WHAT THE PAST CAN PROVIDE: CONTRIBUTION OF PREHISTORIC BISON STUDIES TO MODERN BISON MANAGEMENT

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ABSTRACT—For over 100 years, bison in the Greater Yellowstone Area have been managed intensely. Even during the years of "natural regulation," bison herds have been heavily managed by culling. One of the fundamental goals of the plan for the Greater Yellowstone Area is to maintain the ecosystem's integrity using sound science. In order to reach this goal, it must be recognized that it is a dynamic system, continually undergoing change. However, our knowledge of such changes is extremely limited. In the case of bison, our knowledge is based on non-systematically collected historic records and modern studies of small, isolated populations. In contrast, the prehistoric record can provide a millennia-long record, providing a baseline of pre-European conditions against which the modern situation can be assessed and future management decisions can be made. In this paper, I discuss the application of new and emerging techniques (e.g., stable isotope analysis, pollen and phytolith analysis, and DNA extraction) in the reconstruction of the biology and ecology of prehistoric bison and in contemporary management of bison.

KEY WORDS: bison, ecology, ecosystem, grasses, nutrition, restoration

Introduction

Few animal herds have aroused as much passion as the Yellowstone bison herd. Late in the 19th century, when the North American bison was almost extinct, public outcry at bison slaughter in Yellowstone National

Park forced passage of the Lacey Act in 1894. It provided the legal mechanism for protection of the bison and other wildlife in Yellowstone National Park. More recently, a similar outpouring of support on behalf of the Yellowstone bison followed their execution in the name of protecting the local cattle industry (Peacock 1997). During the winter of 1996-97 over 1000 bison were either executed or sent to slaughter by Montana Department of Livestock officials (National Park Service 1998). These bison were attempting to find food during an especially brutal winter (Baskin 1998:245), following a millennia-old pattern of seasonal migration from the snow-covered high country to the more desirable wintering grounds in the surrounding valleys. A final count of the mortality indicated that nearly one-half of the Yellowstone bison was either killed or died from starvation in that winter (National Park Service 1998).

Watching television reports of "[w]ounded, bleeding, kicking, gut-shot buffalo," people around the country were horrified (Peacock 1997:43). With a mounting body count, even Yellowstone Superintendent Mike Finley felt compelled to make a rather frank comment: "When people describe what's happening here as a national tragedy, I don't disagree with them. . . . We are participating in something that is totally unpalatable to the American people, and it's something we are not convinced that science justifies" (quoted in Peacock 1997:43). The science to which Superintendent Finley refered concerns the bacterium *Brucella abortus*, an infectious microorganism that can cause abortions in ruminants (Baskin 1998).

I would argue, however, that there is another aspect to the science that is being ignored—the prehistoric ecology of the Yellowstone bison. A recent draft of the Environmental Impact Statement for the Interagency Bison Management Plan makes only a passing reference to the prehistoric record of bison in the Park (National Park Service 1998). Recent articles have presented a challenge to students of prehistory. Boyce (1991:196) states that "we do not know and can never completely learn the role of humans during prehistory. Even if we could find 'proof' of substantial Indian predation on elk and other ungulates, we have no way of estimating the number of animals that should be culled to duplicate this source of mortality." This statement goes right to the heart of the matter. I argue that we *can* understand the role of humans as predators through the study of kill sites and bone beds. I suggest, as others have (e.g., Fisher and Roll 1998), that humans were probably the main predator of bison and significantly influenced their behavior, distribution, and evolution. While we may not want to manage bison herds by running them off cliffs, understanding the structure and

predator-prey relations of pre-European bison populations and humans may inform us how to proceed in managing contemporary herds for viable populations.

While I agree "that paleontological, archeological, and historical research completed so far does not allow for reliable comparisons of the abundance of bison . . . at past times with abundance now"(Schullery et al. 1998:327), I would add that these disciplines have much more to contribute to the study of management of modern bison than just an estimate of abundance. By applying a cross-disciplinary approach to understanding bison ecology, we should be able to provide empirical data relevant to such conservation issues as: (1) how long bison have resided in the Greater Yellowstone Area, (2) the characteristics of the pre-park population, (3) the influence of prehistoric humans on bison, (4) how populations have reacted to past climate change, and (5) what management decisions can be made to ensure viable populations, in light of our current understanding of future climate change. Appealing for such collaboration in a recent editorial in *Conservation Biology*, Curt Meine (1999:3) wrote:

> Why should historians pay attention to conservation biologists, and why should conservation biologists pay attention to history? For the same reasons: Both need the other to fulfill their potential in answering to current concerns; both liberate us by allowing us to understand more fully the forces that shape our lives and the lives around us; both allow us to step back, however momentarily, from the always confusing mire of current circumstances; not to escape them, but to comprehend them. Only then can we return to the present prepared to meet the future.

Here I propose the application of various techniques to document the occurrence and biology of prehistoric bison in the Greater Yellowstone Area. These techniques include: (1) the extraction and analysis of phytoliths, pollen, and macrobotanical remains from individual bison teeth for reconstructing the diet of prehistoric bison; (2) stable isotope analysis for reconstructing the trophic level of prehistoric bison and possible migration patterns; (3) metric analyses for determining demographic profiles of populations; and, (4) comparison of genetic diversity in prehistoric populations with that of modern populations. Insights from the application of these techniques should be relevant to management of contemporary bison herds.
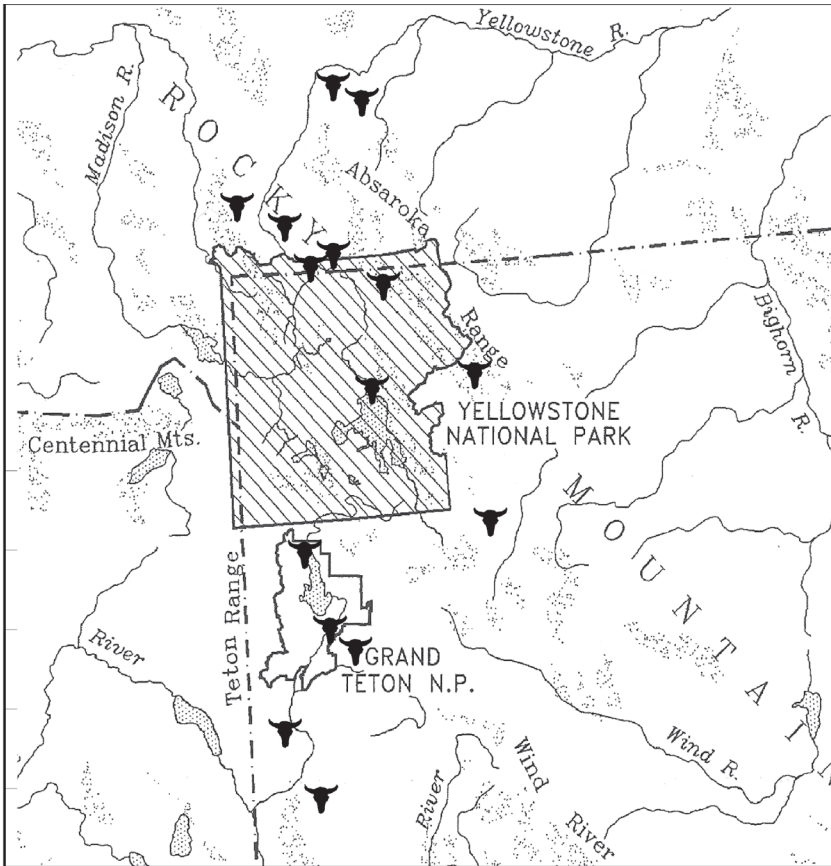
Figure 1. Distribution of sites in the Greater Yellowstone ecosystem which produced prehistoric bison remains.

Yellowstone Bison and Their Environment

An arc of high terrain rising more than 1000 m above the surrounding valleys characterizes the Greater Yellowstone Area (Fig. 1). The high terrain was probably formed as a result of the southwest movement of the North American plate over a stationary thermal mantle plume, causing block faulting and uplift of the landscape over the past several million years (Pierce and Morgan 1992). The area of Yellowstone National Park is a high, mountainous volcanic plateau with an average elevation of 2400 m. In general, the area is a large forested upland incised by numerous drainages
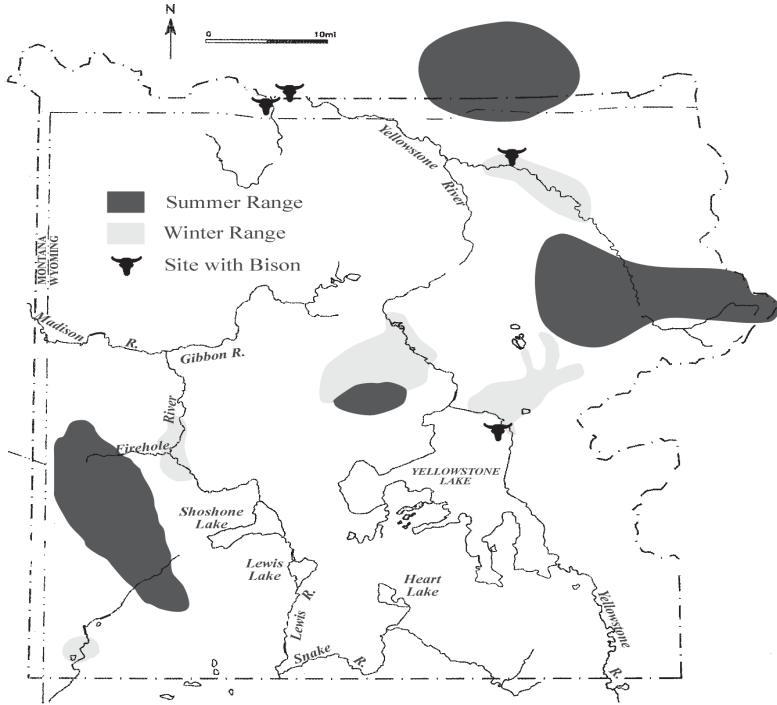
Figure 2. Map of general distribution and seasonal movements of bison mixed-herd groups in Yellowstone National Park (after Meagher 1973).

forming three major rivers and is partially surrounded by rugged mountains (Good and Pierce 1996).

The Central Plateau province, which encompasses over a third of the park's area, is characterized by well-drained sandy soils formed by the weathering of underlying Quaternary-aged rhyolitic rocks. These soils tend to be low in plant nutrients, which probably influenced postglacial colonization by trees (Whitlock 1993). Over 90% of the province is forested by the subalpine fir (*Abies lasiocarpa*) and grouse whortleberry (*Vaccinium scoparium*) habitat type in the grouse whortleberry phase; lodgepole pine (*Pinus contorta*) is the predominant overstory member (Despain 1990:154-55). Bison are typically found in the few large areas of open grasslands. Most of the bison in Yellowstone National Park are seasonally migratory. Migrations during the spring are from the lower wintering valleys to higher summer ranges, with a reverse of this altitudinal migration in the fall (Meagher 1973; see Fig. 2).
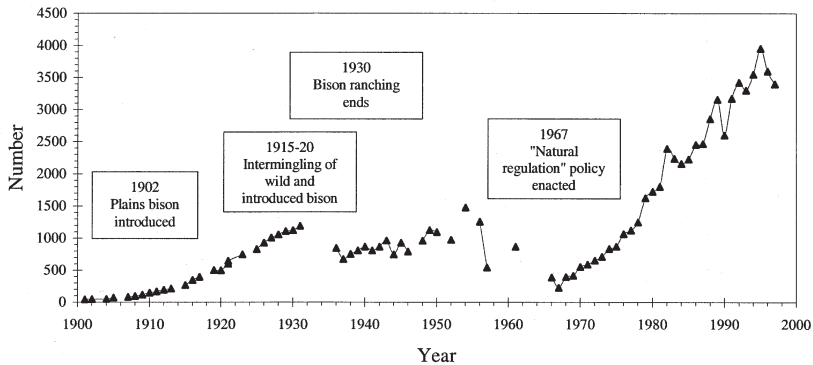
Figure 3. Bison winter counts for Yellowstone National Park, 1901-1997 (Yellowstone National Park 1997). Breaks in lines indicate years for which counts are not available.

The Yellowstone bison herd is one of the few remaining free-ranging herds in North America, rescued from near extinction in the late 19th century by a combination of aggressive protection of the native herd and the introduction of bison from private herds (Keiter 1997:1). During the early part of the 20th century the two herds were managed separately, but eventually they were allowed to interbreed. Over the course of the next 50 years Yellowstone's bison were intensively managed, with culling a common practice (Schullery 1986).

In the 1960s, the National Park Service made a dramatic shift in policy, largely in response to the Leopold Report (Leopold et al. 1963). It began to take a non-interventionist approach to natural resource management, relying instead on natural processes to effect change and to control wildlife population numbers (Keiter 1997:2). Bison numbers responded positively, rising from 397 in 1967 to a high of 3956 individuals in 1995 (National Park Service 1997:113-14; see Fig. 3). Meagher (1973, 1989) and Schullery et al. (1998) provide comprehensive reviews of the history of bison management in Yellowstone National Park.

Bison What Do We Know?

The Prehistoric Record

The prehistoric record of bison in the Greater Yellowstone Area extends back 10,000 years (Cannon 1992), although the record is fragmentary.

A general paucity of bison in the archeological record, as well as low numbers of modern bison in Yellowstone, led Wright (1984:28) to conclude "that bison were relatively rare in northwestern Wyoming, and that they would be too unpredictable in numbers to have provided a stable food source." Wright (1984:24) continued, "[S]ince the populations were small, one successful kill of adults would have reduced the reproductive potential of the herd to a level where it would no longer have been a significant part of the ecosystem." On the other hand, Meagher (1973:14), suggested that "substantial numbers of bison inhabited the Yellowstone Plateau at all seasons, and long before the killing of the northern herd of Great Plains bison in the early 1880s." These two perspectives illustrate the range of opinions concerning past bison populations.

More recent archeological investigations indicate that bison may have been prevalent. My tally of bison remains suggests 65 dated components (67 total, but two are of unknown age; see Appendix). These data represent 29 open archeological sites, one archeological cave site (Mummy Cave), and three paleontological sites (Dot Island, Lamar Cave, and Astoria Hot Springs; see Fig. 1). Not included are the various drive sites in Paradise Valley to the north of Yellowstone National Park. Arthur (1966:45-56) estimated that at least 10 bison kill sites occurred in Paradise Valley, including a large complex of drive lines and rock cairns known as the Emigrant Buffalo Jump. It seems clear that a large number of bison must have been present in the region, at least during some periods, in order to justify the labor involved in mass bison kills.

The earliest evidence of bison in the region is south of Jackson Hole on the Snake River at Johnny Counts Flat near Hoback, Wyoming. During excavation for the development of Astoria Hot Springs, "a layer of mixed *bison* bone and shell was exposed. . . . Several *bison* skulls were retrieved from this layer . . . [and] . . . were not of any *bison* larger than modern populations" (Love 1972:50; italics in original). Mollusk shell, collected from a "trench intersecting 2-ft shell bed at depth of 3 ft" by J.D. Love in 1959 and submitted to the US Geological Survey, produced an age of 11,940 500 yrs BP (Ives et al. 1964:60). I suggest that this age may be problematic, given our current understanding of the process of radiocarbon dating (Goslar and Pazdur 1985), especially in close proximity to geothermal features. For example, Preece et al. (1983:253) explained that a theoretical maximum of 50% of dead carbon could be incorporated into freshwater shell by ingestion, "introducing an apparent error for such shells with respect to contemporaneous terrestrial vegetation of up to one ^{14}C half-life (5730 ± 40 years)."
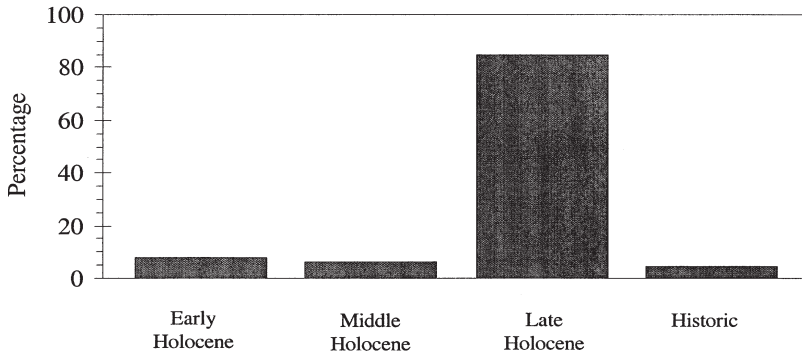
Figure 4. Occurrence of bison bones from components of various ages in the Greater Yellowstone Area.

Thus, the implications of Love's date should be accepted cautiously. However, despite the limits on the data, a tally of the components by time period illustrates an increase in bison remains during the late Holocene (Fig. 4). This trend is also apparent on the Great Plains (Bozell 1995) and may reflect increased biomass during equitable climatic regimes (Reher 1977) or intensification of bison hunting.

If we compare the distribution of paleo-sites in relation to modern herd movements, we see three sites in Yellowstone that are within the modern range (Fig. 2). In Jackson Hole, there is compelling evidence of bison presence from sites south of Blacktail Butte and on the National Elk Refuge that are adjacent to either modern migration routes or within seasonal ranges (Fig. 5). By concentrating archeological investigations in areas currently used by bison, we may be able to develop a model of bison habitat use and selection under various climatic regimes. This information should be useful in managing herds for future climate change. Understanding the relationship between past and future climate change, and its implication for ecosystem management, is recognized as a high-priority research need in Environmental Impact Statement for bison (National Park Service 1998; Appendix).

Our current understanding of Holocene climatic regimes indicates that several major factors have affected weather (i.e., temperature and precipitation), fire history and vegetation in Yellowstone and the intermountain west, and these in turn have affected animal community structure (COHMAP 1988). For example, Hadly's (1995:68-69) analysis of pocket gophers
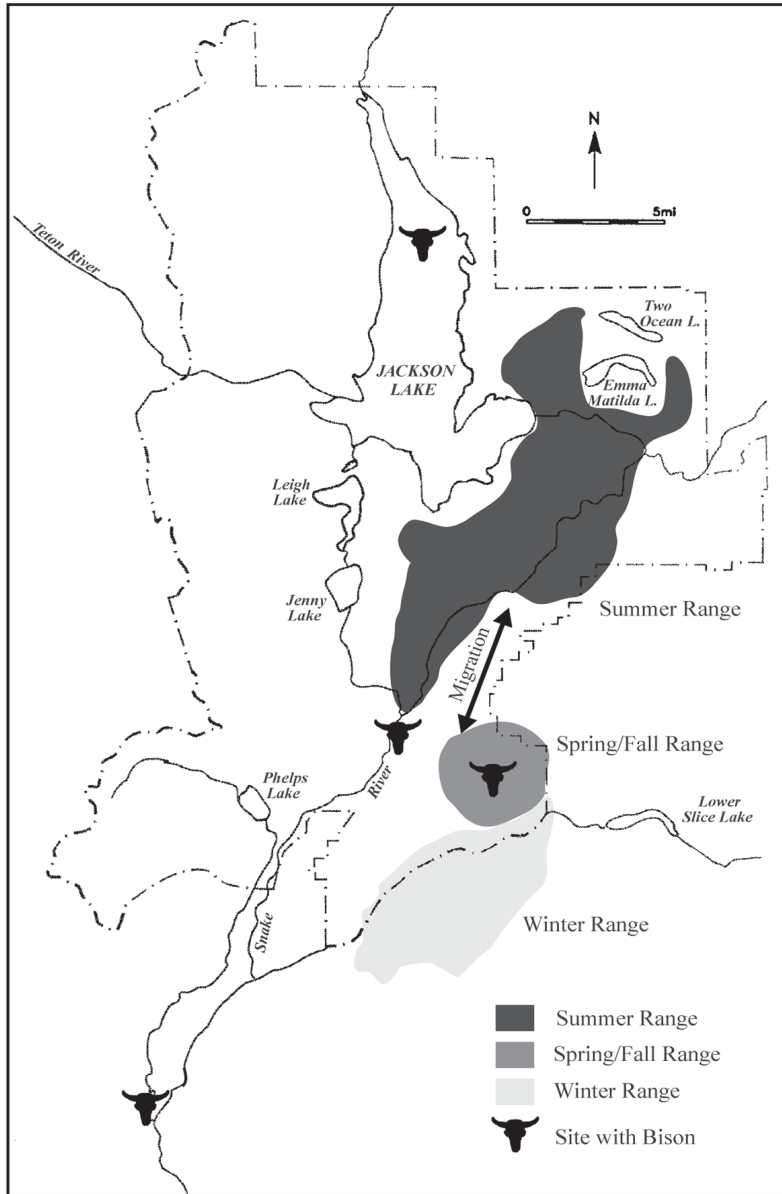
Figure 5. Map of general distribution and seasonal movements of bison in Jackson Hole, Wyoming, in relation to archeological sites with bison remains (modified from the Jackson Hole Bison Herd Management Plan, Grand Teton National Park and National Elk Refuge 1996).

(*Themomys talpoides*) from Lamar Cave in northern Yellowstone found that during wet periods pocket gophers were abundant, but during dry periods they were rare. She also suggested that correlated morphological changes also may have occurred. During the cool, moist regime of the Little Ice Age (450-150 yrs BP)**,** pocket gophers had larger body sizes as well as high population densities.

The decrease and changes in plant biomass during the early Holocene have been suggested as major factors in the diminution in size of bison (Wilson 1975). In particular, Guthrie (1984:271) suggested that change in the duration of the seasonal peak of usable, high-quality forage may account for the dwarfing of Holocene mammals relative to those of the Pleistocene. The quality and quantity of biomass available to bison has also been viewed as an important factor in short-term changes in body size among bison. However, Reher and Frison (1980:85) note that comparison between populations may be complicated by genetic drift, age and sex of individuals, and the characteristics of the plant biomass. In sum, by understanding how bison responded to previous shifts in climatic regimes, we may be better prepared to make empirically-based management decisions concerning bison populations in the face of contemporary changes.

Bison Diet and Ecology

Phytoliths, Pollen, and Macrofossil Remains. Biologists' study of bison diet usually involves the painstaking task of observation and the collection of feces in order to extract plant remains. Guthrie (1980:175-76) found that modern bison are eclectic foragers that, despite versatility, are adaptive specialists who prefer low-growth grasses and forbs. Studies of modern bison indicate that grasses comprise 80% to 90% of their diet (Meagher 1973; Olsen and Hanson 1977; Van Vuren 1984), supplemented by forbs and woody browse (Soper 1941). However, higher consumption of sedges and browse has been observed among bison occupying riverine and woodland habitats (Borowski et al. 1967). For example, in Alaska, where bison were introduced in the 1930s, bison are confined to riverine areas within or adjacent to mountain passes. Several populations of these bison have been studied, illustrating a very different diet from grassland bison. The Fairwell herd ate grasses and sedges through the winter, with browse contributing a little more than 1% of their diet (Campbell and Hinkes 1983). The Delta herd subsisted on river bar grasses and farmers' barley, as well as browse and horsetails (*Equisetum* sp.) (Gipson and McKendrick 1981). Limited

sampling of fecal remains from two smaller herds revealed considerable use of browse in the summer (50% willow, 50% graminoid), and the winter diet consisted of 75% browse with the remaining being graminoids (Miquelle 1985).

In Yellowstone, Meagher's (1973:90-95) study of bison rumen indicated grass and grasslike plants were by far the predominant elements of the bison diet throughout the year. Sedges were the main source of forage in all seasons, averaging more than half the diet. Seasonal shifts in the quantity of sedges correlated well with bison's seasonal use of the landscape. For example, in winter, sedges represented 56% of the diet, which reflected the bison's winter use of river valleys and exposed stream banks where nearly all plant growth was sedges (Meagher 1973:91, see fig. 45). Grass was second in quantity in all seasons except the fall. In the spring, grasses were selected in the highest quantity (46%), reflecting greater palatability, availability, and nutrition of grasses then. Wire rush was another important element of the diet, representing about one-third of the fall diet. Forbs and browse were also represented throughout the year in the bison diet. Meagher (1973:94) suggested that forbs, although a small portion of the diet, were of nutritional importance. Browse was of least importance quantitatively. Six plant species were represented but only in trace amounts.

Several techniques have been used to identify oral food contents. Armitage (1975) applied the botanical technique of phytolith analysis to the teeth of ancient cattle remains from Roman and medieval sites, as well as recent cattle, in order to understand diet. Opal phytoliths were extracted from residual food material found on the cusps of their teeth (calculus). Festucoid grass phytoliths, including *Dactylis glomerata* and *Festuca ovina,* were identified. Also, in another attempt to understand ungulate diet, Guthrie (1990:176-78) recovered and analyzed plant fragments from the infundibula (i.e., infoldings within the body of the tooth's crown down from the occlusal surface). The material extracted from these specimens included the waxy cuticles that cover the plant epidermis. Plant cuticles are characteristic of plant group and are readily identifiable in the laboratory. The results indicated that grass fragments were the predominant food in the teeth of steppe bison (*Bison* sp.), horses (*Equus* sp.), and woolly rhinoceroses (*Coelodonta* sp.). Also, preliminary analysis of prehistoric bison teeth from the region by Linda Cummings (PaleoResearch Laboratories, Golden, Colorado) indicate these techniques are applicable here. For example, isolated bison teeth from mid-Holocene archeological deposits in southern Jackson Hole have produced phytoliths and pollen from festucoid grasses and conifers. The results

were consistent with those from a modern bison from Pelican Valley in Yellowstone National Park (Cummings and Puseman 1999).

Stable Isotope Analysis. Analysis of bone collagen and apatite for carbon isotope variation provides another technique for assessing diet and ecology. Cool (C_3) and warm (C_4) season grasses have distinctive ratios of ^{13}C to atmospheric ^{12}C due to their particular photosynthetic processes. Analysis of the ratio of carbon isotopes in animal bone documents diet composition and suggests range size and seasonal migration patterns. It complements the phytolith and plant macrofossil analyses by providing a second quantitative set of data for interpreting diet and ecology of bison (Tieszen 1994; Tieszen et al. 1996). For example, it provides a method to evaluate the hypothesis that, prior to the establishment of Yellowstone National Park in 1872, bison migrated from the mountains into the valleys to avoid severe winter weather (i.e., deep snows) and to take advantage of seasonally ripening grasses (Cannon 1997a). This seasonal migration occurs today among elk and deer, and it may provide a model for pre-park bison migration.

Another application of the study of ecology and seasonal movement of prey species is to provide a better understanding of past human use of these resources. In areas of the Great Plains, this is even more crucial since bison were a predominant resource for Plains groups. In the Intermountain West, the role of bison in the economy is not well understood, and it may have been more important during certain time periods than others (e.g., Butler 1978; Cannon 2000). Frison (1992) proposed a dichotomy in the economics of Plains and mountain groups based upon their utilization of bison in relation to other food resources. Thus, understanding the bison's seasonal movements provides an important contribution to our understanding of human history in the Plains and West. One way of understanding bison movements is through the study of foraging patterns by applying analyses of diet. If bison move through various ecosystems during annual migrations, and if these environments have different food resources, then we should expect this to be evident in the bison's diet (Chisholm et al., 1986:193). To understand dietary selection, stable carbon isotope analysis has been applied in studies of the population movements of modern ungulates in South Africa (e.g., Tieszen et al. 1979; Vogel 1978), prehistoric bison on the northern Plains (Chisholm et al. 1986), and other fossil vertebrates (e.g., Bocherens et al. 1994; Heaton 1995).

The application of carbon isotope analysis to ecological studies first appeared with the publication of an article by Bender (1968), which de-

scribed a systematic relationship between differences in photosynthetic pathways (C_3 and C_4) and stable isotopic ratios of carbon in grasses (Tieszen 1994:261). Dietary application involves the quantification of ratios of ^{13}C/^{12}C isotopes ($\delta^{13}C$) in bone collagen, which is linked through the food web to the primary producers-photosynthetic plants (Bocherens et al. 1994:214). In terrestrial environments, two main categories of plants are recognized based on their carbon-fixation pathways, which are clearly distinguished by their stable carbon isotope ratios. The C_3 plants include all trees and herbaceous plants from cold and temperate climates. Their $\delta^{13}C$ values range between -23 parts per mil (‰) and -32‰, with an average of about -26‰. Warm weather plants and tropical herbaceous plants, such as maize, sugar cane, and millet, use C_4 photosynthesis and have $\delta^{13}C$ values between -9‰ and -16‰, with an average of about -13‰ (Smith and Brown 1973:505; Bocherens et al. 1994:214). With this understanding of the $\delta^{13}C$ values, the amount of C_3 and C_4—the types of plants consumed by herbivores—can be quantified.

An important aspect in using carbon isotope analysis in reconstructing diets is knowing that atmospheric values of $\delta^{13}C$ have varied in predictable ways, through time and under different environmental conditions. The presence and distribution of C_3 and C_4 plants in the environment are not random and are related to environmental factors, specifically temperature. For example, in systems where the CO_2 released in respiration does not mix freely with the atmosphere, as in closed canopy forests, the ambient CO_2 can become depleted, resulting in higher negative values for both C_3 and C_4 plants (Tieszen 1994:264). One study from the Amazonian forests measured ^{13}C values as negative as -37‰, whereas, open tropical habitats of C_3 grasses averaged about -26.5‰ (van der Merwe and Medina 1991:250). In such depletion, carbon is transferred to other trophic levels, and it must be taken into account when considering diet for forest-dwelling herbivores and humans (Tieszen 1994:264).

In addition, the anthropogenic addition of CO_2 to the atmosphere over the past two centuries through the burning of fossil fuels has had the effect of depleting atmospheric CO_2 of $\delta^{13}C$ (Tieszen 1994:264). The input has also enhanced decomposition associated with agriculture and deforestation. Preindustrial $\delta^{13}C$ values of -6.45‰ have been measured from Antarctic ice cores, compared with modern conservative estimates at -8.0‰. Based on this knowledge, an adjustment must be made in the reconstruction of past diets and paleoecological interpretations. For example, an adjustment of

about 1.5‰ must be made to Holocene samples dated before AD 1800, in comparison to modern values (Tieszen 1994:264).

    With increasing latitude and longitude, a corresponding increase in C_3 species is expected. Changes also occur with elevation. For example, in Kenya, at low altitude in open savannas, all the grasses are C_4 and nearly all trees and shrubs are C_3. However, above 1800 m, C_4 grasses begin to be replaced by C_3 grasses, and at 3000 m nearly all grasses are C_3 (Tieszen 1994:265). Also, in southeast Wyoming, the percentage of C_3 biomass increased with elevation (Boutton et al. 1980, cited by Tieszen 1994:265). Regressions of relative biomass abundance of C_3 and C_4 plants on climatic variables showed that both mean annual temperature and annual precipitation were reliable predictors, (Boutton et al. 1980; Lauenroth et al. 1999: see fig. 3) and influenced the ratios.

    On the Great Plains, increases in the biomass of C_3 grasses are correlated with increasing latitude. In Texas, C_4 grasses represent 68% of biomass in the south and 82% in the southwest. This decreases to 35% in South Dakota. Nongrass species, such as sedges, do not show as clear a temperature-dependent distribution as do grasses. Grass composition for Idaho is estimated to be about 18% C_4 species (Teeri and Stowe 1976: table 2). The genus *Carex*, the most common genus of sedges in the mountains, is C_3 (Tieszen 1994:265). Therefore, it is expected that generalist consumers of grass biomass should have a modern isotopic signal that reflects the mixture of C_3 and C_4 grass species in the environment. However, climatic changes have been demonstrated for various periods during the course of the Holocene (Whitlock 1993). So, vegetation values should be expected to reflect these climatic shifts. This temporal variation creates a complicating factor in the interpretation of isotopic signals from paleo-samples (Tieszen 1994:166).

    Another stable isotope that is related to diet is $\delta^{15}N$, which is linked to trophic level. The main reservoir for nitrogen is the atmosphere. However, it must be transformed from inorganic nitrogen to a form that is available for biological processes. One way this transformation occurs is by specialized organisms, such as those found in bacterial nodules on the roots of leguminous plants. With little or no fractionation, legumes typically exhibit $\delta^{15}N$ values similar to the atmosphere, or 0‰. Most other terrestrial plants take up soil nitrogen that is made available through bacterial degradation of organic material. This process generates $\delta^{15}N$ values that are more positive than atmospheric nitrogen. A bimodal distribution of nitrogen stable isotope ratios is created and nitrogen-fixing plants such as peas and beans form one mode while the nonfixers form the other (Schoeninger 1995).
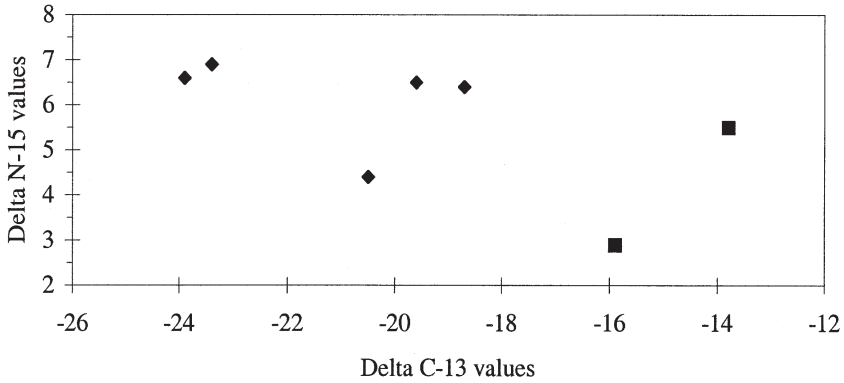
Figure 6. Plot of δ^{15}N against δ^{13}C values for North American bison specimens from high altitude and high latitude (closed diamonds), e.g., Yellowstone and Wood Buffalo, and from Central Plains (closed squares).

The δ^{15}N values recorded in the tissues of animals are positively correlated with their diet. A 2‰-5‰ increase in δ^{15}N values corresponds to an increase in trophic level (Bocherens et al. 1994:214). Potential dietary stress can also be assessed by examining δ^{15}N values. In examining horn sheath annuli of bison from the central Plains, Tieszen et al. (1996) identified a change in δ^{15}N that accompanied changes in δ^{13}C values. They interpreted this as evidence that these individuals had undergone a large degree of stress related to shifts in diet. The cause of stress may have been illness or water drought.

In a recent study for the Salmon-Challis National Forest, the skull of a protohistoric bison from an elevation of 2134 m (7000 ft) was analyzed in order to understand diet and ecology (Cannon 1997a). The results indicated that a significant portion of this individual's diet consisted of C_3 plants. Cool-weather grasses, which would have included genera such as *Festuca* and *Agropyron*, are common at this altitude and latitude. Two bison metatarsals from adult males, excavated from the 800-year-old Goetz site in Jackson Hole, Wyoming, provided similar results (Cannon 2000). The results are similar to the carbon isotope signal from modern bison in Yellowstone, as well as other high latitude bison populations (Fig. 6).

Bison Taxonomy

Prehistoric bison studies can also help resolve the controversy surrounding the species of bison that occupied these regions. The earliest

accounts of trappers, explorers, and zoologists describe the exploits of the
"Woodland or Mountain Bison" (e.g., Christman 1971). Various historical
accounts of the "mountain" bison indicate they "were more hardy, fleet, and
wary, and had darker finer, curlier hair" than the Plains bison (Meagher
1973:14-15). Superintendent P.W. Norris (1880:608) described the bison of
Yellowstone National Park in an early annual report:

> Bison or Mountain Buffalo . . . Bison, so called, in the Park, are
> somewhat smaller, of lighter color, less curly, and with horns smaller
> and less spreading than those of the bison formerly inhabited the
> great parks of Colorado. They have also smaller shoulder humps,
> and larger, darker brisket wattles. They differ materially from the
> buffalo of the Great Plains, being more hardy, fleet, and intelligent;
> their hides also are more valuable for robes, as they are darker,
> finer, and more curly; and these animals are, in all probability, a
> cross between the two varieties just mentioned.

In fact, considering the geographic range of bison in North America, some
authors have suggested there may have been several distinct geographic
forms based on morphological variation (Fig. 7). However, with the near
extinction of the bison in North America a comprehensive study of geo-
graphic variation in bison has been precluded (van Zyll de Jong 1986:1). In
the latter part of the 19th century biologists recognized a distinct form of
bison in northern Canada, formally described as the subspecies *Bison bison
athabascae* by Rhoads (1897) based on a single specimen that he did not
observe directly (van Zyll de Jong 1986:1). While most biologists agreed
with Rhoads, designation of *B. b. athabascae* being at least subspecifically
distinct (e.g., Skinner and Kaisen 1947; McDonald 1981), others felt that
the differences in the two subspecies, *B. b. athabascae* and *B. b. bison*, were
of little consequence (van Zyll de Jong 1986:1).

    According to van Zyll de Jong (1986:1), the decimation of the bison
herds before much study and the small number of specimens available for
study contributed to this diversity of opinions. In one of the first quantita-
tive studies of museum specimens, primarily crania, Skinner and Kaisen
(1947) argued that the distribution of the two subspecies, *B. b. athabascae*
and *B. b. bison*, overlapped along the eastern slopes of the Rocky Moun-
tains. However, their argument was unconvincing because of a lack of
craniometric and postcranial specimens for comparison. More recently,
McDonald (1981) presented metric data from a limited sample that showed
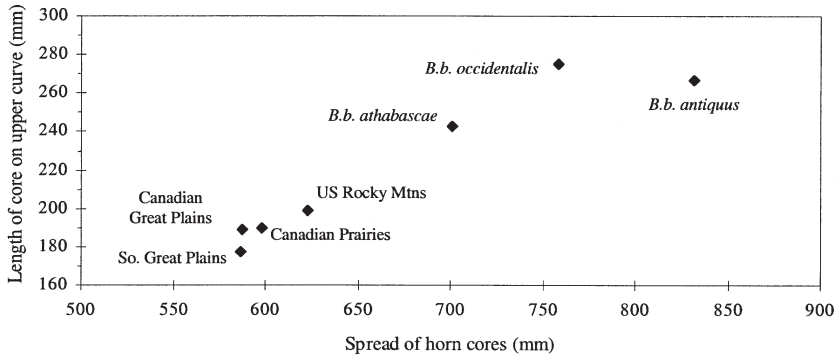evidence that the *B. bison athabascae* range was limited to the northern

Figure 7. Plot of mean horn core measurements of seven historical, Holocene, and late Pleistocene specimens of North American bison. Data from van Zyll de Jong (1986: table 1).

Rocky Mountains and boreal forests of Canada. These data refuted Skinner and Kaisen's earlier model. Instead, he suggested a phylogenesis of modern North American bison from an indigenous Nearctic line (*B. antiquus)*, with *B. b. athabascae* evolving directly from the ancestral *B. b. antiquus*, or a more recent adaptive differentiation from *B. b. bison*, as suggested by the larger body size of *B. b. athabascae*. However, van Zyll de Jong (1986), in studying presumed pure *B. b. athabascae* specimens from northwestern Canada in comparison with other North American fossil and modern bison, suggested body size was just one of a number of presumably genetic characteristics that differentiated the two modern species. According to van Zyll de Jong's analyses, *B. b. athabascae* was more probably "a direct and little differentiated descendant of [Beringian] *B. b. occidentalis*" (van Zyll de Jong 1986:54). His analysis found that *B. b. bison* shows a marked difference in horn core measurements, reflecting a general reduction in horn core size, in comparison to *B. b. occidentalis*, while *B. b. athabascae* illustrate only a reduction in horn core length (van Zyll de Jong 1986:18; see fig. 7).

In arguing for genetic variation, as opposed to ecophenotypic variation, van Zyll de Jong (1986:54-55) illustrated how the interaction of ecological and behavioral factors, gene flow, and natural selection could account for the maintenance of the distinctiveness of the two modern species. Specifically, the boreal forest ecotone acted as a natural barrier to contact by *B. b. athatbascae* with *B. b. bison* in the grasslands to the south. Interbreeding was also minimized due to the limited seasonal movement of the two groups within their respective home ranges. The diverse habitats occupied by the

two populations may also have promoted "differential directional selection" of a specific allele frequency or phenotype (van Zyll de Jong 1986) that would have provided them with a greater degree of fitness in surviving in their respective environments.

Strobeck (1992) recently conducted a molecular study of mtDNA from several populations of Woods and Plains bison in Canada and the United States in an attempt to determine the genetic differentiation of the two subspecies. Based on these data, Strobeck (1992:15) concluded that Woods and Plains bison "do not form distinct phylogenetic groups and are not genetically distinct subspecies." The similarity in mtDNA types from both Woods and Plains eliminate the possibility that they were distinct subspecies in the past (Strobeck 1992). Very recent work by James Derr (1999) of Texas A&M University provided additional support for the genetic similarity of the two taxa. However, geographic isolation of populations may lead to different genotype frequencies among different herds. Strobeck (1992:15-16) contended that "each population represents a geographical isolate of a once vast population of bison." Such genetic evidence of isolation may provide some clues to the morphological variability in bison populations. This observation parallels van Zyll de Jong's (1986:55) morphometric analysis. Furthermore, van Zyll de Jong (1986:55) suggested that similar mechanisms are still in operation among ungulates (e.g., caribou) today, and so they can be studied.

With recent advances in the replication of DNA from fossil populations, the archeological record provides a unique opportunity for addressing issues of both taxonomy and genetic variability of bison populations prior to the 19th century reduction in numbers. The archeological record can also be used to study gene flow among populations (Chambers 1998:156). Chambers (1998) reported on a recent genetic analysis of the Glenrock bison assemblage, a Late Prehistoric bison jump along the North Platte River in central Wyoming (Frison 1970), in comparison to modern populations. Her results indicated that some modern herds are as genetically diverse as the Glenrock sample, while others are not.

Management of the genetic diversity and integrity of threatened populations is an important issue in conservation biology (Meffe and Carroll 1997). In addition to the long-term goal of protecting the germplasm, other conservation issues can be addressed using genetic analyses, such as understanding the effect of hybridization of the native Yellowstone National Park bison with bison introduced in the early 20th century and determining minimal viable population size. DNA analysis of archeological bison herds should provide us with guidance on these issues (Derr 1999; Ward et al.

1999). Archeological kill sites of bison represent frozen moments in time, and so they reflect a cross section of a population at the time of the event. Therefore, these samples can provide information on herd structure (e.g., age profiles and sex ratios), as well as on genetic diversity prior to the genetic bottleneck caused by the near extermination of bison in the late 19th century. The structure and genetic diversity of these groups can then be compared to modern herds to assess how genetic diversity has changed over time. Such comparisons can potentially alert biologists and/or managers to populations that may be at risk to the various consequences of low genetic diversity, for example the increased prevalence of deleterious alleles and inbreeding depression.

Conclusion

Bison ecology has once again become an important management issue. In the Greater Yellowstone Area, it is critical to the bison environmental management plans for both Yellowstone National Park and Jackson Hole (Irby and Knight 1997). Recent expansion of the population and its subsequent migration outside federal lands have caused concern among federal managers, local ranchers, and conservation groups. Much of what we know about bison is based on historic records and modern studies. While both of these are invaluable sources of data, they have limitations. In the case of historic records, the information is often anecdotal, and it was not collected in a rigorous or systematic manner (Bamforth 1987). Modern studies, while of obvious value, are limited by the fact that populations under study are small and isolated and represent only a fraction of the species' original range (Berger and Cunningham 1994). Archeologically-derived data can be an important added tool for providing a baseline of pre-European conditions against which the modern situation can be assessed. Studying subfossil bison in order to understand bison ecology and migration patterns is one of the few ways we have to reconstruct past conditions. Long-term data, such as that available from paleostudies using stable isotope analysis, for example, provide a means to decipher paleoenvironmental conditions that should enable us to make sound management decision for contemporary bison herds.

Acknowledgments

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APPENDIX
INVENTORY OF PREHISTORIC BISON REMAINS FROM THE
GREATER YELLOWSTONE AREA

Site Name, Number	Excavation Provenience	Age (yrs BP)	NISP/MNI[a]	Reference
Dot Island, YNP	Cutbank	Unknown	6/1	Cannon 1997a
Lamar Cave, YNP	Level 5	Late Holocene 960 ± 60	2/1	Hadly 1995
Lamar Cave, YNP	Level 7	Late Holocene	2/1	Hadly 1995
Lamar Cave, YNP	Level 8	Late Holocene	1/1	Hadly 1995
Lamar Cave, YNP	Level 9	Late Holocene 1670 ± 60	1/1	Hadly 1995
Lamar Cave, YNP	Level 10	Late Holocene	1/1	Hadly 1995
Lamar Cave, YNP	Level 11	Late Holocene	2/1	Hadly 1995
Lamar Cave, YNP	Level 12	Late Holocene 1110 ± 60	10/1	Hadly 1995
Lamar Cave, YNP	Level 14	Late Holocene	2/1	Hadly 1995
Lamar Cave, YNP	Level 15	Late Holocene	2/1	Hadly 1995
Corwin Springs 24PA195	n/a	Middle Holocene Late Bitterroot	n/a	L.B. Davis 1992
Emigrant Buffalo Jump 24PA308	n/a	Late Holocene	-/-	Arthur 1966
Meyers-Hindman 24PA504	SU8 5-20 cmbs	Late Holocene 790 ± 90	-/5	Lahren 1976
Meyers-Hindman 24PA504	SU7 20-40.5 cmbs	Late Holocene 1470 ± 70	-/4	Lahren 1976
Meyers-Hindman 24PA504	SU6	Late Holocene 2300 to 1450 BP	-/5	Lahren 1976
Meyers-Hindman 24PA5045	SU5 6-71 cmbs	Late Holocene 2300 ± 120	-/5	Lahren 1976
Meyers-Hindman 24PA504	SU4	Late Holocene 3150 ± 110	-/4	Lahren 1976
Meyers-Hindman 24PA504	SU3	Middle Holocene 4680 ± 220 5950 ± 150	-/3	Lahren 1976
24PA504 Meyers-Hindman	SU1	Early Holocene 8450 ± 190 9400 ± 200	-/2	Lahren 1976
The Sphinx Site 24PA508	Units 1-4, Upper Levels	n/a	-/-	Deaver et al. 1989
Jarrett Site 24SW651	n/a	Late Holocene 2820 ± 120	n/a	L.B. Davis, 1992
24YE353	TU2/F89-1 20-30 cmbs	Late Holocene 1260 ± 50	1/1	Cannon 1997b
24YE366	TU1 Cutbank exposure	Late Holocene	2/2	Cannon 1997b

Site Name, Number	Excavation Provenience	Age (yrs BP)	NISP/MNI[a]	Reference
24YE366	TU1 40-50 cmbs	Late Holocene	2/1	Cannon 1997b
24YE366	TU1 60-70 cmbs	Late Holocene 1420 ± 90	2/1	Cannon 1997b
24YE366	TU1 90-100 cmbs	Late Holocene (?) >1420 BP	1/1	Cannon 1997b
24YE366	TU2A/F89-1 0-10 cmbs	Late Holocene 1220 ± 80	2/1	Cannon 1997b
24YE366	TU2A/F89-1 10-20 cmbs	Late Holocene	1/1	Cannon 1997b
24YE366	TU2A/F89-1 15 cmbs	Late Holocene	1/1	Cannon 1997b
Lookingbill 48FR308	Post-Early Plains Archaic Level	Late Holocene (?)	1/1	Larson et al. 1995
Lookingbill 48FR308	Early Plains Archaic Level	Early Holocene	2/-	Larson et al. 1995
Lookingbill 48FR308	Early Paleoindian Level	Terminal Pleistocene	1/1	Larson et al. 1995
Mummy Cave 48PA202		Early Holocene	1/1	S. Hughes, 1999
Dead Indian Creek 48PA551	Site Area 4	Late Prehistoric	n/a	Jameson 1984
Dead Indian Creek 48PA551	Site Area 5	Late Prehistoric	n/a	Jameson 1984
Dead Indian Creek 48PA551		Middle Holocene 3800 ± 110 4180 ± 250 4430 ± 250	43/4	Scott and Wilson 1984
48PA852	Block B1 15-30 cmbs	Late Holocene		Eakin and Sutter 1991
Stewart Flat 48SU1042	Component 2	Late Holocene <1000 BP	1	Hoefer 1991
Stewart Flat 48SU1042	Component 1	Late Holocene 1050 ± 50 1200 ± 60 1300 ± 70	1	Hoefer 1991
Astoria Hot Springs 48TE342	~ 3 ft.	Terminal Pleistocene 11,940 ± 500	-/-	Love 1975; Ives et al. 1964
Blacktail Butte 7 48TE350	N56/E128	Late Holocene (?) Late Holocene (?)	-/1 -/1	Wright 1975 Wright & Marceau 1981
Blacktail Butte 6 48TE352	Test Pit 1	Late Holocene (?)	2/1	Wright & Marceau 1981
Blacktail Butte 12 48TE391	Test Pits 2-2A, 32-35 cm	Late Holocene (?)	1/1	Wright & Marceau 1981

Site Name, Number	Excavation Provenience	Age (yrs BP)	NISP/MNI[a]	Reference
Goetz Site 48TE455		Late Holocene 800 ± 40	/4	Cannon 2000
48TE1067	Surface	Late Holocene	3/1	Cannon 1991
Crescent H Ranch 48TE1079	Block G	Mid-Holocene	2/2	Cannon et al. 2001
48TE1090	Surface	Late Holocene 770 ± 80	371/17	Cannon 1991
48TE1101	Surface	Late Holocene	63/6	Cannon 1991
48TE1102	Surface	Late Holocene 1380 ± 80	107/8	Cannon 1991
48TE1104	Surface	Late Holocene	6/1	Cannon 1991
48TE1107	Surface	Historic	2/1[b]	Cannon 1991
48TE1111	Surface	Late Holocene	4/1	Cannon 1991
48TE1114	Surface	Late Holocene	91/4	Cannon 1991
48TE1119	Surface	Late Holocene	22/1	Cannon 1991
48YE215	0N/14E Level 2	Late Prehistoric	1/1	Aaberg 1996
48YE215	0N/14E Level 3	Late Prehistoric	4/1	Aaberg 1996
48YE215	12N/12E Surface	Late Prehistoric	4/1	Aaberg 1996
48YE215	12N/12E Surface	Late Prehistoric	15/1	Aaberg 1996
48YE215	12N/12E Surface	Late Prehistoric	15/1	Aaberg 1996
48YE215	12N/12E Surface	Late Prehistoric	2/1	Aaberg 1996
48YE216	Surface	Late Prehistoric	1/1	Aaberg 1996
48YE217	0N/14E Shovel Test	Late Prehistoric (?)	1/1	Aaberg 1996
48YE217	0N/14E Shovel Test	Late Prehistoric (?)	1/1	Aaberg 1996
48YE217	0N/14E Shovel Test	Late Prehistoric (?)	6/1	Aaberg 1996
48YE697	N959/E1025 144 cmbd	Late Holocene (?)	1/1	Cannon et al. 1997
48YE697	N928-9/ E1057-58	Late Holocene 800 ± 60	92/1	Cannon et al. 1997

Notes: n/a = not available; cmbs = centimeters below surface
[a]NISP=number of identified specimens; MNI=minimum number of individuals.
[b]Specimens attributed to *Bison/Bos* due to historic time period and similarity of morphology.