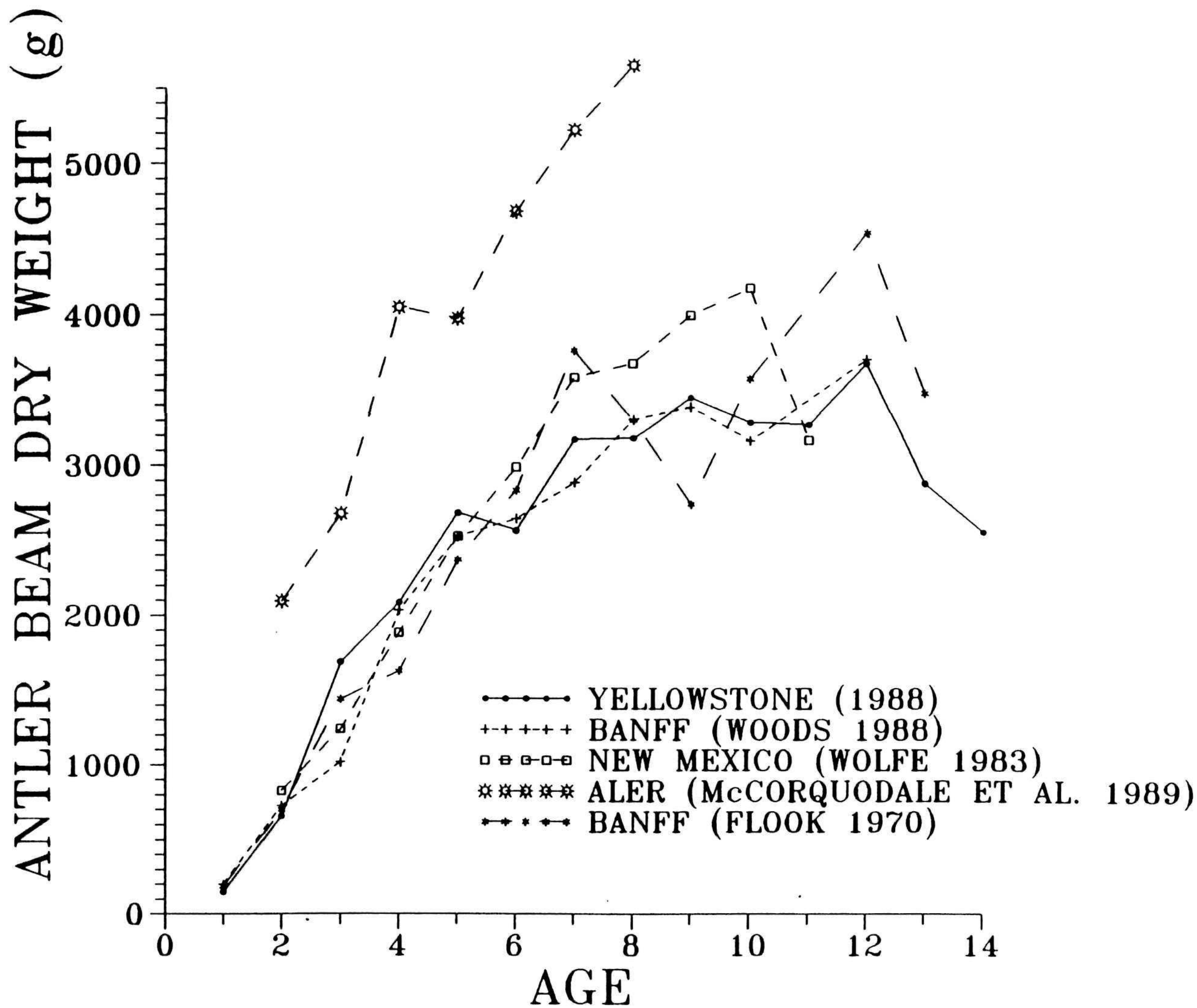
1. Antler mass was allometrically related to dimensions, but the single best predictor of mass was the 2nd-3rd tine minimum circumference squared x length, which gave a linear equation. Equations predicting mass differed between Yellowstone and Banff for ages 2+, but not for age 1 elk.

2. Antler mass of elk in Yellowstone peaked between ages 7-12. The mass over age relationship was similar to that in Banff at present, but less than that of New Mexico and eastern Washington (ALER). Populations in Banff and Yellowstone were at high levels; elk at ALER were colonizing and were at low numbers. Habitat, latitudinal, and growing season length influences need to be explored.

3. Moisture content of antlers averaged 13% for yearlings and 9% for bulls aged 2 and older. No significant differences were found between characteristics of left and right antlers. Antler main beam density averaged 0.95 g/cm^3 for yearlings and 1.21 g/cm^3 for bulls aged 2 and older. Spongy tissue area and mineral content analyses are being processed.



Relationship between dry weight of antler beams and the best predictor variable (minimum circumference between 2nd and 3rd tine squared times beam length) for Yellowstone and Banff National Parks.



Relationship between antler beam dry weight and age in four elk populations.

TITLE: Current distribution of beaver in Yellowstone National Park.

AUTHORS: Susan L. Consolo and Donay D. Hanson

AFFILIATIONS: Resource Management Office, Yellowstone National Park

PUBLICATIONS REPORT STATUS: Included in Wolves for Yellowstone? A Report to the United States Congress, Volume II, Research and Analysis.

PROJECTED PUBLICATION DATE: May 1990.

DATE OF REPORT: December 1989.

SUMMARY OF OBJECTIVES:

As part of on-going efforts to understand the ecology of Yellowstone's northern range and park riparian zones, and to monitor the status of controversial wildlife species, a sampling survey was initiated to document presence and distribution of beaver parkwide. Specific objectives for the initial survey were to 1) identify places with present or recent beaver activity, and 2) assess the likelihood that those sites could support long-term versus highly intermittent beaver activity.

SUMMARY OF MOST SIGNIFICANT FINDINGS:

1. Much of Yellowstone National Park is marginal beaver habitat, but beaver have persisted here since the park's inception.

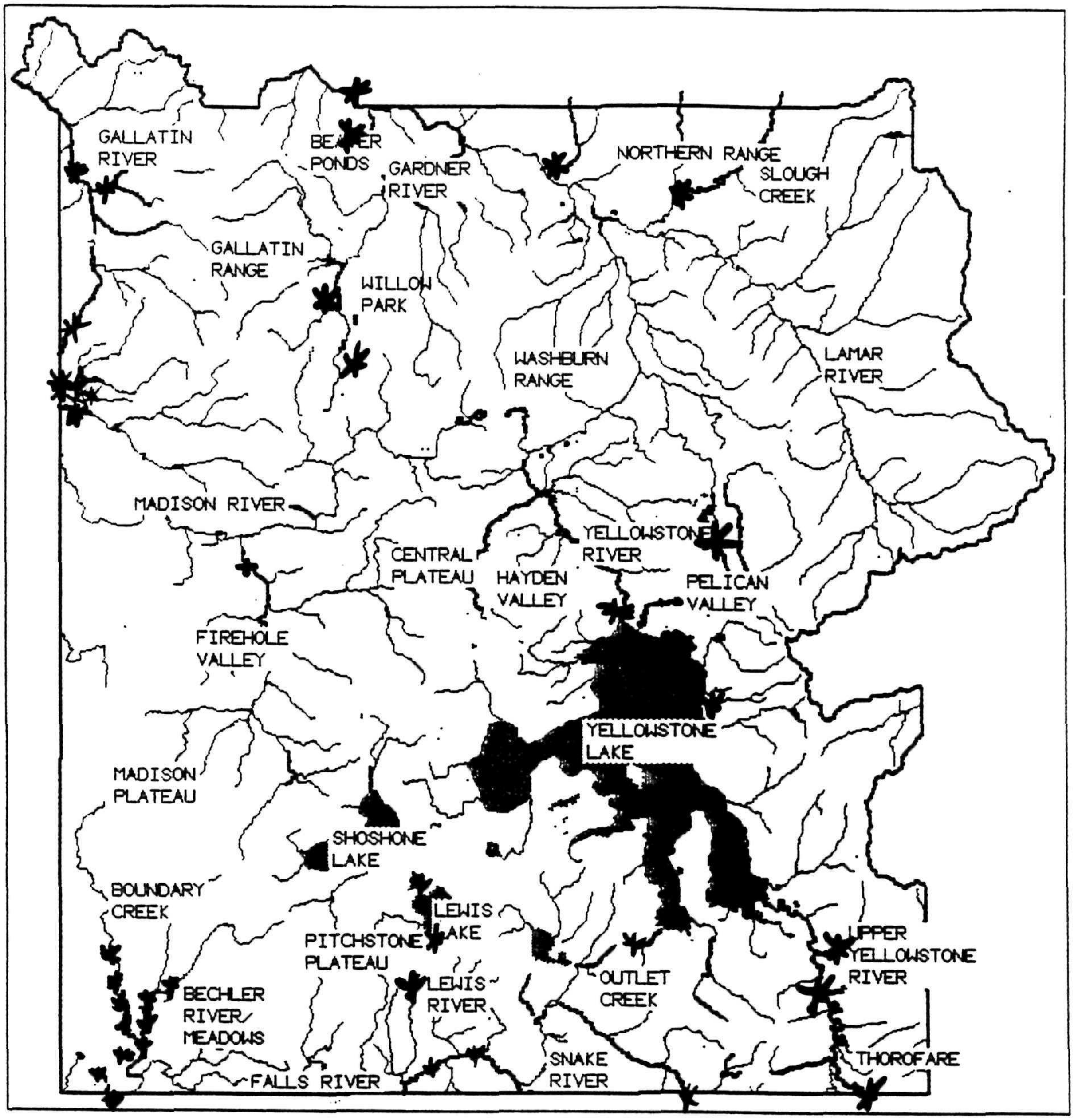
2. In 1988-89, 453 km of riparian habitat in Yellowstone (88% of targeted routes/sites) were surveyed to determine current presence and distribution of beaver. There were 43 stream segments or lakes that had signs of current beaver activity. 42 reliable observations of at least 27 individual beaver were collected during the survey period.

3. There were at least 26 locations with evidence of both present and previous beaver activity, at least 5 of which are on the northern range. Rivers such as the Yellowstone, Gardner, Lamar, and Slough Creek show signs of periodic beaver presence and likely support bank-denning beaver that are difficult to observe. Evidence of moderately persistent activity was found on those waterways, and also in the Beaver Ponds, Slide Lake, and Willow Park areas near Mammoth Hot Springs.

4. Signs of numerous, persistent beaver colonies were found in the upper Yellowstone River/Thorofare region, the Bechler region in the park's southwest corner, the lower elevation reaches of the

Gallatin River drainage, and portions of the Madison River drainage.

5. Observations of beaver and current sign should continue to be collected and surveyed on a periodic basis. Widespread fire activity of 1988 could potentially affect beaver distribution, depending on fire effects on willow and aspen communities as these species are often associated with persistent beaver colonies. However, as a number of stream characteristics have been found to positively correlate with colony size and persistence (Easter-Pilcher 1987), potential beaver habitat in Yellowstone's streams would be better assessed by using a comprehensive stream survey system such as that developed by Rosgen (1985) or Beier and Barrett (1987.)



Areas where beaver or present/recent beaver signs were observed in 1988-89.

TITLE: Elk forage responses in burned and unburned lodgepole forests.

AUTHORS: Francis Singer, James Reardon, Jack Norland, and Jill Oppenheim, Box 168, Yellowstone National Park, WY 82190

PUBLICATION REPORT STATUS: An article for Journal of Wildlife Management is planned.

SUMMARY OF OBJECTIVES:

1. To determine changes in plant species abundance and production in burned and unburned forests on elk summer range.

2. To determine any nutritional changes in elk forages after burning.

3. To determine any differences in elk preferences for forages between burned and unburned habitats. In particular, the hypothesis of Don Despain was investigated, specifically, that some forages species untouched in unburned areas are eaten in burned areas.

METHODS AND STUDY AREA:

1. The study area was located 4 miles southwest of Grant Village in a lodgepole pine forest-wet meadow complex that was partially burned in August of 1988. Three similar burned and unburned sites were selected for both forest and meadow. At each site 10 samples of each forage were collected. The forages were collected, dried and sent to the Composition Analysis Lab in Ft. Collins for analysis of protein content and digestability.

2. Plant sampling was conducted in 1990. Grazing exclosures were erected in forest and meadows in order to determine the amounts of herbage removed by elk. Four replicates of each treatment (grazing, burning) were available.

SUMMARY OF PROGRESS AND FINDINGS:

1. Protein content was higher in burned areas for all four forage samples collected in 1989 (Fig. 1). The magnitude of the increase in protein content is unprecendented in the scientific literature for elk forages. Our explanation for this observation is that most studies of elk forage responses have been conducted near cool fires, e.g. prescribed burns in forest understories, while the Grant fire was a hot wildfire.

2. We found no significant effect on protein content in elk forages in the meadows. These fires were cooler.

3. Digestibility was higher in three burned elk forages in the

forest understory, but not in elk sedge (Table 1). No significant difference was found in any burned elk forages in the meadows. In conclusion, digestibility followed the same trend as for protein content--differences were detected only where the fires were hotter.

4. Vegetation composition of forest understories was dramatically altered by the fires. Huckleberry declined, and grasses and fireweed greatly increased.

5. More intensive field sampling is continuing in 1990.

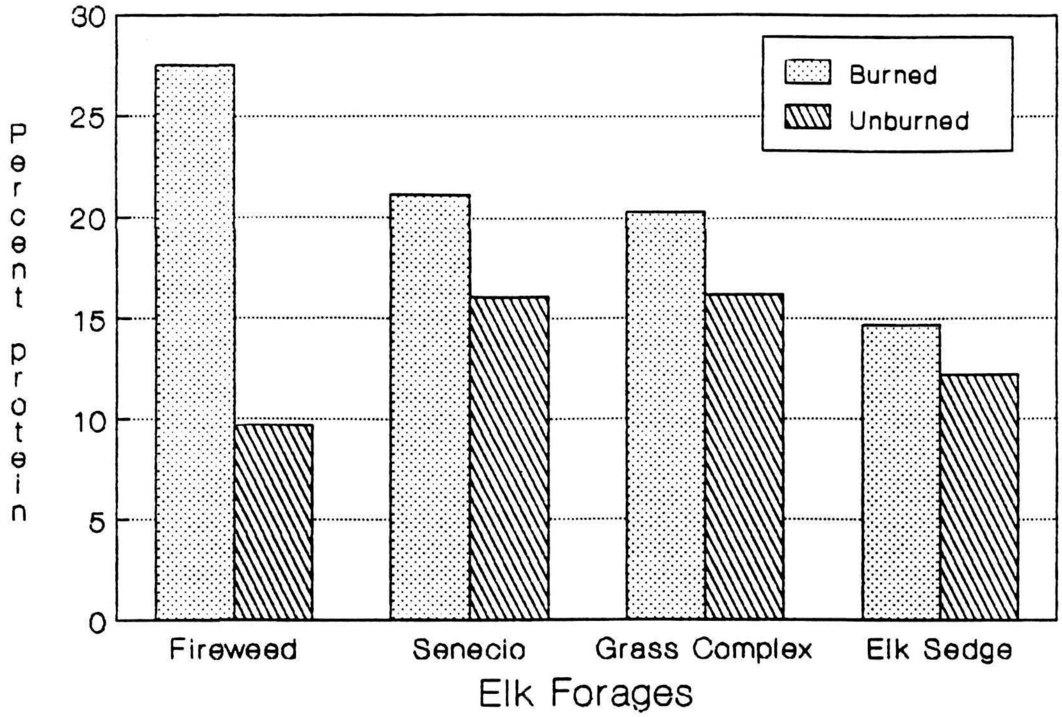


Fig. 1. Percent protein in burned and unburned elk forages in lodgepole forest, 1989.

Table 1. Digestibility of elk forages in burned and unburned meadows and forest understories in the Grant Village area, 1989.

Forage	% Digestibility Burned	Unburned
Forest:		
Fireweed	75	62 *
Senecio	79	71 *
Grass	72	69 *
Sedge	66	64 *
Meadow:		
Forb	79	79
Grass	70	71
Sedge	66	67

TITLE: Effects of the fires of 1988 on elk calf survival rates.

AUTHORS: Francis Singer and Albert Harting, Box 168, Yellowstone National Park, WY 82190.

PUBLICATION PLANS: Journal of Wildlife Management article winter 1990-91.

SUMMARY OF OBJECTIVES:

1. To continue elk calf mortality studies the first two years following the fires of 1988. To compare data gathered on elk calf mortality before the fires to elk calf mortality after the fires.

SUMMARY OF PROGRESS AND FINDINGS:

1. Thirty-two neonatal elk calves were captured in the spring of 1990. Fourteen were captured in the Gardiners Hole study area, and 18 in the Lamar study area. Sixteen were captured by ground and 16 by helicopter. One transmiter was malfunctional, reducing the sample size to 32 calves.

2. We predicted elk calf survival would be improved after the first full growing season following the fires, due to nutritional enhancement of summer and winter ranges. Summer 1990 mortality rates of calves were in fact higher than any previous year (Fig. 1). Apparently, predators were more highly motivated to search for and chase calves in 1990, due to the paucity of winterkilled ungulates during the winter 1989-90.

3. We predicted elk calves would weigh more in 1990 than any previous year, due to range enhancement from the fires of the fall of 1988. This did not prove to be the case (Fig. 2), although 1990 calf weights were improved over weights in 1989 which followed the drought, fires and severe winter of 1988-89.

4. An original goal of this project was to determine the cause of the typically low calf ratios in the northern elk herd in fall and early winter. We have now established that those low fall ratios are due primarily to predation soon after birth of the calves, although accidents and sickness also takes some calves. The relative importance of predators was: grizzlies> coyote> black bear> golden eagle.

5. Houston (1982. The Northern Yellowstone elk. Macmillan) concluded that over-winter mortality of elk calves was density dependent in the northern herd, and was a potential population regulatory mechanism. We did not refute these conclusions. However, our 4-year study demonstrated that predation was more significant than winterkill in the first year mortality of calves (Fig. 3). Additionally, during our study, predation acted in a density independent fashion. For example, predation rates were highest the year of lowest elk numbers.

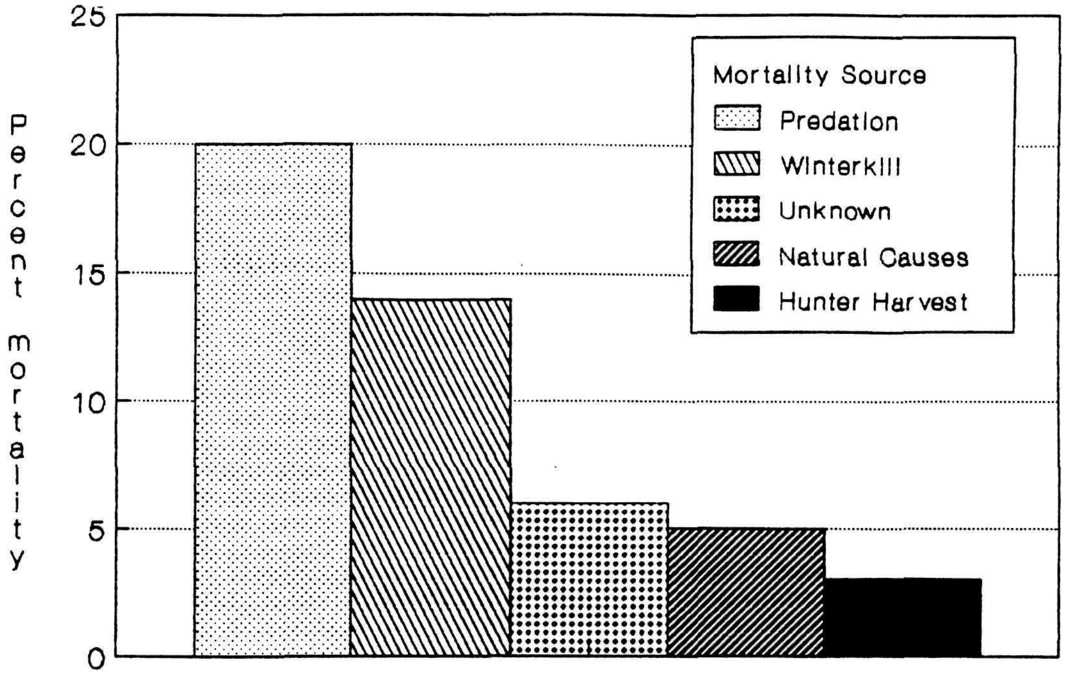


Fig. 3. Sources of elk calf mortality during the 1st year of life, 1987-1990, expressed as a percent of the original marked cohorts (n=128 marked calves), on Yellowstone's northern range.

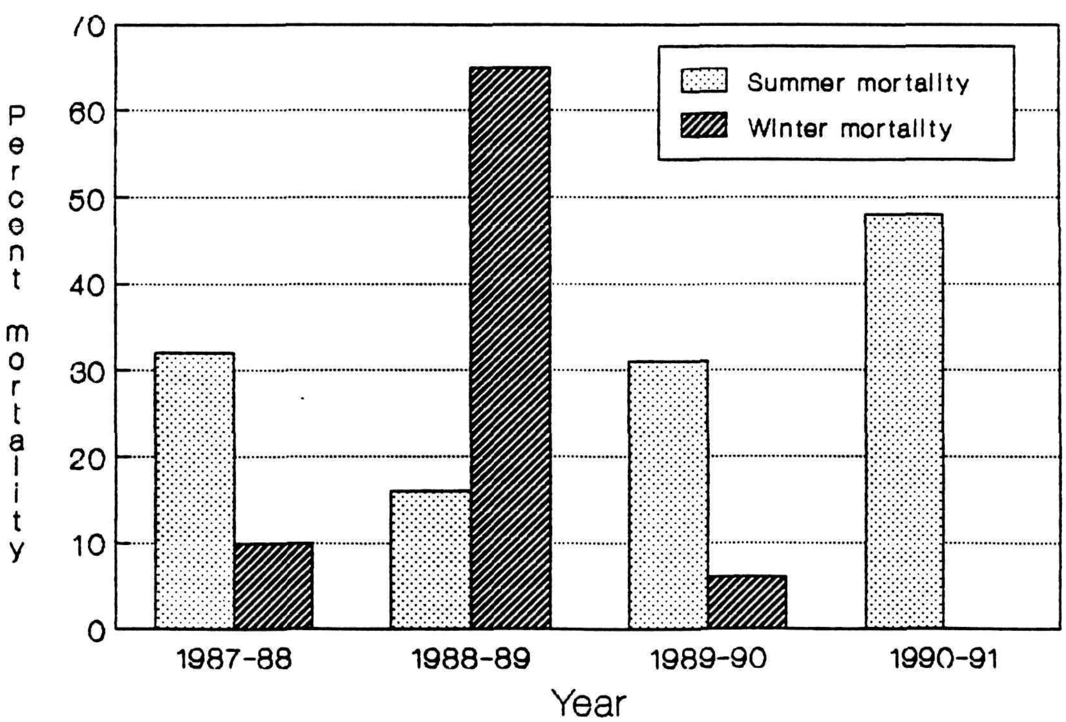


Fig. 1. Elk calf mortality rates, 1987-1990, on Yellowstone's northern range. Percent of initial samples of marked elk calves that died the first summer and the first winter after marking. No data is available yet for the winter of 1990-1991.

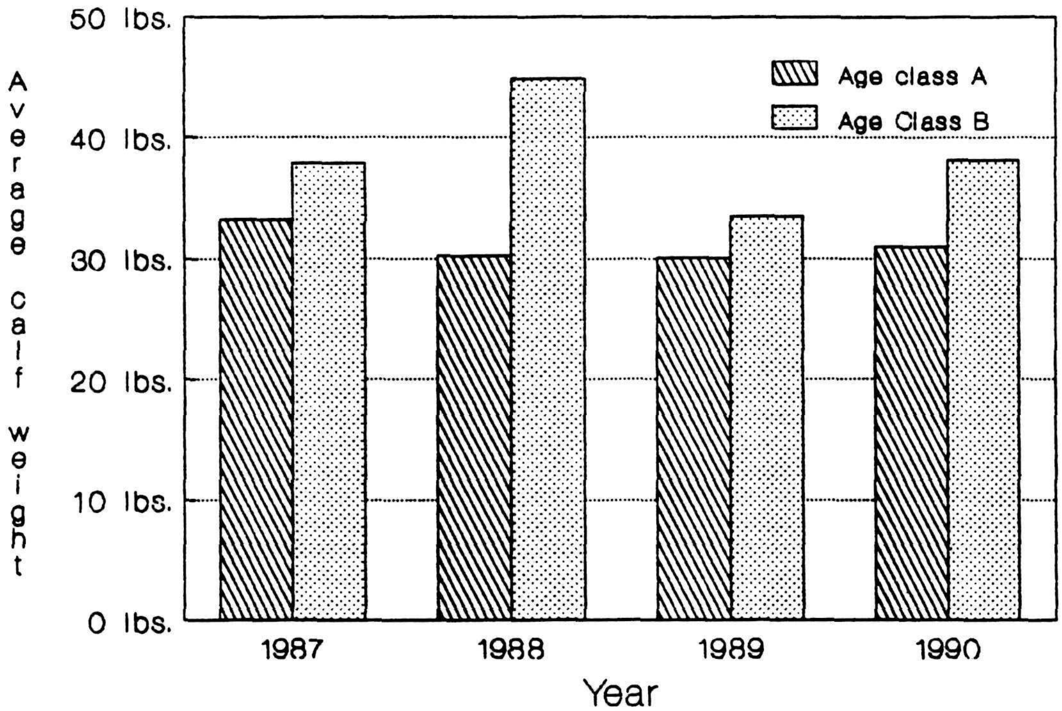


Fig. 2. Elk calf weights in age class A (0-1 day), and age class B (2-4 days), on Yellowstone's northern winter range, 1987-1990.

TITLE: Grazing responses of grasslands to ungulates on Yellowstone's northern elk winter range.

AUTHOR: Francis J. Singer

AFFILIATION: Research Division, Box 168, Yellowstone National Park, WY 82190.

PUBLICATION STATUS: Submitted to J. Range Manage. August 1990.

OBJECTIVES:

1. To determine the effects of ungulate grazing, mostly by elk, upon grassland species abundance, grassland production, grass nutritional quality, and grass heights and morphology.

CONCLUSIONS:

1. Biomass of two grasses, junegrass (Koeleria cristata) and thickspike wheatgrass (Agropyron dasystachum), was greater on grazed plots. Both of these two grasses are widely held to be increasers under grazing(Fig. 1).

2. No consistent difference was observed between 23 other grasses and 87 forbs between grazed and ungrazed sites (Table 1).

3. Minor differences in ground cover was observed on grazed sites. The percent of bare ground averaged about 38% greater on grazed sites, while cover by moss and lichens did not differ in a consistent fashion between grazed and ungrazed sites.

4. No increase in mortality of bunchgrass clumps was observed on grazed sites.

5. Grass morphology varied little between grazed and ungrazed sites. Vegetative culms were shorter on grazed sites, but the total number of vegetative culms did not differ. The heights and numbers of reproductive stalks did not differ between grazed and ungrazed sites.

6. Litter and standing dead vegetation averaged 4 times greater on ungrazed sites. This was a logical consequence of the lack of grazing.

7. There was a very large enhancement in protein and a minor enhancement in other mineral nutrients in 3 common grasses on grazed sites (Fig. 2, Table 2).

JUNEGRASS

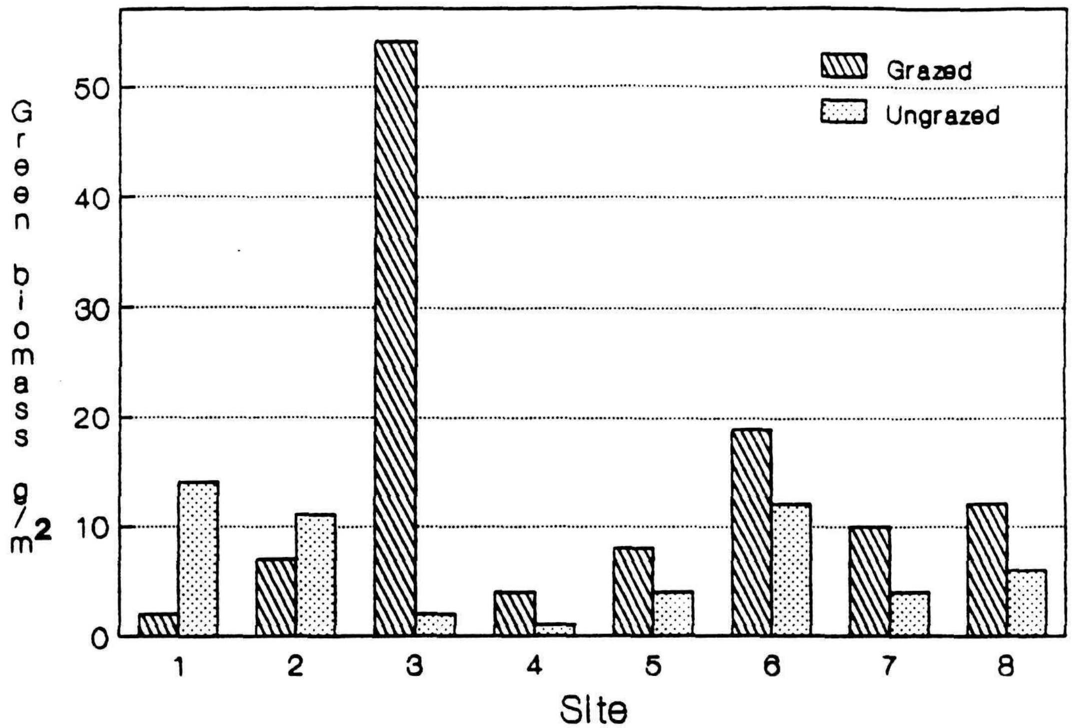


Fig. 1. Biomass of june grass on paired grazed and ungrazed (exclosed) plots on Yellowstone's northern winter range.

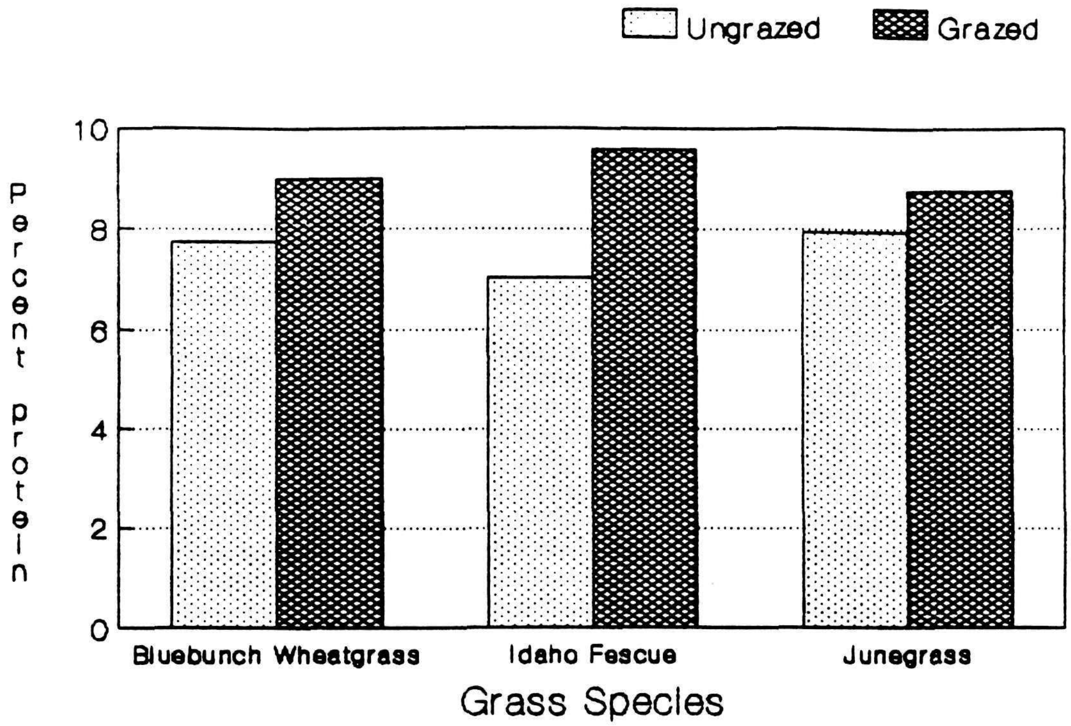


Fig. 2. Protein concentration in live tissue of three common grasses in grazed and ungrazed plots on Yellowstone's northern winter range.

TABLE 1. **BIOMASS DIFFERENCE ON GRAZED PLOTS**

PLANT SPECIES	NO. PAIRED PLOTS	MORE BIOMASS	LESS BIOMASS	NO DIFFERENCE	SUSPECTED EFFECT
Idaho fescue	5	1	2	2	none
Bluebunch wheatgrass	7	2	2	3	none
Bluegrass	5	2	0	3	none
Thickspike wheatgrass	3	2	0	1	none/inc.
Junegrass	8	6	0	2	increase
Litter	8	0	8	0	decrease

TABLE 2.

ENHANCED CONCENTRATIONS IN GRAZED SITES

	IDAHO FESCUE	BLUEBUNCH WHEATGRASS	JUNEGRASS
Ca	*		
P	*		
Mg	*		
K		*	
Mn			
Protein	*	*	*
Digestibility	* (+0.3%)	* (+ 8%)	* (+ 2%)
Fiber			
Ash	*		*

TITLE: Effects of the fires of 1988 on grasses and herbivory at the Blacktail Deer Creek exclosure.

AUTHORS: Francis Singer and Mary Harter, Box 168, Yellowstone National Park, WY 82190

PUBLICATION REPORT STATUS: Article for Journal of Range Management, spring 1991.

SUMMARY OF OBJECTIVES:

1. To document the effects of the fires of 1988 on grassland production and forage quality in grazed and ungrazed areas.

2. To document the effects of the fires of 1988 on soil moisture, seed effort, and spring grazing pressure in a grassland community.

INTRODUCTION:

Eight large grazing exclosures were erected in 1959 and 1962 on the northern winter range to monitor grazing influences by ungulates. Two of these exclosures were influenced by the large fires of 1988. These two exclosures are located on the south facing slopes just west of Blacktail Deer Creek. In the summers of 1989 and 1990, a study was initiated to determine the effects of the fires on elk forage abundance and quality in these grazed and ungrazed (exclosed) sites.

METHODS:

1. Plant cover was measured on 10 macroplots within each of the four treatments of burned and unburned, and grazed and ungrazed sites. Paired plots weres selected with similar slope, aspect, soil, and vegetation type.

2. Within each macroplot, 15-0.25m square subplots were randomly located. Cover by plant species, litter, rock, bare ground, moss, lichens, and animal plants was recorded.

3. Mann Whitnmey U tests were used to test for mean differences between the treatments of burning and grazing.

SUMMARY OF PROGRESS AND FINDINGS:

1. Ungrazed sites responded less rapidly to burning. Ungrazed (exclosed) sites had less plant cover the first summer after the fires (Fig. 1). Litter and standing dead vegetation averages 4 times greater inside of these exclosures (Singer in review). We suspect the fires inside of the exclosures were hotter as Wright and Klemmedson (1965) observed for ungrazed areas, and therefore, vegetation recovery was slower (Wright and Bailey 1982).

2. Grazed plots responded rapidly to the fires, and burned plots

had more plant cover the first season following the fires (Fig. 2) We suspect the fires were cooler on the grazed sites due to less litter. Also, grasses and forbs are less sensitive to burning late in the grwoing season (Wright and Bailey 1982) as occurred at the Blacktail Deer Creek exclosures. Increased soil nutrients following a fire may result in greater plant production.

3. In conclusion, burning of grazed grasslands resulted in more plant cover the first growing season following a fire in comparison to unburned grazed grasslands. However, the trend was the reverse for ungrazed (exclosed) grasslands. Apparently due to the accumulation of litter in ungrazed grasslands, burned sites had less vegetative cover the first season following the fires.

4. Plant nutrient quality (protein, digestibility, other nutrients) has been analyzed by a laboratory, but the results have not yet been analyzed statistically.

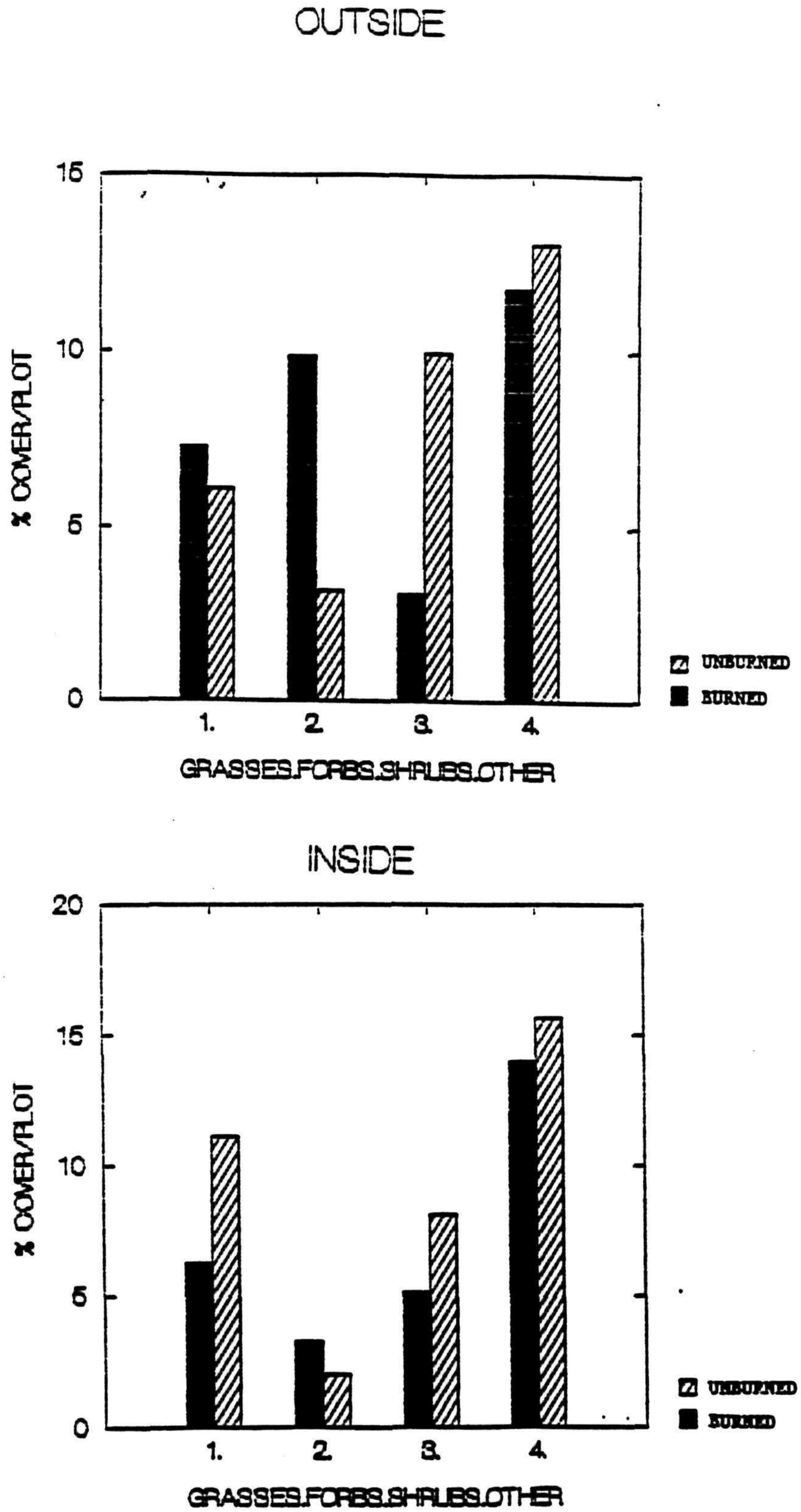


Fig. 3. Vegetative recovery by forage class the first year following the fires in grazed (outside) and ungrazed (inside) plots at the Blacktail exclosures, 1989. Grazed sites responded more quickly to the fires. Forbs responded more quickly than grasses, and grasses responded more quickly than shrubs.

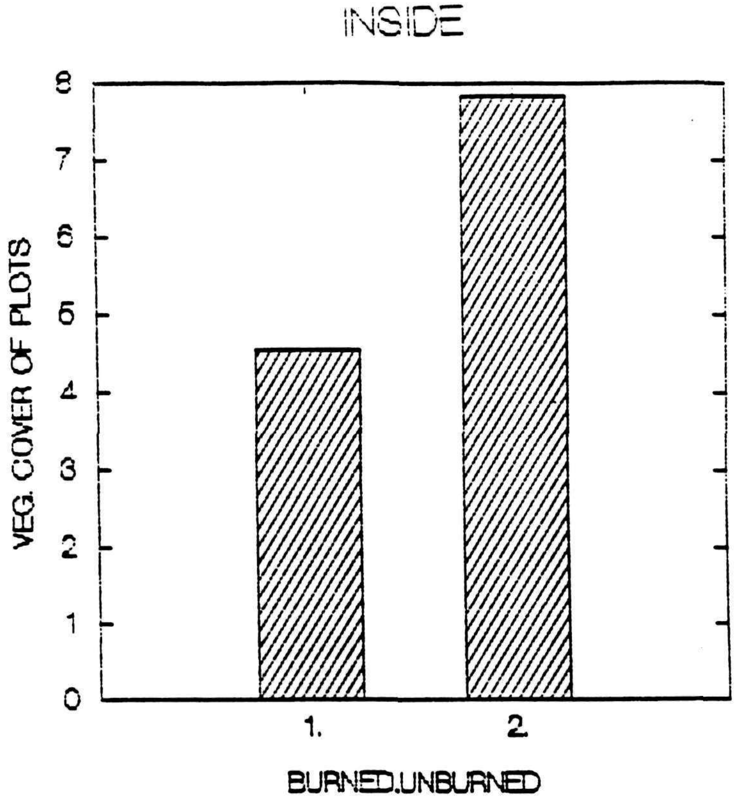


Fig. 1. Vegetative cover of ungrazed (exclosed) burned and unburned plots inside of the Blacktail Deer Creek exclosures in 1989.

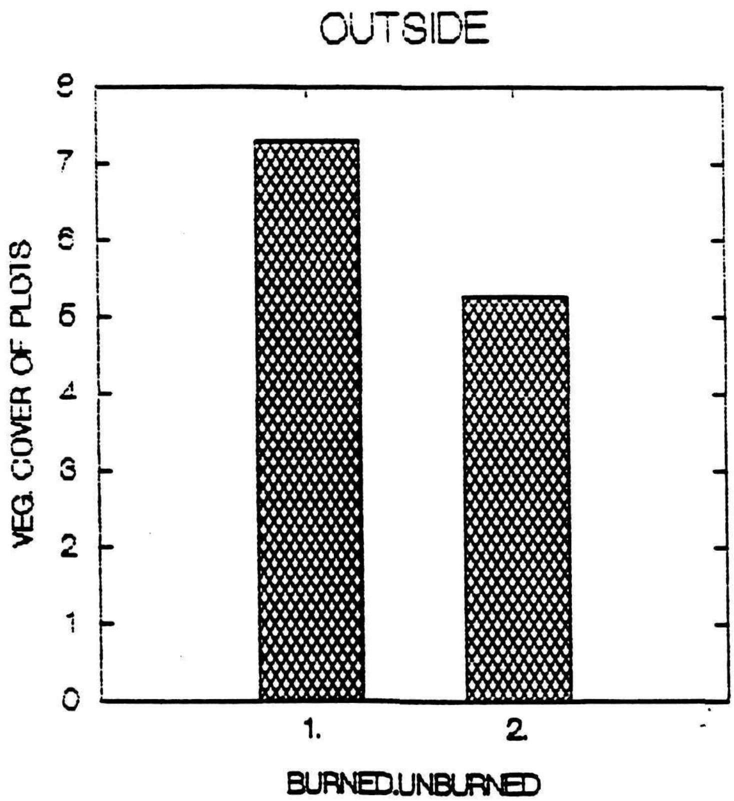


Fig. 2. Vegetative cover in grazed burned and unburned plots located outside of the Blacktail Deer Creek exclosures in 1989.

TITLE: WILLOW SPECIES ABUNDANCE, HERBIVORY, AND THE ROLE OF SECONDARY COMPOUNDS ON THE NORTHERN ELK WINTER RANGE.

AUTHORS: Francis Singer, Lauryl Mack, Research Office, Yellowstone National Park, WY 82190; and Rex Cates, Bringham Young University, Provo, Utah.

PROJECTED PUBLICATIONS: Ecology, Moose Conference in 1991.

SUMMARY OF OBJECTIVES:

1. To describe the distribution and abundance of willows in three drainages located in the northeastern corner of Yellowstone's northern range.

2. To sample the utilization patterns on these willows by large herbivores.

3. To investigate the implications of herbivory, climatic change, and primary sucession upon willow stature, vigor, and nutritional status and, in particuliar, to investigate three primary hypotheses:

   a. That a drier climate in the early part of the twentieth century, especially 1919-1936, contributed to a decline in willows and/or willow stature.

   b. Water and/or browsing stressed willows produce fewer secondary defense compounds than non-stressed willows.

   c. The fires of 1988 may promote vigor and growth in willows and production of secondary compounds and enable some burned willows to escape the height of browsing.

SUMMARY OF FINDINGS SINCE 1989:

1. Willow heights were classified into three categories on the northern range; low stature willows were from 1-37.2cm, intermediate stature was 37.3-176.2cm, and tall stature willows were 176.3cm and above. The mean height of all willows across the northern range was 106.7cm + 69.5. Using these categories, there are two "tall" willow communities (Lower Slough Creek and Soda Butte Creek), two communities which are "low", (Mammoth and Lamar willow belts), and all other communities fall within the

"intermediate" height category. Winter utilization of tall stature willows averaged 38.6% from 1987 to 1990, use on intermediate stature willows averaged 26.2% and use on low stature willows averaged 47.8% 1987-1990 (Fig.1). Shorter stature willows are browsed more heavily than taller willows.

2. Summer utilization rates on low, intermediate and tall stature willows for 1988-1989 are shown in Fig.2. Utilization on all three height categories did not vary greatly. A chi-square test revealed that the differences in utilization rates between the height categories is significant.

3. Our hypothesis is that browse-or ecologically stressed willows are less able to produce secondary compounds such as tannins, and they are therefore subjected to increased browsing. We have collected extensive samples of willows in 1989 and 1990 for analysis of plant defense compounds.

4. The effects of the severe winter of 1988-89 on willow utilization was dramatic. Utilization rates were 3-fold higher than for the previous two winters (Fig. 3). About 24% of the northern elk herd winterkilled and some moose starved to death, so such a dramatic dependence on woody browse was not unexpected.

5. The winter of 1988-89 provided us with another opportunity to test the hypothesis that severely browsed willows are less able to produce secondary defense compounds. Utilization rates on willows remained high during the winter of 1989-90 and summer 1989 rates were higher than summer 1988 rates, in spite of substantially lower ungulate populations. This suggests to us that willows were poorly defended after the tough winter.

6. A widely held belief in the scientific community is that utilization rates of 25-30% can be compensated for, or even stimulate willows, but that utilization rates above that level will result in lowered productivity and eventually death in willows. Few studies in fact have proceeded to the point of eath. However, under this widely-held belief, winter utilization rates on tall willows is acceptable, and use on the intermediate, and short stature willows is excessive.

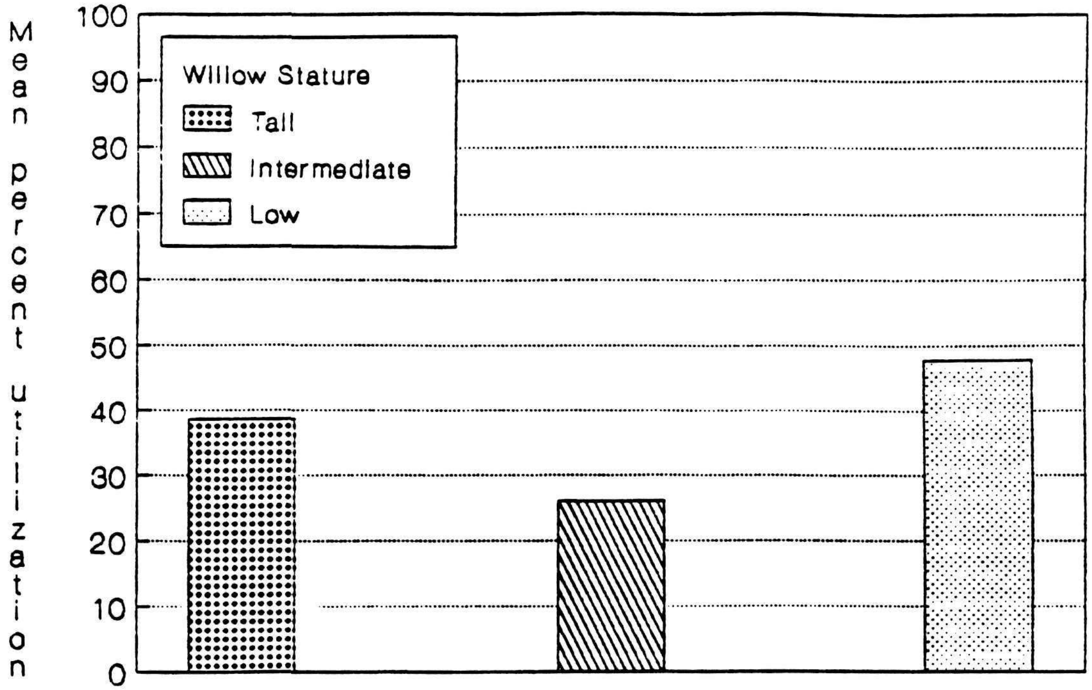


Fig. 1. Average percent winter utilization on tall, intermediate, and low stature willows on Yellowstone's northern winter range, 1987-1990. Low stature willows are more heavily browsed than taller willows.

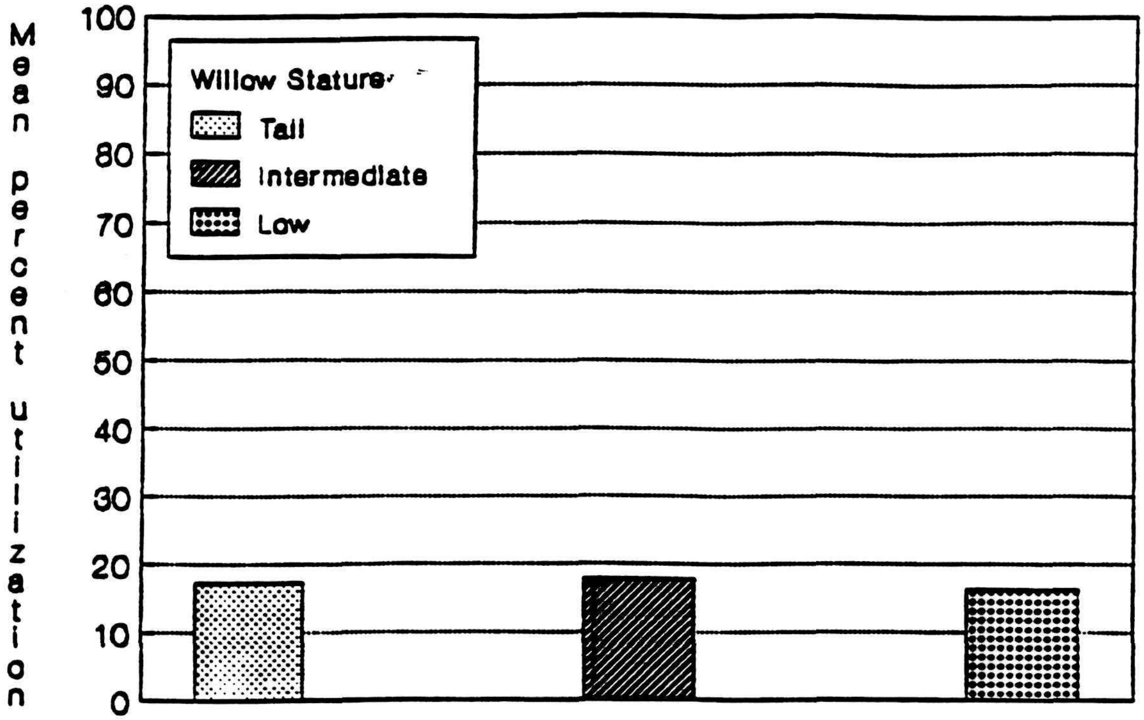


Fig. 2. Average percent summer utilization on tall, intermediate, and low stature willows on Yellowstone's northern winter range, 1988-1989.

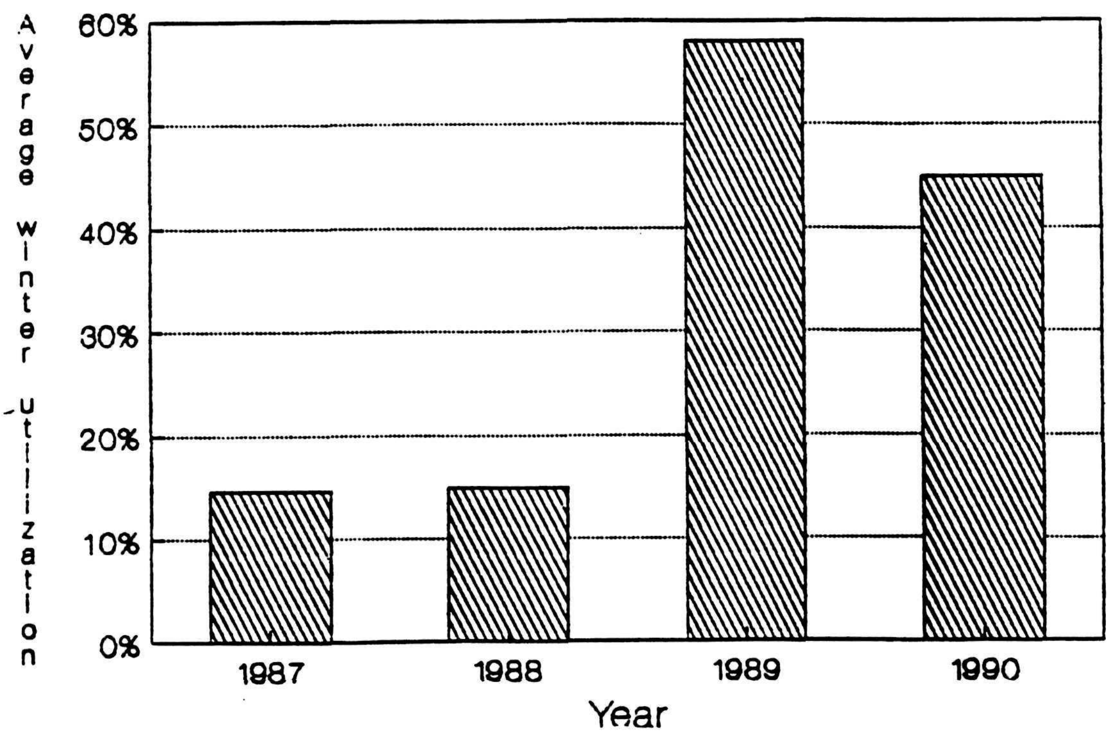


Fig. 3. Average percent winter utilization on willows of the northern range, 1987-1990. Utilization rates for 1987 are based on three areas only.

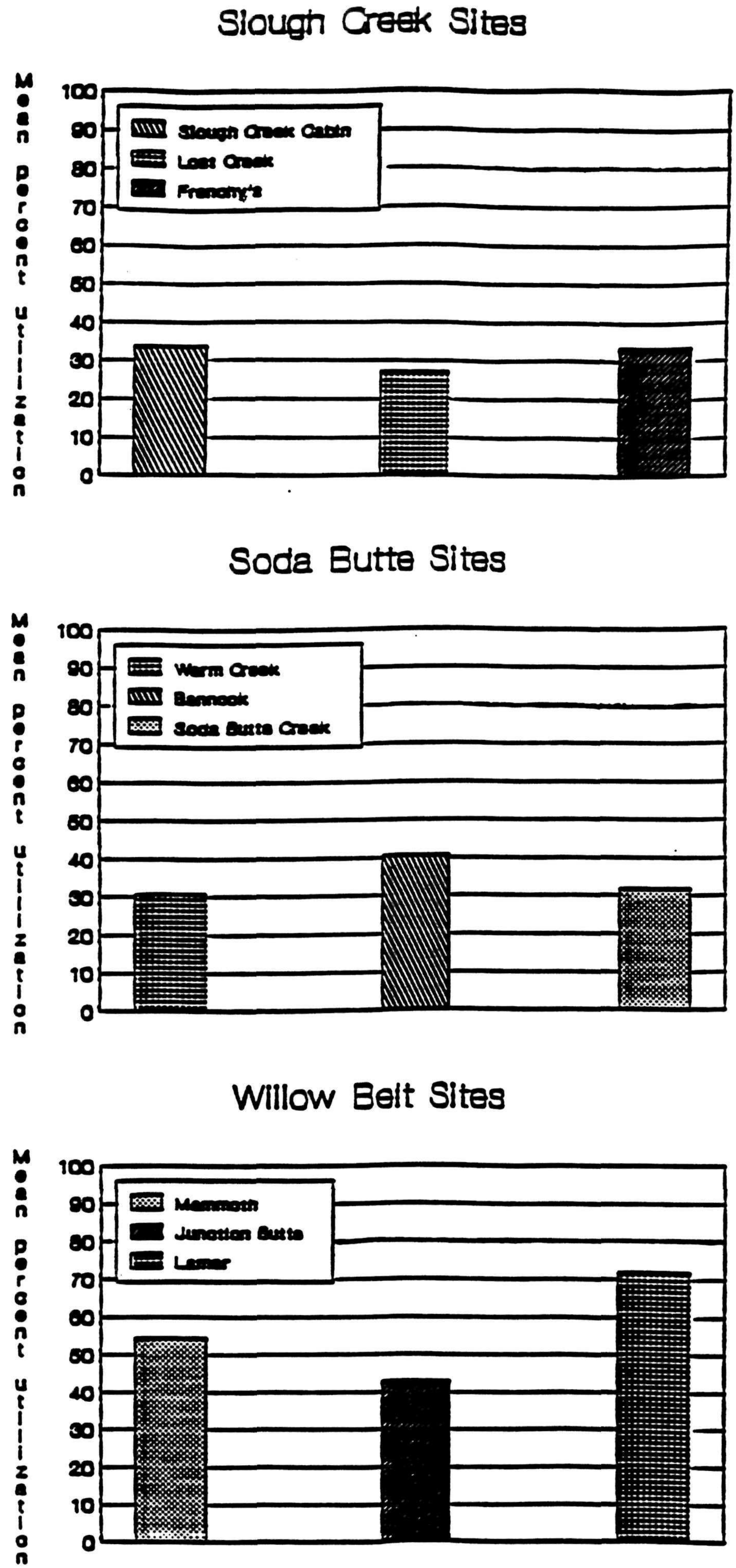


Fig. 4. **Average percent winter utilization rates on willows of the Slough Ck. (1988-1990), Soda Butte Ck. (1987-1990), and Willow Belt (1987, 1989-1990) sites on Yellowstone's northern winter range.**

TITLE: Tall willow communities on Yellowstone's northern range: A test of the "natural regulation" paradigm.

AUTHORS: Steve W. Chadde and Charles E. Kay

AFFILIATIONS: School of Forestry, University of Montana and Department of Fisheries and Wildlife, Utah State University.

PUBLICATION REPORT STATUS: Accepted, Examining the Greater Yellowstone Ecosystem proceedings.

PROJECTED PUBLICATION: Chapter in a book entitled Examining the Greater Yellowstone Ecosystem, Yale University Press.

PROJECTED PUBLICATION DATE: 1990

DATE OF REPORT: Fall 1989.

SUMMARY OF OBJECTIVES:

Prior to 1968, the National Park Service believed than an unnaturally large population of elk was responsible for the decline in tall willow communities on Yellowstone's northern range. However, under "natural regulation" management adopted in the early 1970's, that agency now believes the decline in tall willows is due to normal plant succession, climatic change, or fire suppression, not ungulate browsing. Thus, the status and trend of willow communities on the northern range since establishment of the park in 1872 can be viewed as a test of the "natural regulation" paradigm. The purpose of this paper is first to document historic changes in willow communities on the northern range and then to evaluate what factor or factors may have been responsible for changes in those communities. Successional trend and status were considered as were soils, available water, climatic variation, fire, and ungulate browsing.

SUMMARY OF MOST SIGNIFICANT FINDINGS:

1. Based on 44 repeat photographs, tall willow communities have almost entirely disappeared from the northern range since establishment of Yellowstone Park.

2. Willows protected from ungulates exhibit significantly greater growth and canopy-coverage than unprotected plants and in physical stature, resemble the willows which existed in the park during the late 1800's.

3. The decline and current suppression of willows over the entire northern range is due primarily to frequent,

repeated ungulate browsing, and not climatic change, plant succession, or suppression of lightning fires.

4. Ungulate browsing has not only changed the stature and abundance of willow communities on the park's northern range, but also animal communities which are usually associated with those riparian habitats. Entire communities have been affected, not just willows.

5. Ungulate browsing has acted to competitive exclude beaver from nearly all the northern range.

6. The near elimination of beaver may well have had a marked negative feedback effect on the extent of willow communities by lowering water tables and reducing stream flows.

7. These findings do not support the "natural regulation" hypothesis.

TITLE: Aspen regeneration on Yellowstone's northern range following the 1988 fires.

AUTHOR: Charles E. Kay

AFFILIATION: Department of Fisheries and Wildlife, Utah State University.

PUBLICATION REPORT STATUS: None - this is only the first year of a multi-year study.

PROJECT PUBLICATION: (?)

PROJECTED PUBLICATION DATE: 1994(?)

DATE OF REPORT: Preliminary findings were presented at the 1989 and 1990 Yellowstone Research meetings.

SUMMARY OF OBJECTIVES:

Based on 81 repeat photo sets, aspen on the northern range has declined over 95% since Yellowstone Park was created. Park Service biologists attribute this decline to the suppression of naturally occurring lightning fires, not to repeated browsing by an "unnaturally" large elk population. Park Service biologists have postulated that if burned, aspen stands would produce root-sprouted, regenerated stems greater than 2 m tall which, in time, will successfully regenerate those stands. To test this hypothesis, I established 131 photo points containing 773 photo frames in recently burned aspen stands on Yellowstone's northern range. Those sites were photographed in October 1988 and again after the 1989 growing season. In addition to these photo stations, I established several 2 x 30 m permanent belt transects to measure aspen regeneration.

SUMMARY OF MOST SIGNIFICANT FINDINGS:

1. Despite what was the worst fire season in the park's history, many aspen stands were not overly susceptible to burning. In many cases, fire either swept around the aspen stands, or lightly burned through the stands with little fire-induced mortality of older aspen trees apparent in 1989.

2. Aspen regeneration rates were highly variable one year after the 1988 fires and ranged from 1,000 to over 200,000 stems per ha.

3. In areas without summering elk, fire regenerated aspen suckers averaged 64 cm tall with individual stems approaching 2 m in height. In areas where elk summer on

the winter range, those animals browsed each and every aspen sucker despite an apparent abundance of other forage. In those areas, fire regenerated aspen suckers averaged just over 15 cm in height.

4. I spent 3 days in April 1990 checking many of my aspen burn study plots and found that wintering elk had browsed all those suckers often to within a few cm's of the ground.

5. Measurements in subsequent years will allow me to test the hypothesis that high intensity, infrequent fires which burn a major portion of the winter range are necessary to regenerate aspen stands under the level of ungulate use that presently occurs on the park's northern range. If Yellowstone's burned aspen stands are not able to successfully regenerate, this would falsify the Park Service's "natural regulation" experiment.

6. Experimental aspen burns conducted by the Park Service on the northern range prior to 1988 have failed to produce aspen stems greater than 2 m due to repeated elk browsing.

TITLE: Woody debris movement dynamics in Yellowstone National Park's northern range following the 1988 fires.

AUTHORS: Deron E. Lawrence and G. W. Minshall

AFFILIATIONS: Stream Ecology Center, Idaho State University.

PUBLICATION REPORT STATUS: Submitted to the Proceedings of the 3rd Annual Northern Range Meetings.

PROJECTED PUBLICATION: Summer 1990.

DATE OF REPORT: April 1990.

SUMMARY OF OBJECTIVES:

Woody debris within stream channels is being used to document the effects of the 1988 Yellowstone National Park fires on stream stability. One-hundred meters of stream channel within 22 streams in the Park have had woody debris mapped immediately following the fires, in August of 1989, and in August of 1990. Disturbance was measured by counting the number of pieces of wood lost to or gained within the channel reach of each stream. In addition, wood was tagged in both burned and reference watershed streams (six total) to determine movement patterns.

SUMMARY OF MOST SIGNIFICANT FINDINGS:

1. More pieces of wood moved in burn streams than in their corresponding reference streams. No data were available for first order reference streams, but it is commonly accepted that these streams are very retentive and stable systems which probably experienced little change (see Figure 1B).

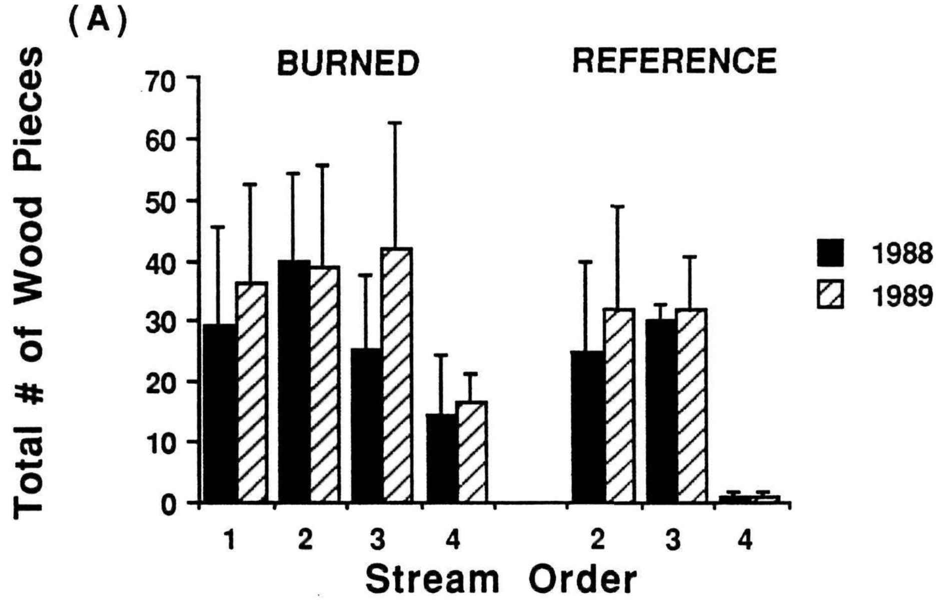
2. Although more wood moved in burn streams, the total number of pieces of wood in a given stream reach remained about the same. This means wood is being exchanged within a reach, but no trend of net gain or loss is occurring. Thus, as the turnover rates decrease to the reference stream values and wood stabilizes within the channel, a similar number of pieces of wood should be present as compared to the pre-fire abundances (see Figure 1A).

3. Wood in the stream channel was tagged in two streams with high spring run-off discharge and two streams with spring base-flow discharge. The maximum distance moved in the former streams was 17.8m, while no wood moved in the stable flow streams. Between 82% and 100% of the tagged wood was found. Reference stream wood was not tagged until 1989, so comparative data is not available yet.

4. In order to determine how far wood moves immediately following its entrance to a stream, wood from the riparian zone was tagged and placed in the streams discussed in (3). Maximum distance moved for high spring flow streams was 83.2m, while stable flow stream wood movement did not exceed 7.5m. The maximum length of a piece moved in peak flow streams was 3.25m (40m movement), while the largest piece of wood moved in the stable flow streams was 2.00m (6m movement).

SPECULATION:

Peak flow discharge is the driving force behind woody debris movement dynamics, and is the direct cause for greater movement in burn streams. Standing crop of woody debris will be determined by the severity of spring run-off or summer storms, and as watershed vegetation biomass increases the peak discharges will decrease. The Yellowstone Park streams were most susceptible to extreme wood rearrangement and channel cutting during spring run-off of 1989, and had the peak flows been more severe then the woody debris in burn streams could have been nearly completely removed. It appears woody debris loading has remained about the same following the fires (woody debris volume still needs to be analyzed), and recovery for the streams to the pre-fire conditions will occur relatively quickly.



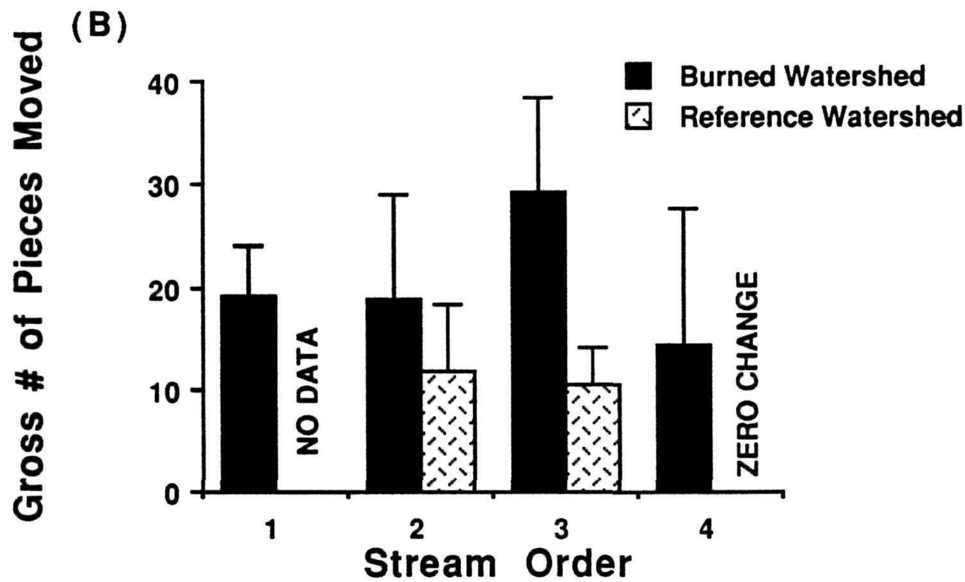


Figure 1. (A) Total number of pieces of wood in 1988 and in 1989 for burned and reference watershed streams of different order. (B) Gross change (total lost added to total gained) in number of pieces of wood in burned and reference watershed streams of stream order 1-4. Error bars represent standard deviations.

TITLE: Interactive ecology of plants, herbivores and climate in Yellowstone's northern range.

AUTHORS: Douglas A. Frank and Samuel J. McNaughton.

AFFILIATION: Syracuse University, Syracuse, New York.

PUBLICATION REPORT STATUS:

1. Aboveground biomass estimation with the canopy intercept method: a plant growth form caveat. Oikos 57, 57-60.
2. Stability increases with diversity in plant communities: empirical evidence. Science (submitted).
3. Dissertation in preparation.

OTHER PROJECTED PUBLICATIONS:

1. Interactive ecology of plants large mammalian herbivores and climate in Yellowstone National Park. Ecol. Monogr.
2. The effect of climate and large herbivores on plant community species composition. Ecology or Vegetatio.
3. The effect of climatic variation on ecosystem function. Am. Nat.
4. The role of ecosystem science in developing Park Service policy. Science.

PROJECTED PUBLICATION DATE FOR WORK IN PREPARATION: 1991.

DATE OF REPORT: June, 1990.

SUMMARY OF OBJECTIVES:

Our major focus was to measure rates of primary production and herbivory, principally in this study by elk and bison, in a variety of plant communities in all seasonal ranges in Yellowstone National Park's northern range. We also estimated the amount of dung deposited in the communities to index the rate of nutrient flow from ungulates to soil microbes. At 4 sites, large permanent exclosures were erected to quantify the effect of large herbivores on primary production in the northern range. We were fortunate to obtain data for 1988 and 1989, 2 very different years in regards to herbivore numbers and climate. This allowed us to examine the impact of these disparate years on ecosystem processes.

SUMMARY OF MOST SIGNIFICANT FINDINGS:

1. Primary productivity was stimulated by herbivores. In 3 of the 4 communities, primary production was significantly higher in grazed vegetation in comparison to ungrazed vegetation (Fig. 1). Results were consistent between years for sites there is 1988 and 1989 data. Site s4, which was unaffected by herbivores, was located in the summer range.

We believe the lack of a herbivore response in s4 during both years was due to the 1988 drought, which likely was most severe in the summer range.

2. Primary production and consumption declined from 1988 to 1989. The decline in consumption is not suprising, since there were fewer ungulates in 1989 than in 1988. However, higher primary production in 1988, a drought year, than 1989, a cool and more moist year, is counter-intuitive. The explanation, we believe, involves a combination of drought-induced death of plants that reduced the basal primary production potential of plant communties, and less consumption in 1989 that concomitantly reduced the stimulation of primary production by herbivores throughout much of the northern range.

3. There was a positive linear relationship between herbivore consumption and aPn. This indicates that as primary production increases among patches in the landscape, so will consumption at a constant rate per unit production.

4. The rate of consumption (grams consumed per gram produced) declined in the winter range from 1988 to 1989, while it was unchanged in transitional and summer range sites.

5. There was a linear positive relationship between dung deposited in the sites and consumption. The relationship was indistinguishable between years. This indicates that grazing and nutrient cycling are coupled in the Yellowstone landscape.

6. There was a positive linear relationship between timing of grazing and timing of plant growth. In off-winter range sites, rate of daily production explained 92% and 80% of the variance in daily consumption in 1988 and 1989, respectively. This indicates that during their migration off the northern winter range beginning in spring, ungulates are preferentially grazing in a band of young, nutritious tissue as it progresses through the season from low to high elevations in the park.

7. There was a positive relationship between species diversity and resistance to plant community species composition change during the 1988 drought. These data are the first of their kind that show stability of plant community species composition increases with species diversity.

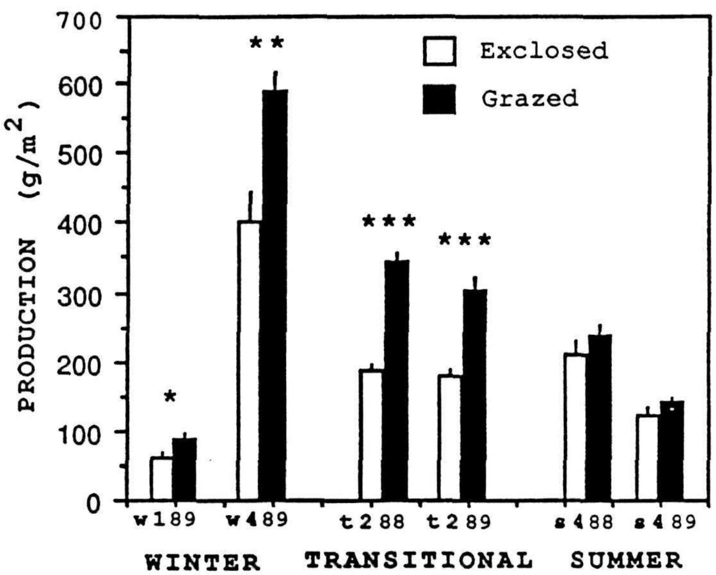


Figure 1. Net aboveground primary production in grazed and ungrazed vegetation in four communities. Sites t2 and s4 were sampled during both 1988 and 1989. * denotes P<.05. ** denotes P<.01. *** denotes P<.001.

TITLE: Forage species response to grazing

AUTHOR: Linda L. Wallace

AFFILIATION: Department of Botany and Microbiology, University of Oklahoma

PUBLICATION REPORT STATUS: Two manuscripts in preparation

PROJECTED PUBLICATION: Ecology, Oecologia

PROJECTED PUBLICATION DATE: 1991

DATE OF REPORT: May, 1990

SUMMARY OF OBJECTIVES:

1. Determine which forage species were most preferred by bison and elk.
2. Determine how plant community structure is influenced by grazing by both bison and elk.
3. Determine what grazing intensity exists across the northern range.
4. Determine how the most heavily utilized forage species respond to grazing pressures simulated by clipping.
5. Determine whether there are interactive effects of plant competition and grazing on plant growth and survival.
6. Determine what the physiological limits to herbivory are for the most heavily utilized forage species.

SUMMARY OF MOST IMPORTANT RESULTS:

1. At five sites across the northern range that represent winter, summer and transitional range sites, the three most heavily utilized forage species at each site were found to be graminoids. These include both native and introduced (exotic) species. These sites were grazed by both elk and bison.

2. Plant community structure was monitored over a three year period from 1987 through 1989. During the drought year of 1988, species diversity was reduced inside of temporary exclosures. However, the greatest difference in plant community structure was found between years with percent similarity between community measurements at any site averaging 62%. Percent similarity measured between inside and outside exclosures at each site averaged 75%. Therefore, yearly climatic variation will cause a greater change in plant community structure than will the presence of grazing animals.

3. Grazing intensity averaged 75% of the aboveground biomass removed from the preferred forages at the five sites in 1988. Grazing intensity averaged 30% in 1989. These could be attributed to both greater plant growth in the moist summer of 1989 as well as reduced ungulate populations.

4. All of the forage species examined were capable of compensating for tissue lost to herbivory in 1989. Compensation occurs when grazed plants grow at a more rapid rate than ungrazed plants. No

compensation occurred during the drought year of 1988.

5. In the experimental manipulations, plant competition and grazing did significantly interact to influence plant response to herbivory. If a target plant and all its surrounding neighbors were grazed, then the target plant was able to compensate for herbivory. If only the target plant was grazed, then it undercompensated for herbivory; if the target was ungrazed but all its neighbors were grazed, then the target also undercompensated. Therefore, if grazing is selective (such as occurs when only elk graze an area) then plants may undercompensate. However, when grazing is nonselective (such as occurs when bison graze in an area) then plants can compensate for herbivory. Therefore, it appears that bison may be a stabilizing influence in the northern range ecosystem.

6. In a laboratory study where plants were grown in isolation with adequate supplies of water and fertilizer, only one species could be killed by extremely severe levels of clipping. All of the other Yellowstone species possess the ability to tolerate high levels of herbivory.

7. Based upon these results, I feel that the northern range ecosystem is capable of tolerating high levels of herbivory. It is important, however; that both bison and elk are present since if only selective herbivory occurs, plant community structure and system productivity could be altered. I suggest that these data obtained from experimental manipulations be tested by field observations in areas that support only elk.

TITLE: The interaction of fire and grazing on plant productivity and community structure.

AUTHOR: Linda L. Wallace

AFFILIATION: Department of Botany and Microbiology, University of Oklahoma

PUBLICATION REPORT STATUS: Field work still in progress

PROJECTED PUBLICATION: Functional Ecology

PROJECTED PUBLICATION DATE: 1991

DATE OF REPORT: May 1990

SUMMARY OF OBJECTIVES:

1. Determine grazing intensity in burned and unburned grasslands during the two years following the 1988 fires.
2. Determine plant productivity in burned, unburned, grazed and ungrazed grasslands over the above time frame.
3. Determine plant community structure in the above combinations of areas over the same time frame.
4. Determine how plant community structure has changed in permanent transects that were burned by the fires of 1988 at both Junction Butte and Hayden Valley.

SUMMARY OF MOST IMPORTANT RESULTS:

1. Plant community structure was affected variably by the fires. At Blacktail, species richness was greatest at intermediate levels of disturbance with values highest in burned, ungrazed areas and lowest in both unburned, ungrazed areas and burned grazed areas. The site at Mt. Norris exhibited the greatest species richness in unburned areas regardless of the grazing regime. The site at Crystal Creek in the understory of a burned Douglas fir community had the greatest species richness in unburned, ungrazed and burned, grazed areas. Since all sites exhibited such disparate responses, further work will be conducted on these areas to determine what may be responsible for this variance.

2. Species richness was greater after the fire at the Junction Butte site. The transect which did not burn exhibited a reduction in species number while the transect which did burn had many more species present. At Hayden Valley, results were opposite to those at Junction Butte. Species richness was dramatically reduced in the burned transect. This may be due to the area (near Alum Creek) being on thermally influenced soils which are an additional stress to plant growth. Since only a few species are capable of growth on these thermally altered soils, then few opportunists were able to grow in these communities following the fires.

3. Work is continuing on plant samples collected in 1989 and field work will continue in 1990 to determine how grazing intensity and productivity were influenced by the fires.

TITLE: Grassland recovery after burning: a remote sensing approach.

AUTHORS: Evelyn H. Merrill and Ronald W. Marrs

PUBLICATION REPORT STATUS:

1. Annual reports, University of Wyoming- Yellowstone National Park
2. Remote sensing of grassland phytomass. J. Range Management, accepted.
3. Elk dynamics and summer range. Book Chapt. Yellowstone Symposium. in press.

OTHER PROJECTED PUBLICATIONS

International Journal of Fire Management, 1992.

PROJECTED PUBLICATION DATE FOR WORK IN PREPARATION: 1992

DATE OF REPORT: July 1990

SUMMARY OF OBJECTIVES:

(1) Improve pre-fire remote sensing techniques for estimating green phytomass on grasslands sites to monitor vegetation recovery in the initial post fire years and

(2) Determine factors across the landscape that may have influenced the patterns of vegetation recovery.

SUMMARY OF PROGRESS AND FINDINGS:

1. Landsat Thematic mapper (TM) spectral data were acquired for August 2, 1989 for the Yellowstone National Park and mounted on the University of Wyoming remote sensing image processing system.

2. Spectral data were used to derive the 2-D Perpendicular index (PVI) and the 6-D Green vegetation index (GVI) for 40 ground truth sites. These indices are a special class of spectral indices which are linear combinations of n-spectral bands in n-dimensional space. The indices are useful for discrimination of vegetation from soil background.

3. During late July and early August 1989, 40 ground truth plots were sampled for green herbaceous phytomass (Table 1). Ground truth data are being used to calibrate PVI and GVI models.

4. Spectral models built using 1989 data will be tested using Landsat imagery for the same area and additional ground truthing in the summer of 1990.

5. Once GVI/PVI models are validated, we intend to use the models in a GIS system to monitor vegetation recovery and determine landscape factors influencing vegetation recovery.

Table 1. Summary of plots sampled July 27-August 10, 1989.

Plot	Location	Burn[1]	Elev	Asp	Slope	CT-DD[1]	Azm
			Plot Characteristics				
101	Lower Norris	T3	7520	180	15	TFG	135
102	Lower Norris	No	7720	196	25	TFG	322
103	Middle Norris	T1	7800	254	20	TFG	190
104	Middle Norris	T2	7520	328	10	TFG	34
105	Lower Cache	T2	7460	250	10	TFG	280
106	Lower Cache	No	7680	235	5	FN	298
107	Upper Cache	No	8100	230	20	FN	290
108	Upper Cache	No	7940	230	1	TFG	234
109	Upper Cache	T3	8025	283	5	TFG	190
110	Upper Cache	No	7960	195	20	TFG	80
111	Upper Cache	No	7850	184	3	TFG	200
112	Upper Cache	No	7760	295	4	TFG	218
113	Upper Cache	T3	7750	230	10	TFG	322
114	Lamar Flat (52)	T1	6630	0	0	TF	165
115	Lamar Flat (51)	No	7160	206	25	TFG	36
116	Upper Lamar Flat	T4	6710	0	1	TF	65
117	Floating Island (28)	No	6480	0	0	TFG	137
118	Floating Island (29)	T2	6680	0	0	TFG	135
119	Y-L Confluence (30)	T1	6120	80	2	TF	255
120	Y-L Confluence (31)	No	6080	310	4	TF	210
121	Opal Creek	T2	8800	145	5	FNG	50
122	Opal Creek	T2	8740	95	15	FNG	8
123	Opal Creek	T4	8800	95	7	FNG	11
124	Above Opal Camp	No	8960	90	7	FNG	130
125	Above Opal Camp	No	8880	190	15	FNG	120
126	Above Opal Camp	T3	8760	356	3	FNG	170
127	Opal Creek	T4	8800	15	1	FNG	15
128	Opal Creek	No	8660	305	6	FNG	32
129	Specimen Ridge Trail	T2	8770	90	5	TFG	8
130	Mirror Plateau	No	9120	192	20	FNG	272
131	Mirror Plateau	No	9170	0	2	FNG	23
132	Top Specimen Ridge Tr	No	8840	150	20	FNG	76
133	Above Norris Hot Sp	T2	6980	233	5	TFG	138
134	Lower Norris	T1	7250	230	12	TFG	148
135	Lower Norris Rdge Top	No	7800	218	1	FA	136
136	West Of Norris Cliff	T2	7440	180	15	FA	238
137	Upper Norris	No	8130	121	5	TFG	196
138	Pk Midway To Norris	No	8250	171	10	FNG	247
139	Top/Draw Mid-Norris	No	7880	338	10	TFG	326
140	Norris/Next To Cliff	No	7760	302	5	TFG	220

[1]Burn descriptions:

T1= hot fire, all shrubs & litter burned, ground fire complete.

T2= all shrubs killed but some aboveground woody material not consumed, ground fire mostly complete.

T3= some shrubs survived or at least some leaves present, ground fire >50% complete.

T4=light burn, > 50% ground vegetation survived.

[2]Vegetation types follow D. Despain cover map.

TITLE: Report on 1989 suspended sediment and turbidity in the Yellowstone River and selected tributaries from Yellowstone Lake, Yellowstone National Park, Wy., to Tom Miner Basin, Park County, Montana following the 1988 wildfires.

AUTHORS: Roy Ewing and Jana Mohrman

AFFILIATIONS: National Park Service, Yellowstone National Park

PUBLICATION REPORT STATUS: Preliminary Report finished April 1990, final report in late 1990.

PROJECTED PUBLICATION: U.S.Fish & Wildlife Technical Report, Aquatic Ecology Studies, Yellowstone Fisheries Assistance Office.

PROJECTED PUBLICATION DATE: Late 1990 for final report.

DATE OF THIS SUMMARY: May 1990

SUMMARY OF OBJECTIVES: The objectives of the post-fire sediment project were to measure streamflow, suspended sediment, and turbidity in the Yellowstone River and selected tributaries in northern Yellowstone Park that had been monitored for these characteristics in 1985, 1986, and 1987. 1989 measurements will be compared to the pre-fire data.

SUMMARY OF SIGNIFICANT FINDINGS:
<u>CLIMATE</u>, <u>PRECIPITATION</u>, <u>AND</u> <u>STREAMFLOW</u>:

1. The area in and around northern Yellowstone Park received more October-June precipitation in 1989 than in the pre-fire years 1985-1987.

2. Despite greater October-June precipitation, 1989 snowmelt period saw less runoff in the Yellowstone River (Corwin Springs) than in 1986 due to the gradual, cool nature of the 1989 snowmelt season.

3. 1989 summer precipitation in the area was less than in the pre-fire years. 1989 summer streamflow in the Yellowstone (Corwin Springs) was less than in 1986 but greater than 1985's. The greater 1989 summer streamflow in the Yellowstone for less summer precipitation (than in 1985) was probably a lag effect of the thick snowpack and gradual snowmelt since unburned streams in the area also experienced the same precipitation-streamflow relations.

4. Streams in the Yellowstone Park area had two high-flow periods during snowmelt, May 10-11 and June 16-17. The Yellowstone River at Corwin Springs, receiving streamflow from severely to lightly burned drainages, had peak mean daily flow on June 16. With one exception, date of peak flow

seemed to relate to basin elevation, lower basins peaking in May and higher basins peaking in June. The Lamar River, a high basin with large burned areas, peaked in May. This could be a fire effect.

5. Streamflow for all seasons in 1989 in the Lamar River (Tower Junction) was about equal to 1986 values. Since 1986 streamflow was greater than 1989's on the Yellowstone (Corwin Springs) and for most monitored tributaries, this could be a fire effect.

<u>SUSPENDED</u> <u>SEDIMENT</u> <u>AND</u> <u>TURBIDITY</u>.

1. Suspended sediment and turbidity in the Yellowstone (Corwin Springs) and several of the monitored tributaries followed the trend of average streamflow, with 1989 values exceeding those of 1985 but less than the 1986 averages, for all seasons.

2. Fire effects on streamflow, suspended sediment, and turbidity during snowmelt season were minimized by the cool, gradual 1989 snowmelt. The lower snowmelt values caused overall averages to also lower.

3. Post-fire suspended sediment and turbidity were greater than pre-fire values in the Lamar River only for the summer season. Other monitored, burned tributaries also experienced elevated post-fire summer sediment and/or turbidity.

4. Post-fire increases in turbidity were most noticeable in previously non-turbid streams, such as Slough and Lava Creeks.

5. Summer fire effects on stream suspended sediment and turbidity were probably mitigated by the dry 1989 summer.

6. The fact that increases in summer sediment in the Lamar River and other monitored tributaries were not reflected in the Yellowstone at Corwin Springs suggests that sediment from storm runoff may be stored in stream channels upstream from Corwin Springs and may be moved through the stream system during the 1990 snowmelt.

7. Post-fire sediment rating curves for the Yellowstone River at Corwin Springs, the Lamar River at Tower, and several other monitored tributaries show a general decline in slope of the best-fit curves indicating either an increase in low-discharge sediment or a decrease in high-discharge sediment following the 1988 fires. This may have been caused by the mild, low streamflow 1989 snowmelt season.

Fig. 1. SEASONAL AVERAGES OF MEAN DAILY DISCHARGE, CONCENTRATION, SEDIMENT DISCHARGE AND TURBIDITY IN THE YELLOWSTONE RIVER-CORWIN SPRINGS, 1989-1985

	STREAMFLOW (CFS)							CONCENTRATION (MG/L)						
	1986		1989		1985		1987	1986		1989		1985		1987
SNOWMELT	10949	>	9000	>	7821	>	5072	219	>	171	>	90	>	44
SUMMER	4348	>	3158	>	2737	>	2009	30	>	22	>	14	<	18
ENTIRE	6980	>	5487	>	4595	>	3230	106	>	81	>	42	>	28

	SUSPENDED SEDIMENT DISCHARGE (TONS/DAY)							TURBIDITY (NTU)						
	1986		1989		1985		1987	1986		1989		1985		1987
SNOWMELT	8979	>	4718	>	2287	>	672	22	>	14	>	10	>	8
SUMMER	532	>	243	>	113	<	129	11	>	6	=	6	<	8
ENTIRE	3901	>	2027	>	908	>	345	17	>	9	>	7	<	8

TITLE: Effects of Charcoal on Postfire Nitrogen Dynamics in Streams.

AUTHOR: James W. Check

AFFILIATIONS: Department of Biological Sciences, Idaho State University

PUBLICATION REPORT STATUS: Project just initiated, no publishable findings to date.

SUMMARY OF OBJECTIVES:

The objectives of this study are to determine if charcoal affects nitrogen dynamics in streams, and which processes are involved. It was hypothesized that charcoal could: 1) remove nitrogen from the water column by adsorption, and 2) store nitrogen in sediment-buried charcoal and release it later in time, or 3) concentrate nitrogen on the charcoal substrate for microbial processes (nitrification and denitrification).

SUMMARY OF MOST SIGNIFICANT FINDINGS:

1. Charcoal was found to comprise up to 40% of the benthic organic matter of streams sampled in August 1989. At reference sites not burned by the fires of 1988 streams sampled had up to 15% charcoal in benthic organic matter.

TITLE: Characterization and comparison of soils inside and outside of grazing exclosures on Yellowstone National Park's northern winter range.

AUTHORS: John R. Lane and Cliff Montagne

AFFILIATION: Montana State University, Bozeman, MT 59715

PUBLICATION REPORT STATUS: Thesis in review

PROJECTED JOURNAL PUBLICATION: Journal of Range Management

PROJECTED PUBLICATION DATE: Spring 1990

SUMMARY OF MOST SIGNIFICANT FINDINGS:

1. The effects of winter grazing by elk on soil chemical and physical properties in Yellowstone National Park's northern winter range were examined inside and outside of eight grazing exclosures. Soil nutrients in the 0-15 cm, 15-30 cm and 30-45 cm depths, soil surface bulk density and double ring infiltration were studied and soil profiles were described for two exclosures each at Gardiner, Blacktail and Lamar Valley and one exclosure each at Mammoth and Junction Butte. A rainfall simulator study comparing sediment yield and surface runoff inside and outside was conducted at two exclosures each at Gardiner and Blacktail and one exclosure at Lamar Valley.

2. Soil profiles were generally similar inside and out, though there were differences. Percent clay in the surface horizon differed by more than (+/-) 5% at Gardiner west, Blacktail east, and Lamar Valley east. Soil texture in the surface horizon was different at both Gardiner exclosures, Blacktail east, Lamar Valley west, Mammoth and Junction Butte.

3. There was no apparent trend in soil nutrient differences inside and outside the exclosures. NO_3-N and NH_4-N for all depths were consistently higher outside at Junction Butte. Blacktail east and Lamar Valley east had consistently higher amounts inside the exclosure. However, not all differences were significant. Soil organic matter was consistently higher at all depths outside of three exclosures; Gardiner west, Blacktail west, and Junction Butte. Differences at Blacktail west were significant ($P=0.10$) for all depths. Other soil nutrients: phosphorus, sulfur, calcium, sodium, magnesium, potassium, zinc, copper, manganese, and iron had no trends. Some exclosures had higher amounts of a nutrient inside for a particular depth while others had higher amounts outside. Some differences were significant others were not.

4. All exclosures but Blacktail east trended toward higher soil surface bulk density outside the exclosure compared to inside. At Gardiner east, Lamar Valley east, Mammoth, and Junction Butte the differences were significant at the 90% confidence level.

5. All exclosures except Blacktail east and Gardiner west had higher double ring infiltration rates inside. None were significantly different. Double ring infiltration rates mostly followed the pattern of higher infiltration associated with lower surface bulk density inside the exclosures.

6. A triple replication rainfall simulator study was conducted to measure the effects of three treatments on runoff and sediment yield inside and outside of five exclosures. The treatments were: 1) vegetation undisturbed, 2) vegetation clipped and left on the surface, and 3) clipped vegetation and litter removed from the soil surface. Surface runoff and sediment yield were higher outside the exclosure for all three treatments. The differences were not significant ($P=0.10$) for treatment 1, vegetation undisturbed. For treatment 2, vegetation clipped and left on the surface, Gardiner east, Blacktail east and Lamar Valley east had significantly higher surface runoff outside the exclosures; none of the differences in sediment yield were significant. When the clipped vegetation and litter were removed, treatment 3, surface runoff at Blacktail east and west and sediment yield at Blacktail east and Gardiner west were significantly higher outside.

7. These results display some statistically significant differences as well as nonsignificant trends. Further replicates may or may not demonstrate statistical significance of these trends. Because soils data were not collected prior to exclosure establishment, it is difficult to ascertain if significant differences inside and outside of exclosures are due to no grazing inside, increased intensive grazing outside, or more likely a combination of both.

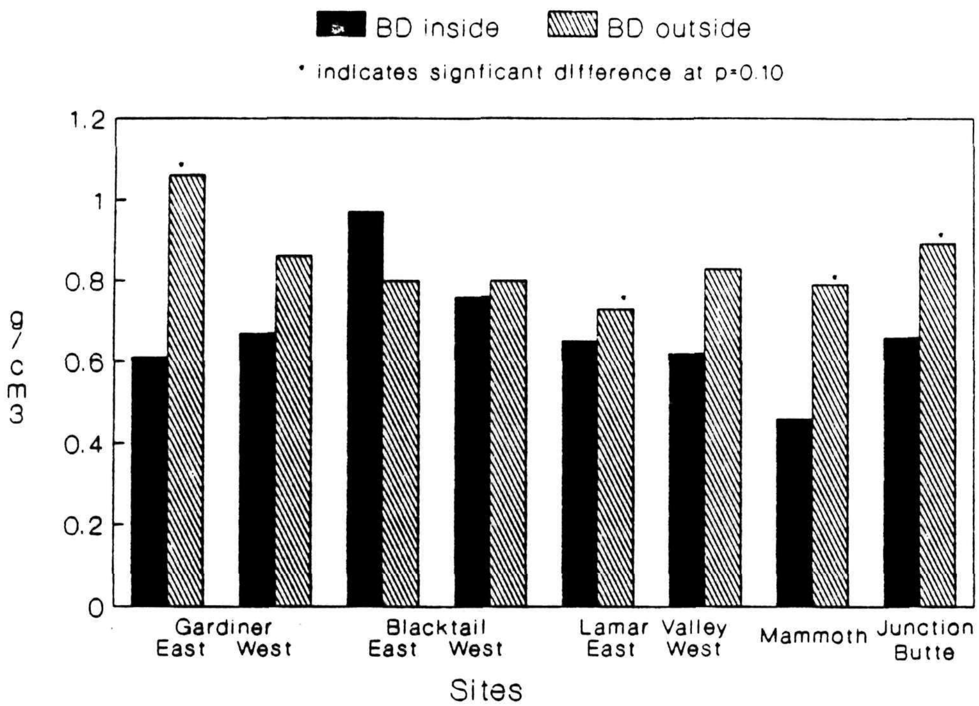


Figure 1. Soil surface bulk density of soils inside and outside of eight exclosures.

Abstract from
Plants and Their Environments: First Biennial Scientific Conference on the Greater Yellowstone Ecosystem
September 16-17, 1991
Mammoth Hot Springs
Yellowstone National Park, Wyoming

EFFECTS OF LONG-TERM PROTECTION FROM ELK GRAZING ON BUNCHGRASS AND BIG SAGEBRUSH COMMUNITIES ON YELLOWSTONE'S NORTHERN RANGE

Singer, F.J. (Research Division, P.O. Box 168, Yellowstone National Park, WY 82190), and M.K. Harter

The effects of long term protection of plant communities from elk grazing were studied at 8 large (2 ha) exclosures constructed in 1958 and 1962. Shrub transects were read at approximately 5-year intervals during the 1958-1990 period. Grassland measures were taken inside of and in adjacent grazed sites in 1986-1987 at all of the exclosures and during four of the years, 1986-1990, at the Blacktail Deer Creek exclosure.

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 ($P > 0.05$). Biomass of two grasses, junegrass (*Koeleria cristata*) and thickspiked wheatgrass (*Agropyron spicatum*), were more abundant on grazed sites, while only one grass, *Poa sandberghi*, and 2 nongrasses, *Artemesia frigida* and *Phlox hoodii*, were less abundant on grazed sites ($P < 0.05$). Morphological characteristics were not influenced by grazing, with the exception that vegetative culms of grasses were shorter on grazed sites. There was one-quarter the litter and one-third more bare ground on grazed sites. Grazing enhanced the protein content of common grasses 10-36%, but grazing did not significantly influence the digestibility of grasses. Protein content varied 8-20% between years. Grazing slightly enhanced other nutrients (Ca, Mg, K) in Idaho fescue (*Festuca idahoensis*) ($P < O.05$), but not in junegrass or bluebunch wheatgrass (*A. spicatum*). Heights of seed stalks of bluebunch wheatgrass were shorter in 1986 than in the other 3 years, further suggesting that growing conditions in 1986 were less than optimum. Seed heights are often used as an indicator of grass vigor. About 16% more grass biomass was produced under big sage cover than in open bunchgrass communities. Soil moisture was not influenced by grazing, and soil moisture did not vary between sage and open grass stands.

Protection from ungulates benefitted big sagebrush growth and reproduction at the lower exclosures near Gardiner. Pronghorns (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) also winter in this area and the big sage subspecies involved is the more palatable *Artemesia tridentata wyomingensis*, or Wyoming big sage. Numbers of big sage increased 348% and cover increased 828% inside the exclosures, 1958-1962, while numbers of big sage declined 40% and cover declined 29% on grazed sites.

Big sage trends were similar on grazed and protected sites at the remaining higher elevation exclosures. Numbers of big sage declined an average of 20% on both grazed and protected sites, but the big sage individuals were taller and larger, 1958-1990. Big sage canopy volumes increased 440% on protected sites and increased 210% on grazed sites. Only elk and bison (*Bison bison*) winter at the higher sites; they eat less big sage, and the big sage subspecies are the less palatable Basin and Mountain big sage (*A. t. triaentata* and *A. t. vaseyana*).

All shrubs, except common rabbitbrush (*Chrysothamnus nauseosus*), were shorter and smaller in volume on grazed sites. Big sage averaged 16% taller on protected sites, horsebrush (*Tetradeymia canescens*) was 91% taller and green rabbitbrush (*C. viscidiflorus*) was 42% taller. Common rabbitbrush individuals were 36% taller and crown volumes were 200% larger on grazed sites. Shrub seedling reproduction was more common and age class distributions were younger on grazed sites. Apparently either the reduction in competition through reduced shrub size or trampling by ungulates enhanced shrub establishment on the grazed sites.

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Mammoth Hot Springs
Yellowstone National Park, Wyoming

AN OVERVIEW OF WILLOW- LARGE HERBIVORE INTERACTIONS ON YELLOWSTONE'S NORTHERN WINTER RANGE

Singer, F.J. (Research Division, P.O. Box 168, Yellowstone National Park, WY 82190), and L. Mack

Trends in willow abundance were sampled from 1958-1990 on a series of permanently marked transects located within ungulate exclosures (protected) and on adjacent grazed sites. Protected individuals averaged 65% taller than grazed willows at 4 exclosure sites, and crown volumes were 600% larger. Ungulate browsing, however, apparently stimulated root sprouting and suckering. Numbers of suspected individuals of Bebb willow (*S. bebbiana*) and Booth's willow (*S. boothii*) averaged 4 times greater on grazed sites, numbers of roses (*R. spp.*) were 2 times greater, and shrubby cinquefoil (*Potentilla fgruticosa*) were 12 times more numerous. Some of the suspected different willow individuals may actually have been part of the same clone—this was not verified by digging up root systems.

Willow production, percent of total twigs browsed, and average bite sizes were monitored during 4 years, 1987-1990, on a series of marked plots within both elk and moose winter ranges. Twenty percent of the willow stands in Slough Creek were classified as suppressed in height (1-80 cm), 60% were intermediate (81-120 cm), and 20% were tall (121+ cm). Sixty-one percent of the willow stands in the Lamar Valley-Soda Butte drainage were suppressed, 9% were intermediate, and 30% were tall. Percent of total twigs browsed in winter average 59% on suppressed stands, 43% on intermediate stands, and 32% on tall stands. Suppressed willow stands produced only 20% of the biomass each year (g/25 m^2) as produced by intermediate height stands, and 13% as much as tall stands. Percent of total twigs browsed varied greatly between years. Twenty-two percent of twigs were browsed in the winter of 1987-1988, but use increased to 60% in 1988-1989 following the drought and fires of 1988, and use then declined, but remained higher, at 43% the second winter following the fires (1989-1990).

Wolf's willow (*S. wolfii*) was the most abundant willow on the study plots (29% of available twigs), followed by Booth's willow (*S. boothii*)--16%; Geyer's willow (*S. geyeriana*)--13%; Drummond's willow (*S. drummondiana*)--13%; Farr's willow (*S. farriae*)--11%; and mountain willow (*S. pseudomonticola*)--1%. Use versus availability was tested with a statistical procedure. Bebb, Booth's, and Geyer's willows were in the most preferred category, use of Drummond's willow was variable, and Wolf's and Farr's willows were consistently used less than availability. The latter willows rarely, if ever, grow beyond 0.8 m in height and they are suspected to be well-defended by secondary compounds. Therefore, they may be less palatable than the other willow species. Correlations between preferences of willows and levels of secondary compounds are currently being analyzed with Dr. Rex Cates of Brigham Young University and those results will also be presented at the meeting.

Abstract from
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SYSTEM STABILITY AND PERTURBATION IN YELLOWSTONE'S NORTHERN RANGE: THE EFFECTS OF THE 1988 DROUGHT ON GRASSLAND COMMUNITIES

Wallace, L.L. (Department of Botany & Microbiology, University of Oklahoma, Norman, OK 73019)

Grasses and grasslands have evolved in the presence of a number of perturbations including fire, grazing, and drought. The morphological structure of grasses adapts them to each of these means of tissue loss. However, grasslands consist of species that vary in their adaptability to these perturbations; hence system structure will be altered by their presence. Community structure was monitored over 3 years (1987, 1988, 1989) at five sites across the Northern Range of Yellowstone National Park which were representative of summer, winter, and transitional ranges. This time frame spanned a major, system-wide drought in 1988. Data were collected both inside and outside of exclosures at each site using line transects with an interval length of 20 cm. Grazing intensity was monitored at each site by comparing aboveground volume of marked individuals of the major forage species both inside and outside of exclosures.

Community structure parameters of diversity (Shannon's index), richness, and evenness were calculated for each of the 3 years. There was a general trend of increasing diversity at each site due to increases in the richness component. Largest changes in diversity from the 1987 pre-drought levels were noted in the lowest elevation sites with a corresponding decrease in change of diversity indices at higher elevation areas. There were no significant correlations between change in diversity and grazing intensities. Coefficients of community similarity were calculated at each site for comparisons between inside and outside exclosures as well as for between years. There was uniform agreement among all sites that there were greater differences between years with community structure remaining fairly similar inside and outside of exclosures within a year.

The conclusions that can be drawn from these comparisons indicate that climate has a stronger control on system structure than does grazing. Also, systems at lower elevations tend to be less stable since they show a lack of resilience (return to pre-disturbance values) and a lack of resistance (resist change during the disturbance). Systems at higher elevations exhibit stronger resistance and resilience thereby making them more stable. Possible reasons for this difference will be discussed.