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ARTICLES

What is "Natural"?: Yellowstone Elk Population —A Case Study

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Ecology analyzes the structure and function of ecosystems at all points along the continuum of human disturbance, from so-called pristine forests to urban backyards. Undisturbed systems provide reference points at one end of the spectrum, and nature reserves and parks are highly valued because they can provide unique examples of such ecosystems. Unfortunately the concept of "natural" or pristine is not that easy to define. Indeed, although ecologists have considered pre-Columbian, western-hemisphere ecosystems to have been largely unaltered by human action, and have termed their state "natural" or "pristine," evidence from archaeology challenges this view. U.S. and Canadian national parks are charged with preserving the "natural," and thus need to be able to understand and manage for the "natural." A pivotal "natural" question in Yellowstone National Park management is the size of the northern-range, wintering elk population at Park establishment in 1872, argued both to have been small and large. Integrating and quantifying several sources of evidence provides a consistent picture of a low population (ca. 5,000–6,000), largely migrating out of the northern range in winter, with little vegetation impact. If we accept this conclusion about what is natural for the Yellowstone ecosystem, then it dramatically alters how we view management alternatives for the Park, which currently supports a northern wintering herd of up to ~ 25,000 elk.

KEY WORDS: natural ecosystems, pre-Columbian, elk, Yellowstone, national parks, archaeology, fire ecology

The science of ecology has for some time recognized the need for ecological systems minimally altered by human action to serve as reference points. The world's ecosystems exist along a spectrum of human disturbance. Ecology strives to understand the structure and function of systems at all points along the spectrum in order to (1) understand the effects of human use; (2) detect thresholds beyond which human use becomes unsustainable; and (3) perceive break points at which systems are irrevocably changed, and no longer able to return to more intact conditions once disturbance is removed. Relatively undisturbed systems are crucial for providing understanding at one end of the spectrum.

Characterizing such minimally disturbed systems is a major emphasis in ecology today, and a number of epithets are being used to identify them: "healthy" (e.g. the new professional society International Society of Ecosystem Health and its new journal "Ecosystem Health"), "natural,"[1] and "pristine" or with "ecological integrity".[2] All imply little or no human alteration. Providing this reference-point function has long been a major reason for establishing different kinds of natural areas. Over a half century ago, Leopold[3] advocated preservation of wilderness areas on the grounds that "A science of land health needs ... a base datum of normality, a picture of how healthy land maintains itself as an organism ..." And a 1963 National Academy of Sciences/National Research Council study on U.S. national park research[4] urged their protection "because of their scientific value as outdoor natural laboratories."

Although a large and growing archaeological literature is reporting that the character of western-hemisphere landscapes was significantly altered by Native Americans,[5–10] there is an enduring assumption among American ecologists that North American ecosystems were not materially modified by their pre-European human inhabitants. Consequently such prehistoric systems are assumed to have been healthy, natural, intact, pristine, or with integrity. If their nature were known, they could provide the reference-point service needed for a thorough understanding of ecosystem structure and function.

Preservation of pre-European conditions is a recurring theme in U.S. national park policies. In a frequently cited quote, a 1963 panel of scientists appointed by Interior Secretary Stewart L. Udall urged: "As a primary goal, we would recommend that the biotic associations within each park be maintained or where necessary recreated, as nearly

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as possible in the condition that prevailed when the area was first visited by the white man. A national park should represent a vignette of primitive America."[11]

A Yellowstone National Park policy document states: "The primary purpose of Yellowstone National Park is to provide present and future visitors with the opportunity to see and appreciate the natural scenery and native plant and animal life as it occurred in primitive America."[88]

And the 1916 National Park Organic Act stipulates: "The fundamental purposes of said parks is to conserve the scenery and the natural and historic objects and the wildlife therein and to provide for the enjoyment of the same in such a manner and by such means as will leave them unimpaired for the enjoyment of future generations."

More contemporary ecology points out that ecological systems change over time in the absence of human influence, and to freeze them with management in the conditions that prevailed at European contact is neither natural nor possible.[12] Yet there is a persisting sense that knowing and restoring those conditions are somehow desirable. Thus Anderson[13] proposes as one criterion of the degree of naturalness of an area the proportion of species present at the time of European settlement which persist today. And a massive National Park Service (NPS) management manual states: "As a point of reference, natural conditions are defined as those that would have existed today in the absence of the effects of European man."[14]

Thus there is a continuing impetus in ecology to reconstruct the character of pre-European North American ecosystems. Boyce has commented that it will never be possible to learn their exact nature.[12] But by using a number of tools and sources—archaeology and paleontology, palynology, early historic accounts, early land surveys, evidence of fire history, photographic archives—ecology has succeeded in developing a substantial knowledge of pre-Columbian North American landscapes. This paper engages in one such reconstruction by estimating the size of the wintering northern herd of the Yellowstone National Park (YNP) elk (*Cervus elaphus*) population prior to Park establishment in 1872. It synthesizes a diverse array of evidence, and quantifies what are otherwise anecdotal, subjective, and nonparametric observations. It reveals, we think, the ironies and pitfalls of paying so much attention to the holy grail of "natural" without an ecologically precise definition of the concept, or clear evidence of its character.

DEPENDENCY OF YELLOWSTONE MANAGEMENT ON THE NATURAL CONDITION

As the first national park in the U.S. and in the world, YNP is the flagship of the American system. Policies first set in YNP can become general policies for the entire system.[15] Some 3 million tourists visit the Park each year from many parts of the world. Hence management actions in the Park are crucial both to its own welfare and that of the entire system, and thus are highly visible. The number of elk wintering prehistorically in a 100,000 ha area inside the northern boundary of YNP, "the northern range," has been a pivotal question from both an ecological and policy standpoint for more than a century. There is general agreement among all observers that such woody vegetation as aspen (*Populus tremuloides*) and willow (*Salix* spp.) on the northern range has declined significantly since Park establishment in 1872 (Figs. 1 and 2). But trends in the elk population, and its role in the decline of vegetation and related ecosystem components, are a highly contentious issue.

There is an enduring assumption among American ecologists that North American ecosystems were not materially modified by their pre-European human inhabitants.

The crux of the argument has centered on two paradigms proposing explanations of the situation. One, henceforth the Cole-Houston view, holds that before establishment of YNP large numbers of elk (i.e. 12,000–15,000)[16] wintered on what is now the northern range, and their influences on the ecosystem were not very different before Park formation from what they are today.[17–19] Any vegetation decline has variously been ascribed to climate change, fire suppression, and natural succession. Elk influence has generally been held to be secondary or minimal.

Advocates of the other paradigm, which both predates and is contemporary with the Cole-Houston view, infer that elk did not winter in large numbers on what is now the northern range. In its most recent form,[8,20,21] this paradigm maintains that elk occurred at low densities in the Yellowstone region in prehistory. The animals that did occupy the higher elevations in summer migrated out of what is now the northern range as far as 150–300 km to more extensive, lower-elevation winter range.[22–24] Following Park formation, increased hunting and European settlement around the Park eventually restricted seasonal migration and forced the northern herd to winter in the northern portion of the Park.[22,24,25] Advocates of this paradigm agree that herbivore pressure on what is now the northern winter range was light prior to Park establishment. Protection from hunting in the 1870s, elimination of large predators, and artificial feeding allowed the northern herd to increase to contemporary numbers (ca. 20,000[26]). Changes in woody vegetation and associated ecosystem components have been profound, have occurred in this century, and have been induced primarily by the unprecedented build-up of the northern elk herd.[20,21,27]

In addition to the obvious ecological conundrum, answer to this question has become the fulcrum for the Park's ungulate-management policy which has varied back and forth over the past century depending on which paradigm was in vogue.[28] And importance of the

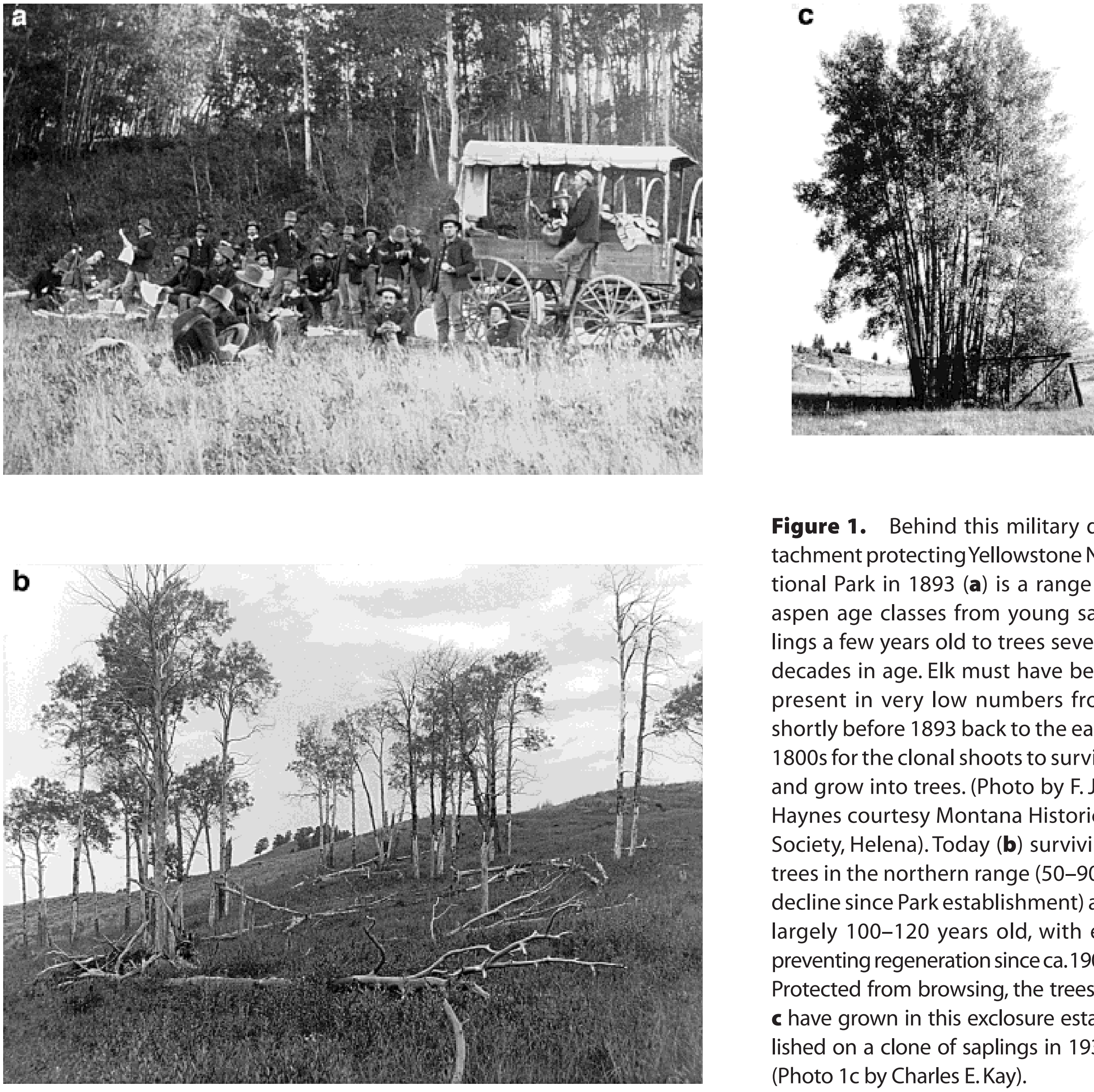

Figure 1. Behind this military detachment protecting Yellowstone National Park in 1893 (**a**) is a range of aspen age classes from young saplings a few years old to trees several decades in age. Elk must have been present in very low numbers from shortly before 1893 back to the early 1800s for the clonal shoots to survive and grow into trees. (Photo by F. Jay Haynes courtesy Montana Historical Society, Helena). Today (**b**) surviving trees in the northern range (50–90% decline since Park establishment) are largely 100–120 years old, with elk preventing regeneration since ca. 1900. Protected from browsing, the trees in **c** have grown in this exclosure established on a clone of saplings in 1936. (Photo 1c by Charles E. Kay).

question has expanded beyond YNP in that the current policy has been extended to become the prevailing one for the entire National Park System.[15] Thus a reasonably dependable sense of wintering abundance on YNP's northern range prior to Park establishment is a crucial ecological and policy question. This paper reviews previous efforts to arrive at that sense, summarizes and quantifies diverse sources of evidence bearing on the issue, and presents a simple population model for developing a more quantitative approximation than has hitherto been attempted.

PERILS AND PITFALLS OF SIMPLISTIC INTERPRETATIONS OF HISTORICAL ACCOUNTS

Since there were no censuses of wintering elk numbers on the northern range in the 1870s and before, all attempts at approximating them, including the one we propose, have been based on interpretation of anecdotal reports by early trappers, miners, explorers, hunters, tourists, and military personnel in diaries, journals, oral accounts, and a variety of publications. There is a consistent core of accounts used by all the authors, but some drew on a wider range of sources than others. The differing impressions of abundance result from which accounts have been used, and how they have been analyzed.

Inferences of Scarcity by Early Biologists

M.P. Skinner,[29] probably the first NPS biologist to investigate the northern-range situation, cited accounts in the Lewis and Clark journals of game abundance on the plains, but scarcity once the party reached the mountains. This

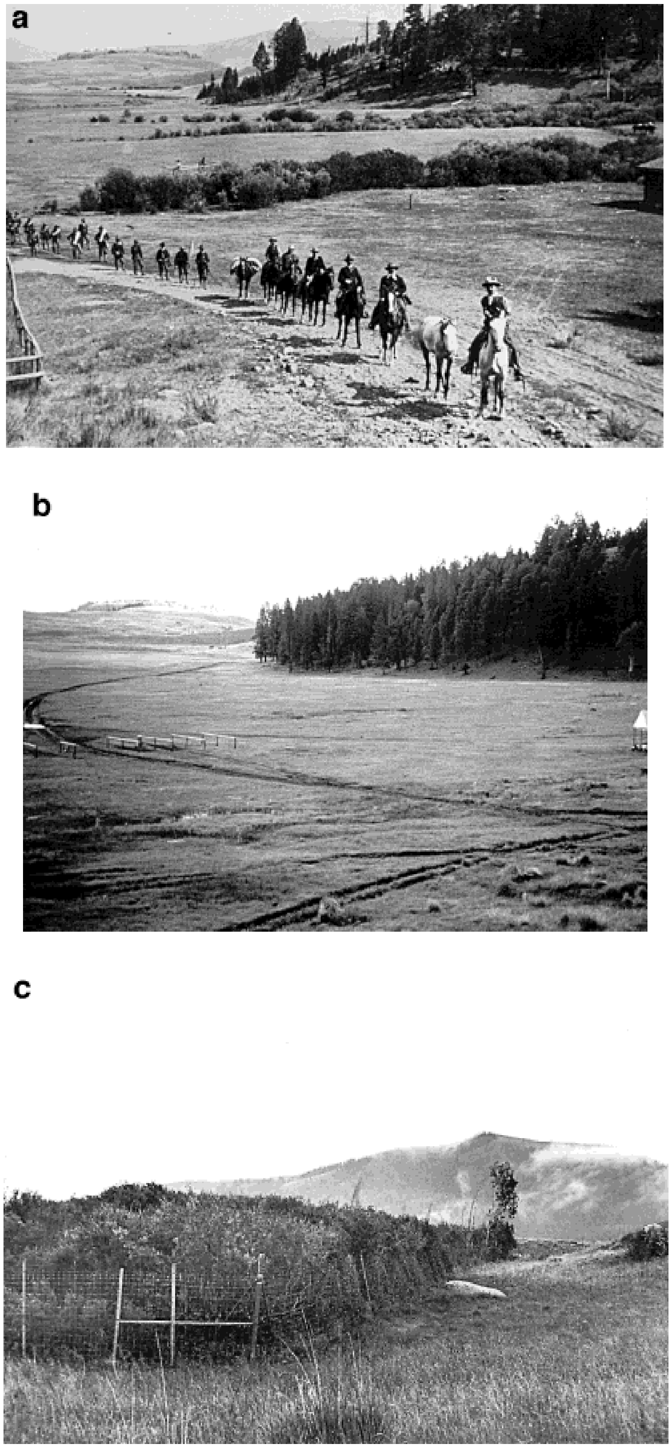

Figure 2. The horizontal strips behind the horsemen in this 1893 Park photograph (**a**) are riparian willow growths along small streamlets flowing to a creek outside the photo on the left. (Photo by F. Jay Haynes, courtesy Haynes Foundation Collection, Montana Historical Society, Helena). Before this 1986 photo (**b**), the riparian shrubs had been eliminated by elk browsing in this area as they have throughout the northern range. Where protected with fencing in the Park, (**c**) willows grow in profusion in moist areas. (Photo 2b by Charles E. Kay.)

impression was reinforced by Seton's map[23] of prehistoric elk distribution which showed it to be a plains animal roughly coinciding with bison (*Bison bison*) distribution.

Rush[30] quoted from the Lewis and Clark journals at length regarding comments on game scarcity and Native Americans subsisting on foods other than meat. Recently, Martin and Szuter[31] cited the Lewis and Clark accounts of abundant game on the plains, and scarcity in the mountains and westward along the Columbia River. In the latter area, the expedition was obliged to trade with the tribes for dogs and horses to provision their party with meat. The authors emphasized that regions of game abundance coincided with Indian

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nations at war where hunters were reluctant to venture freely and far from tribal centers. Skinner[29] also cited reports from the 1870 Washburn, Langford, and Doane expedition through the Yellowstone area to the effect that they "found very few animals." He inferred from the accounts of the 1871 Hayden survey that the party only saw one deer. This inference of scarcity was generally repeated by later investigators.[24,30]

Later Analyses Concluding Abundance

Murie[32] was apparently the first agency biologist to challenge the early impressions of scarcity. Citing accounts from some of the same expeditions as those referred to by Skinner[29] as well as others, Murie pointed out that some of these reports included instances where large numbers of animals were seen. He argued that positive evidence must take precedence over negative. In his view, failure to see game could not be taken as certain indication of its absence. He compiled approximately 17 early accounts and observations of wildlife abundance and concluded that it must have been abundant in the Yellowstone area during the 1800s.

Houston[18] cited 20 accounts of wildlife numbers from 1836 through 1881, many of the same sources used by Skinner and Murie. All of Houston's sources reported seeing and/or shooting elk, with accounts ranging from individual animals to such epithets as "scattered flocks, large band, elk everywhere, abundant, all manner," etc.

The most extensive effort in this vein has been the compilation of such accounts by YNP historians Schullery and Whittlesey.[33] These authors reviewed statements from 168 sources for the period 1806 through 1881. Reports of 131 sightings of individual elk, "small groups," and "herds"; 9 of sounds; 25 of meat, hides, bones, or antlers; 31 of tracks, trails, or other sign; and 84 general statements of presence totaled 280. Of the 56 statements by observers who commented one way or the other on game abundance in the Park area, 91% noted that game was, in Schullery and Whittlesey's words, "very abundant."

These authors concluded from this evidence that:

(1) "Elk were common in appropriate habitats in the Greater Yellowstone Ecosystem in this early historical period..."
(2) "... elk were common throughout the park, and were observed at various times in large numbers in virtually every part of the park where large numbers now occur ..."
(3) "... elk were abundant throughout the Greater Yellowstone Ecosystem prior to 1882 ..."
(4) "The record is not sufficiently detailed, for example, to allow us to say with any confidence that elk numbers on the Northern Range during any given year in that period equaled, exceeded, or were less than, at present ...."
(5) "Elk were widely distributed throughout the park area, and were observed, often in groups and occasionally in large herds, in every portion of the park where such observations would be expected today."

This is an extensive compendium, and in reading through the ca. 117 pages of historical accounts, one inevitably develops a sense of great elk abundance from the sheer number of reports. That sense is heightened by frequent allusions to abundance in other wildlife: six other species of ungulates, beaver (*Castor canadensis*), numerous species of carnivores, flocks of waterfowl, streams brimming with trout, etc. But with further analysis, that sense of abundance is tempered with several reservations:

(1) The perspective of these early observers cannot be judged from our own. What they considered abundance may or may not match our mental image. It is not possible to get any reasonably quantitative sense from subjective words or comments like "abundant, numerous, hunter's paradise," etc. used more than a century ago by people who had very different outdoor experiences from our own.
(2) Some observers exaggerated. Kay[20] recognized this in the 1866 reports of prospector A. Bart Henderson, and chose not to use Henderson's accounts in his tabulations. Schullery and Whittlesey chided Kay for inferring that Henderson, in their word, "lied." But they conceded that in his frequent use of theword "thousands" Henderson probably meant something more like "lots."
(3) Most importantly, the Murie, Houston, and Schullery and Whittlesey reviews set out primarily to compile reports of game abundance, evidently to support the contention that wildlife was abundant in the YNP area in the 1800s. In so doing, they almost certainly did not compile comments on game scarcity, inability to shoot game for food, food shortage, etc. with equal thoroughness. Murie and Houston reported none; Schullery and Whittlesey referred to only a few. Hence their compendia are based on selected evidence.

We agree with the latter authors and Murie that focusing only on anecdotal reports of failure to see wildlife cannot provide an objective indication of its absence, or necessarily its scarcity. But it is equally true that reporting only observations of abundance, as Murie and Houston have done, biases inferences in the opposite direction. And when reports of scarcity are numerous from large parties of mounted, experienced outdoorsmen who depended on shooting game to provision lengthy excursions, they begin to carry weight and discount reports of game abundance to some degree. Kay[20] raised this issue in pointing out Houston's[18] reference to two passages from prospector Walter DeLacy's journal of his 1863 trip. Houston cited two passages in which DeLacy observed elk, but did not point out that these were the only reports of elk by a party of 25–40 prospectors on a 27-day excursion. Hence any balanced assessment of this type of evidence depends on equally thorough consideration of abundance and scarcity reports.

In sum, we agree with Schullery and Whittlesey that their evidence indicates the presence of elk at points in time and prior to 1882 over most of what is now YNP, and in substantial numbers at times and in places. But without any temporal or spatial scaling, it is not possible to say whether the 131 sightings reported in 168 sources scattered over a 26-year period imply general abundance or scarcity in the 1800s over the nearly 9,000 km^2 area that now comprises the Park. Clearly, the challenge is to devise some quantitative approach to analyzing this type of information.

QUANTIFYING THE HISTORICAL RECORD POINTS TO SCARCITY

Aware of the above difficulties in deriving any reliable quantitative sense from anecdotal reports, Kay[20] devised a means for quantifying such observations. He analyzed the journals of 20 expeditions through the Park area in the 1800's on what he called a "continuous-time" basis. He adopted the historian's discipline of using only first-person accounts placed on record in journals or diaries at the time of observation, and tabulated these in terms of occasions on which wildlife was seen, occasions on which sign was observed, number of animals killed, and number of references to lack of game or lack of food. His major results were:

(1) The 20 parties ranged in size from 3–60, averaged around 20, and spent a total of 765 party days in the Yellowstone area. The mean number of days per party was 765/20=38.
(2) The 20 parties reported seeing elk on 42 occasions, or approximately two times per party and once per 18 party days (765/42). Kay did not attempt to estimate the number of elk seen because it was impossible to determine the number of animals in a reported "herd" or "group."
(3) The parties recorded lack of game or lack of food 45 times, or approximately the same number of times they reported seeing elk.
(4) The parties reported seeing ungulates of six species on 121 occasions, and the 42 elk observations thus constituted 35% of the total ungulate observations. He contrasted this with the fact that elk today make up 79% of the collective ungulate populations in the Greater Yellowstone Ecosystem. Mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), and bighorn sheep (*Ovis canadensis*) in that order, were the next most common ungulates seen. (White tailed deer (*Odocoileus virginianus*), though effectively absent today, originally occurred in the Park in small numbers. Most of the historical accounts did not distinguish them from the more abundant mule deer. Hence we treat all references to deer as mule deer or simply "deer.")

Kay concluded from these calculations that elk were "... not abundant throughout the Greater Yellowstone Area during the period of early historical records ...." and "... elk were rare throughout the Greater Yellowstone Ecosystem ..." (p. 365). Moreover, the elk that were present constituted a much smaller fraction of the collective ungulate population than they do today. One reviewer questioned this procedure and inferences on the grounds that differences in the species' behavior might make them differentially visible and bias inferences about comparative abundance. This is a valid question, and it has prompted us to analyze it in some detail. But rather than interrupt the flow of the discussion here—we conclude from the analysis that the evidence does not point to a serious problem—we present the analysis in Appendix A.

Kay's method for quantifying historical reports provides a more objective and accurate picture of early elk abundance.

Schullery and Whittlesey[33] criticized Kay's work at several points in their report, largely taking issue with some of Kay's interpretive or editorial comments. They did not take issue with Kay's efforts at quantification. But they implied that because their compilation was so much more extensive than Kay's, their conclusions of game abundance were more valid than Kay's inference of scarcity. Since the data sources used were so different we do not consider this a valid comparison. But the results of the two studies can be compared by analyzing the Schullery and Whittlesey data with the same quantitative procedures Kay used. Schullery and Whittlesey did not restrict their sources to first-person, on-the-spot accounts, as did Kay. They used some newspaper and magazine sources, published accounts after time lapses of months to years from original observations, and some second-hand accounts. Nevertheless, we will accept these at face value and analyze the entire data set. The results are as follows:

(1) Their 168 sources reported seeing elk on 131 occasions, only 0.78 times per source, and only about one-third as often as Kay's twice per party. We did not attempt to tabulate the total source- or party-days because of the greater variety and indirectness of some of the authors' sources. But if the time for each source was anywhere near similar to Kay's mean of 38 days per party, the number of source- or party-days per elk observation was 38×168/131=49, far less often than Kay's 18 party days per elk observation.
(2) Schullery and Whittlesey's sources reported seeing ungulates on 330 occasions. The 131 elk occasions thus constituted 40% of all ungulate observations, not very different from Kay's 35%. Mule deer, pronghorn, and bison, in that order, were the next most frequently seen ungulates other than elk, again similar to Kay's results except that bison replaced bighorn sheep at third in the order.
(3) Although they reported seeing signs of, or hearing, wolves (*Canis lupus*) and mountain lions (*Felis concolor*), Kay's 20 parties did not report seeing either species during their 765 party days. He considered this another indication of low ungulate densities since, in other parts of the world with large ungulate (prey) populations (e.g. East Africa, the early North American plains), large predators are numerous and readily seen.

Schullery and Whittlesey's sources did report seeing wolves and mountain lions, and again on the basis of their more extensive survey and these observations, questioned Kay's inference of large-predator scarcity. But again when quantified on a per-source basis, their evidence tends to support Kay's position rather than their own. These authors' 168 sources only reported actually seeing wolves on 5 occasions, mountain lions on 3. Thus over 95% of their sources failed to report seeing these two species, supporting Kay's inference of low abundance.

We conclude that the more extensive Schullery and Whittlesey results provide the same indication of low elk abundance in the Yellowstone area that Kay inferred from his data. These authors and Schullery[34] have emphasized that 90% of the 56 writers who commented on wildlife abundance judged it to be "abundant." But they drew from 168 sources, 131 of which reported seeing elk. Hence only a third of their sources commented on wildlife abundance, and 22% of their sources did not report seeing elk. More generally, Kay's methods for quantifying historical reports provides a more objective and accurate picture of early elk abundance in the northern range than subjective appraisal of anecdotal accounts.

WAS THE NORTHERN RANGE A MAJOR ELK WINTERING AREA IN PREHISTORY?

Part of the northern-herd debate involves the question of whether elk occupying the higher-elevation summer ranges of the Park area, whatever their numbers, migrated north to lower-elevation winter ranges beyond present Park boundaries before its establishment in 1872. By some accounts, elk migrated down the Yellowstone River valley to the north beyond the present town of Livingston, Montana (89 km from the Park's north entrance at Gardiner) as far as 100–300 km.[22, 25, 35, 36] Yellowstone Park historian Haines[37] wrote "... Crow Indians who lived along the lower Yellowstone River... [called it] 'E-chee-dick-karsh-ah-shay' ... which means 'Elk River', a name derived from the fact that it provided a migration route for those animals while passing between their summer range on the Yellowstone Plateau and their wintering grounds at lower elevations." Park Superintendent Harris commented 15 years after Park establishment:[38]

"The professional hunters who surround the Park commenced their operations in good season, and great activity and vigilance by scouting parties were requisite to prevent them from operating within the borders of the Park. It is the practice of these hunters to locate camps on the tributaries of the Yellowstone River just outside the limits of the Park on its northern and eastern borders, and thus to intercept the game when, driven out of the mountains by the deep snow, it seeks the lower valleys ..."

Migration reports by the earliest biologists[35, 39] could conceivably have been based on eye-witness accounts. As we will comment below, northern-range elk have continued to show inclinations well into the present century to migrate out of the Park.

Since the early visitors to the area cited by Murie,[32] Houston,[18] and Schullery and Whittlesey[33] travelled largely from May–October, there were few if any direct observations of wintering elk prior to 1872. Nevertheless, Houston[18] questioned the reality of seasonal migration, basing his argument on three lines of indirect evidence or reasoning. First, he noted that early travellers to the area observed large numbers of cast antlers in what is now the northern range. He surmised that these were shed by wintering animals. Second, he reasoned that an exodus from the northern range would leave an improbable biological vacuum in an area that today winters large numbers of animals. Third, within a few years after Park establishment, Park employees wintering in the area were seeing wintering animals. Schullery and Whittlesey[33] reviewed this evidence and accepted Houston's conclusion, but conceded that early historic accounts "... only rarely provide meaningful information on ... [elk] numbers."

We do not find this a compelling case for a number of reasons. First on the matter of antler shed, Skinner[40] observed the dates of elk antler shed during 7 years. The average starting and ending dates were March 16 and April 26. It is entirely possible that bulls could be returning from distant wintering grounds to the northern portion of the park by these dates, especially in mild winters. Moreover, Yellowstone bulls are less prone to migrate to wintering areas than are cows and calves,[35] or even come down to lower-elevation winter range.[36] Boyce[12] reports that the observed number of bulls/100 cows in Grand Teton National Park in summer is 2–3 times the number/100 that winter on the National Elk Refuge near Jackson, Wyoming. At the Hardware Ranch elk feed grounds in northern Utah, the older bulls tend not to join cows and calves except in extremely severe winter conditions. Mature YNP bulls may well have remained in the higher elevations, at least in mild winters, while cows and calves migrated to lower levels. In especially mild winters, migration of the entire population could have been light. Over decades and centuries, large numbers of antlers could have been deposited without large wintering populations typically on the northern range.

On the matter of vacating the northern range, Houston's[18] hypothesized biological vacuum might have credence if winter conditions on the current northern range were similar to those in the Paradise Valley (i.e. the Yellowstone River valley north of the Park). But elevations down the river valley drop as much as a third from the northern range inside the park: 1,900 m at Tower near the north-range center, 1,610 m at the Gardiner north entrance, 1,359 m at Livingston, MT, and 1,234 m at Big Timber, MT 56 km from Livingston. Moreover, there is a significant difference in snowpack between YNP and the Paradise Valley. In 1875, Strong[41] was informed by Bottler, a rancher ca. 50 km north of Gardiner, that snow rarely fell in the Paradise Valley and that livestock was never sheltered or fed during the severest winters. In contrast, the winter range within and adjacent to YNP is typically snow-covered.

Elsewhere, contemporary elk populations characteristically migrate between seasonal ranges, in some cases considerable distances. Many animals migrate from southern YNP to the National Elk Refuge over a distance of 100 km.[42] The present wintering herds on the YNP northern range show tendencies to move out of the Park during severe winters but are intimidated by hunting to remain inside the boundaries.[43] In intensive observations on this behavior, Vore[87] has shown this constraint on movement out of the Park by hunting, and immediately following by tourist activity.

Schullery[34] commented that the animals shot by market hunters were shot in winter. But Strong[41] makes it clear that they were shot at the end of fall and beginning of winter when they were moving out of the higher elevation summer ranges en route to wintering areas: "When the snow falls and the fierce winter storms begin in November and December, the elk, deer, and sheep leave the summits ... and come in great bands to the foot-hills and valleys where they are met and shot ... by these mercilous human vultures."

On the whole, the early accounts of seasonal migration out of the Park area seem likely in view of the species' behavior. And it seems unlikely that the early accounts to that effect were pure fabrication. By 1887, Superintendent Harris commented on the tendencies of the elk to seek "the safety afforded by the Park" during the winter.[38]

QUANTIFYING THE ARCHAEOLOGICAL DATA COMPLEMENTS THE HISTORICAL EVIDENCE

Modern-day archaeologists systematically quantify the plant and animal remains of the sites that they explore in order to develop an understanding of the abundance and use of resources by earlier cultures. Along with anthropologists studying contemporary subsistence cultures, and borrowing such questions of ecological theory as the degree to which resources limit (human) populations, the effects of humans on their resources, and optimal foraging theory, these scientists are finding significant exploitation effects on animal populations and alteration of landscapes with fire, deforestation, and cultivation.[6, 44, 48]

In an effort to use archaeological data as one source of evidence on the early abundance of elk in the Yellowstone area, Kay[20] surveyed the entire archaeological literature for the region. Some 274 sites have been catalogued in what is now YNP, more than 300 in Jackson Hole, Wyoming, south of the Park, and over 1,000 in other parts of what is now considered the Greater Yellowstone Ecosystem (GYE). While the region has been surveyed extensively, no major archaeological sites within present-day Park boundaries have been excavated. But there have been a number of excavations in areas surrounding the Park, and archaeologists have shown that the GYE was inhabited by Native Americans beginning some 10,000 years BP.

Kay[20] summarized the ungulate remains unearthed at four sites ranging from 4–80 km north and east of YNP according to archaeologists' parameters MNI (minimum number of individuals [animals]) and NISP (number of individual specimens). Among 313 ungulate MNI and 3,708 NISP, elk made up only 5% and 3%, respectively. Deer and bighorn sheep together made up 75% and bison 15% of the MNI, and 59%and 37% respectively of the NISP. Kay contrasted these results with the contemporary makeup of the GYE ungulate populations in which elk comprise 79%.

At the time of Park formation, the northern herd numbered on the order of 5,000–6,000.

Kay[20] also summarized the extensive work of archaeologists G.C. Frison and G.A. Wright in Jackson Hole. Wright[49] had spent 10 years excavating "more than two dozen sites" in the area. He found some bison, mule deer, and bighorn bones, but not a single one of elk in an area where today 2,000–4,000 elk summer on the floor of Grand Teton National Park on the west side of Jackson Hole, and where 7,000–10,000 winter on the National Elk Refuge.[42] Frison[50] also found bison and mule deer remains in Jackson Hole, but no elk. In total, ungulates in Jackson Hole were a minor part of the native people's diet, and elk no amount of that part.

Wright[51] proposes a subsistence model of the early inhabitants termed a "High Country Adaptation." Hunter-gatherer cultures depended heavily on plant resources. They harvested root crops such as blue camas (*Camassia quamash*) and bitterroot (*Lewisia rediviа*), moving to higher elevations as the seasons advanced. Fishing was also important between late spring and early fall. Winter was spent outside the area hunting ungulates, the inhabitants of the Park area moving north to the plains where bison jumps have been found. Jackson Hole occupants moved southeast in winter to the Green River-Red Desert area or west into Pierres Hole. No evidence was found that large numbers of elk occurred in Jackson Hole in either winter or summer.

Rush[30] quoted the Lewis and Clark journals in which they commented on the scarcity of game in the mountains. When they met the Shoshoni Indians at the headwaters of the Jefferson River "even the Indians had only salmon and berry cakes to trade them ..."

Frison[52] comments on the "strong orientation toward Archaic plant gathering" among early inhabitants of the Wind River and Bighorn Basins south and east of Yellowstone. He too, comments on the scarcity of elk among the ungulate remains of archaeological sites: "It is difficult to understand why elk remains are lacking in prehistoric sites if they were present in any numbers. They are particularly desirable meat animals and they are not difficult to hunt. No evidence is known of artificial elk traps or of communal procurement practices."

Kay[20] further compiled results of excavations in 202 sites in seven northwestern states. Here again, ungulate remains were a minor component of the diets dominated by plant foods. Within the ungulate components, elk comprised 4% and 3%, respectively, of 3,345 MNI and 52,624 NISP. Deer and bighorn combined, the commonest species, made up 67% and 79% respectively. From these and other sources, Kay[8,20] developed his aboriginal-overkill hypothesis proposing that ungulate populations in the Intermountain West of North America, and particularly elk and moose, were held at low densities in pre-Columbian times by a combination of aboriginal hunting and predation by large carnivores.

Schullery and Whittlesey[33] generally questioned this view for Yellowstone and cited a number of authors who reported finding occasional elk bones in sites. The thrust of their argument appears to be simply to prove that elk were present in the region, and perhaps by some unstated inferential extension that this demonstrated early elk abundance. But the question of elk *presence* has not been at issue. Neither we nor Kay[20] suggest that elk were totally absent. Our point is rather that elk were present in low numbers. Schullery and Whittlesey's sources present no archaeological evidence that contradicts this conclusion.

These authors also comment approvingly on Hadly's[53] statement: "This argument [that elk were not prehistorically abundant in the Park area] is refuted by evidence from Lamar Cave .... The occurrence of elk in the Lamar Cave fauna establishes its presence in Yellowstone prior to historic disturbances ..." Here again, Kay has not questioned the presence of elk in prehistory. And in our view, Hadly's ungulate data are too few to shed any light on early elk abundance or to justify her statement about refuting the conclusion of elk scarcity. If any inference is to be drawn, it is that her data are compatible with our conclusions.

Lamar Cave is a small cave in the YNP northern range. Hadly[54] concluded that the major taphonomic agents carrying material into the cave were packrats (*Neotoma cinerea*) and carnivores. There was no evidence of human activity. She excavated a single pit 175×200 cm wide and 272 cm deep. She subdivided the fill vertically into 16 stratigraphic levels, the deepest of which she aged at ca. 2,030–2,860 yrs BP.

Hadly identified 10,597 mammalian specimens (NISP) of which only 196 were ungulate bones: 76 elk, 20 mule deer, 25 pronghorn, 23 bison, and 52 bighorn sheep. Thus to begin with, ungulate bones only comprised 1.9% of the mammalian specimens.

Of the 76 elk bones, 42 (55%) were in the surface layer and 59 (78%) were found in layers 1–3. Three radiocarbon ages were obtained from level 3: 0–40 yrs, 0–40 yrs, and 0–333 yrs. Thus, over three-fourths of the elk bones were in the modern layers (0–333-yr accumulation) while only 17 (22%) were distributed down through the remaining >2,000-yr-old column. In layers 1–3, elk bones comprised 70% of all ungulate bones. In levels 4–16 they comprised only 15%.

If any inferences are to be drawn from these small numbers, they are that elk have increased in numbers in recent times, and have become a much larger proportion of the combined ungulate population. And while deer and bighorn outnumbered elk in the earlier times, elk have outnumbered the other two species by a factor of 2.5 in the recent period.

Bishop et al.[55] queried Hadly on a similar interpretation of her data by Wagner et al.[15] In her reply she opined that the latter authors did not know the nature of the taphonomic agents (pack rats and carnivores) which were not sufficiently adept at bringing in larger bones to allow any such quantitative judgments. But as indicated above, we are aware of the agents. We do not suggest that they were able to bring in large bones with anywhere near the facility of humans. Our only implicit assumption is that whatever their facility, it was roughly the same over the 2,030–2,860-year period sampled by her excavation; and that the presence of 59 elk bones in the recent strata and 17 through the remaining ~2,000 years of the column are compatible with Kay's inference of early elk scarcity and recent abundance. We do not see any basis for inferring that these results refute Kay's interpretations, whatever the taphonomic agents.

We have discussed the matter recently with Hadly (August 27, 1998). Her cogent point was that small numbers of bones of large mammals brought in by small taphonomic agents like packrats and raptors cannot reliably be used to reconstruct population abundances of those species. The point is certainly well made. We have only raised the issue here because she did make a judgment in the above quotation[53] on Kay's hypothesis of early elk scarcity, because Schullery and Whittlesey[33] quoted that judgment, and because Bishop et al.[55] reiterate it.

More generally, we conclude that a large mass of archaeological evidence—which Schullery and Whittlesey somehow dismiss as "... this extremely small archaeological research effort ..."—portrays a pattern similar to that of the historical records: ungulates occurred in relatively low numbers in the Yellowstone area in prehistory and far below numbers of this century. Moreover, the species composition of the combined populations was quite different, with mule deer and bighorn sheep together comprising a much higher fraction, and elk comprising a much smaller fraction, than what prevails today. That too was implied by quantification of the historical evidence.

USING POPULATION-BIOLOGY CONCEPTS TO ESTIMATE ACTUAL NUMBERS FROM HISTORICAL ACCOUNTS

A population's rates of change can be calculated from a few reasonably dependable counts or estimates over time. In turn, those rates can be used (1) to estimate population numbers at other points in time and reconstruct time series; and (2) estimate a population's size from its response to measured, exploitive removals. We use these techniques for approximating the northern herd size in 1870.

Until 1870, a few elk appear to have been shot mainly for subsistence in the YNP area, according to historic accounts. But from 1871 through 1877, larger numbers of elk were killed by market hunters for their hides and tongues. The magnitude of this removal, and associated population response, provide a basis for modeling the 1870 population.

Four travelers to the Park described the number of elk killed in the area of the northern range in the 1870s: Norris,[56,58] Ludlow,[59] Grinnell,[60] and Strong.[41] All first visited the northern range in the summer of 1875, hence could only know the number of animals shot prior to that time from hearsay. Strong, Ludlow, and Grinnell were only in the area for a few days, so could not have witnessed any kills after 1875. Norris became the second Park superintendent in 1877 and continued in that role until 1882. All of the 1875 travellers depended on local guides Jack Baronett, and Fred and Phillip Bottler whose ranch was established in the Yellowstone River valley 50 km north of the present Park boundary in 1868. These guides were intimately familiar with the market hunting scene and should have provided similar information. Norris had frequent contact with Baronett and the Bottlers during his 5-year tenure as superintendent, and was the only one of the four who had ample opportunity to clarify the market-hunting history. The accounts of the travelers are as follows.

Norris[56] reported: "The Bottler Bros. assure me that they alone packed over 2,000 elk skins from the forks of the Yellowstone [its confluence with the Lamar] ... and other hunters at least as many more [thus ca. 4,000]." After he became superintendent in 1877, he wrote[57] "... that over 2,000 hides [of elk] ... were taken out of the park in the spring of 1875, probably 7,000 or an annual average of 1,000 [have been killed] ..." Somewhat confusing the picture, Norris[58] commented 3 years later in his superintendent's report: "As stated in my first report, at least 7,000 of these valuable animals were slaughtered between 1875 and 1877 for their hides, or perhaps for their carcasses, which were stripped and poisoned for bear, wolf, or wolverine bait."

Strong[41] reported on his 1875 summer visit: "Over four thousand [elk] were killed last winter [1874–75] by professional hunters in the Mammoth Springs Basin alone ... The terrible slaughter ... has been going on since fall of 1871 ..." Mammoth Springs (Soda Mountain)—in the northwest corner of the Park, near its north entrance, and in the northern range—was the base camp for explorations during that era. While at Mammoth Springs, Strong described their next destination as the "Yellowstone Basin—distant thirty-six miles." Strong's trip log indicates that the Lamar-Yellowstone confluence is less than 26 miles distant from Mammoth Springs. In fact it is approximately 15 air miles (24 km). Thus Strong's allusion to hunting within the Mammoth Springs Basin appears to include the confluence area of the Yellowstone and Lamar Rivers and coincides with the area referred to by Norris and next by Ludlow.

Ludlow[59] reported "... no less than 1,500–2,000 of these [elk] ... were thus destroyed within a radius of fifteen miles of the Mammoth Springs." Like Strong, his comments were based on his brief 1875 summer visit. Sheridan[61] reported he has "been credibly informed that ... as many as 4,000 elk were killed by skin hunters in one winter ..." Grinnell[60] reported: "It is estimated that during the winter of 1874–75, not less than 3,000 ... were killed between the mouth of Trail Creek and Mammoth Hot Springs." This area extends 60 km north of the present Park boundary. It is not clear whether any of these animals were included in the Bottlers' reports.

Our inference from these accounts is as follows. The figure of approximately 4,000 killed between Mammoth Hot Springs and the confluence of the Yellowstone and Lamar Rivers for the winter of 1874–75 appears repeatedly: Strong,[41] Norris in 1875,[56] Sheridan,[61] and possibly Ludlow[59] ("no less than 1,500–2,000"). We therefore assume that it has some validity. (Schullery[34] presents an alternative set of inferences from these reports which differ from ours. We present them in Appendix B so that the reader is fully informed on the alternative views on this issue, and we explain why we consider our interpretation the more probable.)

Norris[57] provides the only description for the entire period 1871–77, placing the total kill at 7,000. We conclude that the peak of market hunting occurred during the winter of 1874–75. If the 7,000 count is valid for the 7 years, then 3,000 were killed in the other 6 years, or an average of 500 for each of the 6. We assume that the account of 7,000 killed from 1875–77 in Norris's 1880 report is either an inadvertent misstatement or a transcription error. His 1877 proration of 7,000 over 7 years to derive an annual average of 1,000 is too explicit to reject in favor of the 1880 statement made 3 years later. Norris sought protection of the elk, and any bias would likely reflect an effort to dramatize the extent of the killing. By the summer of 1875, Strong[41] commented that market hunting had reduced the game "until it is a rare thing now to see an elk, deer, or mountain sheep along the regular trail from Ellis [now Bozeman, Montana] to Yellowstone Lake." Jack Baronett advised Strong's 1875 expedition that there was "very little game to the west of the Yellowstone." Norris[57] deemed "the game in most of the park, especially along the main routes of travel, as too much decimated to justify extra efforts for its protection west of the Yellowstone Lake, River, and Grand Cañon."

In 1877, Norris appealed to the market hunters to cease the slaughter.[57] By 1879, hunting abated and "choice animals" were deemed to "have increased" in number.[62] In 1883, it was reported "that between the Mammoth Springs and Cooke City [at the northeast entrance to the Park and near the eastern extreme of the northern range] there are at least 5,000 elk; that the yearly increase, to place a low estimate, is 1,000."[63] Three years later Harris[64] reported that "there is more game in the Park now of every kind than was ever known before." The following year, several thousand elk were estimated to winter in the Lamar River Valley and its tributaries.[38] During the 1870s, wolves (the elk's chief carnivorous predator) were killed as well. Norris[65] reported that "their easy slaughter with strychnine-poisoned carcasses of animals have nearly led to their extermination."

We infer from these sources that herd increase began in 1879 with the population low in 1878[62] because 1879 was the first year a population increase was noted. We also assume for the purpose of calculation, and from the above report, that the northern-range population numbered approximately 5,000 in 1883.[63] We then calculated population rates of change and observed population responses to different removal rates to test Houston's surmise[43] that (1) the pre-1870 population numbered on the order of 12,000–15,000; and (2) the herd was reduced to 5,000–8,000 during the market-hunting era.[18]

The rates of population change of which the northern herd is capable at low density can best be calculated from the Park censuses of the 1960s and 1970s. Subject to stringent Park control efforts in the 60's, the northern herd had been reduced to a censused 3,172 in 1968. At that point, control was terminated and the herd increased in the ensuing 5 years to a count of 9,981.[18] We calculate a mean, annual, instantaneous rate of increase, $\bar{r}$, over this period as:

$$\bar{r}_{1968-1973} = \frac{\log_e 9{,}981 - \log_e 3{,}172}{5} = 0.23.$$

This rate, transposed to a percentage rate of increase by

$$[(\text{antilog}_e\ 0.23) - 1.0] \times 100 = 26\%,$$

characterized the first years of population recovery. It corresponds well to increase rates in other elk populations. Eberhardt et al.[66] calculated growth rates for an elk population on the Arid Lands Ecology (ALE) Reserve (recently renamed the Fitzner-Eberhardt Reserve) in eastern Washington over an 18-year period. Mean annual increase rates from the censuses was 20%. That calculated from reproductive and survival data was 24%. These authors concluded that a "feasible maximum" rate for elk could be "as high as 28%." We do not suggest that the 0.23 $\bar{r}$-value continues through the full range of YNP population increases. Boyce[12] projected a logistic model for the northern herd implying a linear, density-dependent decline of r as the population increased. And Wagner et al.[15] fit a negative linear regression to the census-based annual $\bar{r}$-values as functions of each year's census, with $\bar{r}$ approaching zero at approximately 16,000. This was conservative since the population continued to increase to a census of 18,913 in the winter of 1987–88.[67] Our purpose here is only to approximate the herd's growth rates at low density.

One additional rate estimate for a single year is possible from the above anonymous report of 5,000 elk in 1883 between Mammoth Springs and Cooke City, and the observation of 1,000 yearly increase. This implies that the 1882 population was 4,000, and the 1,000 increase computes to an $\bar{r}$-value of 0.22, very close to the above 1968–73 estimate. We reconstructed the time series from 1870–1883 by working backward from 5,000 in 1883 with an r of 0.23 (Fig. 3):

$$N_{1878} = N_{1883} e^{-0.23(5)} = 1{,}583.$$

With the low point of 1,583 reached in 1878 and cessation of heavy market hunting, the population rose to 5,000 in 1883. We suggest that between 1875 and 1878, the herd was roughly stable at somewhere between 1,500–1,600. At this size the herd could increment each year through reproduction at a rate of 0.23 by fall. A fall-spring market-hunting removal of approximately 500 would then restore a pre-calving population of around 1,500 each year.

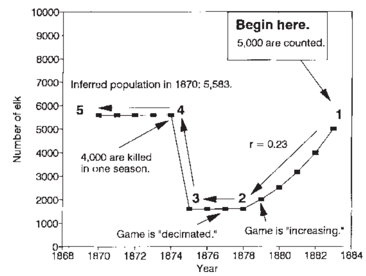

Figure 3. Simulated number of elk in the northern herd 1870–1883. The simulation begins at point 1 and proceeds backward in time to 1870. See text for explanation.

That the 1875–78 low of 1,580 was established by the 4,000 elk killed between fall and spring 1874–75 implies a pre-1874 population of approximately 5,000–6,000. We are suggesting roughly this size as the pre-European population, held at this level by a combination of predation by wolves, mountain lions, black (*Ursus americanus*) and grizzly (*U. horribilis*) bears reported in Schullery and Whittlesey's historic accounts;[33] by Native American hunting;[20] and by severe winter weather in some years.

Some comment is needed on the plausibility of using the same increase rate for 1878–83 as we calculated for 1968–73. Predator poisoning evidently began in the 1870s,[58] and wolves were noticeably reduced by 1881.[65] But some predation doubtless continued for a time as it does today. The heavy market hunting had been curtailed by 1879[62] although some poaching persisted for a time along with some game killing to provision the dining rooms of the Park hotels.[68] Thus there were some sources of attrition in the early Park years not experienced by the herds of 1968–73. However, the forage conditions, consequent nutritional state of the animals, and winter survival must have been superior in the earlier years to what has prevailed in the latter 1900s following decades of browsing by a large herd that has eliminated much of the woody vegetation. The different conditions must have offset each other to some degree.

The plausibility of both our population reconstruction and Houston's[42] hypothesis that the pre-1870 herd numbered 12,000–15,000 can be examined by analyzing the responses of known population sizes during Park history to measured removals. Prior to 1969, Park elk-management policy decreed that the northern herd had to be controlled in order to prevent it from increasing to levels at which it degraded the northern-range ecosystem. Known numbers of animals were removed each year by Park personnel trapping and shooting, and by hunters taking animals outside the Park that had moved beyond the boundaries.

In 1935, 10,112 elk were counted during the winter census on the northern range.[18] If this census underestimated the herd by 20%, the actual 1935 population numbered approximately 12,000. From 1935 to 1949, a total of 33,657 elk were removed (Fig. 4). The average annual removal was 2,244. In 1943, 7,230 animals were removed; this number is similar to Norris's account of the total market kill from 1871–1877. In 1949, 9,496 elk were counted during the winter census, only 616 fewer than in 1935. Hence a population of 10,000–

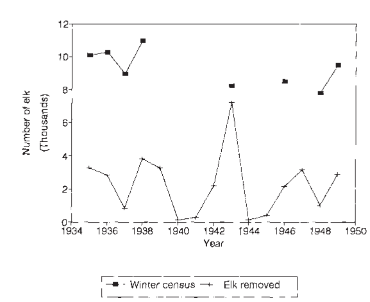

Figure 4. The number of northern-herd elk counted in winter censuses, and number removed through the period 1935–1949. Data are from Houston.[18] Removals were a combination of reductions by NPS and hunter kills outside the Park.

12,000 was able to maintain its numbers with a 2,244 mean, annual removal.

In the winter of 1961–62 the Park carried out a major herd reduction of 4,744 elk.[18] After reduction, the residual herd was censused at 5,725, similar to what we are proposing for 1870. In the ensuing 6 years, annual removals averaged 1,649 which progressively reduced the counted numbers to 3,172 in 1968, a 45% reduction.

We conclude that a herd of 10,000–12,000 can sustain an annual removal of approximately 2,000 and maintain its numbers. But a herd of nearly 6,000 could not withstand a 4,000-animal removal in 1 year plus smaller kills in subsequent years without declining over half in a 6-year period. A herd of 10,000–12,000 could withstand removals of this magnitude and not decline to scarcity. Thus the evidence suggests that the population was far below Houston's[16,18] projected 12,000–15,000, probably on the order of magnitude of our proposed 5,000–6,000, and conceivably less.

"NATURAL" YELLOWSTONE EVIDENTLY SUSTAINED LOW ELK NUMBERS AND LIGHT HERBIVOROUS PRESSURE

We conclude that at the time of Park formation, the northern herd numbered on the order of 5,000–6,000. We base this on integrating archaeological, historical, and vegetation evidence (to be discussed elsewhere), and the fact that a one-time market kill of 4,000 and 500 in each of 6 years thereafter sharply reduced the population. A censused population of 8,000–11,000 during the 1930s and early 1940s declined only slightly in the face of 2,244 average annual removals. Obviously this is a crude estimate, based as it is on the single, anonymous 1883 report of 5,000, and we look on it as little more than an order-of-magnitude number. And the prehistoric population doubtless fluctuated to some degree over the years with environmental variations, as do other ungulate populations. We are also persuaded by the anecdotal, historical accounts that elk occurred in substantial numbers in localized areas at points in time.

But quantification of the historical and archaeological evidence and the photographic record of the vegetation are all consistent in indicating low elk numbers. And the archaeological evidence gives no suggestion of continuous, large elk populations for prolonged periods during recent millennia. We consider the most probable hypothesis is Kay's[20] that populations were held at low prehistoric levels by a combination of aboriginal hunting, predation by large carnivores, and winter weather.

Our reading of the historical reports places market hunting largely in the period 1871–1878. Houston[18] states that market hunting continued into the early 1880s, but Superintendent Norris[57] began appealing for cessation of hunting in 1877, and there was already a reported elk population response by 1879. Some lesser amount of shooting did continue for a short time thereafter, in part simply to provide meat for the Park hotels. But our calculated 1878 low of ca. 1,583 could have recovered to the reported 5,000 animals between Mammoth and Cooke City in 1883[63] with an increase rate equal to that achieved by the contemporary population after the 1968 low. We also conclude that the evidence supports early accounts[35,39] of the northern herd migrating to an ancestral winter range north of its present winter range and that access to that ancestral range was blocked by EuroAmerican settlement and hunting. It seems unlikely that those authors would suggest such an extensive migration without basis.

Fire-ecology research in the Sierra Nevada and northern Rockies discloses frequencies and intensities of "natural," pre-Columbian fires and vegetation condition.

As a result of the low population density and migration out of the present northern range in the Park, we believe that the range sustained little use by elk. This conclusion is well supported by the early photographic evidence compiled by Kay.[8,20,27,69]

PURPOSES AND FEASIBILITY IN RECONSTRUCTING THE "NATURAL"

Managing the world's natural resources for sustainable use requires an understanding of how different forms and intensities of human use influence the structure and function of ecosystems from which the resources are extracted. Ecology operates on the premise that this understanding is best provided by insights into the character of systems both with and without human use. After all, this is the modus operandi of classical experimental science: controls and treatments.

Clearly, systems minimally altered by human use serve as important reference points. An entire lexicon—healthy, intact, natural, pristine, integrity—has been developed to characterize such systems. Highly diverse systems, often resulting from minimal human disturbance and thus considered healthy, are being shown to be more stable[70,71] and more resistant to invasion by nonnative species.[72,73]

Resource use and management are often conceptualized in terms of their effects on ecosystem "health" or "integrity." The impetus to conceptualize proper resource use in terms of proximity to what today we consider ecosystem health began at an early date. The discipline of range ecology evolved in the context of Clements'[74] ideas of plant succession, with the formal concepts and terminology developed by E.J. Dyksterhuis in the 1940s.[75] Grazing systems that today we would call "healthy" are commonly considered to be those that approach the undisturbed successional end points, and largely composed of species termed "decreasers" in Dyksterhuis' terminology. The term describes the trend in the species under grazing disturbance. More recently foresters are evaluating the effects of timber cutting on forest ecosystem health and integrity.[76]

As discussed above, a major purpose of natural areas is to preserve unexploited systems as reference points at the unaltered end of the human disturbance scale. This is a major function of U.S. national parks, and the Canadian National Parks Act requires maintenance of ecological integrity as a first priority for park management. Although the assumption that pre-Columbian, western-hemisphere ecosystems were largely unaltered by Native Americans—and thus "natural"—may be about to change, the view remains that these systems were in some sense healthy or natural and should be preserved to the extent possible in natural areas. Hence there is a need to reconstruct their character on areas now in national parks to fulfill their charge of preserving natural conditions.

In some cases reconstructing the natural requires estimating prehistoric population sizes of large mammalian herbivores which have the potential of significantly altering ecosystem structure and function. We have engaged in one such analysis for elk in YNP as have Baker et al.[77] and Fettig[78] for Rocky Mountain National Park and Bandelier National Monument, respectively. In eastern and midwestern U.S., similar efforts are underway for white-tailed deer.[79–81] In other cases, extensive effort has gone into reconstructing pre-European fire patterns.[82–84] The resulting knowledge has been the basis for using prescribed burning as a management tool in the Sierra Nevada national parks to simulate aboriginal burning that maintained the prehistoric mixed-conifer forests.[85]

U.S.D.A. Forest Service fire research has shown profound changes in vegetation composition in the northern Rocky Mountains since it instituted fire suppression in the early 1900s.[86] Prior to European settlement, fires on south-facing slopes were largely low-intensity ground fires with a mean interval of approximately 10 years. Stand-replacing crown fires were less than 20% of all fires. Vegetation, largely of an open, park-like, early-successional form, is thought to have prevailed since the last glacial retreat. Since fire protection, vegetation has filled in to mature forest stands, mean fire intervals have increased to ~100 years, and 90% of fires are crown fires.

In prehistory, north-facing slopes also experienced low-frequency (e.g. 10-year) fire intervals. But fires in these moist environments were of low-intensity and burned small patches (e.g. 250 ha). Herb-, shrub-, and sapling-vegetation occupied 50% of the terrain, with tree canopy cover at ~65%. Today, pole and mature trees dominate 90% of the vegetation while canopy cover has risen to 95%. The fire interval is now approximately 80 years; 60% of the total are crown fires with an average patch size of ~1,200 ha.

Risbrudt[86] has commented: "These changes have occurred because we did not understand the structure and function of pre-Columbian ecosystems, and the ecosystem consequences of our management decisions .... Today, the wildfires that land managers are facing are often of a type for which we do not have the technology, manpower, or equipment to control."

Reconstructing the early conditions is always problematic and entails some uncertainty. But accessing and synthesizing as many data sources as possible, particularly those of disciplines with which we ecologists do not ordinarily interact, reduces the risk of biases that can result from using only one. And it is always desirable to devise means for quantifying evidence that might otherwise be anecdotal or qualitative in order to avoid the biases of prior disposition which subjective appraisal can bring. A great deal has been learned about the nature of pre-Columbian, western-hemisphere ecosystems. And much more remains to be disclosed by a broad array of methodologies. It is doubtful that we will ever clearly know what is "natural," and certainly not until we have an explicit definition of the term. But we are increasingly assembling the tools and methodologies to reconstruct pre-Columbian conditions.

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APPENDIX A

One reviewer appropriately commented that Kay's[20] calculated proportions of the different species in the collective ungulate populations in his data sources, and ours in the Schullery and Whittlesey[33] data, do not consider possible visibility differences associated with differing behavior patterns of the species. We have examined this question and conclude the following.

Five characteristics of the species would seem to be potential influences on visibility: (1) body size, the larger animals being more visible; (2) color, the darker animals standing out in the landscape; (3) social behavior, the species forming aggregations more readily seen than those of solitary behavior; (4) habitat preference, the species occupying open terrain being more visible than those occupying woody cover or dissected topography; and (5) seasonal migration, whether or not a species occupies more wooded, high-elevation terrain in summer and moves to more open, lower-elevation winter range versus one that spends the entire year in open, lower-elevation range.

We rank-ordered the five species in question for each of these characteristics from most to least visible as follows:

(1) Size: bison, elk, sheep/deer, pronghorn
(2) Darkness of color: bison, elk, deer/sheep, pronghorn
(3) Aggregation tendency: bison, pronghorn/elk, sheep, deer
(4) Habitat preference: pronghorn/bison, elk, sheep, deer
(5) Seasonal habitat change: pronghorn, bison, elk/sheep/deer.

Aggregate scores for the five species, from most to least visible, order them: bison, pronghorn, elk, sheep, and deer. Thus, in terms of these criteria, elk tend to be intermediate in the visibility scale, possibly being underrepresented vis-a-vis bison and pronghorn, and overrepresented vis-a-vis bighorn and deer.

One data-analytic procedure tends to overrepresent deer. The observational units in both Kay's analysis and ours of Schullery and Whittlesey are reported instances in which a species was seen without any provision for the number of animals observed. Thus a single observed animal carries as much weight as a herd or harem. Since deer are the one species of the five with solitary behavior, they are most likely to be seen as singles or perhaps as pairs during the fall rut. We have implicitly inferred relative abundance from frequency of observation, and this behavioral trait and our analytic procedure may be one factor tending to exaggerate relative deer abundance vis-a-vis the other species and their proportion within the aggregate ungulate population. But that tendency would be offset to some degree by the deer's lowest visibility score based on the above five criteria.

One behavioral trait, bugling, would tend to call attention to elk and bias its visibility score upwards. Kay's 20 parties largely travelled in July, August, and September.[20] The ear-piercing squeal of the bulls during the rut can be heard for several kilometers during late August and September. This would tend to attract hunting parties afield in search of game for food.

In total, a complex of factors, in many cases offsetting each other, tend to reduce and enhance the relative visibility of each species and its proportionate rankings in the aggregate ungulate populations. Kay's 20 sources were expeditions averaging 20 individuals who were experienced outdoorsmen, traveling horseback, often spreading out in small hunting parties to find game to provision their tours. It seems likely that the size, duration, and skills of these parties would tend further to override any biases associated with these animals' characteristics.

While we do not suggest that our calculated percentages represent the exact percentages of the species present at the time, we have no reason to suspect that they are grossly in error in approximating those proportions, or negate the inference that elk were a much smaller fraction of the collective ungulate populations than they are today. The fact that the archaeological evidence, based on very different procedures for sampling the ungulates, implies a similar picture—in fact places elk at substantially lower percentages—supports Kay's and our conclusions.

APPENDIX B

Where we have inferred an 1874–1875 kill of 4,000 elk by market hunters, Schullery[34] concluded 8,000: "Norris and Strong's reports yield a total of 8,000 elk taken from the park in less than a year." This would imply a large enough population to withstand such a kill and not be eliminated, and "... should lay to rest any remaining notions that large mammals were not abundant in the Yellowstone area."

The authors' 8,000 figure assumes that Norris and Strong described separate instances, 4,000 killed in each. Four lines of evidence suggest that Strong and Norris described the same events:

(1) Neither man was present at the time of the killing. Both depended on secondhand accounts. Both visited with a principal—the Bottler brothers. (Norris had many contacts with them; the Ludlow party camped at their ranch.) It seems unlikely that the Bottlers would not discuss the market hunting, and that they would describe one instance to one party and a separate instance to the other.

(2) In those days when there were few settlements, geographic boundaries were larger compared to today. The Mammoth Springs area was a focal point for travel in northern Yellowstone. When in the Mammoth Springs basin, Strong described his next destination as the "Yellowstone basin—distant thirty six miles." By Strong's trip log, the Lamar/Yellowstone confluence is less than 26 miles distant from Mammoth Springs. Thus, the confluence area apparently includes the geographic area referred to as the Mammoth Springs basin.

(3) After 1875 Norris returned to the park where, over a period of years, he had frequent contact with the Bottlers. Of all the witnesses, Norris had the greatest opportunity to correct any false impression that he may have gained on his trip in 1875.

(4) Norris's 1877 estimate of 7,000 for 1871–77 and his calculated mean of 1,000 per year, leave no doubt about his view of the numbers except what was apparently the misstatement of 7,000 for 1875–77. In neither case is there any suggestion of 8,000 being killed in 1 year.

Hence we consider 4,000 to be the more probable estimate of the number killed in 1874–75, and as well the implication of a relatively low population. If the population had been in the range of 12,000–15,000 as Park personnel have maintained, and given an annual recruitment rate of around 20%, a 4,000 removal would not have reduced them to scarcity.