

BIOGEOGRAPHY OF HOLOCENE BISON IN THE
GREATER YELLOWSTONE ECOSYSTEM

by

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BIOGEOGRAPHY OF HOLOCENE BISON IN THE
GREATER YELLOWSTONE ECOSYSTEM

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University of Nebraska, 2008

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The role of bison in the pre-Euroamerican settlement of the Greater Yellowstone Ecosystem (GYE) has been debated for decades by biologists, historians, and archeologists. However, we do know that bison have been a member of the regional ecosystem for more than 10,000 years. Despite this long-term presence, knowledge of their ecology has largely been gained through the study of modern herds who have been subjected to various management practices for over 100 years. In this study, I examine the Holocene record of bison from the region to reconstruct their relative abundance through time in the context of Holocene climate models. More detailed analysis of individual bison was also conducted. Craniometric analysis of 10 bison suggests a bull-dominated assemblage. The demographics of these individuals may be reflective of a larger hunting pattern of either pursuing lone bulls or an encounter-type hunting pattern. Discriminant function analysis of these crania was also conducted and suggests possible genetic isolation of mountain populations. Stable carbon and oxygen stable isotope analysis of downtown samples from third molars of precontact and modern individuals were also conducted. The sample includes 14 individuals from eight archeological sites in the GYE that range from the early Holocene Horner site on the western edge of the Bighorn Basin to the late Holocene bison from the Goetz site in Jackson Hole. Three modern individuals from Yellowstone National Park and two individuals from the Henry Mountains, Utah were also analyzed. Each of the individual stable isotope data provides a pattern that is probably reflective of seasonal use of available vegetation and water sources. While each of the Holocene individuals illustrates greater variability than the modern samples, the early Holocene Horner site individuals have the greatest variability. The results of this analysis suggest variability of bison migration patterns that may be reflective of the influence of large-scale climate patterns on vegetation and the behavioral response of these individuals to resource availability.

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Chapter I

Introduction

Background on Bison in the Greater Yellowstone Ecosystem

The North American bison (*Bison bison*) has aroused the curiosity of scientists and the general public for many years. Steeped in myth and legend, the North American bison, or buffalo, was nearly exterminated in the late nineteenth century (Geist 1996). Its demise occurred before its role as a member of North America's native fauna could be fully understood (Hornaday 2002 [originally published in 1889]). Over the past 100 years there have been numerous studies of bison (e.g., McHugh 1972) and compilations of the state of knowledge (e.g., Roe 1972). Over twenty years ago Arthur (1985) published a bibliography of bison studies in which he cited 2521 scientific publications on the topic. Over the last few years there has been a renewed interest in the study of the North American bison, which has again precipitated an assessment of the state of our knowledge (e.g., Irby and Knight 1998; Franke 2005).

A number of social, economic, and ecological factors also have focused attention on public herds in the United States (e.g., Gogan et al. 2001) and in the Canadian Provinces (e.g., Gates et al. 2001). Specifically, increased herd size on public lands has caused range expansion, potentially placing bison in close proximity to cattle. While bison and cattle interaction may not seem problematic, the potential for the transmission of the bacterium *Brucella abortus*, an infectious microorganism that can cause abortions in ruminants (Baskin 1998), could have widespread economic consequences for the cattle industry (Newby et al. 2003). For humans exposure to the bacterium can cause various symptoms of "undulant fever" (Corbel 2006). The disease was initially detected in Yellowstone National Park (YNP) bison in 1917 and has been present ever since (National Research Council 1998). Management and eradication of the disease in the YNP herd has been a concern since the 1930s (Franke 2005), and the efforts have cost \$4.5 billion (McMillion 2006). A consequence of this disease has been the annual winter vigilance of the Yellowstone National Park boundaries for bison migration into Montana, where they are met

by an array of well-intentioned individuals, with a series of sometimes conflicting solutions that range from chasing bison back into the park to controlled hunting to roundup for butchering (Franke 2005).

When the harsh winter of 1996-1997 forced bison to leave the park in record numbers in search of forage, national attention was focused on the fate and management of Yellowstone's bison (Peacock 1997). In response to the public discussion, the Secretary of Interior Bruce Babbitt asked the National Academy of Sciences to undertake a 6-month study of brucellosis in the Greater Yellowstone Ecosystem (National Research Council 1998:1). It was about this same time (fall 1995) that the Yellowstone Center for Resources contacted the National Biological Service to discuss information needs relative to the ecology of Yellowstone bison (Gogan et al. 2001). Two initial studies were implemented in 1996 (Dawes 1998; Ferrari 1999), the study area was expanded to include the Jackson Hole bison, and several research topics were identified (Gogan et al. 2001:68-69):

- A synthesis of trends in bison numbers and habitat use between 1968 and 1998;
- Statistically reliable estimates of the number of bison in Yellowstone;
- Bison seasonal movement patterns and habitat use;
- The role of extrinsic factors (such as snow conditions and forage availability) in seasonal distribution;
- Effects on bison of winter grooming of portions of the road system within Yellowstone;
- Impacts of bison on the vegetation communities within Grand Teton and Yellowstone;
- Impacts of killing or removing bison on bison population dynamics;
- An ecosystem-level model to calculate bison ecological carrying capacity within Yellowstone; and
- An ecosystem model-based analysis of bison and elk population dynamics and habitat-use relationships in the southern Greater Yellowstone Area (GYA).

Officials in YNP initiated a related study that focuses on the critical evaluation of the movement, distribution, and management of YNP bison (Gates et al. 2005).

What is surprising is that despite this seemingly comprehensive list of research needs, understanding the ecology of bison prior to the establishment of YNP in 1872 was not considered (Cannon 2001). This is striking in light of management documents, such as the Greater Yellowstone Ecosystem Vision Statement (Greater Yellowstone Coordinating Committee 1990) and statements by the National Research Council (2002:32) such as this:

Yellowstone is a dynamic landscape, and we cannot determine whether management actions have forced components of the system beyond their historical range of variability unless we place recent dynamics in a longer time frame. *Knowledge of prehistoric and historical environments is essential for creating a context for this evaluation* (italics added).

Driving the movement to understand ecological systems within a longer time frame is the realization that the community-based approach is no longer tenable (cf., FAUNMAP Working Group 1996). Individual species respond in their own particular way to environmental perturbations, and it is only through the study of individual species that we will be able to understand how these larger ecological systems have evolved (cf., Grayson 2006).

One of the fundamental goals of the Greater Yellowstone Area Vision Statement (Greater Yellowstone Coordinating Committee 1990) is the maintenance of the ecosystem's integrity based on sound scientific research. In order to reach such a goal, the study of the ecosystem must be grounded in the fact that it is a dynamic system, continually undergoing change, whether this be by forest fire, the shifting weather patterns, or plant competition—processes that have been affecting the system for thousands of years. The ecosystem today is a result of its history. By utilizing evidence of past variability, it only follows that this information can be used to inform future decisions. In order to do this, a management context must be devised that integrates modern ecological studies and prehistoric data. Bison, while they may represent a keystone species, are an excellent species to study in the context of changing climatic and environmental conditions at an ecosystem level, because they will reflect these larger-scale patterns. Prehistoric

data can be an essential tool for providing a baseline of pre-Euroamerican conditions against which the modern situation can be assessed (National Research Council 2005).

In the case of bison, knowledge is largely based on non-systematically collected historic records (Bamforth 1987) and modern studies of small, isolated populations (Berger and Cunningham 1994). The prehistoric record, however, can provide a millennia-long account, providing a baseline of pre-European conditions against which the modern situation can be assessed and future management decisions can be made (Cannon 2001). While ecologists, conservation biologists, and resource planners and managers have typically been trained to view ecosystem function in synchronic terms, (although this situation seems to be changing), paleoscientists have been trained to think in terms of diachronic processes and long temporal spans (Lyman and Cannon 2004). By the very nature of the data, archeologists can provide the long-term view of ecosystem change. Bringing the geologically historic record to bear on this issue is a goal emphasized not only for the GYE (National Research Council 2002), but for other public lands as well (National Research Council 2005).

Understanding bison ecology and migration patterns through the study of sub-fossil bison is one of the few methods for the reconstruction of past conditions. Bison today are confined to small isolated herds that are not allowed to range freely within their historic ranges. If the few surviving undisturbed areas are to be managed in a meaningful way, there must be an effort made to study how ecosystems have developed through time. Today, ungulate management is a very politically charged issue, and much of the information used to make the management decisions is based on modern studies of herds under confined situations (e.g., Berger and Cunningham 1994). Few, if any, studies incorporate long-term data, such as that available from paleostudies. New methodologies, such as stable isotope analysis provide, a means to decipher paleoenvironmental conditions in order to model future changes and the restoration of habitats. Long-term historic records provide an original perspective for examining bison populations. By analyzing the skeletal remains of bison within an interdisciplinary framework, it is possible to reconstruct a

record that has a temporal span of not just a few decades, but many centuries. This is the type of resolution that is necessary for examining long-term ecological processes.

Objectives

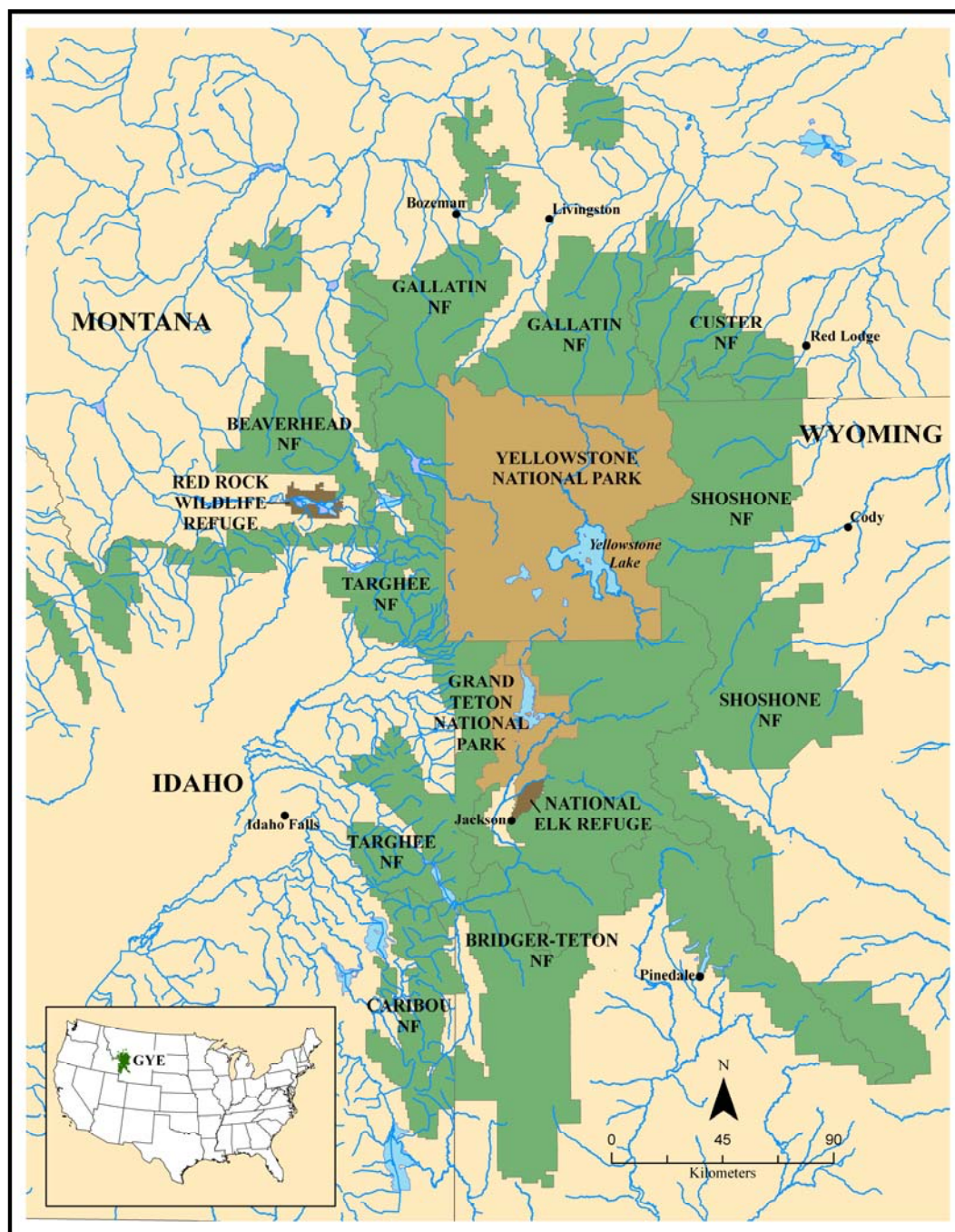
The primary goal of this study is to provide an ecological and historic context for bison within a prescribed spatial setting, the GYE, through the examination of a subset of precontact bison recovered from Holocene contexts in the region. At a fundamental level this research follows Gleason's (1926) hypothesis that individual species react to environmental perturbations based upon their individual tolerances and behavior, a hypothesis that has been supported by Quaternary mammalian patterns (FAUNMAP Working Group 1996). More recently, Grayson (2008) has emphasized the importance of "Gleasonian individualism" by arguing that in order to build explicit model of past ecosystems we must first build detailed life history models of individuals species, particularly those that have either been extirpated from their former ranges or those that have become extinct. In the broadest sense this is the traditional goal of biogeography, to study the distribution of species, both past and present (Brown and Gibson 1983). However, the research focus of biogeographers has expanded to include all aspects of an individual's life history within the context of contemporary issues wildland management and climate change (e.g., Grayson 2005).

This dissertation applies metric analysis and stable isotope analyses to prehistoric and modern bison remains to reconstruct the biogeography of prehistoric bison in order to make reasoned recommendations for contemporary management of the GYE. The research is focused on Holocene specimens recovered from the GYE (Figure 1.1). Ecosystem boundaries were first proposed in the 1970s and 1980s based on the range of the local grizzly bear (*Ursus arctos*) (Schullery 1997). The study area was chosen, because it is a largely intact system with a wealth of published ecological research.

The broader purpose of this study is to develop a longer-term historical perspective on the mammalian community of the Greater Yellowstone Area, as identified in recent National

Research Council (2002, 2005) reports, with bison as the initial focus. The lack of knowledge of the local mammalian community is notable considering all that is known concerning the glacial, climate, and vegetation history.

Figure 1.1. Map of the Greater Yellowstone Ecosystem.



The focus of the research is the application of stable isotope analysis, carbon and oxygen, to the recovered teeth of early and late Holocene bison. Samples from modern specimens are also analyzed to provide controls against which the ancient samples can be compared. The application of carbon isotope analysis to ecological studies became apparent with the publication of an article by Bender (1968) which described a systematic relationship between differences in photosynthetic pathways (C_3 and C_4) and stable isotopic ratios of carbon in grasses (Tieszen 1994, p. 261). The dietary application of carbon isotope studies 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, p. 214). Therefore, generalist consumers of grass biomass (bison) should have a modern isotopic signal that reflects the mixture of C_3 and C_4 species utilized in the environment. The theoretical relationship of the stable carbon isotope signature to diet is well developed, as are the methodological means for extracting the signature (Tieszen 1994).

Oxygen isotopic analysis of bones can also be used to elucidate bison ecology. As Shikha et al. (2004) have argued, bovid (including bison) teeth are an archive of paleoclimatic information. Experimental studies have demonstrated a strong linear relationship between $\delta^{18}O$ values and temperature and, therefore, have value in paleoclimatic reconstruction (Fricke and O'Neil 1996; Schoeninger et al. 2000), and tooth enamel is considered to be a superior reservoir of oxygen isotope signatures to any of the other oxygen-bearing hard tissues (Fricke et al. 1998). As meteoric water is ingested either through surface water sources or vegetation, the oxygen isotopic composition is reflected in the enamel apatite. While most studies of oxygen isotopes are focused on paleoclimatic changes, the signals preserved in bison teeth also provide information on seasonal migration. For example, bison should be drinking water from wetlands and lakes that experience evaporation and will have an isotopically enriched signature. If they are exclusively drinking from streams and rivers filled by snow runoff there should be less seasonal variation and

the signature should be isotopically depleted. A more detailed discussion is presented in Chapter VI of this study.

Preceding the section on the isotopic analysis Chapter II will provide an overview on the environment and ecology of the GYE; Chapter III will provide a historical perspective on bison in the region; Chapter IV will discuss the climate change and its influence on bison, the study set, followed by a concluding section. All ages presented in the text are uncorrected radiocarbon years before present, unless otherwise noted.

Chapter II

Environment and Ecology of the Greater Yellowstone Ecosystem

Introduction

The Greater Yellowstone Ecosystem (GYE) is a 4.6 million-ha (18,000-mi²) region in northwestern Wyoming, southwestern Montana, and northeastern Idaho. It includes two national parks and seven national forests (Figure 1.1). Ecosystem boundaries were first proposed in the 1970s and 1980s based on the range of local grizzly bears (*Ursus arctos*) (Schullery 1997). More recent definitions expanded the size of the GYE and change the focus from individual species to more general ecological principles (Keiter and Boyce 1991; Schullery 1997).

The high-elevation mountains and plateaus that characterize the GYE are the result of uplift associated with the Yellowstone hot spot. This arc of high terrain rises more than 1000 m above the surrounding valleys (Figure 2.1). The high terrain was probably formed as a result of the southwestward movement of the North American plate over a stationary thermal mantle plume causing block faulting and uplift of the landscape during the past several million years (Pierce and Morgan 1992). During the mid-Quaternary (150,000-12,000 BP), the GYE experienced several episodes of glaciation. The 900-m-thick Pinedale glaciation was centered along a north-south axis through Yellowstone Lake, with ice flowing radially to the northeast, west, and southwest (Good and Pierce 1996; Pierce 1976). The annual temperature during full glaciation was probably 12 °C colder than present (Thompson et al. 1993; Whitlock 1993). Today, 80 percent of the GYE is forested, although many vegetational communities are present (Despain 1990) ranging from sagebrush grasslands at 1,370 m to alpine tundra at elevations over 3,900 m (Figure 2.2). Topographic relief provided by the uplift created a mosaic of biotic communities within relatively small areas (Clark 1999).

Figure 2.1 Topographic map of the Greater Yellowstone Ecosystem. Map was created using NED shaded relief 1/3 arc second downloaded from www.seamless.usgs.gov.

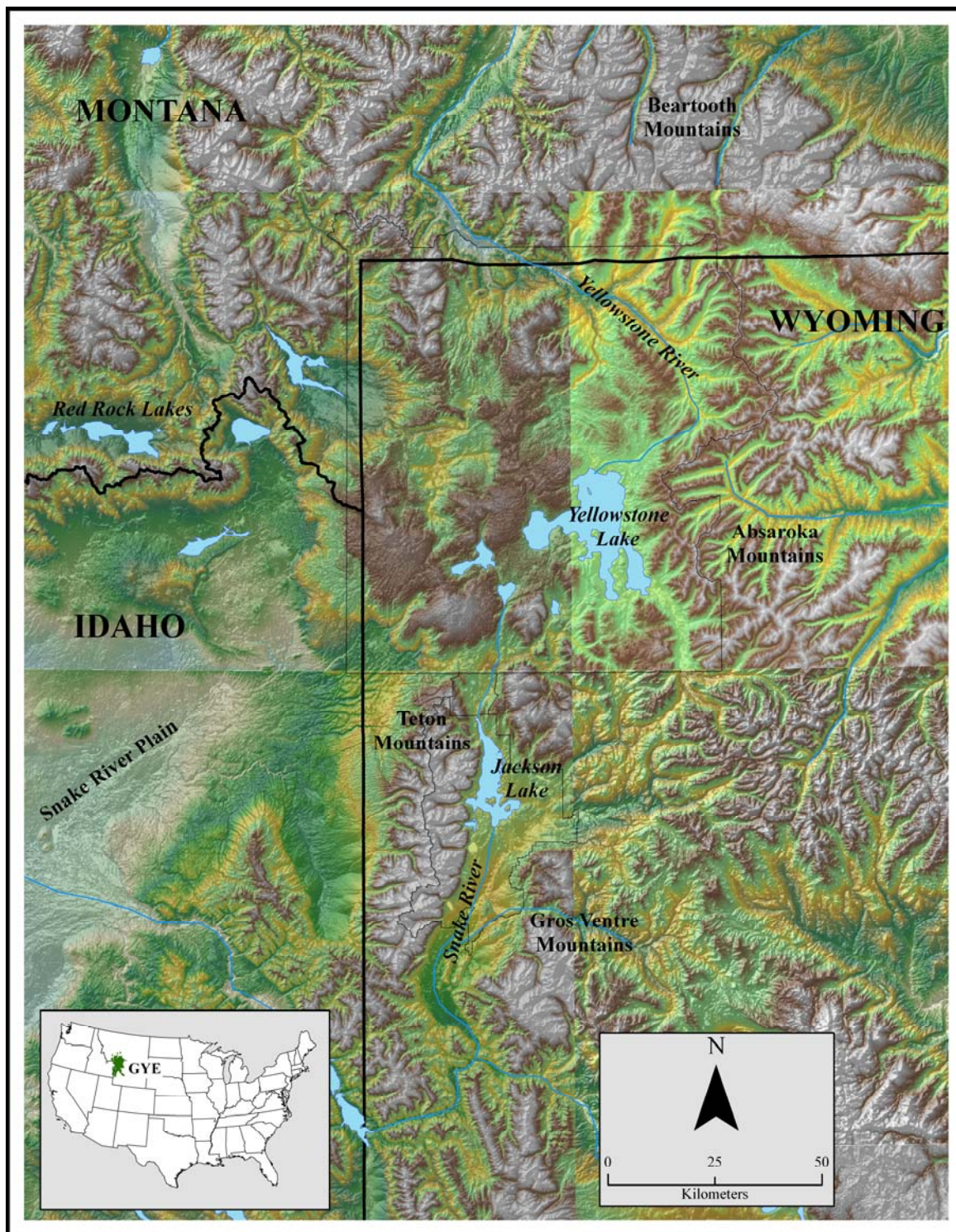
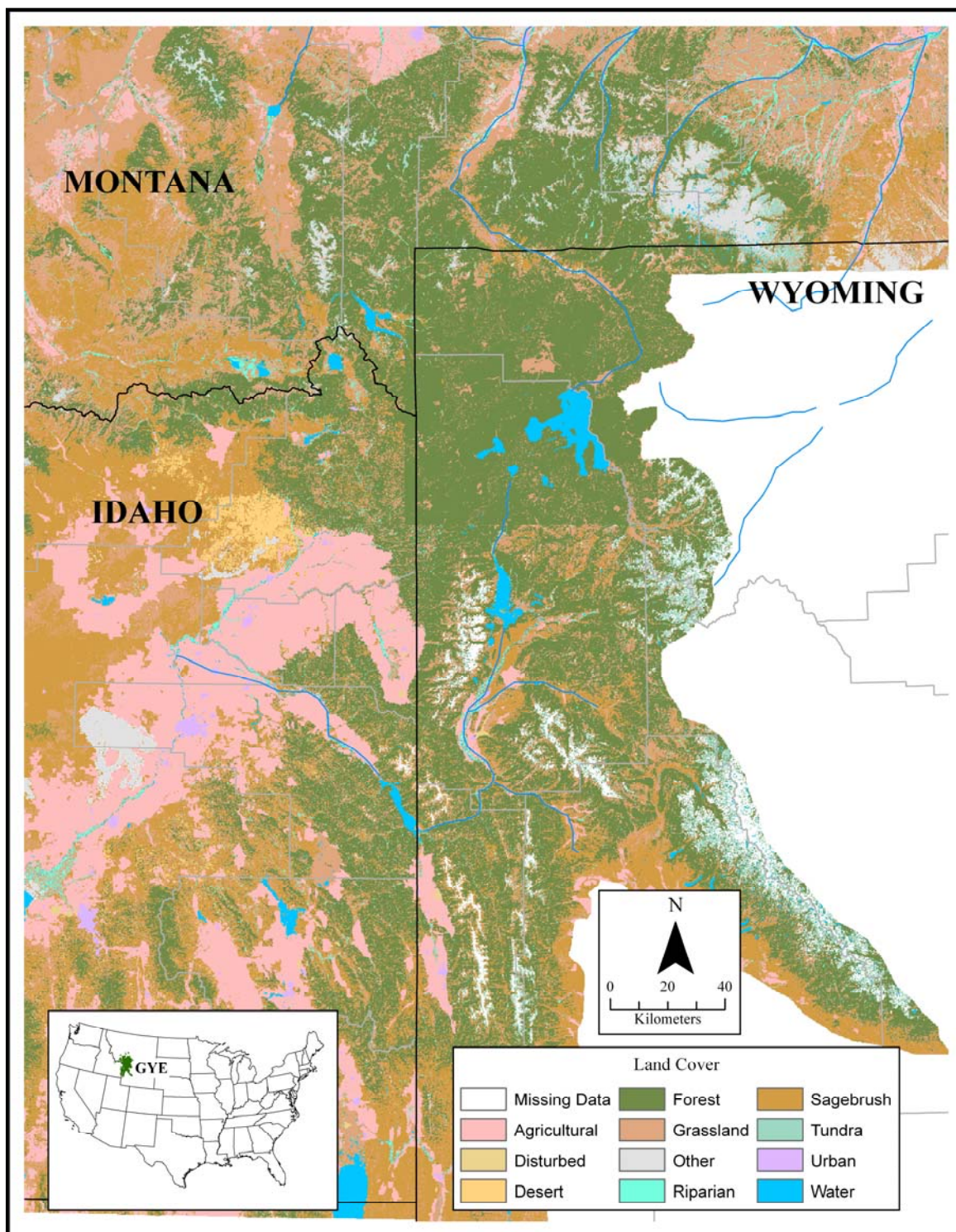


Figure 2.2 Vegetation map of the Greater Yellowstone Ecosystem. Vegetation map was constructed from published maps utilizing GAP data. Vegetation categories were simplified to reflect general vegetation patterns of forested and non-forested areas.



Yellowstone National Park

They are several major topographic features of the GYE, two of which have been preserved as national parks: Grand Teton National Park and Yellowstone National Park. Yellowstone National Park is a high, mountainous plateau region lying within the Rocky Mountains of northwestern Wyoming and adjacent parts of Montana and Idaho. The great plateau of Yellowstone is actually an undulating volcanic plateau with an average elevation of 2400 m (8000 ft). In general, the area is a large forested upland incised by numerous drainages that form the headwaters of three major rivers (Snake, Yellowstone, and Missouri), and is partially surrounded by rugged mountains rising 600 to 900 m (2000 to 3000 ft) above the plateau.

Along the eastern boundary of the plateau, and extending northwestward, is the Absaroka Range. There are only three passes through these peaks: Sylvan Pass, east of Yellowstone Lake; Colter Pass, in the northeast; and, the Thorofare, a pass at the headwaters of the Yellowstone River in the southeastern portion of the park. In the northwestern corner of the park is the southern portion of the Gallatin Range.

The high terrain surrounding Yellowstone on three sides has been described as the Yellowstone crescent that extends both south and west from highlands to the north and east of the park. Interspersed within the mountainous terrain are basins of alluvial fills that were deposited in late- and post-glacial time (Rodman et al. 1996). This pattern of high dissected mountains may have resulted from a thermal mantle plume that has caused uplift, volcanism, and faulting in the southwest-moving North American plate. Large, caldera-forming eruptions migrated about 300 km along the present Snake River Plain in the last 10 million years, arriving in the present Yellowstone area about 2 million years ago (Christiansen and Blank 1972). The track of the hot spot (Snake River Plain) has also influenced climatic patterns, permitting moist oceanic air masses to move up the Snake River Plain to where the orographic rise up onto the Yellowstone Plateau causes the deep snowfall (Pierce and Morgan 1992).

The area of focus for this study (the area where all the specimens are from) is the south-central portion of the park, which is within the Central Plateau's geovegetation province, bounded on the east by the Absaroka Range (Despain 1990). This province encompasses more than a third of the park's area and 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 colonization of trees (Whitlock 1993). More than 90 percent of the province is forested by the subalpine fir/grouse whortleberry habitat type in the grouse whortleberry phase, with lodgepole pine as the predominant overstory member (Despain 1990).

During the Holocene, climatic fluctuations, which in turn influenced vegetative patterns and animal populations, have been documented for the region (e.g., Whitlock 1993). The modern composition of the Yellowstone ecosystem is probably a very recent occurrence, possibly as recent as the last 200 years. However, this system is constantly under flux in relation to a number of processes that operate at local scales in very short (i.e., decadal) time scales (Barnosky 1998).

The modern climate of Yellowstone is extreme and variable. The mean annual temperature at Mammoth is 0°C (32°F) (<http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?wylyel>). However, precipitation and temperature are dependent on topographic features, specifically elevation. Despain (1987), in analyzing records from weather stations across the Park, identified two general climatic patterns. One pattern is similar to the Great Plains climatic type to the east and is characterized by a spring peak in precipitation. This climate type can be found in the interior and low valleys. The second type is characterized by winter peaks in precipitation, similar to patterns on the west coast and mountains of northern Idaho and northwestern Montana. This pattern is common on the western plateaus and the mountains of the western and eastern part of the Park (Despain 1987). These climatic patterns are important for understanding vegetation distribution and paleoclimatic reconstruction. Whitlock and Bartlein (1993) refer to these patterns as summer-wet/winter dry and summer-dry/winter-wet, respectively.

Baker (1976) recognized five broad vegetation zones for the Yellowstone Plateau that represent elevation zonation of vegetation. The lowest vegetation zone, the *Artemisia* (sagebrush) steppe association, occurs between Mammoth and Gardiner in the northern part of the Park and along the boundaries below 1900 m (6000 ft) (Baker 1976:E10). Next in elevation is the *Pseudotsuga* association, which is dominated by *Pseudotsuga menziesii* (Douglas fir) with locally common constituents of *Pinus flexilis* (Limber pine), *Populus tremuloides* (quaking aspen). This vegetation zone is located at elevations between 1900 and 2400 m (6000 to 8000 ft) (Baker 1976:E10). The most extensive vegetation zone in the Park is the *Pinus contorta* (lodgepole pine) forest association that covers 80 percent of the forested area. Common species include *Picea engelmannii* (Engelmann spruce), *Abies lasiocarpa* (subalpine fir), and *Juniperus communis* (common juniper). This vegetation community is common between 2100 and 2600 m (7000 and 8500 ft [Baker 1976:E12]). From about 2600 m (8500 ft) to tree line the *Picea-Abies-Pinus albicalis* (spruce-fir-whitebark pine) forest association is dominant. Engelmann spruce and subalpine fir are the dominant species, with whitebark pine a common associate locally (Baker 1976:E12). At the highest elevations in the Park, alpine communities dominate. Species in this association include members of the Gramineae (Grass family), Cyperaceae (Sedge family), and the Juncaceae (Rush family [Baker 1976:E12]).

The modern faunal assemblage of the GYE has probably been intact since mid-Holocene times, although fluctuations in population dynamics and migration patterns have probably occurred in relation to changing climatic patterns (Hadly 1990), and in relation to human predation and settlement. A recent overview of the paleontological data from the region is presented by Walker (1987a) and Cannon (1992) and need not be repeated. However, it should be noted that bison have long been an important element of mammalian faunal community. Cannon (1992:Table 2) notes that bison are present at over 67 percent (21 of 31 sites) of Pleistocene and Holocene sites in the region. Only bighorn sheep (29 of 31 sites) and elk (24 of 31) are more ubiquitous in the prehistoric record.

Jackson Hole and Grand Teton National Park

Grand Teton National Park lies partially within a large upland valley known as Jackson Hole. This large intermountain valley sits at an elevation of approximately 2000 m. Soils in the valley are generally derived from glacial outwash. The valley is drained by the Snake River, which heads in the Pitchstone Plateau and the Pinyon Peak Highland of southern Yellowstone. The valley is flanked by the Teton Range to the west and the Gros Ventre Mountains to the east (Good and Pierce 1996).

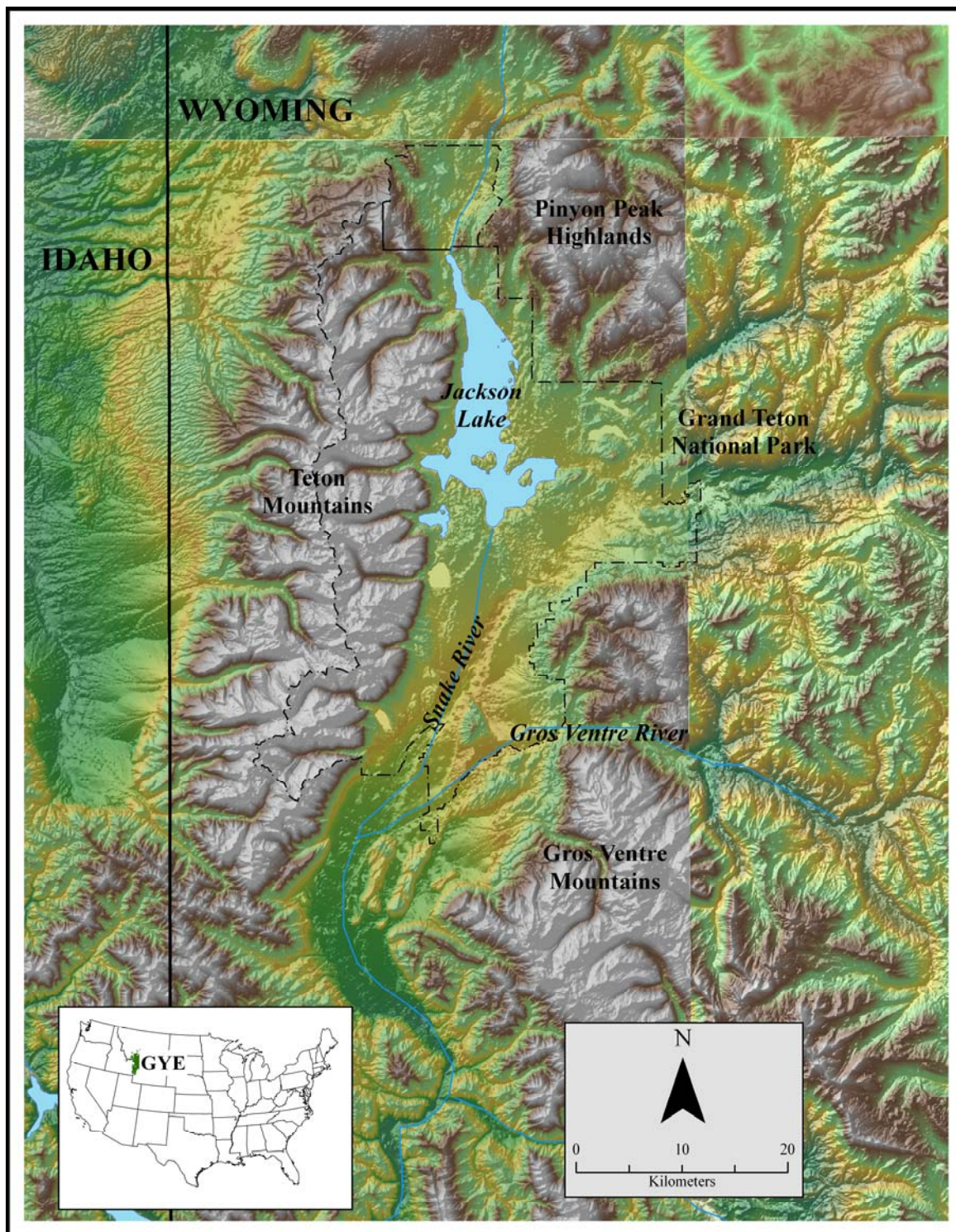
Jackson Hole represents a major topographic feature of the Greater Yellowstone Ecosystem (Figure 2.3). This location is in the central portion of the Middle Rocky Mountains physiographic province (Fenneman and Johnson 1946). The town of Jackson is situated within Jackson Hole, which is an intermountain basin drained by the Snake River and flanked by the Teton Range to the west and the Gros Ventre Mountains to the east. Jackson Hole is a topographic, structural, and depositional basin (Thornbury 1965).

Jackson Hole is immediately west of the continental divide and is drained by the Snake River and its tributaries. Once in Jackson Hole, the river flows into the artificially dammed Jackson Lake Reservoir (2,064 m; 6,772 ft). Jackson Lake reservoir lies in a basin formed by down-faulting along the Teton Fault, which has been scoured and deepened by glaciation. Prior to being dammed, this basin was occupied by Jackson Lake, which maintained an average shoreline elevation of 2,052 m (6,732 ft).

Soils of the Jackson Hole area reflect a cold, semi-humid precipitation regime (Young and Singleton 1977). Mountain slope soils are formed in residuum derived from sedimentary rocks and granite and also from glacial deposits. Soils on the forested areas vary by age. Older soils have clay-enriched B horizons (Cryoboralfs), whereas younger soils are characterized solely by the accumulation of humic organic material (Cryoborolls). Soils on the floor of Jackson Hole formed in glacially and glacio-fluvially redeposited materials. Upland settings commonly support

sagebrush steppe and have organic-enriched A horizons (Cryoborolls). Lowland soils support riparian communities and are poorly drained (Cryaquolls).

Figure 2.3 Topographic map of Jackson Hole and vicinity.



Like much of Wyoming, Jackson Hole is characterized by varied topographic features and vast differences in elevation. From the valley floor at an elevation of 1,920 m (6,300 ft), the Tetons rise over 2,200 m (7,200 ft) in only a few miles. Within this lateral and vertical distance are a number of life zones, with a variety of plant and animal species in relatively close proximity to each other (Figure 2.3). Many of these species are confined to one zone or another, yet many more range through several of these zones on annual or seasonal cycles. Pika (*Ochotona princeps*) and bighorn sheep (*Ovis canadensis*) are frequently found above the timberline, but in the winter the bighorn sheep migrate to lower elevations.

In his book *The Natural World of Jackson Hole*, Tim Clark (1999) describes four extant life-zones for Jackson Hole, following the system developed by Cary (1917). These include the *Arctic-Alpine*, the *Hudsonian*, the *Canadian*, and the *Transition*. Each of these communities is based upon the association of living organisms inhabiting a specific area or physical habitat (Clark 1981:40). While this was an early means of organizing and classifying communities, it provided little in the way of explaining the complex interaction of species competition and energy flow. However, it is still heuristically useful for describing the ecology of the region, and it suggests how prehistoric groups may have organized themselves in relation to these communities and their particular resources.

The modern vegetation distribution in Jackson Hole and the surrounding mountains is largely related to altitudinal gradients of moisture and growing-season temperature, although the substrate is also an influencing factor. Higher elevations support a spruce-fir forest, with the lower slopes dominated by a Douglas fir forest. Much of this area is covered with sub-climax lodgepole pine forest. Above about 2,900 m (9,500 ft) is the treeless zone of the Arctic-Alpine community. This area includes the highest mountain peaks where soils are very shallow and boulder fields are common. In these marginal environments, vegetation consists of low-growing species such as lichens, phlox, and pussytoes. In alpine meadows, sedges, grasses, and shrubs are present. The Hudsonian community exists in a narrow zone just below the timberline exists. The

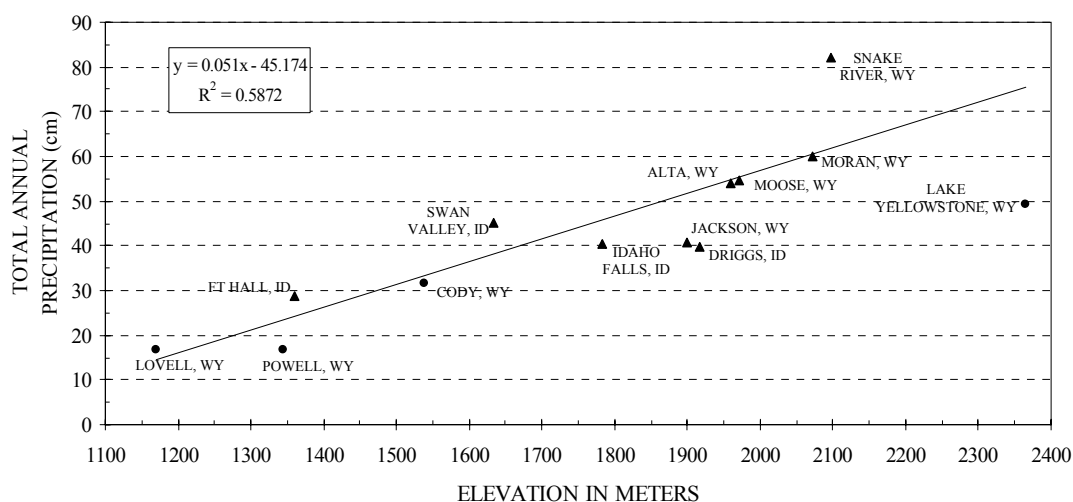
predominant overstory species of this community are whitebark pine, dwarf Engelmann spruce, and subalpine fir. The Canadian community, found at middle elevations of the mountains and along the highest foothill slopes consists of Engelmann spruce, subalpine fir, lodgepole pine, and aspen. The Transition community exists on the valley floor and on the lower slopes and foothills. Predominant species include sagebrush and lodgepole pine. Bison have been known to use each of these communities, including the high altitude alpine meadows, during various times of the year (Meagher 1973; Cannon 2007).

Regional Climate and Paleoclimate

The climate in northwestern Wyoming is strongly influenced by topography. Brown (1980) defined the local climate as *alpine*, characterized by humid continental weather with ample precipitation and cool summers. At Jackson the mean annual temperature is 3.33°C, and the mean annual precipitation is 38.61 cm (Martner 1986; records from 1951–1980). In the higher mountain peaks, climate is classified as *alpine tundra* and is very cold and windy. The correlation between temperature and elevation is quite clear in the area, with an adiabatic lapse rate (cooling rate) of 9.8°C/1,000 m (Dirks and Martner 1982).

Precipitation is also strongly influenced by elevation. The prevailing storms move up the Snake River Plain from the southwest, and, as this air mass moves over the mountains, it cools and condenses, falling as either rain or snow. This orographic effect is well illustrated in Figure 2.4, which shows that lower elevation sites, such as Fort Hall and Idaho Falls, receive less moisture than those sites at higher elevations. On the leeward side of the mountains, a “rain-shadow” is created in which descending air masses warm, and the potential for evaporation is greater than for precipitation. Weather stations, such as Cody and Powell, illustrate this effect.

Figure 2.4. Plot of mean annual precipitation (MAP) against elevation. Closed triangles represent weather stations west of the continental divide and closed circles represent stations to the east.



In the past, a similar movement of storms up the Snake River Plain probably fed the region's glaciers. The increasing height of the late Wisconsin Pinedale ice from southwest to northeast mimics the current distribution of moisture (Good and Pierce 1996:Figure 9.4), and moisture distribution may have had an influence on prehistoric settlement, particularly during winter months. To date, the only identified winter occupation site in the region, the Pagoda Creek site, 48PA853, is along the North Fork of the Shoshone River east of Yellowstone National Park (Eakin 1989). While still cold, the valley receives considerably less snow than the Yellowstone Plateau, a plausible reason for its mid-winter use.

Whitlock and Bartlein (1993) have also demonstrated how circulation interacts with topography to influence local seasonal distribution of precipitation. They describe the climate regime in Jackson Hole and southern Yellowstone as summer-dry/winter-wet. This pattern of precipitation results from the influence of the eastern Pacific subtropical high-pressure system, which suppresses precipitation through large-scale subsidence during the summer. In the winter, precipitation is generated by storms tracking along the jet stream as it migrates south. Mountain ranges, such as the Tetons, intercept these storm systems moving in from the Pacific. The

northern portion of the GYE features summer-wet/winter-dry conditions. This regime receives precipitation that originated as onshore flow of moisture from the Gulf of California and the Gulf of Mexico as part of a summer monsoonal flow that extends to the northern part of Yellowstone and the eastern Snake River Plain, where convectional precipitation occurs along orographic boundaries (Whitlock and Bartlein 1993).

While the contrast between these two climate regimes is evident even at a spatial scale as small as northwestern Wyoming, it may have been more dramatic during earlier portions of the Holocene. Vegetation records from northwestern Wyoming show that Jackson Hole and southern Yellowstone were drier during the early Holocene probably because of the expanded subtropical high. These warmer drier conditions allowed lower-elevation species, such as Douglas fir, to grow above their elevational range. In the middle and late Holocene, the subtropical high began to weaken, summer drought was less severe, and mesophytic conifers became abundant (Whitlock and Bartlein 1993). In the northern part of Yellowstone, the greatest summer moisture occurred during the early Holocene, when the monsoonal circulation was stronger. During the middle and late Holocene, summers became drier as the onshore flow from the Gulf of Mexico attenuated (Whitlock and Bartlein 1993).

The Regional Prehistoric Bison Record

The prehistoric record of bison in the GYE extends back 10,000 years (Cannon 1992), although the record is fragmentary. Nineteenth-century observations suggest that bison ranged throughout the lower-elevation meadows, with probable summer migrations into the high alpine meadows (Meagher 1973:Appendix II; Fryxell 1926). Today, bison are restricted to public lands in YNP and Jackson Hole. Migrations beyond these political boundaries result in either hazing or death (Peacock 1997). A general paucity of bison in the archeological record, as well as low and fluctuating numbers of modern bison in Yellowstone and Jackson Hole, led Wright (1984: 28) to conclude that “bison were always relatively rare in northwestern Wyoming, and that they would have been too unpredictable in numbers to provide a stable food source.” Wright continues,

“since 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.” Mary Meagher (1973:14), on the other hand, suggests 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.” While these two perspectives illustrate extreme views, it is clear there is still much to learn about the details.

Since the time when both Wright and Meagher presented their views, new information has become available concerning both modern and prehistoric populations. Part of Wright’s argument for low numbers of bison in the prehistoric record came from the extrapolation of population dynamics of modern bison in both Yellowstone and Jackson Hole. While bison in both these areas received protection from the Department of Interior, Wright failed to mention that bison were often removed from the herds based upon various management decisions. If we look at winter counts for bison in Jackson Hole, we see that since the mid-1960s, when the NPS implemented a noninterventionist approach to natural resource management, bison numbers have increased to a high in 1999 of 438. In 1969, the Jackson Hole herd was begun with 16 founders and subsequently high fecundity rates caused exponential population growth rates of 16–19 percent a year (Cain et al. 1998).

Despite the characterization of the Yellowstone National Park herd as free-ranging, much of its history during the 20th century has been based upon management decisions to control the population. Following a period of management practices that allowed the herd to grow in the early 20th-century, during the mid-20th century the herd was intensively managed, with culling a common practice (Meagher 1973; Schullery 1986, Schullery et al. 1998). Shortly after the Leopold Report (Leopold et al. 1963) was issued, the National Park Service took a noninterventionist approach to natural resource management, relying on natural processes to effect change and to control wildlife numbers (Keiter 1997). Bison responded by increasing their numbers from 397 in 1967 to a high of 3,956 individuals in 1995 (National Park Service 1997).

While it is problematic to draw comparisons in bison population dynamics between prehistoric populations and modern managed herds, it is apparent that the region can support a fairly sizable population. Based upon new information, it may be time to reevaluate the role of bison in the regional ecosystem and in the prehistoric economy.

A review of the prehistoric record of the GYE provides a minimum of 66 components from 30 archeological and 3 paleontological sites that produced bison remains (Table 2.1). These components represent 29 open archeological sites, one archeological cave site (Mummy Cave), and three paleontological sites — Dot Island, Lamar Cave, Astoria Hot Springs — but do not include the various drive sites in Paradise Valley north of YNP (Cannon 2001b). George Arthur (1966:45–56) estimated that at least 10 bison kill sites are present in Paradise Valley, including a large complex of drive lines and rock cairns known as the Emigrant Buffalo Jump (24PA308). Table 2.2 provides a list of archeological sites with bison based upon counties within the GYE (Figure 2.5).

Figure 2.5. Map of counties in the GYE illustrating the number of sites that have reported bison remains. Distribution is probably more reflective of the amount of excavations in the county than the actual distribution of bison in the past.

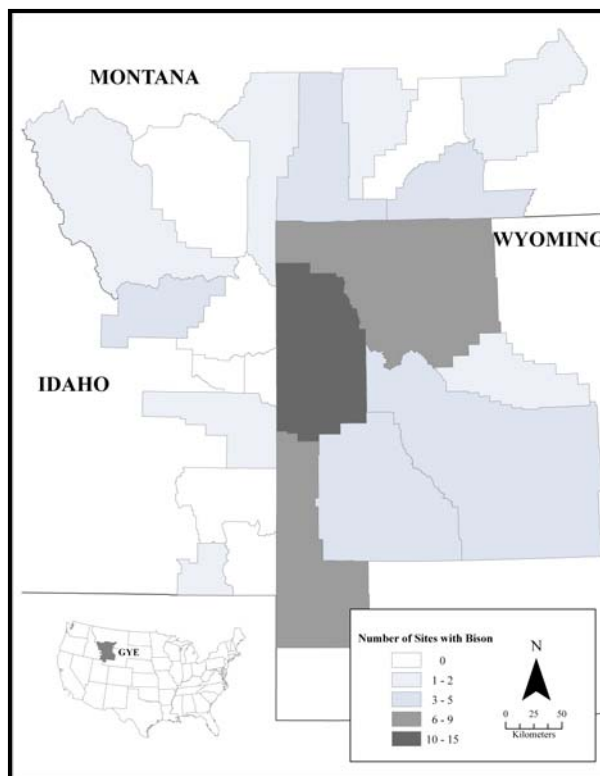


Table 2.1. Inventory of prehistoric locales with bison remains from the Greater Yellowstone Ecosystem.

State	County	Site Name and Number	Excavation Provenience	Age	NISP/MNI ¹	Reference
Idaho	Bonneville	10BV30 Owl Cave	Bison Bone Layer	6700-8160	-/60	Miller 1972
			Proboscidean Layer	10000-14000	1/1	
Idaho	Clark	10CL10 Bison Rockshelter	Layer 1	100-948	1/1	Swanson 1972
			Layer 2	100-948	2/1	
			Layer 3	100-948	5/2	
			Layer 4	370-948	1/1	
			Layer 5	370-2350	155/13	
			Layer 6	370-2350	1/1	
			Layer 7	370-2350	1/1	
			Layer 8	370-2350	4/3	
			Layer 9	370-2350	14/2	
			Layer 11	370-2350	4/1	
			Layer 12	370-2960	1/1	
			Layer 13	2350-2960	1/1	
			Layer 14	2350-2960	9/1	
			Layer 15	2350-2960	1/1	
			Layer 16	2350-3995	1/1	
			Layer 17	3360-6030	1/1	
			Layer 18	5870-6925	1/1	
			Layer 22	5870-6925	16/6	
			Layer 28	5870-6925	4/1	
			Layer 29	5870-6925	4/2	
			Layer 32	6700-12000	1/1	
Idaho	Clark	10CL3 Veratic Rockshelter	Layer 8	0-370	1/1	Swanson 1972
			Layer 15	0-370	1/1	
			Layer 18	0-370	2/2	
			Layer 19	100-948	17/5	
			Layer 20	100-948	2/2	
			Layer 21-23	370-2920	1/1	
			Layer 24	2900-3500	5/4	
			Layer 25-26	2900-3995	3/1	

State	County	Site Name and Number	Excavation Provenience	Age	NISP/MNI ¹	Reference
			Layer 27	3360-4500	65/12	Swanson 1972
			Layer 29	3995-6030	1/1	
			Layer 30	6282-12,000	2/1	
			Layer 31	12,000-35,000	2/2	
Idaho	Clark	Jimmy Olsen Rockshelter	n/a	5400 BP	-/-	Lohse and Sammons 1994
Idaho	Clark	10CL105 Warm Springs Creek	n/a	n/a	-/-	Plew and Sundell 2000
Idaho	Franklin	Weston Canyon Rockshelter	Layer 4-5	2000-3740	1/1	Miller 1972
			Layer 6-7-8	2000-5000	5/1	
			Layer 9	3740-5000	1/1	
			Layer 12-13	5000-7200	1/1	
Montana	Beaverhead	24BE230 Red Rock Springs		690 ± 90	-/-	Keller 1991
Montana	Carbon	24CB75 Big Lip		2000-4000	-/-	Graham et al. 1987
Montana	Carbon	24CB221 Mangus	Occupation III	1050 ± 70 1070 ± 70	8/-	Husted 1969
			Red Silt	1050-1070	7/-	
Montana	Carbon	24CB91 Shield Trap	Occupation I	1270 ± 55 1745 ± 65	-/-	Graham et al. 1987
			Occupation II	2185 ± 60 2675 ± 65 3190 ± 60	-/-	
			Occupation III	5490 ± 75 7165 ± 225 7245 ± 70 7540 ± 215	-/-	
Montana	Carbon	24CB202 Sorenson	Occupation II	7560 ± 250 7800 ± 250	-/-	Husted 1969
			Occupation III		-/-	
			Occupation VI	1310 ± 100	4/-	
Montana	Carbon	24CB384 False Cougar Cave	Natural Stratum I	1600 ± 90 2210 ± 90 5670 ± 110	-/-	Graham et al. 1987

State	County	Site Name and Number	Excavation Provenience	Age	NISP/MNI ¹	Reference
				5690 ± 110 5830 ± 110		
			Natural Stratum II	6105 ± 230 6290 ± 285 10530 ± 140 14590 ± 300	-/-	
Montana	Gallatin	24GA660 Antonsen	Area A	180 ± 180	-/-	Davis and Zier 1978
			Area B		-/-	
			Area C	1605 ± 90	-/-	
			Area D		-/-	
Montana	Park	24PA195 Corwin Springs	n/a	Middle Holocene Late Bitterroot	n/a	L.B. Davis, personal communication, 1992
Montana	Park	24PA308 Emigrant Buffalo Jump	n/a	Late Holocene	-/-	Arthur 1966
Montana	Park	24PA504 Meyers-Hindman	SU8 5-20 cmbs	Late Holocene 790 ± 90	-/5	Lahren 1976
			SU7 20-40.5 cmbs	Late Holocene 1470 ± 70	-/4	
			SU6	Late Holocene 2300 to 1450 BP	-/5	
			SU5 56-71 cmbs	Late Holocene 2300 ± 120	-/5	
			SU4	Late Holocene 3150 ± 110	-/4	
			SU3	Middle Holocene 4680 ± 220 5950 ± 150	-/3	
			SU1	Early Holocene 8450 ± 190 9400 ± 200	-/2	

State	County	Site Name and Number	Excavation Provenience	Age	NISP/MNI ¹	Reference
Montana	Park	24PA508 The Sphinx Site	Units 1-4, Upper Levels	n/a	-/-	Deaver et al. 1989
Montana	Sweetgrass	24SW651 Jarrett Site	n/a	Late Holocene 2820 ± 120	n/a	L.B. Davis, personal communication, 1992
Montana	Yellowstone National Park	24YE353	TU2/F89-1 20-30 cmbs	Late Holocene 1260 ± 50	1/1	Cannon 1997b
Montana	Yellowstone National Park	24YE366	TU1 Cutbank exposure	Late Holocene	2/2	Cannon 1997b
			TU1 40-50 cmbs	Late Holocene	2/1	
Montana	Yellowstone National Park	24YE366	TU1 60-70 cmbs	Late Holocene 1420 ± 90	2/1	Cannon 1997b
			TU1 90-100 cmbs	Late Holocene (?) >1420 BP	1/1	
			TU2A/F89-1 0-10 cmbs	Late Holocene 1220 ± 80	2/1	
			TU2A/F89-1 10-20 cmbs	Late Holocene	1/1	
			TU2A/F89-1 15 cmbs	Late Holocene	1/1	
Wyoming	Fremont	48FR1398 Castle Gardens Access Road		660 ± 100 750 ± 100 789 ± 110	995/-	Todd and Walker 1984
Wyoming	Fremont	48FR308 Lookingbill	Post-Early Plains Archaic Level	Late Holocene (?)	1/1	Larson et al. 1995
			Early Plains Archaic Level	Early Holocene	2/-	
			Early Paleoindian Level	Terminal Pleistocene	1/1	
Wyoming	Fremont	48FR5657				Wyoming SHPO site files
Wyoming	Hot Springs	48HO364 Additional Creek Bison Site				Wyoming SHPO site files
Wyoming	Lincoln	48LN74	Feature 1.2		-/-	Brown 1980

State	County	Site Name and Number	Excavation Provenience	Age	NISP/MNI ¹	Reference
Wyoming	Lincoln	48LN317 Skull Point	T-7	300 ± 50 1375 ± 55	2/-	McGuire 1977
Wyoming	Lincoln	48LN127 Cow Hollow	Component 3	Late Archaic	4/-	Schock et al. 1982
			Component 4	1280 ± 85	1/1	
Wyoming	Lincoln	48LN350 Barnes Site		1060 ± 80		Thompson and Pastor 1995
Wyoming	Lincoln	48LN373	Component 3, Occupation 13	1030 ± 80		Wheeler et al. 1986
			Component 3, Occupation 12	1170 ± 70	-/1	
			Component 3, Occupation 11	1790 ± 80	-/1	
Wyoming	Lincoln	48LN373	Component 2, Occupation 9	2960 ± 80	-/1	Wheeler et al. 1986
Wyoming	Lincoln	48LN1296	Area E, Component 3	1460 ± 80	n/a	Wheeler et al. 1986
			Area E, Component 2	1590 ± 70	n/a	
Wyoming	Lincoln	48LN1468 Taliaferro Site	Component VII	960 ± 60	n/a	Smith and Creasman 1988
			Component IV	1500 ± 70	n/a	
			Component III	2590 ± 90 2850 ± 90	n/a	
Wyoming	Lincoln	48LN3573 Laster's Bison Kill	n/a	n/a	n/a	Wyoming SHPO site files
Wyoming	Park	48PA202 Mummy Cave		Early Holocene	1/1	S. Hughes, personal communication, 1999
Wyoming	Park	48PA29 Horner Site	Horner I	6151 ± 500 6619 ± 350 7132 ± 350 7880 ± 1300 7690 ± 850 9390 ± 75	-/200	Frison and Todd 1987
			Horner II	9875 ± 85 10,060 ± 220	-/65	

State	County	Site Name and Number	Excavation Provenience	Age	NISP/MNI ¹	Reference
Wyoming	Park	48PA551 Dead Indian Creek	Site Area 4	Late Prehistoric	n/a	Jameson 1984
			Site Area 5	Late Prehistoric	n/a	
				3800 ± 110 4180 ± 250 4430 ± 250	43/4	Scott and Wilson 1984
Wyoming	Park	48PA602	n/a	n/a	n/a	Wyoming SHPO site files
Wyoming	Park	48PA605	n/a	n/a	n/a	Wyoming SHPO site files
Wyoming	Park	48PA607	n/a	n/a	n/a	Wyoming SHPO site files
Wyoming	Park	48PA612	n/a	n/a	n/a	Wyoming SHPO site files
Wyoming	Park	48PA852	Block B1 15-30 cmbs	Late Holocene		Eakin and Sutter 1991
Wyoming	Park	48PA950	n/a	n/a	n/a	Wyoming SHPO site files
Wyoming	Sublette	48SU301 The Wardell Buffalo Trap	Top level of kill area	990 ± 100	-/150	Frison 1973
Wyoming	Sublette	48SU301 The Wardell Buffalo Trap	Firepit, meat-processing area	1170 ± 100		Frison 1973
			Bottom level of kill area	1580 ± 110		
Wyoming	Sublette	48SU867 Harrower Site	Component 5	680 ± 50 850 ± 70		Thompson 1995
			Component 6	280 ± 60		
Wyoming	Sublette	48SU1013 Kyle's Site		Late Archaic (?)	n/a	Wyoming SHPO site files
Wyoming	Sublette	48SU1042 Stewart Flat	Component 2	Late Holocene <1000 BP	1	Hoefler 1991
			Component 1	Late Holocene 1050 ± 50 1200 ± 60 1300 ± 70	1	
Wyoming	Teton	48TE342 Astoria Hot Springs	~ 3 ft.	Terminal Pleistocene 11,940 ± 500	-/-	Love 1975; Ives et al. 1964
Wyoming	Teton	48TE350 Blacktail Butte 7		Late Holocene (?)	-/1	Wright 1975

State	County	Site Name and Number	Excavation Provenience	Age	NISP/MNI ¹	Reference
Wyoming	Teton	48TE352 Blacktail Butte 6	Test Pit 1	Late Holocene (?)	2/1	Wright and Marceau 1981
			N56/E128	Late Holocene (?)	-/1	
Wyoming	Teton	48TE391 Blacktail Butte 12	Test Pits 2-2A, 32-35 cm	Late Holocene (?)	1/1	Wright and Marceau 1981
Wyoming	Teton	48TE455 Goetz Site		Late Holocene 370 ± 40 800 ± 40	/4	Cannon 2001, this volume.
Wyoming	Teton	48TE1067	Surface	Late Holocene	3/1	Cannon 1991
Wyoming	Teton	48TE1079 Crescent H Ranch	Block G	Mid-Holocene	2/2	Cannon et al. 2001
Wyoming	Teton	48TE1090	Surface	Late Holocene 770 ± 80	371/17	Cannon 1991
Wyoming	Teton	48TE1101	Surface	Late Holocene	63/6	Cannon 1991
Wyoming	Teton	48TE1102	Surface	Late Holocene 1380 ± 80	107/8	Cannon 1991
Wyoming	Teton	48TE1104	Surface	Late Holocene	6/1	Cannon 1991
Wyoming	Teton	48TE1107	Surface	Historic	2/1 ²	Cannon 1991
Wyoming	Teton	48TE1111	Surface	Late Holocene	4/1	Cannon 1991
Wyoming	Teton	48TE1114	Surface	Late Holocene	91/4	Cannon 1991
Wyoming	Teton	48TE1119	Surface	Late Holocene	22/1	Cannon 1991
Wyoming	Yellowstone National Park	Dot Island, YNP	Cutbank	Unknown	6/1	Cannon 1997a
Wyoming	Yellowstone National Park	Lamar Cave, YNP	Level 5	Late Holocene 960 ± 60	2/1	Hadly 1995
			Level 7	Late Holocene	2/1	
			Level 8	Late Holocene	1/1	
			Level 9	Late Holocene 1670 ± 60	1/1	
			Level 10	Late Holocene	1/1	
			Level 11	Late Holocene	2/1	
			Level 12	Late Holocene 1110 ± 60	10/1	

State	County	Site Name and Number	Excavation Provenience	Age	NISP/MNI ¹	Reference
Wyoming	Yellowstone National Park	48YE215	Level 14	Late Holocene	2/1	Aaberg 1996
			Level 15	Late Holocene	2/1	
			0N/14E Level 2	Late Prehistoric	1/1	
			0N/14E Level 3	Late Prehistoric	4/1	
			12N/12E Surface	Late Prehistoric	4/1	
			12N/12E Surface	Late Prehistoric	15/1	
			12N/12E Surface	Late Prehistoric	15/1	
			12N/12E Surface	Late Prehistoric	2/1	
Wyoming	Yellowstone National Park	48YE216	Surface	Late Prehistoric	1/1	Aaberg 1996
Wyoming	Yellowstone National Park	48YE217	0N/14E Shovel Test	Late Prehistoric (?)	1/1	Aaberg 1996
			0N/14E Shovel Test	Late Prehistoric (?)	1/1	
Wyoming	Yellowstone National Park	48YE217	0N/14E Shovel Test	Late Prehistoric (?)	6/1	Aaberg 1996
Wyoming	Yellowstone National Park	48YE697	N959/E1025 144 cmbd	Late Holocene (?)	1/1	Cannon et al. 1997
			N928-9/E1057-58	Late Holocene 800 ± 60	92/1	

Table 2.2. List of counties by state within the Greater Yellowstone Ecosystem and number of sites with bison remains.

State	County	Number of Sites with Bison	Number of Components with Bison
Idaho	Bear Lake	0	0
Idaho	Bonneville	1	2
Idaho	Caribou	0	0
Idaho	Clark	4	35
Idaho	Franklin	1	4
Idaho	Fremont	0	0
Idaho	Madison	0	0
Idaho	Teton	0	0
Montana	Beaverhead	1	1
Montana	Carbon	5	11
Montana	Gallatin	1	4
Montana	Madison	0	0
Montana	Park	4	10
Montana	Stillwater	0	0
Montana	Sweetgrass	1	1
Montana	Yellowstone National Park	2	8
Wyoming	Fremont	3	5
Wyoming	Hot Springs	1	1
Wyoming	Lincoln	8	15
Wyoming	Park	9	11
Wyoming	Sublette	4	8
Wyoming	Teton	15	16
Wyoming	Yellowstone National Park	6	16

Thirteen sites in Jackson Hole produced bison remains. The earliest evidence of bison in the region was reported from south of Jackson Hole on the Snake River at Johnny Flats Count near Hoback. Because the association of cultural material with the bison remains has not been demonstrated, these deposits are considered paleontological. During excavation for the development of Astoria Hot Springs (48TE342), “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; underlining in original). Mollusk shell was collected from a “trench intersecting 2-ft shell bed at depth of 3 ft” by J.D. Love in 1959 and submitted to the U.S. Geological Survey, which produced an age of $11,940 \pm 500$ BP (W-1070; Ives et al. 1964:60). With the current understanding of the process of radiocarbon dating (e.g.,

Goslar and Pazdur 1985), especially in proximity to geothermal features, this age might be problematic. For example, Preece et al. (1983:253) explain that a theoretical maximum of 50 percent 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).” The implications of this work should be reviewed with these issues in mind.

The Goetz site, 48TE455, located on the National Elk Refuge in Jackson, was initially investigated by Dr. George Frison and his student at the time, Charlie Love. The investigations were in response to dragline excavations to draw water from a spring for elk and other wildlife. Love (1972:69–71; underlining in original), in his master’s thesis entitled *An Archeological Survey of the Jackson Hole Region, Wyoming*, provides the following narrative of the investigations:

A dragline operation to open up the spring brought up quantities of butchered bison bone and flake materials. An incomplete bear mandible was recovered from this site in an earlier test hole. A 5 by 10 foot test pit into an undisturbed portion revealed the scattered remains of three separate butchered bison as well as numerous flakes, choppers, bifacial fragments, and projectile point pieces. Over twenty pounds of flakes, core pieces, scrapers, and chopper or knife-like bifaces were obtained from the single test pit. ... A thin layer of carbon at a depth of approximately 9 inches was collected and subsequently dated at A.D. 1560 ± 115 . At this level and below were found a reworked obsidian edge-ground lanceolate point, a thin straight-edged, square-based, unnotched brown chert point, a piece of obsidian corner notched point, and what appears to be a McKean-like stem base of an obsidian point. ... A great deal of fire-cracked rock was distributed throughout the test pit as well as other undiagnostic tools. ... Possibly two layers of bone and materials are present, though a specific dividing line between them could not be drawn.

According to Frison, the excavation was salvage in nature (personal communication, October 1999). The relationship of the bone and the cultural material is difficult to assess, and Love’s radiocarbon age should be considered minimum.

Bone from the site was reanalyzed by Cannon (2001). The results indicate that a minimum of four bison, two of which are males, are represented in the assemblage. A more

accurate age for the assemblage is provided by the direct dating of a right metatarsal. An age of 800 ± 40 BP was returned on the specimen. A second age was obtained from the direct dating of the roots from a lower third bison molar (FS455.2) from the University of Wyoming 1971 investigations. The age, 370 ± 40 yrs BP (Beta-241894; $\delta^{13}\text{C} = -18.8\text{‰}$), indicates a more complex history of the site with multiple kill events. Both ages are older than the minimum age that reported by Love (1972).

Four sites, including the Goetz site, are within the current bison habitat. The sites, at the southern end of Blacktail Butte, were investigated by Wright and his students in the 1970s and produced bison remains. Blacktail Butte 6 (48TE352) produced “two cranial fragments of a large mammal, apparently a bison” in Test Pit 1 (Wright and Marceau 1981:5). The reporting of the faunal remains from the Tiny Pine site, or Blacktail Butte 7 (48TE350), is confusing. However, it appears that remains from a minimum of two bison were recovered during the test excavations. Wright and Marceau (1981:6) indicate the “midden included parts of a butchered bison ... while a second section of the site [Area 2] ... produced a bison ulna at a depth of 40 cm.” They also report two obsidian-hydration dates on artifacts recovered from the midden — AD 92 and AD 172; however, those dates may be problematic.

At the extreme southwestern end of Blacktail Butte is site 48TE391, Blacktail Butte 12, which was documented in 1974 and tested in 1975. Faunal remains were recovered from at least two contexts. While the majority (>95 percent) were unidentifiable fragments, at least three elements are probably of bison and represent a minimum “of at least two butchered bison” (Wright and Marceau 1981:4). “Level 1 [Test Pits 2 and 2A] ... produced ... a fragment of tooth enamel from a large mammal, possibly bison. ... [In] Level 4 we found ... at a depth of 32–35 cm ... the proximal end of a bison radius” (Wright and Marceau 1981:3). Thirty-five bone fragments were recovered from Level 1 of Test Pits 3 and 3A, one of which “is part of a long bone, probably bison” (Wright and Marceau 1981:4). Despite the fact that the predominant species recovered by Wright was bison, he still felt that they were unimportant.

To date, the largest assemblage of bison from Yellowstone National Park and Jackson Hole comes from late Holocene contexts on the former Snake River delta, now inundated by Jackson Lake. Archeological investigations by MWAC in 1987 and 1988 under the direction of Connor (1998) produced the remains of at least 39 bison (Cannon 1991). While it is unclear whether humans were responsible for the entire assemblage, the association of the bone with artifacts and the limited evidence of butchering suggest some of the animals were the result of human predation.

While the results of this review are not conclusive, it does suggest that bison may have been more prevalent in the region than previously thought. In a review of bison and other large mammals, Cannon (1992) found bison to be the second most ubiquitous large mammal occurring at 21 of 31 sites (67.74%), second only to elk (24 of 31 sites). If bison were a more common member of the precontact Jackson Hole faunal community, they may have provided a significant resource to aboriginal groups in the valley, especially prior to the early nineteenth century. It may be time to dust off the model of the local prehistoric economy of GYE and reassess the role of bison (Figures 2.6 and 2.7).

Figure 2.6. Frequency of bison bones based upon number of individual specimens (NISP) at key archeological sites in the GYE in comparison to other mammals.

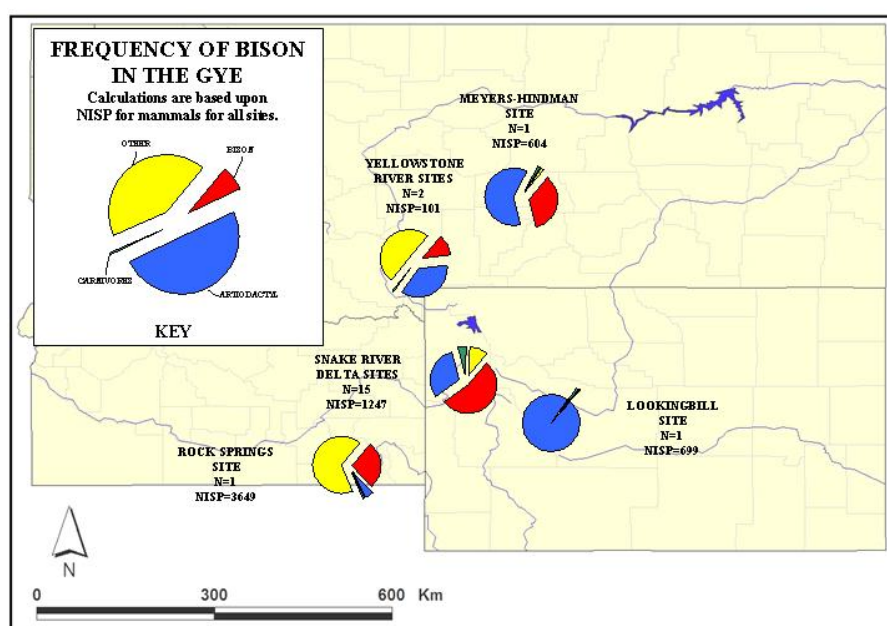
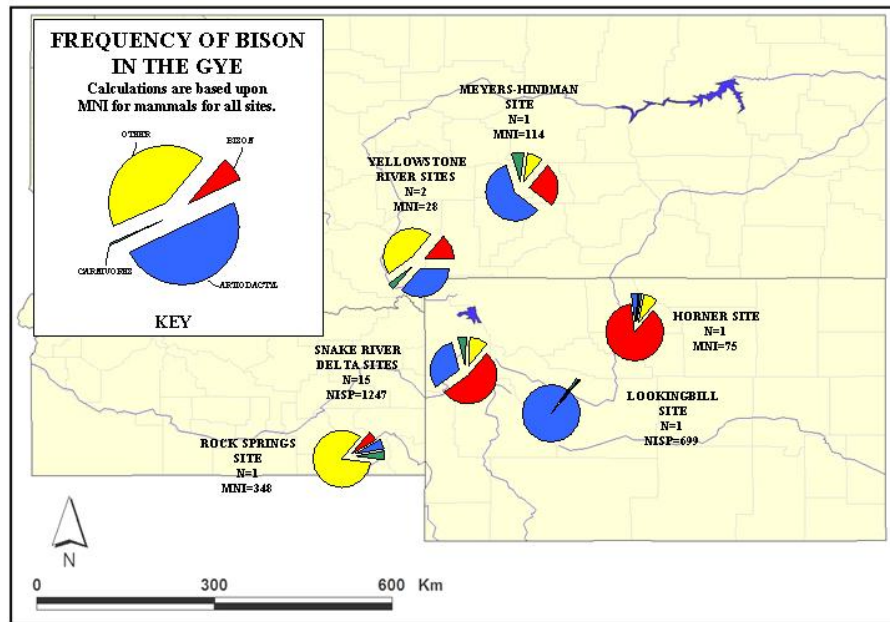


Figure 2.7. Frequency of bison bones based upon minimum number of individuals (MNI) at key archeological sites in the GYE in comparison to other mammals.



The Regional Historic Bison Record

The management policies concerning the GYE have intimately involved bison. Expressions of this range from the public outcry over the slaughter in the late 19th century that produced the Lacey Act (1900) to the current outpouring of support on behalf of the Yellowstone bison slaughtered during the winter of 1996-97 in the name of protecting the local cattle industry (Peacock 1997), and the recent call for the listing of the Yellowstone bison as an endangered species (Federal Register 50 CFR Part 17, Vol. 72, No. 157, Wednesday, August 15, 2007).

The earliest written record of bison in the GYE comes from the Corps of Discovery led by Meriwether Lewis and William Clark (Moulton 1993). In mid-July of 1806, a party under the command of Clark approached the western and northern edge of the GYE. Traveling west they traversed the Gallatin Valley, camping near the site of present day Bozeman, Montana. They continued their eastward trek through the Yellowstone River Valley of present-day Montana. Their brief citation "we had not proceeded on far before I saw a buffalow [sic] & Sent Shannon to kill it" is typical of the early citations (William Clark entry dated 16 July 1806 in Moulton 1993:190). More than 135 citations with specific references to bison were collected for the 19th

century (Table 2.3). The following are examples of the more compelling journal entries from the GYE that provide insight into bison presence there in the 19th century.

Table 2.3. List of observers, year of observation, and number of citations used in this study. The individual citations are stored in Access database maintained by the author as part of GIS project (Cannon and Ratcliffe n.d.).

Traveler	Years in Region	Number of Citations
William Clark	1806	7
Warren A. Ferris	1833	3
Osborne Russell	1835-1839	14
Capt. W.F. Raynolds	1860	5
Walter DeLacy	1863	2
James Stuart	1863	3
A. Bart Henderson	1866, 1867,1870,1871, 1873	44
D.E. Folsom with the Cook-Folsom- Peterson Party	1869	3
Lt. G.C. Doane with the Washburn-Lang- Doane Expedition	1870	3
Calcium Clawson	1871	2
Henry Bird Calfee	1871	2
A.C. Peale with the Hayden Survey	1871-1872	6
J.W. Barlow and D.P. Heap with the Hayden Survey	1871	2
William Holmes with the Hayden Survey	1872	1
William Blackmore	1872	2
E.A. Maynard	1873	2
Theodore Comstock with Capt. W.A. Jones Party	1873	3
R.C. Wallace	1874	1
The Earl of Dunraven	1874	1
P.W. Norris	1830, 1875, 1881	4
General W.E. Strong	1875	2
Lt. G.C. Doane	1876	2
Warren and White with Doane Expedition	1876	1
O.M. Poe	1877	1
William Holmes	1878	1
William Henry Jackson with Hayden Party	1878	2

Traveler	Years in Region	Number of Citations
J.E. Mushbach with Hayden Party	1878	5
Richard B. Hassell	1879	1
Colonel W.D. Pickett	1879-1880	3
Harry Yount	1880	1
George Marshall	1881	2
H. Barnard Leckler	1881	4

In the early nineteenth century, bison (*Bison bison*) may have been a common component of the Jackson Hole fauna, as suggested by this quote by Ferris:

[We] found a large herd of buffalo in the valley, and killed several; also a large bear, which paid with his life [for] the temerity of awaiting our approach (Ferris 1940:163, relating his experience of 31 May 1833 about four miles west of the Gros Ventre River in Jackson Hole).

Yet within a few short decades they were reduced to just two remnant herds, one of which was in YNP (Meagher 1973). Bison were protected in YNP, but by the 1880s they were extirpated in the region outside the park:

There are no buffaloes whatever in the vicinity of the Yellowstone Park, either in Wyoming, Montana, or Idaho, save what wander out of that reservation, and when any do, they are speedily killed (Roe 1972:465, quoting Hornaday 1889:552).

Small, isolated herds may still have been in the GYE, as indicated by this quote from Beaver Dick Leigh of 2 October 1875 in reference to the Henry's Fork area:

Some Indians came here. They had shot a buffalo bull breaking his hind leg on the Middle Fork. He ad [sic] come here and crossed to the west side of the river. The Indian hunters crossed this evening to hunt him up. This is the first buffalo that as been seen since the spring of 1871. It is likely there is a band of cows and calves in the vicinity of the Middle Fork of the North Fork.

The final demise that Leigh was witnessing had begun a few decades before. A quote from Osborne Russell (Haines 1965:138–139), an earlier trapper (1830s–1840s) in the region, also bears witness:

The Buffaloe is already a stranger, altho numerous 10 years ago, in that part of the country which is drained by the sources of the Colorado, Bear, and Snake Rivers and occupied by the Snake and Bannock Indians.

In the Jackson Hole Bison Management Plan (Grand Teton National Park and National Elk Refuge [GRTE–NER] 1996:5), it is noted that bison were absent from Jackson Hole between “at least 1840 and 1948.” The modern Jackson Hole bison herd was created in 1948 with the introduction of 20 individuals (3 bulls, 12 cows, and 5 calves) from YNP to the 1,500-acre Jackson Hole Wildlife Park near Moran. This private, non-profit endeavor was sponsored by the New York Zoological Society, the Jackson Hole Preserve, Inc., and the Wyoming Game and Fish Commission. This population was maintained at between 15 and 30 individuals until 1963, when brucellosis was detected in the herd, and the bison, with the exception of four vaccinated yearlings and five new calves, were destroyed (GRTE–NER 1996).

The herd was revitalized in 1964 with the introduction of 12 bison from Theodore Roosevelt National Park, bringing the herd size up to 21. In 1968, the herd size was down to 11 adults and 4 or 5 calves, who later in the year escaped the confines of the wildlife park. The herd was eventually allowed to range freely in 1969, partially because of the Leopold Report (Leopold et al. 1963), which called for the implementation of ecological principles into the management of natural resources. The free-ranging herd soon established fairly well defined movement patterns in Grand Teton, with summers in the Potholes/Signal Mountain/Snake River bottoms area and winters in the Snake River bottoms and further south. Since the winter of 1975–76, with the exception of the 1976–77, the herd has wintered on the NER (GRTE–NER 1996:6).

Herd size has also grown substantially since becoming free-ranging. Growth in the 1970s was relatively slow, but in 1980 the bison began feeding on supplemental winter feed, intended for elk, on the NER. Herd growth has been dramatic since 1980, probably in large part due to the supplemental feed and the subsequent decrease in winter mortality (GRTE–NER 1996:6).

Chapter III

Questions of Taxonomy

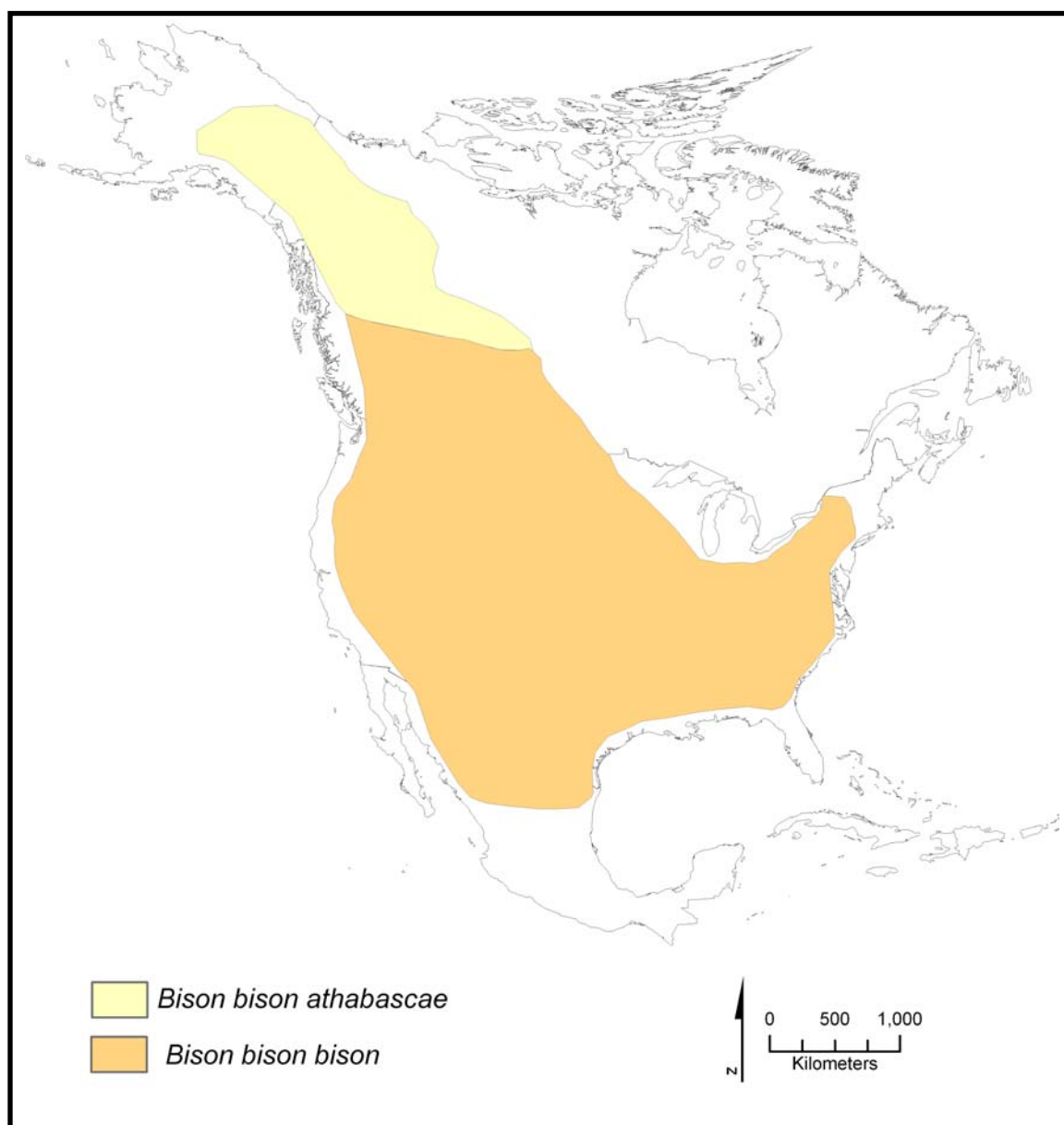
Introduction

Since the nineteenth century, when trappers, explorers, and zoologists first ventured into the Rocky Mountains, there has been controversy surrounding the species of bison occupying these regions. The earliest accounts are filled with descriptions of 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 Norris (1880) described the bison of Yellowstone National Park in the Superintendent’s 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 that 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 (Figure 3.1). However, with the near extinction of the bison in North America, a comprehensive study of its geographic variation has been precluded (van Zyll de Jong 1986). In the latter part of the nineteenth century, biologists recognized a distinct form of bison in northern Canada, formally described as the subspecies *B. b. athabasca* by Rhoads (1897), based on a single specimen he did not directly observe (van Zyll de Jong 1986). While most biologists agreed with Rhoads’s designation of *B. b. athabasca* as at least subspecifically distinct (e.g., Skinner and Kaisen 1947; McDonald 1981a), some felt that the differences in the two subspecies, *B. b. athabasca* and *B. b. bison*, were of little consequence (van Zyll de Jong 1986).

Figure 3.1. Map of geographic distribution of *Bison bison bison* and *Bison bison athabasca* following McDonald (1981a:Figure 23).



According to van Zyll de Jong (1986), the decimation of the bison herds prior to first-hand study and the small number of specimens available for study contributed to the diversity of opinions. In one of the first quantitative studies of museum specimens—primarily crania—Skinner and Kaisen (1947) argued for an overlap in distribution of the two subspecies—*B. b. athabascae* and *B. b. bison*—along the eastern slopes of the Rocky Mountains. However, their argument was unconvincing due to the lack of cranial and postcranial specimens for comparison.

More recently, McDonald (1981a) presented metric data from a limited sample that shows evidence that the *B. b. athabascae* range was limited to the northern Rocky Mountains and the boreal forests of Canada. This model refutes Skinner and Kaisen's earlier model. He suggests a phylogenesis of modern North American bison from an indigenous Nearctic line (*B. 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), studying presumed pure *B. b. athabascae* specimens from northwestern Canada and comparing them to other North American fossil and modern bison, suggests that body size is just one of a number of presumably genetic characteristics that differentiate the two modern species. According to his analysis, *B. b. athabascae* is 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*, whereas with *B. b. athabascae* there is only a reduction in horn core length (van Zyll de Jong 1986).

Arguing for genetic variation, as opposed to ecophenotypic, van Zyll de Jong (1986:54-55) illustrates how the interaction of ecological and behavioral factors, gene flow, and natural selection can account for the maintenance of the distinctiveness of the two modern species. Specifically, the boreal forest ecotone acted as a natural barrier to contact with *B. b. bison* in the grasslands to the south. Interbreeding was also minimized due to the limited seasonal movement

of the two populations 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 that provided them with a greater degree of fitness for surviving in their respective environments.

In a preliminary molecular study from several populations of wood and plains bison in Canada and the United States, Strobeck attempted to determine the status of the two subspecies. Based on this study, Strobeck concluded that wood and plains bison “do not form distinct phylogenetic groups and are not genetically distinct subspecies” (Strobeck 1992:15). With the similarity in mtDNA types from both “wood” and “plains,” the possibility that they may have been distinct subspecies in the past is also refuted, Strobeck asserts.

Geographic isolation of populations may have the effect of creating different genotype frequencies in different herds. Strobeck (1992:15-16) contends in his study that “each population represents a geographical genetic isolate of a once vast population of bison.” This genetic isolation may provide some clues to the morphological variability we see in bison populations. This observation is similar to what van Zyll de Jong (1986:55) found in his morphometric analysis. He goes on to suggest that similar mechanisms are still in operation among ungulates (e.g., caribou) today and can be studied.

In a more inclusive study Wilson and Strobeck (1999) surveyed 11 microsatellite loci of 11 bison populations in order to calculate the genetic variation and genetic distances of wood and plains bison. Their expectation was that large genetic distance should exist between wood and plains bison. One result of their study was that all the sampled bison populations are genetically distinct from one another. According to the authors, this was not unexpected and probably a result of the founder effect and genetic drift, which resulted “from the small number of transfers between herds that have occurred, are probably responsible for the uniqueness of these populations” (Wilson and Strobeck 1999:493). Of particular interest to this study is that the genetic distance between the Yellowstone bison is not as large as expected if these bison were a

distinct population (i.e., mountain bison). The authors indicate indigenous Yellowstone bison were “driven to the area by hunters” (Wilson and Strobeck 1999:493), and, therefore, represent *mountain-dwelling plains bison* (emphasis added).

Understanding the taxonomy of the archeological bison cannot be adequately addressed without genetic analysis (Shapiro et al. 2004), but morphological differences in adult skulls have been commonly used to determine how individual animals, or populations, compare (e.g., Skinner and Kaisen 1947; Walker 1992). In differentiating between *B. b. athabasca* and *B. b. bison*, McDonald (1981a) used horn core morphology as a key characteristic both in size and shape. By comparing the archeological specimens to known taxonomic groups, it may be possible to begin to explore questions concerning their ecology. For example, were these groups geographically and genetically isolated? Or, was there frequent (seasonal) migration between the high elevation valleys and the lower basins that allowed for periodic reinforcement through inbreeding? McDonald (1981a) has suggested that populations of Plains bison periodically reinforced wood bison populations by dispersing into the boreal parks from the adjacent northern grasslands. Researchers interested in the taxonomic relationship of prehistoric bison have often applied a number of descriptive and statistical analyses involving craniometric data (e.g. Walker 1992). In order to assess the relationship of the Grand Teton and Yellowstone specimens to other bison populations, I will apply descriptive and statistical analyses using published data from McDonald (1981a).

Metric Analysis

The Grand Teton and Yellowstone specimens represent late Holocene individuals that should be considered fully modern (Figures 3.2 and 3.3). Three of the individuals were radiocarbon dated with an age range of 770 ± 80 yrs BP to 1380 ± 80 yrs BP making it difficult to argue for a breeding population (Table 3.1). However, the sample, although limited, provides

Figure 3.2. Male archeological specimens from Grand Teton National Park used in study.

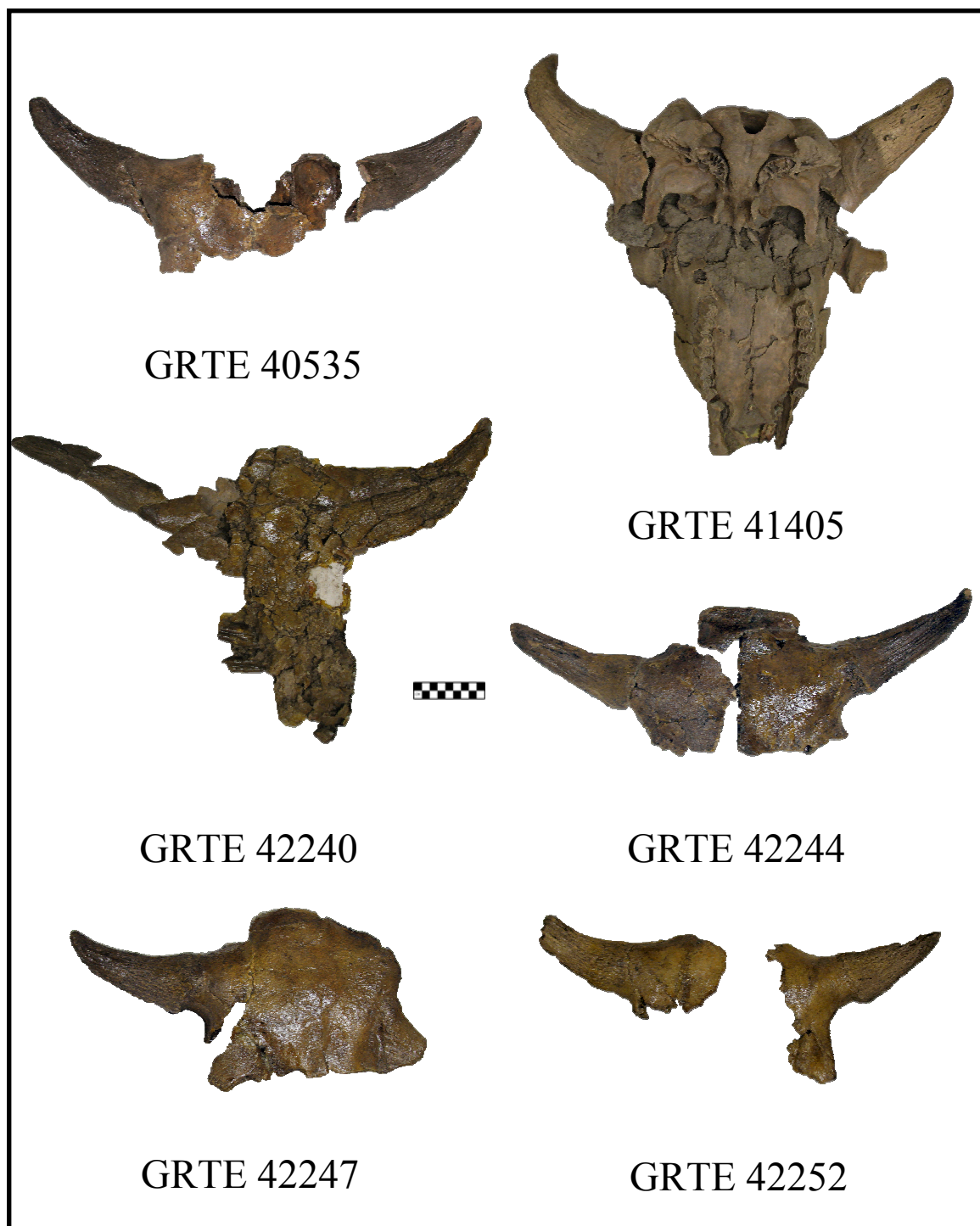


Figure 3.3. Female archeological specimens from Grand Teton National Park used in study.

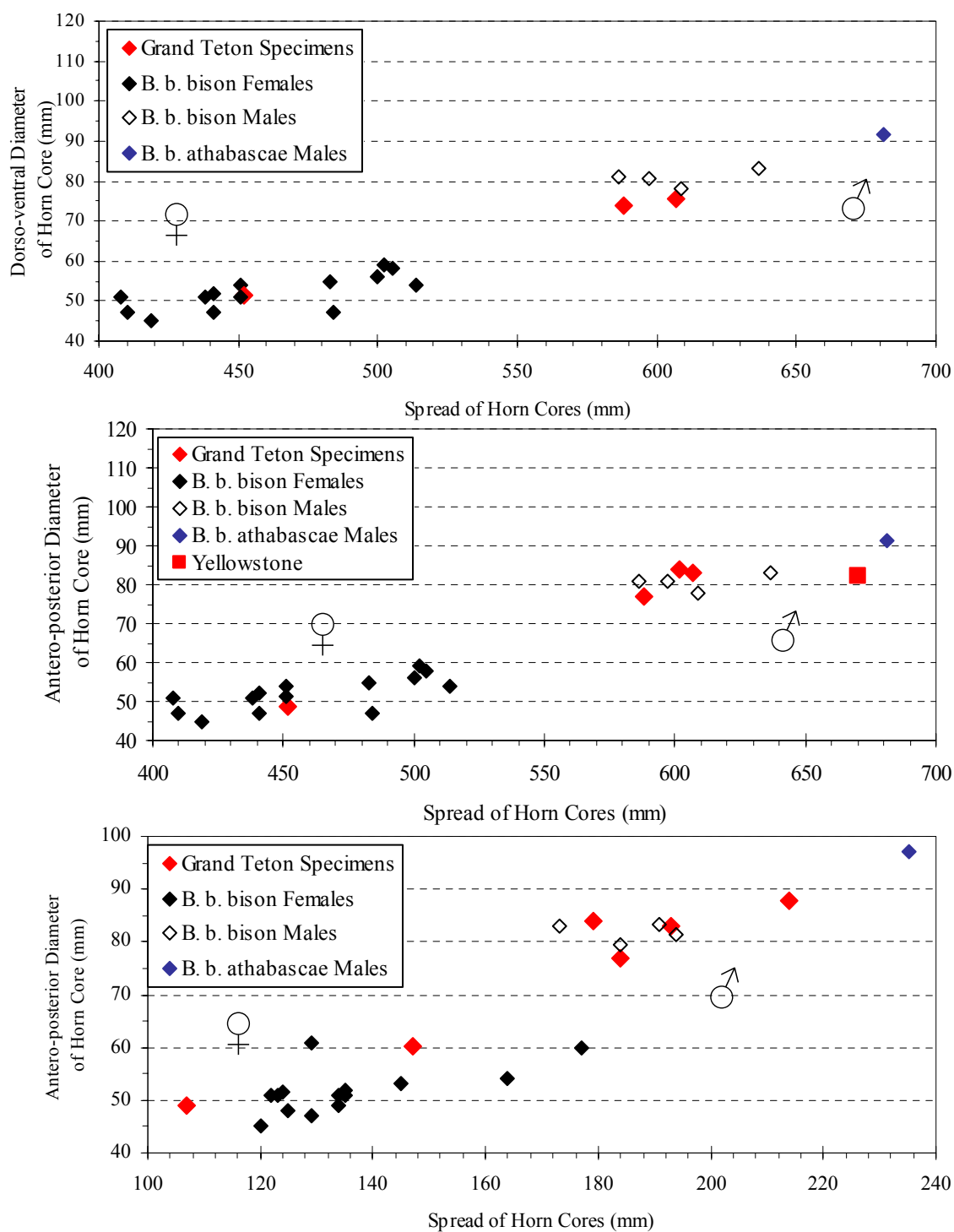


information on how these bison compare to other taxonomic and geographic groups. The sample consists of eight males and two females from Grand Teton, while the Yellowstone specimen is represented by a male. The sex of the specimens was determined visually during the measurement process, with males having more robust features (e.g., burrs on the horn cores). The classification was verified less subjectively through comparison with published data. Sexual dimorphism is clearly illustrated in the robustness of the horn cores (Figure 3.4). Measurements and supporting data for this study are presented in Appendix A.

Table 3.1. Provenience information of archeological specimens from Grand Teton and Yellowstone National Parks.

Specimen Number	Site Number	Sex	Age
GRTE-40535	48TE1102	Male	Late Holocene
GRTE-40553	48TE1114	Female	Late Holocene
GRTE-40555	48TE1090	Female	Late Holocene
GRTE-41404	48TE1102	Male	Late Holocene
GRTE-41405	48TE1090	Male	770 ± 80 yrs BP
GRTE-41406	48TE1102	Male	1380 ± 80 yrs BP
GRTE-42240	48TE1090/1102	Male	Late Holocene
GRTE-42244	48TE1090/1102	Male	Late Holocene
GRTE-42247	48TE1090/1102	Male	Late Holocene
GRTE-42252	48TE1090/1102	Male	Late Holocene
YELL-111083	48YE697	Male	800 ± 60 yrs BP

Figure 3.4. Plots of Grand Teton and Yellowstone National Parks archeological bison skulls in relation to mean bison skull values from United States populations. United States population values from McDonald 1981b: Tables and values for archeological specimens presented in Appendix A.



Using a ratio diagram (Simpson 1941) it is possible to explore how the Grand Teton and Yellowstone specimens compare to other populations. The ratio diagram was applied by van Zyll de Jong (1986) in trying to establish an evolutionary history between modern bison species and the extinct *Bison antiquus occidentalis*. The ratio diagram is a univariate technique in which measurements can be compared to a standard. To replicate van Zyll de Jong's study (1986: Figure 16), as well as that of Walker (1992: Figure 6), *B. antiquus occidentalis* is used as the standard. The technique is a plot of the difference between the log of a measurement from a comparative specimen or the mean of a population and the log of the measurement of a conspecific specimen. The comparative or standard specimen, in this case *B. antiquus occidentalis*, is set to zero with dimensions with negative values indicating the specimen is smaller with a positive value indicating a larger specimen (Lyman 2004). The mean of the Grand Teton male specimens and the Yellowstone specimen measurements were compared to the standard (Figure 3.5). While smaller in all dimensions, the specimens are within the published range of the other modern groups (Figure 3.6).

Figure 3.5. Ratio diagram comparing skull dimensions of the Grand Teton specimens and Yellowstone National Park in comparison with *Bison bison bison*, *Bison bison athabasca*, and *Bison antiquus occidentalis*, with the latter serving as a standard. All measurements included in analysis are from male skulls. (*B. antiquus occidentalis* (N=31) data from van Zyll de Jong 1986: Table 1; *B. b. athabasca* and *B. b. bison* from McDonald 1981a: Table 29 and 34, respectively). Missing data is indicated by breaks in line.

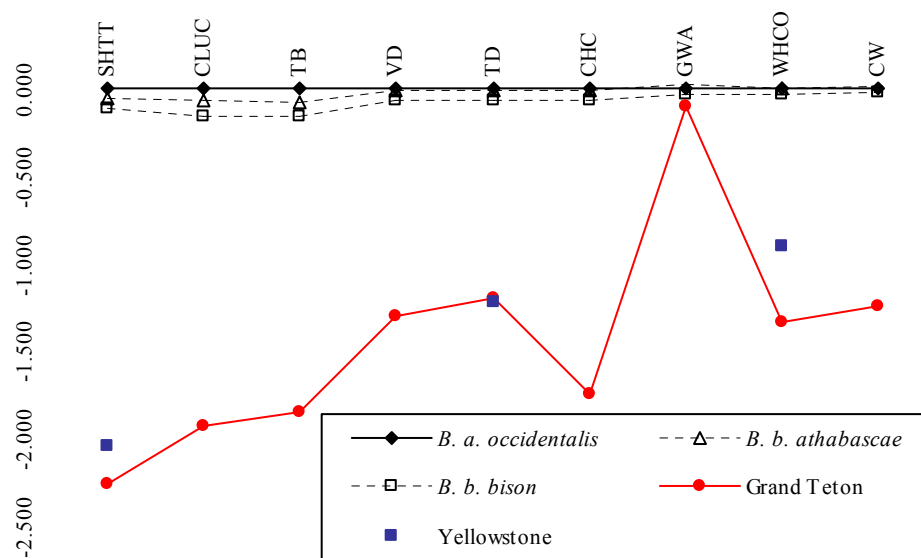
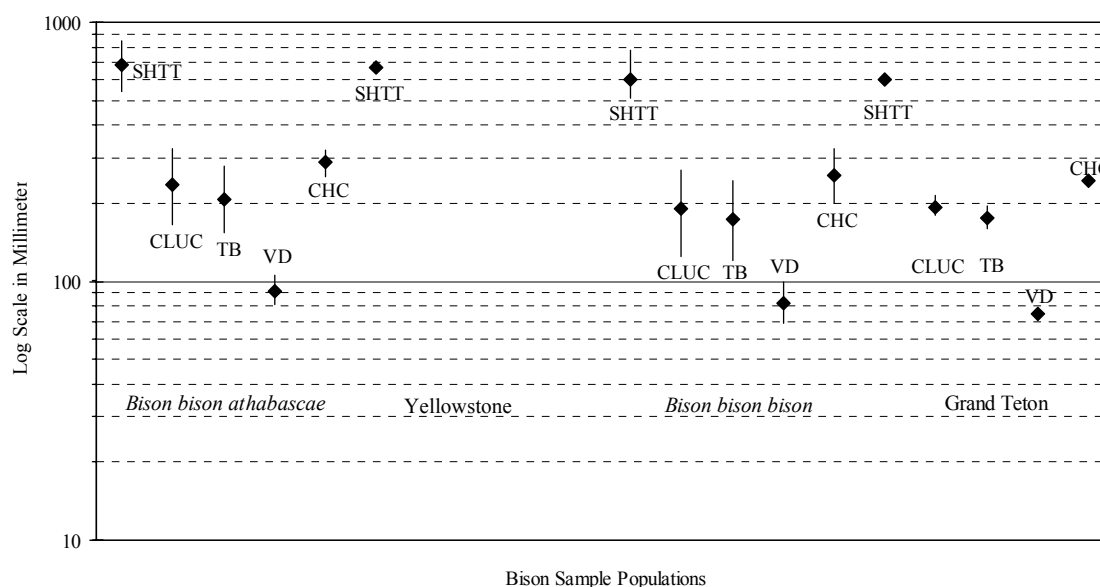


Figure 3.6. Comparison of select horn core measurements of Grand Teton and Yellowstone specimens with other taxonomic groups to illustrate amount of overlap in range of measurements. See Table A1 for measurement abbreviations.



The results of this comparison illustrate that each group is significantly smaller in all dimensions than the *B. antiquus occidentalis* and the other groups. The only characteristic in which Grand Teton sample is close to the other groups is in the width of the skull at the auditory openings. The incomplete set of measurements may be influencing the results. Another possibility exists that genetic isolation of populations may be expressed in the phenotype (see Wilson and Strobeck 1999). Wilson (1974b) illustrates a similar situation from the Casper site in which phenotypic characteristics of two populations may have contributed to the single herd. However, he suggests that gene flow between the two populations occurred. Genetic isolation of intermountain populations in the West may be expressed phenotypically, as discussed by van Zyll de Jong (1986:54-55). A more definitive understanding of the genetic relatedness of intermountain populations will have to wait for genetic analysis.

In order to explore further the taxonomic and potential genetic, relatedness of the archeological specimens to known taxonomic groups I used the discriminant function analysis of the SPSS program (ver. 11.5). Discriminant analysis is useful for building a predictive model of

group membership based on observed characteristics of each case. Discriminant function analysis of craniometric data has been widely used by physical anthropologists in discerning relatedness of archeological populations (Key and Jantz 1981; Keita 1992). The discriminant function analysis technique has been utilized by other researchers seeking to identify the taxonomy of subspecies. Most appropriately, Walker and Frison (1982) applied discriminant function analysis to aid in the classification of archeological specimens of canid skulls from Wyoming. The results showed that specimens originally classified as wolves were actually wolf/dog hybrids exhibiting constant and continual backbreeding to the local wolf populations. The procedure generates a discriminant function (or, for more than two groups, a set of discriminant functions) based on linear combinations of the predictor variables that provide the best discrimination between the groups. The functions are generated from a sample of cases for which group membership is known; the functions can then be applied to new cases with measurements for the predictor variables with unknown group membership. This can provide information on the relatedness of groups.

Given a set of independent variables, discriminant analysis attempts to find linear combinations of those variables that best separate the groups of cases. These combinations are called discriminant functions and have the form displayed in the equation. Using the stepwise method (Wilks'lambda) this procedure automatically chooses a first function that will separate the groups as much as possible. It then chooses a second function that is both uncorrelated with the first function and provides as much further separation as possible. The procedure continues adding functions in this way until reaching the maximum number of functions as determined by the number of predictors and categories in the dependent variable, or until the remaining variables will not aid in the discrimination.

One discriminant analysis was run for this study due to the limited number of archeological specimens and their fragmentary nature, which limited the number of measurements that could be made. Bison are highly sexually dimorphic, so in order to reduce the

chance that any discrimination would be due to sexual variation only males were used in the analysis. In addition to the archeological specimens from Grand Teton and Yellowstone National Parks (n=10), known groups included 69 *Bison bison bison* from the Central Great Plains and 11 *Bison bison athabasca*. Data from these specimens are reported by McDonald (1981b). Six horn core measurements were used in the analysis: spread of horn core (SHTT), horn core length (CLUC), straight line distance of dorsal horn core (TB), dorso-ventral diameter of horn core base (VD), minimum circumference of horn core base (CHC), and antero-posterior diameter of horn core base (TD). The analysis was limited to these measurements based on preservation of the skulls and the history of horn core morphology for discerning taxonomy (McDonald 1981a).

Results of the analysis are presented in Tables 3.2-3.4. Table 3.2 lists the statistics for all discriminant functions derived in the analysis, illustrating the relative importance of each function by several statistical methods. Table 3 shows the results of the prediction and classification stages of the analysis. Of the 89 potential specimens, 71 (79.8%) had enough measurements for analysis. The total percentage of the original groups classified correctly is 88.2%, reflecting the relative ease in discriminating between the groups. The third table in the series reports the standardized discriminant function coefficients. These scores, regardless of the negative or positive sign, indicate the relative power of each variable in the analysis—the higher the coefficient's value the greater the impact of the variable in the analysis (Table 3.4). For this study, the dimensions of the horn core base were the most powerful discriminating variables.

Table 3.2. Statistical table of functions derived during the discriminant function analysis of the archeological and known taxonomic bison specimens.

Function	Eigenvalue	% of Variance	Canonical Correlation	Wilks' Lambda	Chi-square	Degrees of Freedom	Significance
1	0.629	79.7	0.621	0.529	42.950	4	0.000
2	0.160	20.3	0.371	0.862	10.016	1	0.002

Table 3.3. Classification prediction results of the bison groups.

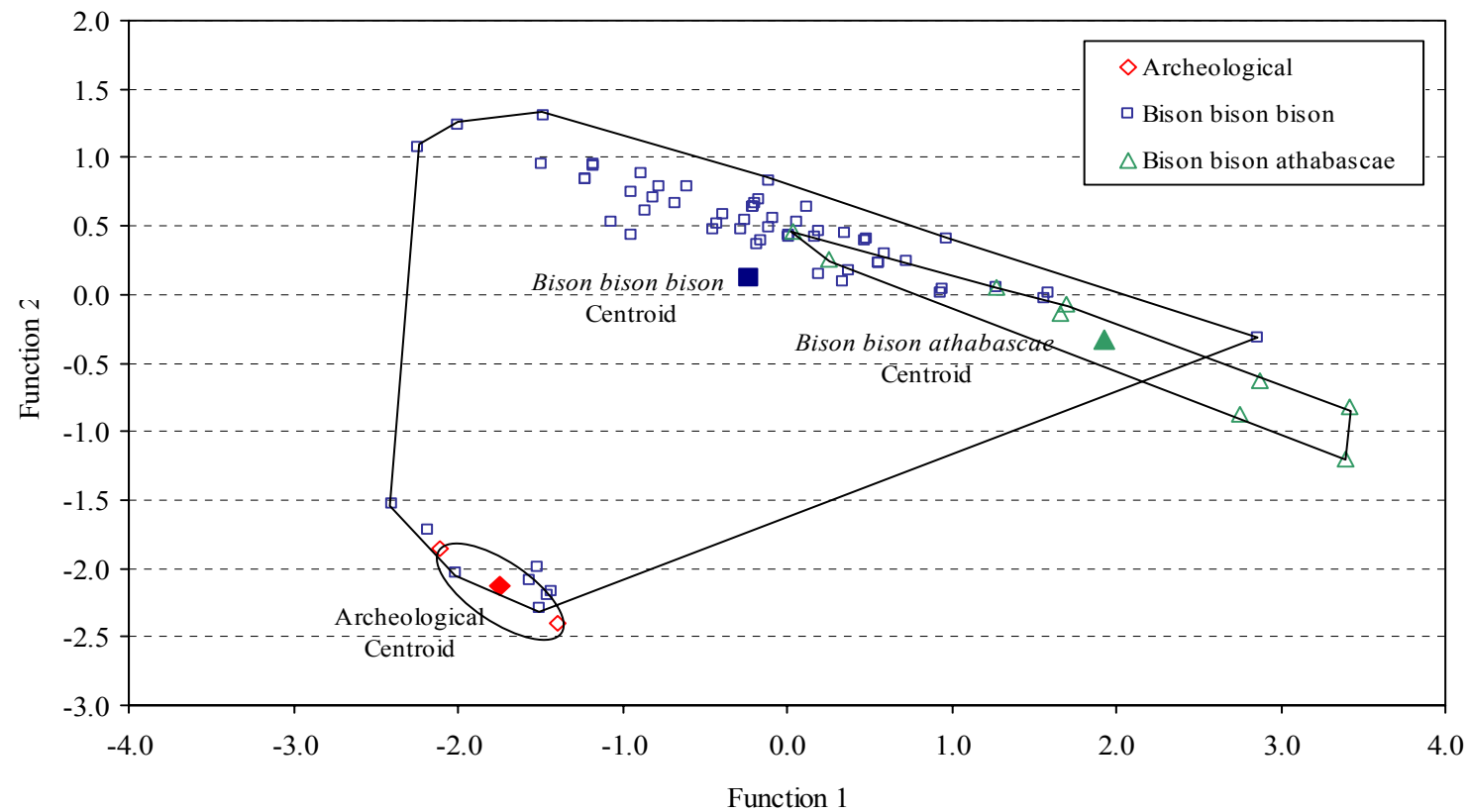
Actual Group	Predicted Group		
	Archeological	<i>Bison bison bison</i>	<i>Bison bison athabasca</i>
Archeological	2 (100%)	0 (0%)	0 (0%)
<i>Bison bison bison</i>	3 (4.6%)	61 (93.8%)	1 (1.5%)
<i>Bison bison athabasca</i>	0 (0%)	5 (55.6%)	4 (44.4%)
88.3% of original grouped cases correctly classified.			

Table 3.4. Standardized canonical discriminant function coefficients of bison groups.

	Function 1	Function 2
VD	0.457	0.919
TD	0.793	-0.652

Figure 3.7 illustrates the discrimination between the groups, but also the overlap and variability between the two known taxonomic groups. Eigenvalues for Function 1 are relatively high (0.629) illustrating the variability between the groups, although Walker and Frison (1982) indicate that only values >1.0 should be considered significant. Two of the Grand Teton archeological specimens were correctly grouped and suggest possible genetic isolation of these populations. Of additional interest are the three *Bison bison bison* specimens misclassified with the archeological group represent high altitude specimens. These include a specimen from Mt. Audubon, Colorado (3438 m AMSL), a specimen from the Beartooth Plateau, Wyoming (3042 m AMSL), and a specimen from the Yogo Peak in the Little Belt Mountains of Montana (2683 m AMSL). While by no means definitive, these results suggest that bison occupying high elevation environments may have similar characteristics. It may also reflect periodic crossbreeding by mountain-dwelling and Plains bison as suggested by the mtDNA analysis of Wilson and Strobeck (1999). Five specimens classified as Woods bison were predicted by this analysis to belong to the Plains bison

Figure 3.7. Discriminant function analysis scores for archeological and *Bison bison bison* and *Bison bison athabasca* groups.



group. Again, this may be reflective of periodic crossbreeding of these two populations (McDonald 1981a).

The results of the various analyses of the taxonomic relationship of the archeological specimens suggest a potential genetic isolation of Grand Teton bison. These results are preliminary considering the limited sample size. However, one thing it does provide is testable hypotheses for further study:

- If bison occupying the high elevation valleys of Jackson Hole and Yellowstone National Park are genetically isolated populations living year-round at high elevations, this may be illustrated by low variability in their stable isotope signatures.
- Bison herds in the region have a high degree of group integrity. Herds staying within restricted ranges and intermixing and interbreeding is limited.
- Discriminant function analysis suggests that crossbreeding between populations has probably occurred. This would indicate seasonal migrations between high altitude and low altitude range. Again, this should be reflected in the stable isotopic signatures.

In summary, the results of the metric analysis of the bison skulls:

- Indicates a predominance of male bison. If each of these bison is the result of hunting it suggests a pattern of pursuing isolated bulls. This pattern is different from the more typical Plains-style of taking mixed cow-calf herds in mass kills that utilized topographic features to either trap or jump bison (Frison 1991). However, the hunting of isolated or small groups of bulls has been documented in other mountain settings (Reeves 1978), including other sites in Jackson Hole (Cannon 1999) and Yellowstone National Park (Cannon et al. 1997).
- Applying the ratio diagram analysis, all of the archeological specimens were significantly smaller in all dimensions than either the early Holocene *Bison antiquus occidentalis*, or the modern Plains and Woods bison.

- A preliminary study applying discriminant function analysis suggests a potential genetic isolation of the Grand Teton specimens. While genetic isolation conjures up patterns of physical anomalies, the result of depression of the gene pool, genetic drift may be a more likely vehicle for this pattern.

Chapter IV

Holocene Climate

Introduction

Delineation of regional and local paleoclimatic dynamics during the terminal Pleistocene and Holocene has been an important aspect of archeological investigations over the past three decades (e.g., Lipe 1995). During this time period, interdisciplinary studies, under the rubric of *environmental archeology*, have sought to understand the dynamic relationship between human cultural systems and the ecological system in which they live (Reitz et al. 1996). These studies have compiled a picture of large-scale shifts in climatic regimes, and these shifts have significantly affected vegetational suites, animal populations, and presumably human settlement and subsistence, with the most dramatic shift being the Pleistocene–Holocene transition. However, to fully understand the influence these climatic shifts had on human socioeconomic systems it is imperative that problem-oriented studies be generated that focus on further refinement of the effect that climate had on prey species, such as bison. As Grayson (2008) has noted focusing on the histories of individual species allows a more complete understanding of the evolution of these systems, but also how humans have interacted and influenced them. This information is also important for modeling the Holocene development of biotic communities (Grayson 1977:512; Lyman 1996), as well as the thoughtful management of ecosystems (Lipe 1995; Cannon 2001).

Other areas to be investigated include the development of new methods of data-model comparison (Whitlock and Millspaugh 1994), as recent compilations of paleoclimatic data by Barnosky et al. (1988; Whitlock 1993; Whitlock and Bartlein 1993; Whitlock and Millspaugh 1994), emphasize that patterns of paleoclimatic change are not continuous across the continent, but are time transgressive. Therefore, a more concerted effort must be placed on delineating the *local* paleoenvironmental sequence using a variety of proxy data (e.g., paleoentomology, paleontology, and palynology) at the finest resolution possible. For example, applying a time-

stratigraphic term, such as the Altithermal or Hypsithermal (cf. Antevs 1955), to vast areas of the west in hopes of explaining patterns of human occupation is no longer valid or desirable. Recent research has shown that the occurrence of post-glacial maximum warmth and aridity is complex and affected by solar insolation and atmospheric circulation patterns (Whitlock and Bartlein 1993). While originally thought to represent a single climatic event in the west, it has now been demonstrated to have spatial and temporal variability (Whitlock and Millspaugh 1994). As this example suggests, local level investigations of paleoclimatic conditions are an essential aspect of contemporary archeological investigations if we are truly to understand the complex interaction of humans and their environments.

The following chapter provides a contextual overview of regional paleoclimatic patterns for interpreting bison migration and behavior. In addition to the regional pattern, local conditions, both geomorphic and vegetative, will also be discussed. All ages are presented as uncalibrated radiocarbon years before present, unless otherwise noted.

Regional Paleoenvironmental Reconstruction

In recent simulation models, large-scale climatic shifts have been shown to result from changing atmospheric circulation patterns caused by changes in the orientation of the earth's axis (COHMAP 1988). At 18,000 BP, the Laurentide ice sheet caused a split in the jet stream, while cooling temperatures continent-wide. A deflection of the southern branch of the jet stream brought moister conditions to the southwest, while anticyclonic winds, generated by the ice sheet, brought prevailing easterlies and dry air to the northwest instead of the moisture-laden westerlies that are the common pattern today (Thompson et al. 1993). Cooler than present conditions existed in the region, depressing tree lines and vegetative communities hundreds of meters in comparison with modern distributions.

Prior to about 18,000 BP, full-glacial conditions existed in the Intermountain West. The timing of the transition from full-glacial to late-glacial conditions in the region occurred between 15,000 and 12,000 BP. By about 12,000 BP, orbitally increased solar radiation enhanced the

thermal contrast between land and sea, producing strong summer monsoons that raised lake levels in arid regions worldwide. With increased insolation and glacial retreat, readjustments in vegetation communities followed (COHMAP 1988).

At Late Glacial Maximum (LGM) winters were probably no harsher than at present, but seasonality was much reduced, resulting in colder summers. Annual temperature in the study region was $\sim 12^{\circ}\text{C}$ colder than at present. The summer monsoon was absent, and the Pacific subtropical high was very weak. Cold, dry conditions are retrodicted for the study region. Proxy data support this model (Thompson et al. 1993). Glaciation was extensive (Andrews 1987; Clayton and Moran 1982; Porter et al. 1983; Richmond 1986), with active mountain glaciers in the Lemhi Range, the Lost River Range, and the Tetons, and a large ice cap covered the Yellowstone Plateau (Porter et al. 1983). Permafrost conditions existed on the Snake River Plain and in the Wyoming Basin at this time (Fosberg 1965; Malde 1964; Mears 1981), and permafrost appears to have been preserved in special environments well into the Holocene (Dort 1968). Streams had higher capacities and competencies during this time (Baker 1983; Harrold and Dort 1987), and vegetation zones were elevationally depressed (Barnosky et al. 1987). Pleistocene megafauna were also common in the surrounding area (Butler 1978; Grayson 1991; Walker 1987a), although none have been recovered in Jackson Hole or Yellowstone.

Around 15,000 BP, changes in the geometry of the earth's orbit and axial tilt initiated a trend toward warming and an increase in seasonality (COHMAP Project Members 1988). The Pacific subtropical high was beginning to strengthen and to provide some moisture, but the area was generally arid (Whitlock and Bartlein 1993). Regional data are in close agreement with the model's retrodictions for this period (Thompson et al. 1993). Haynes (1990) suggests that this period ended with a millennium of severe drought (12-11 ka [thousands of years before present]). This drought coincides with the earliest human presence in the region (Frison 1991; Gruhn 1961; Gruhn 1965) and also with the extinction of the Pleistocene megafauna (with the exception of the bison). Deglaciation progressed (Richmond 1986; Teller 1987), and vegetation zones shifted

upwards in elevation (Barnosky et al. 1987). A wide variety of now-extinct Pleistocene megafauna was regionally present (Butler 1978; Walker 1987a), including bison (*Bison bison antiquus* and *Bison bison occidentalis*), musk ox (*Symbos* sp.), mammoth (*Mammuthus* sp.), horse (*Equus* sp.), and camel (*Camelops* sp.). On the Yellowstone Plateau a number of minimum ages for deglaciation have been obtained (Cannon et al. 1997:Table 3). The oldest of these is $14,490 \pm 350$ yr BP from Solution Creek on the southeastern shore of Yellowstone Lake (Richmond 1976). More recently, Licciardi et al. (2001) have provided additional minimum cosmogenic ages for deglaciation. The oldest of these is from the Eightmile moraines near Chico, Montana (16.5 ± 0.4 ^3He ka and $16.2 \pm$ ^3Be ka).

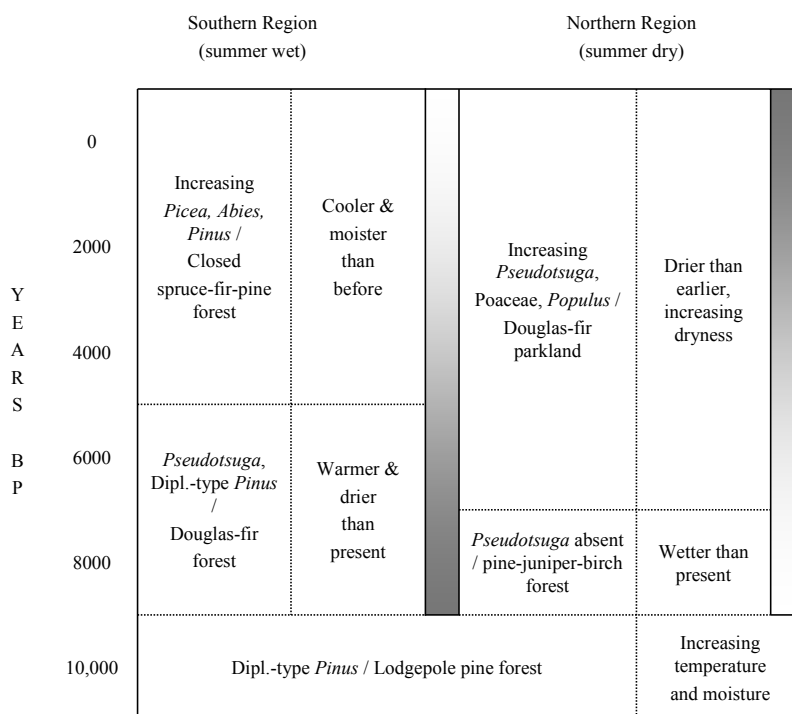
Worldwide temperatures were as much as 2–4°C higher than at present during this time period (COHMAP Project Members 1988). In response, seasonality was very pronounced, and summer warming caused the jet stream to shift northward (Thompson et al. 1993). The general circulation model predicts post-glacial maximum values of solar radiation 8 percent higher in summer and 8 percent lower in winter than at present.

The changing position of the jet stream caused regional variation in the timing of periods of maximum post-glacial moisture and maximum post-glacial aridity (Beiswenger 1991; Davis and Sellers 1994; Whitlock and Bartlein 1993). Under modern climatic conditions, the seasonal shift of the jet stream northward in the summer and southward in the winter produces distinctive seasonal patterns of precipitation in the western United States (Hidore and Oliver 1993). In the winter, the jet stream is positioned over the northern tier of western states. At this time of the year, Pacific storms track the jet stream inland from Washington–Oregon eastward to Idaho–Montana–Wyoming. These winter storms drop their moisture over the Pacific Northwest and into the Northern and Middle Rocky Mountains. However, during the summer, aridity prevails in the Middle and Northern Rockies when the jet stream and its associated storm track migrates northward into Canada. The northern migration of the jet stream during the summer produces stronger onshore flow along the Gulfs of Mexico and Cortez, drawing moisture northward from

these areas but generally not as far north as the Jackson Hole area. Wind velocity was probably greater than present, which contributed to increase precipitation in northwestern Wyoming (Whitlock 1993).

The study region is situated in the present-day summer-dry/winter-wet zone of precipitation. Whitlock and Bartlein (1993) document regional pollen data that indicate that the maximum post-glacial aridity occurred in summer-dry/winter-wet areas, such as the Snake River Plain and the southern portion of the Northern Rocky Mountains, during the latest Pleistocene/earliest Holocene. On the other hand, maximum Holocene aridity occurred in the late Holocene in summer-wet/winter-dry areas, such as the Colorado Plateau, Great Plains, and northern Yellowstone National Park (Figure 4.1). Conversely, summer-dry/winter-wet areas experienced moist conditions during the Neoglacial, while in summer-wet areas drying progressed into the late Holocene (Figure 4.1).

Figure 4.1. Modified Whitlock and Bartlein's (1993:Figure 1) summary of pollen, vegetation, and climate change in the Greater Yellowstone Ecosystem. Increased shading indicates increased aridity.



Davis and Sellers (1994) developed a similar model of post-glacial climatic change that predicts a north–south gradient in the timing of both a late Pleistocene/early Holocene pluvial and the period of maximum Holocene aridity. In the Pacific Northwest, within the present-day summer-dry/winter-wet regime, they predict a post-glacial pluvial to have occurred at 11,500 BP, whereas in the American Southwest, a summer-wet regime, the pluvial peaked at 9000 BP. The model predicts maximum post-glacial aridity beginning at 10,000 BP in the summer-dry/winter-wet zone but not until 6000 BP in the summer-wet Southwest.

Regionally, a brief increase in effective precipitation may have occurred between 11,500 and 10,000 BP. This is documented most strikingly in Lake Bonneville's rise to the Gilbert Shoreline (Currey 1990) and in the very moist conditions evident in Folsom and early Plano sites (Albanese and Frison 1996; Butler 1978; Haynes 1990; Swanson 1972).

The pollen record from Grays Lake in southeastern Idaho suggests *Pinus* and other conifers grew in the foothills (Beiswenger 1991). Other proxy data (e.g., faunal records [Mead and Mead 1989; Graham and Mead 1987], fossil insect assemblages [Elias and Toolin 1990], and permafrost features [Mears 1981]) from the region also contribute to this model of cool, dry conditions with open vegetation.

Whitlock (1993) estimates that between ~14,000 and ~11,500 BP, the climate in Yellowstone National Park was ~5-6°C colder than present. By 12,000 BP, the continental ice sheet diminished significantly, and with it the predominant easterlies also diminished. A resultant increase in January and July temperatures and in January precipitation also occurred (Whitlock 1993:192).

In montane regions, *Picea* was present between 12,000 and 11,000 BP, with *Pinus albicaulis*-type and *Abies* recolonizing these areas after 11,500 BP (Davis et al. 1986; Mehringer et al. 1977; Mehringer 1985; Whitlock and Millspaugh 1994). The pollen record from this time period demonstrates the recolonization of subalpine forests in the recently deglaciated mountains from the surrounding basins (Thompson et al. 1993). Increased moisture and temperatures

between about 11,500 and 11,200 BP are indicated by the pollen spectrum of Grays Lake, which illustrates an abundance of spruce and *Artemisia*, as well as other taxa (Beiswenger 1987, 1991). However, it should be noted that temperatures were still cooler than present.

Individual faunal species and communities also were affected by climatic and vegetation shifts. Mammalian biogeographers have referred to late Pleistocene faunal communities as “disharmonious,” “intermingled,” and “nonanalog assemblages” when describing the heterogeneous nature of the species composition in relation to modern, pre-European community patterns (FAUNMAP Working Group 1996). In their recent paper, the FAUNMAP group uses a number of statistical methods to test two models of community response to environmental change. The Gleasonian model (Gleason 1926) assumes “that species respond in ecological time to environmental change in accordance with their individual tolerance limits, resulting in shifts with varying rates, at different times, and in divergent directions” (FAUNMAP Working Group 1994:1601). In contrast, the Clementsian model (Clements 1916) assumes that large groups of species are in equilibrium and their organization is determined primarily by biological interaction, which results in communities being long-lived geologically. Based on their analyses, faunal communities conform to the Gleasonian model. As such, modern community patterns have only appeared in the last few thousands years through the process of individual species addition and subtraction throughout the late Quaternary (FAUNMAP Working Group 1994:1602).

Characteristics of biogeographic regions also were investigated as part of this study (FAUNMAP Working Group 1994:1602-1603). For the late Pleistocene, eastern Idaho shares characteristics of several faunas: species that generally prefer dry, open habitats (e.g., pocket gopher, desert shrew, and black-tailed jackrabbit), and species indicative of northern grasslands (northern pocket gopher, Richardson’s ground squirrel, and sagebrush vole), alpine tundra (pika), and coniferous forests (yellow-bellied marmot, heather vole, and bushy-tailed woodrat). Faunas in northwestern Wyoming are characterized by a mixture of species indicative of northern grasslands, alpine tundras, and coniferous forests. Extinct megafauna also were part of this

community. These include mammoth (*Mammuthus* sp.), sloth (*Nothrotherium* sp.), bison (*Bison antiquus*), camel (*Camelops* spp.), and horse (*Equus* spp.). Some of these species were of economic importance, particularly the mammoth (Miller 1989) and the bison (Butler et al. 1971).

Several extralimital species from eastern Idaho sites demonstrate the nature of change from the late Pleistocene to late Holocene. One of the most significant shifts in range is illustrated by the collared lemming (*Dicrostonyx torquatus*), a species now limited to well-drained tundra habitats north of the boreal forest. A minimum of four individuals were identified from late Pleistocene deposits ($11,530 \pm 250$ BP) in Jaguar Cave (Guilday and Adams 1967:29). Other late Pleistocene deposits in Wyoming and north-central Nebraska indicate this species was widespread south of the ice sheet (Walker 1987a:348). The presence of this species indicates cold conditions in an open environment. Based on physiological evidence, Walker (1987a:121) has suggested the collared lemming is more indicative of cold environments with heavy snow cover than of the extant Arctic tundra conditions.

Pika (*Ochonotona princeps*) are common along talus slopes and rockslides, usually near timberline (Burt and Grossenheider 1976:202). During the late Pleistocene and early Holocene, pika were found at lower elevation sites, such as Moonshiner Cave (White et al. 1984) and Wilson Butte Cave (Gruhn 1961) along the Snake River Plain, as well as Jaguar Cave (Swanson 1972) in the Birch Creek valley. Walker et al. (1985) suggest pika remained at lower elevations until at least 7000 BP. During the mid-Holocene, that pika appear to have migrated upslope, a possible response to changing vegetation community structure. Walker (1987a:380) notes that *Ochonotona* remains are absent from late Holocene and modern assemblages in the Pryor Mountains of Montana. Pika also become less common through the Holocene at sites in the northern Bighorn Mountains (Chomko 1987). At lower elevations (1,830 m) near the basin of the Beaverhead Mountains, Swanson (1972:Table 12) reports *Ochonotona* from essentially modern deposits in Unit 15 ($<370 \pm 80$ BP) at Veratic Rockshelter.

The presence of the black-footed ferret (*Mustela nigripes*) in the late Pleistocene deposits of Jaguar Cave was problematic to Guilday and Adam (1967:30), especially in consideration of the absence of prairie dog remains, a major prey item of the ferret (Hillman and Clark 1980:2). Guilday and Adam (1967:30) suggest that the presence of these “active predators” is not unexpected and may be more behavioral than a response to climate change. However, more recent excavations in Idaho have produced additional remains of black-footed ferret (e.g., early Holocene deposits at Moonshiner), as well as white-tailed prairie dog remains (*Cynomys leucurus*) from two late Pleistocene faunas in southern Idaho (Rainbow Beach and Duck Point). Since at least the early Holocene, the ranges of both of these species has spread to the east and south.

The boreal red-backed vole (*Clethrionomys gapperi*) has been recovered from three locales on the Snake River Plain, areas that are today xeric and dominated by sage–grassland communities. Although its present range in Idaho overlaps with its paleo-distribution, its ecology and distribution from valley sites is consistent with the paleovegetation record. For instance, Walker (1987a:350) notes that the boreal red-backed vole “prefers moist habitats with abundant litter stumps and logs in coniferous forests but has been found in hardwood deciduous forests as well.” The presence of the boreal red-backed vole from late Pleistocene–early Holocene deposits is consistent with the pollen record of coniferous forests present in the valleys at this time. In Idaho, the only records of the boreal red-backed vole are from late Pleistocene and early Holocene deposits.

Caribou (*Rangifer tarandus*) were recovered from three sites in eastern Idaho, which illustrates a slight southern extension of their range during the late Pleistocene and early Holocene. Modern distributions extend as far south as northern Idaho, although major populations are further north in Canada and Alaska (Miller 1982). Across their modern geographic range, caribou encompass a variety of habitat types from tundra to taiga to the eastern woodlands. The

habitat of the western woodland caribou includes mountain summits above timberline, as well as alpine meadows and open subalpine forests (Edwards 1958).

In sum, the latest Pleistocene and earliest Holocene was a period of dramatic climatic change. Climatic shifts were most likely the result of increased solar radiation and its effect on the wasting of the continental and cordilleran ice sheets. With the reduction of the continental ice sheet, previously predominant easterlies diminished and the January jet stream moved northward to about the latitude of the northern Great Basin. Greater than present wind velocity also helped to increase precipitation. While temperatures were still cooler than at present, a trend towards warmer conditions began.

“Disharmonious,” “intermingled,” and “nonanalog assemblages” are terms that have been used to describe sympatric relationships of species within late Pleistocene communities that today are allopatric. Paleontological and archeological deposits in eastern Idaho and Wyoming have revealed members of such diverse habitats as alpine tundra and xeric grasslands living within the same community. Several extinct megafaunal species have also been recovered from deposits of this age. Biotic communities during this period were much more diverse than modern communities, thereby presenting a number of subsistence options to groups living at the time. While paleogroups (e.g., Clovis and Folsom) have historically been viewed as big-game hunters, recent evidence is emerging from the northern Rockies that suggests that they practiced a more diverse economy (Davis 1993:270–271). Understanding the parameters of this economy (e.g., its spatial and temporal range) should be an important pursuit of archeologists working in the region where a diverse range of ecosystems exist within relatively short distances of each other.

Regionally, effective moisture began to gradually decrease around 10,000 BP (Currey 1990). This was generally a period of increased warming and drying. Davis (1984) believes that changes in the season of maximum solar insolation caused by orbital changes may have influenced the timing of vegetative response to warming and drying. He sees a xeric vegetation response at low elevations in the early Holocene, and at high elevations later in the middle

Holocene. Essentially, modern Holocene vegetation conditions were prevalent by 9000 BP (Mehring 1985). The Great Salt Lake record indicates that effective moisture began to gradually decrease around 10,000 BP (Currey 1990). Murchison (1989) suggests that the lake fell to an early Holocene low between 8800 BP and 7800 BP. A minor rise occurred between 7600 BP and 7000 BP before dropping to post-glacial low levels between 6000 and 6800 BP.

By about 9000 BP, spruce–whitebark pine and limber pine–fir parkland are dominant in the higher elevations of western Montana and Idaho (Mehring et al. 1977; Davis et al. 1986). Although a time-transgressive pattern of increasing temperatures was in evidence throughout the west, summer temperatures in general were warmer than present (Thompson et al. 1993). On the Snake River Plain, increasing aridity began about 10,200 to 10,000 BP, with a peak in warm, xeric conditions around 7300 BP (Beiswenger 1987, 1991). However, altitude, edaphic conditions, and plant autoecology also may have modified the effect of climate on local communities (e.g., Davis et al. 1986).

There is no evidence that cirque glaciers reactivated during this period (Davis 1988). Beiswenger (1991) reports that maximum Holocene aridity occurred around 8200 BP at Greys Lake, Idaho, whereas at the Lost Trail Pass bog the period of maximum Holocene warmth occurred between 7000 and 5000 BP (Mehring et al. 1977).

In the summer-dry/winter-wet regime of Jackson Hole, maximum warmth and aridity occurred around 9500 BP, lasting until about 5500 BP (Whitlock and Bartlein 1993; Figure 4.1). The pollen record from Loon Lake, located south of the Yellowstone National Park boundary, indicates the forests were composed of lodgepole pine, with Douglas fir, whitebark or limber pine, and subalpine fir as minor constituents. Dry, open habitats were also present, as indicated by higher than present percentages of *Artemisia*, *Sarcobatus*, other Chenopodiaceae, and *Selaginella densa*-type spores (Whitlock et al. 1995).

The mid-Holocene of western North America is often viewed as a period of maximum warmth and aridity, initially defined by Antevs (1948) and labeled the Altithermal interval.

However, post-glacial climate and vegetation community response in the region appears to have been complex. Davis et al. (1986), in their examination of pollen records from several sites on, or adjacent to, the Snake River Plain, identified evidence of multiple thermal maxima. Their evidence displays a consistent difference in climatic histories in which low-elevation sites reflect xerothermic conditions prior to about 6000 BP, while higher elevations indicate maximum warmth after 6000 BP. Mountain cirque glaciation during the middle Holocene is rare for the Rocky Mountains (Davis 1988). It is unclear if fluvial aggradation occurred in the middle Holocene (Knox 1983). However, it seems fair to infer that dry conditions would have caused vegetation denudation and hillslope instability, resulting in increased slope wash, debris flow, and colluviation at a time when streams were least able to remove laterally derived sediment, thus facilitating valley filling.

A number of pollen fossil records from Idaho, western Montana, and northwestern Wyoming suggest that climatic conditions at 6000 BP were warmer and drier than at 9000 BP. However, at some sites the evidence indicates conditions were either not significantly different at these two time periods, or, as is the case at the high elevation Lost Lake site in Montana (Barnosky 1989), conditions became more mesic (Thompson et al. 1993).

In southern Idaho and on the western Snake River Plain the pollen spectra have been interpreted as indicating that moister conditions existed around 9000 BP than present (Davis 1981; Henry 1984). However, more recent studies involving regional pollen spectra and paleoclimatic modeling indicate the climatic maximum was time-transgressive. In northwestern Wyoming for example, a rise in *Pseudotsuga* (Douglas fir) and *Populus* (aspen) pollen between 9500 and 5000 BP indicates this was the period of maximum warmth for this region. Other indicators from the region of increased warmth and aridity are provided by upslope migration and local extinction of more mesic species, such as spruce, fir, and whitebark pine (Baker 1976; Whitlock 1993).

The effects on mammalian community structures have not been well investigated for the region. Guilday (1969:49), in his analysis of small mammals from the Wasden Site, noticed a significantly larger number of them and a more diverse assemblage in pre-Mazama layers (ca. 7000 BP), which he interpreted “as indicating progressive desiccation in the upper layers.” Building on Guilday’s analysis and the geomorphic data from the Wasden site, Butler (1972) provides a model for a greater abundance of grasses and forbs in the sagebrush–grass biome on the Snake River Plain prior to 7000 years ago than has occurred since. Such a community could have supported, according to his model, “either larger numbers of or larger big game than now” (Butler 1972:53).

Additional information may also be gained from this faunal assemblage for interpreting biotic responses to climate change. Guilday (1969:Table 1) notes a large number of individuals of the genus *Sylvilagus* sp. (cottontail rabbit). The two potential species, *S. audubonii* and *S. nuttallii*, have different habitat requirements, “arid regions” (Chapman and Willner 1978:1) for the former and sagebrush (Chapman 1976:1) for the latter. These species also differ in size, with *S. audubonii* being generally larger than *S. nuttallii*. It may be possible to separate these two species based on skeletal metric data, which then may be used to further test climatic models, such as those proposed by Davis et al. (1986) and Butler (1972). A similar study was conducted by Grayson (1977) for *Lepus* spp. (jackrabbit) recovered from the Connley Caves fauna in south-central Oregon. In this study Grayson was able to metrically separate two species of jackrabbit, and he was then able to determine that the pre-Mazama species were predominantly *L. townsendii*, which tend to occupy higher elevations and grassier habitats, and *L. californicus* was predominant in post-Mazama deposits. *L. californicus* occupies more southern regions at lower elevations and shrubbier habitats. In other words, prior to Mazama conditions were cooler and more moist than after the Mazama ash fall.

Regionally, shadscale and sagebrush communities were at their greatest extent between 7000 and 4000 BP, and they were expanding at the expense of grasses and conifers (Mehring

1985). These vegetational changes resulted in the reduction of big game populations and the development of an archaic, or more diverse, lifestyle in the late Paleoindian period (Butler 1978; Frison 1991), a trend which continued relatively unabated until the reintroduction of the horse.

Late Holocene (5000 BP to present)

The late Holocene (5000 BP to present) has previously been viewed as a period when little change occurred (e.g., Mehringer et al. 1977); however, with improved methodological techniques researchers have been able to interpret climatic proxy data in greater detail and have thus been able to show that discernible shifts in climate and vegetation occurred (Thompson et al. 1993). The moister and cooler conditions of the late Holocene have been labeled the *Neoglacial* and *Neopluvial*, but regional studies have shown these conditions to be time-transgressive and elevationally variable even over relatively short distances (Thompson et al. 1993:492, 495). For example, at Grays Lake in southeastern Idaho cooler and moister conditions occurred between 7100 and 5800 BP (Beiswenger 1991), while in Yellowstone National Park this occurred around 1600 BP (Gennett and Baker 1986). In Jackson Hole, climatic conditions became cooler and moister after 5000 BP (Whitlock and Bartlein 1993; Figure 4.1).

A pollen record from Lost Trail Pass, at an elevation of 2,152 m, in the Bitterroot Mountains provided a 6.7-m sediment core that records the vegetation history of the last 12,000 years (Mehringer et al. 1977). The record of the last 4,000 years did not reveal any “readily interpretable fluctuations in pollen content that suggest important changes in forest composition” (Mehringer et al. 1977:367). A cooler and/or moister climatic interval is suggested by deepening water at the pond between 3700 and 3450 BP. Although no drastic changes in the vegetation are indicated, an increase in charcoal during the last 2,000 years is interpreted as evidence for frequent small, or low- to medium-intensity, fires, possibly due to changing patterns of human land use (Mehringer et al. 1977:366).

Frequent and recurrent fires can produce a mosaic of different-aged stands, or an environment of high diversity (Cannon 1996). Post-fire studies of lodgepole pine succession

indicate that the number of species of plants, birds, and mammals increases continuously for about 25 years following fires, then decreases rapidly following canopy closure (Taylor 1969). The increased fire frequency and the opening of forests may have had significant effects on local bison populations occupying the forested mountains.

Bryson's (1994) model combines the influence of solar input and volcanic aerosols to predict Holocene climatic change. It predicts that the 5000-4000 BP period was transitional between the generally dry winters and the warm and wet summers of the mid-Holocene and the warmer and wetter winters of the Neoglacial episodes after 4000 BP. Thus, as modeled, the early Neoglacial was transitional.

The Lake Bonneville record (Currey 1990) indicates that conditions of relatively low effective precipitation continued into the period between 5000 and 3500 BP (early Neopluvial). Murchison (1989) suggests that lake levels fell after a minor, late Altithermal high-stand that occurred between 6000 and 5200 BP. A low-stand, equivalent to the average Altithermal lake level, prevailed from 5000 to 3500 BP. Currey and James (1982) correlate a wide variety of geological and biological data from the northeastern Great Basin. Most of these studies suggest continued arid conditions within the time frame traditionally designated the "early Neoglacial" (5000-4000 BP).

Pollen records from the southern Yellowstone area indicate that xeric conditions began to ameliorate after 5000 BP, a trend that has continued up to the present. This is documented at Divide Lake (Whitlock and Bartlein 1993) and Buckbean Fen (Baker 1976). Beiswenger (1991) documented aridity continuing through the early Neoglacial at Ice Slough in the Wind River basin. As mentioned above, Holocene drying began much later in the Plains to the north and east of the study area, with aridity beginning after 7000 BP and intensifying after 3000 BP (Whitlock and Bartlein 1993). In basin regions, grassland began to expand slightly at the expense of desert shrub during this period (Butler 1978; Mehringer 1985).

There is evidence that eolian sand activity continued in some portions of the Wyoming Basin through the “early Neoglacial” period of 5000-3500 BP. At the head of the Killpecker dune field, eolian sand began to accumulate in the Upper Sand unit after 5845 ± 115 yr BP, marking the end of a long deflationary period (Ahlbrandt 1974). Ahlbrandt et al. (1983) suggest that sand deposition prevailed from 5800 to 4200 BP. Gaylord (1990) indicates that sand accumulation continued after a stable, mid-Altithermal period dating to 6400-5900 BP, and that a post-Altithermal peak in sand accumulation occurred between 5900 and 4500 BP. Continued but lessened sand accumulation occurred from 4500 to 2200 BP, at which time the Seminoe–Ferris dune field stabilized.

Eckerle (1989, 1997) has documented a well-developed paleosol (Vonalee–Hiland paleosol) formed on eolian sand in the Wyoming Basin during the middle Neoglacial. Dates generated by this research indicate that eolian activity (deposition with intermittent deflation) began in the Altithermal and continued into the early Neoglacial. Eolian activity ceased by the middle Neoglacial, giving the soil an opportunity to form. Albanese (1989; Albanese and Frison 1995) has noted the presence of this soil in the Lost Soldier area, where he documented eolian activity spanning both the Altithermal and the early Neoglacial, with a similar soil forming on stabilized sand after 3600 BP. Several sites in southwestern Wyoming have evidence of eolian sand activity (deposition and deflation) spanning the Altithermal to the early Neoglacial and followed by stability (non-deposition and non-deflation) during the middle Neoglacial (Eckerle 1991; Rood et al. 1992; Eckerle 1993; Eckerle and Hobey 1995). Evidence for renewed soil formation on moraine and till slope soils after 4800 BP has been observed in the Wind River Mountains dating (Dahms 1994).

Evidence for early Neoglacial cirque glaciation is based on dates with rather poor context (Davis 1988). There are a few radiocarbon dates suggesting early Neoglacial glacial activity in the Wind River Mountains, but their context is not ideal (Davis 1988). Benedict’s (1973) type section for the Triple Lakes glaciation (Front Range, Colorado) was originally dated at between

5000 and 4500 BP but is now considered to be a Temple Lake equivalent, which dates in excess of 10,000 years old (Davis 1988). A few other localities in the Front Range have some evidence for minor rock glaciers and expanded snowbanks at this time (Benedict 1985; Birkeland et al. 1987). A possible early Neoglacial advance in the Tetons (Richmond 1986) is also poorly dated. However, there is some evidence for a resurgence of cool conditions with higher timberlines and renewal of some cirque glaciers at this time (Benedict 1985; Currey and James 1982; Denton and Karlén 1973; Zielinski 1987).

The alluvial record for the early Neoglacial indicates that conditions remained similar to those that existed earlier. Powder Wash in the Washakie Basin (48SW7933) was aggrading by foot slope and lateral fan encroachment during this period (Eckerle and Hobey 1994). Similar relationships that show a continuation of Altithermal depositional processes are present at Indian Creek, Montana (Albanese 1987a; Ottersberg 1987), Barton Gulch, Montana (Davis et al. 1989), and Dead Indian Creek (Eckerle 1990).

The highest Holocene lake levels in the Great Salt Lake basin occurred between 3500 and 1800 BP (Currey and James 1982; Murchison 1989). Pollen records indicate a continuation of previously established trends, with summer-dry areas becoming more moist and summer-wet areas becoming more dry (Whitlock and Bartlein 1993). Packrat middens in the Bighorn Mountains indicate increased moisture from 4400 to 2700 BP, with increased aridity following 2700 BP (Lyford et al. 2002). Ahlbrandt et al. (1983) indicate that dune fields were generally not active during the beginning of the middle Neoglacial. As mentioned above, Eckerle (1989; see Albanese and Frison 1995) identified a prominent soil formed on eolian sand in some parts of the Wyoming Basin which developed in response to long-term surface stability (non-deposition/non-deflation) after 3600 BP. There is evidence for a resurgence of cool conditions with higher timberlines and a renewal of cirque glaciers at this time (Benedict 1985; Currey and James 1982; Denton and Karlén 1973; Zielinski 1987). The alluvial history of the region is subject to diverse interpretations for this period, with few regionally consistent patterns (compare Albanese [1990],

and Miller [1992]). Mesic indicator species dominate small mammal collections from deposits in Yellowstone National Park dating from 3200 to 1100 BP (Hadly 1996). However, drought-related forest fires increased on the Yellowstone Plateau at ca. 3000 BP, 2000 BP, and 1000 BP (Meyers et al. 1995).

The hydrographic record of Lake Bonneville indicates that transitional-to-dry conditions returned from 1800 to 900 BP (Currey 1990) during the early-late Neoglacial. Apparently, conditions began to shift back to those that dominated the early and middle Holocene (Butler 1978). Mountain glaciation was rare during this time span (Davis 1988). Dahms (2002) reports on a warm interval from the Wind River Range between 1500 and 500 BP. According to Ahlbrandt et al. (1983), dune fields reactivated between 2000 and 1000 BP. Benedict (1985) dates his Audubon mountain glacier resurgence to this period; however, supporting evidence for mountain glaciation is rare during this time span (Davis 1988). Bison procurement seems to become more common during this time at sites with possible Avonlea affiliations (1200–900 BP). This increase in bison procurement may be the result of purely cultural processes; however, a return to slightly more moist conditions during this 300-year span is also possible. Cannon (1999) has also noted an increase in bison utilization in the Greater Yellowstone Ecosystem during this time.

Recently published records from various parts of North America suggest a period of aridity occurred which correlates to the Medieval Warm Period of Europe (Graumlich 1993; Pielou 1991). Lake levels in the Great Salt Lake fell to post-Altithermal low levels during this time (Currey 1990; Murchison 1989). Chatters (1982) has documented aridity at Pahsimeroi Valley in eastern Idaho from AD 962 to AD 1375. There are no glacial episodes dating from this time (Davis 1988). Higher frequencies of forest fires are noted on the Yellowstone Plateau around 1000 BP (Meyers et al. 1995). One of the few studies to suggest cooling and increased moisture at this time is Gennett and Baker (1986). Local pollen records have not provided definitive data for this time period, but aridity is strongly expressed in Northern Plains records (Pielou 1991; Campbell 1998). An episode of post-Altithermal eolian activity dating to 1000–500 BP correlates

with this aridity (Ahlbrandt et al. 1983). There are also no glacial episodes dating from this time period (Davis 1988). Xeric indicator species dominate small mammal collections from deposits in Yellowstone National Park, during this middle-late Neoglacial time interval (Hadly 1996).

A final high-stand of Great Salt Lake occurred in the terminal prehistoric era (Currey 1990). Murchison (1989) places this event at about 450–150 BP. Thereafter, the lake dropped to modern levels, suggesting a drier historic climate such as that documented by Chatters (1982) in the Pahsimeroi Valley. The best evidence for Holocene glaciation dates to the Little Ice Age. This glaciation is termed the Gannett Peak in the Wind River Range, where it dates to 500–150 BP (Richmond 1986). Similar aged glacial deposits have been reported from both the Front Range (Benedict 1973) and the Teton Range (Richmond 1986). Albanese (Albanese and Frison 1995) suggests that the Little Ice Age was the most pronounced of the Neoglacial episodes. Mesic indicator species reappear in small mammal collections from deposits in Yellowstone National Park dating to the Little Ice Age (Hadly 1996). Butler (1978) suggests that bison achieved their highest post-Altithermal populations during this period.

As Thompson et al. (1993:492) have been able to illustrate “large-scale coherent patterns” were present across the west. However, local, small-scale variability, which is dependent on a number of factors, is of most importance to archeological and biogeographic research (e.g., Finley 2003). The regional models of climatic history (i.e., Anathermal, Altithermal, and Medithermal) proposed by Antevs (1948) over fifty years ago have been shown to be invalid (Thompson et al. 1993:495).

Shifts in climatic patterns can have significant influences on local vegetational communities, depending on a number of factors that include elevation, edaphic conditions, slope and aspect, among others. As a result, climatic change and the accompanying vegetational changes can have different results on the populations of foraging ungulates. During periods of cool and moist conditions, forage quality can be expected to improve, with a corresponding increase in ungulates. This is generally what is believed to have occurred on the Great Plains

between AD 1500 and AD 1700 (Reher 1978; Bozell 1995) and possibly in the Pahsimeroi Valley during a similar time period (Chatters 1982).

In a recent simulation model for historic vegetation communities in the Upper Columbia River Basin, Keane et al. (1997) suggest that Douglas fir sites were more open prior to 1850, with lodgepole pine numbers reduced. The openness of these sites is believed to have been maintained by more frequent non-lethal, ground fires. Under these more open conditions, grasses and forbs, which require higher intensity light, were probably more abundant.

However, as grassland biomass increased so too did forest cover. With increased effective moisture, disturbances such as fires will also decrease, allowing forest canopies to close, accompanied by encroachment on open meadows. This pattern would reduce bison populations in these areas due to a reduction in forage. While this scenario may be overly simplistic, it does provide a model of how “improved” climatic conditions have significantly different effects upon bison populations in two different, but adjacent biomes.

As is apparent from this short review, proxy climatic data have shown significant differences in local environmental conditions over relatively short distances. These patterns may be due to a number of factors including preservation and the ability to discern small-scale shifts, as well as orographic effects. How these changes affected local community structure and resource availability to bison and other mammalian populations is an important research question.

Although detailed studies exist for the pollen record, and a detailed reconstruction of climate history has followed, the structure of animal communities is poorly understood (Cannon et al. 1997). Future problem-oriented studies should focus on geomorphic settings that foster the preservation of faunal material (i.e., caves and rockshelters).

Can We Use Modern Climate to Understand Past Climatic Influences on Bison?

The Archeological and Historic Records

Archeologists have long tried to understand the impact of climate on bison (e.g., Butler 1978). For example, Wilson (1975) and Butler (1978) have suggested that reduced biomass and

nutritional quality of grasses correlates with diminished stature of bison during the early Holocene, a However, these studies tend to look at changes in bison populations in relation to generalized climatic regimes that extend over hundreds, often thousands of years. However, our more recent understanding of climate change suggests greater climatic variability and frequency (e.g., Laird et al. 1996). Reher and Frison (1980:41) argue that bison populations with a generation span of only three years, high mobility rate, and fertility rate dependent on the individual's condition should be quite sensitive to fluctuations in grassland productivity at a time scale of less than a decade. Under drought conditions bison populations should have increased mortality and lower fertility which would be reflected in irregular age pyramids. Age structure and survivorship rates would also be influenced by how close the population is to carrying capacity. Behavioral responses would include migration to river valleys, foothills, or montane areas. Longer drought cycles (ca. 200 years) would drastically depress survivorship rates and regional population levels.

Using forage quality to model bison herd responses, Bamforth (1988: Table 6-1) proposed bison response to poor forage would be low population density, small herds, and herds which moved faster, farther, and more frequently across larger home ranges. High forage production would lead to high population density, large herds, and herds which move slowly, over shorter distances, and within smaller home ranges.

Bozell (1995) built on Bamforth's predictions and proposed the following trends in relation to climatic episodes for the Central Plains. The moist and cool Sub-Atlantic (1000 BC-AD 250) and Neo-Boreal (AD 1550-1880) episodes and perhaps the warm, moist Neo-Atlantic (AD 750-1150) episode should have favored large, slow moving bison herds predictable to hunting parties. The cool, dry Pacific episode (AD 1150-1550) and perhaps the Scandic (AD 250-750) regime should have witnessed poor forage for bison resulting in small, fast-moving, unpredictable herds.

Applying the archeological record of unmodified bison bone density (identified specimens/excavated m³), Bozell (1995) concluded that bison population levels fluctuated significantly during the late Holocene probably because of climate shifts. While bison populations ebbed and flowed during climatic episodes, humans adapted by changing their social structure either through smaller aggregations or through the employment of maize horticulture and a diverse hunting-gathering strategy.

The Vore site, a Late Prehistoric bison kill site in northeastern Wyoming, contains a high resolution archeological record of bison kills that date between AD 1500 and 1800. The high-resolution record makes it an important site for testing ideas concerning cultural and climatic influences on local bison populations. The time period of the record is also of significance, because it falls within a climatic period identified as the Little Ice Age, which is characterized by a significant increase in effective moisture. As Reher (1978) suggests this increase in effective moisture would have had a positive influence on the productivity of the shortgrass prairie and bison carrying capacity.

While Great Plains archeologists have long sought to understand the influence of climate on bison populations, they have been hampered by limited samples and resolution. Therefore, these studies typically look at gross trends across long time periods or across regions. Bamforth (1990:36) recognized this problem and argued that:

“climatic reconstructions for any specific region must ultimately be assessed empirically, against data which derive directly from that region. ... the apparently great year to year variation in Little Ice Age conditions implies that climatic reconstructions must incorporate analyses of such variation.”

Osborn (1983, 2003) also addressed this issue. While not specifically considering the effect of climate on bison, Osborn (1983) examined the effect of winter severity on domesticated horse herds used by historic western North American tribes. He found that 66% of the variation in horse herds was due to winter severity. Osborn argued that the low-quality forage and snow cover imposed significant constraints on feeding and reproduction. More recently, Osborn (2003:210)

has stated that “[s]evere winter conditions have adverse, limiting effects on ungulate distribution, abundance, body condition, reproduction, and mortality.”

Winter severity is not the only climatic factor influencing bison populations, as suggested by Bamforth (1988), but decreases in forage availability and quality during periods of reduced precipitation can also have physiological effects on bison. In examining Early Holocene (8500-6300 BC) bison remains from the Lubbock Lake site in Texas, Johnson and Holliday (1986) found a high incidence of dental abnormalities that they attributed to poor range conditions and excess grit on the vegetation. It is also during this time period, and into the Middle Holocene, that environmental stress was being expressed phenotypically through the diminution of bison size (Holliday 1987).

Historic, albeit anecdotal, references to bison having been severely impacted by severe winters is related by Roe (1970:181): “when, according to the reports of mountaineers and Indians, the snow fell to the depth of ten feet on a level. The few buffaloes that escaped starvation are said to have soon afterwards ‘disappeared.’”

What archeologists have demonstrated is that climate can have significant influences on bison population density, migration, and physiology. Unfortunately, temporal resolution is not adequate to address these changes at a finer scale. Higher resolution sites, such as the Vore site, and proxy data (e.g., dung fungus *Sporormiella*) may provide more pronounced evidence of past climate influences on herbivore and bison populations.

Contemporary Studies

Recently biologists have shown a keen interest in the effect of climate on ungulate populations. A major impetus for this has been concern over how to manage expanding populations, particularly when they come into conflict with other management and economic interests. Yellowstone National Park has been an important setting for these investigations mainly because of the long and detailed records of weather conditions and ungulate populations (Taper et al. 2005). For example, Coughenour (1994), in examining the influence of climate on elk carrying capacity, found that calf mortality in particular was negatively correlated with precipitation in the prior year which indicates an effect of forage quality on pregnant and nursing cows. Urine analysis of wintering elk supports the influence of nutritional deprivation (Delguidice et al. 1991).

Climate as an environmental regulator of bison was an important aspect of early studies of the Yellowstone bison herd (e.g., McHugh 1958). McHugh observed that yearlings and 2-year-olds were particularly vulnerable to severe winter conditions, such as deep snow that would inhibit travel and effective foraging. Calves, on the other hand, may have been less vulnerable because of their close association with the cows. While deep snow and limited forage quantity did not appear to be directly related to winter mortality, the combination of severe winter weather effects (i.e., deep snow, cold temperatures, distribution of available forage) would impose incremental physical stresses on the bison, particularly subordinate individuals. However, winter severity, particularly snow hardness and crusting, may have greater influences on elk carrying capacity than depth (Barmoer 1980). Crust hardness impedes the ability of elk to migrate and forces them to expend greater energy.

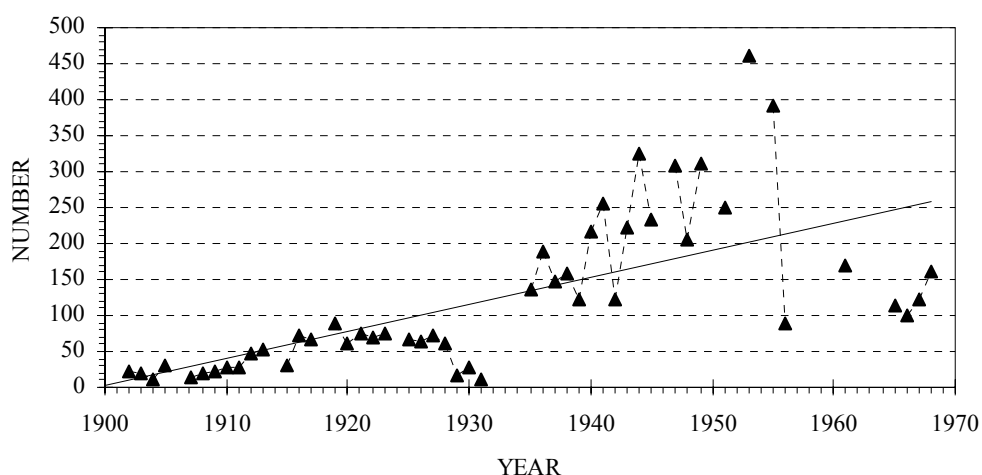
Yellowstone bison are an important population for studying the influence of climate on demography and range expansion. The Yellowstone bison represent one of the few herds in North America that represent a free-ranging population with limited management interference (Taper et al. 2005). The population has a long historic record extending back to 1860. The bison have been intensively managed for the last four decades (Meagher 1970; Meagher et al. 1997). Weather data

is also available and has a long, detailed historic record, in some instances extending back to the 19th-century.

Meagher's (1973) seminal study of Yellowstone bison sought to understand climate as a mechanism influencing bison populations. Her study population consisted of the Pelican Valley herd, which she felt had "been regulated for many years without interference by man" (Meagher 1973:110; Figure 4.2). Between 1902 and 1968 only two episodes of culling occurred—118 in 1958 and 34 in 1965. For Meagher (1973:111) "exceptionally severe winters appeared most important in Yellowstone."

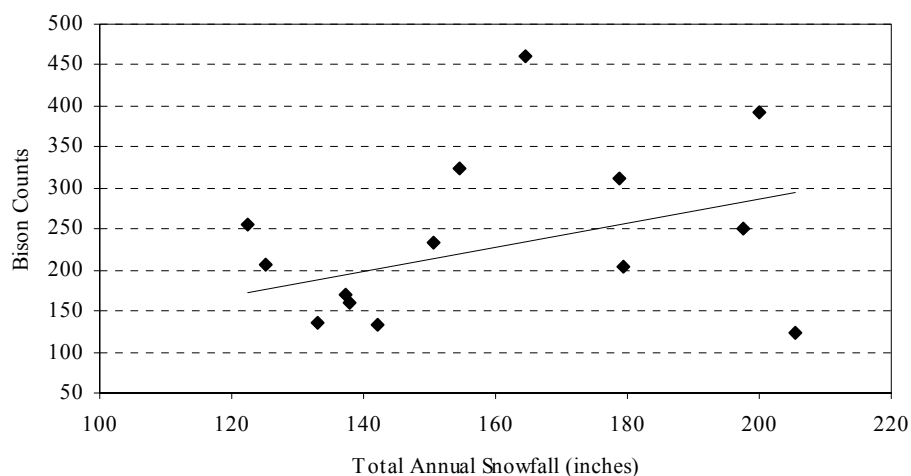
Differential mortality among sex and age classes indicated to Meagher that the combination of low temperature and snow depth were critical factors. She goes on to argue that the slow growth rate of the Pelican Valley herd may be the result of a population approaching winter carrying capacity. Being able to survive the severe winters of interior Yellowstone may have to do with particular features of Pelican Valley, and elsewhere in the Park, such as thermal areas, open streams due to warm water, extensive sedge bottoms and open side hills for both forage and movement (Meagher 1973:113).

Figure 4.2. Pelican Valley bison winter counts from Meagher (1973: Appendix IV). Two episodes of culling occurred during this time period—118 in 1956 and 34 in 1965. Growth rates were gradual, but steady over this period ($y=3.7592x-7140.3$; $r^2=0.4407$).



Simplistically comparing the relationship between the Pelican Valley herd and snow depth at the Lake Yellowstone weather station indicates a slight positive correlation (Figure 4.3; $y=1.4746x-7.5085$; $r^2=0.1333$). Obviously, this is counterintuitive and may be because of a number of factors: (1) bison herd size had not reached carrying capacity; (2) annual snowfall may not be a true indicator of winter severity; and (3) the limited dataset represents 13 of a possible 68 winters due to years of incomplete weather records and/or bison winter counts.

Figure 4.3. Linear correlation between Pelican Valley actual winter bison counts (Meagher 1973: Appendix IV) and total annual snowfall as recorded at the Lake Yellowstone weather station. To dampen possible effects of culling, bison culled during the years 1956 (n=118) and 1965 (n=34) were added to the total bison count for that winter. The dataset includes only the years 1931-1968, but only 13 years are presented in the dataset due to missing data from either winter counts or snow depth. Correlation is weak ($r^2=0.1332$).



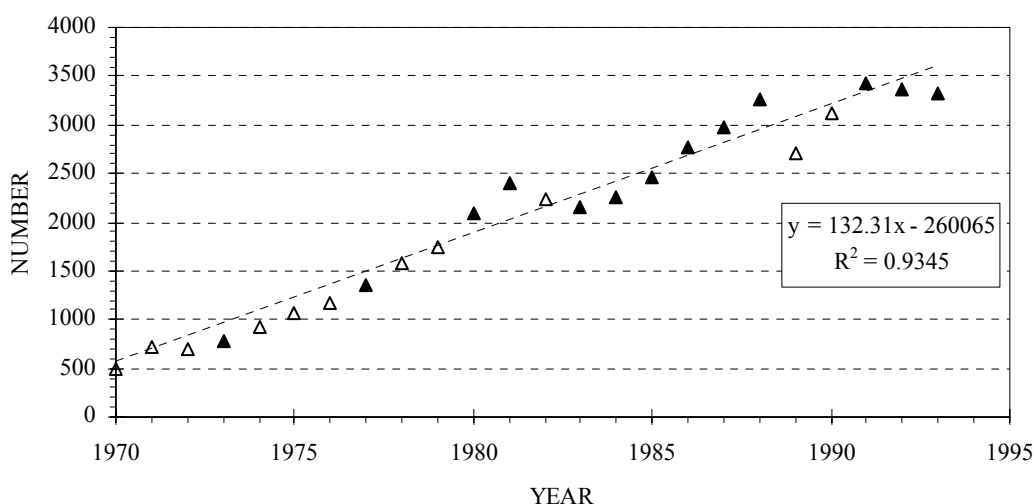
Farnes (1997) has been examining the snows of YNP for nearly six decades and has developed a more sophisticated understanding of the relationship of winter snows to vegetation and herbivores. He argues that a number of environmental factors affect overwintering wildlife, including the availability of forage, the amount and condition of snow, air temperature, and variability between winter ranges. Farnes argues a more meaningful measure for understanding the influence of snow on the following year's vegetation is the Snow Water Equivalent (SWE)¹. However, the condition of the snow may be even more important in winter survival. Deep snow, hard crusts, cold air temperature, and limited access to forage may result in greater mortality. A

simple correlation between snow depth and mortality may not be a robust index for understanding winter severity. For example, early snows followed by mid-season rain and freezing can create a hard crust on the surface of the snow, limiting herbivores ability to access forage. Prolonged exposure to cold air temperatures, strong winds, and deep snow will further deplete fat reserves of animals. While some herbivores, such as bison, are bigger and stronger and can travel and forage in deeper snows, their condition going into winter also has an influence on survival (Farnes 1997:10).

Farnes (1996:Table 1) presents variables and indices to determine an index of winter severity for the lower winter range. This area encompasses the lower elevations of the Yellowstone River drainage including Crevice Creek, Lava Creek, and Blacktail Deer Creek and north to Gardiner and Corwin Springs. While Farnes (1996) developed a severity index for elk, Cheville et al. (1998) in looking at the effect of winter severity of bison movements emphasized different variables for bison based upon their physiology. In their index they weighted the snow water equivalent and temperature. I calculated the snow severity index using the weighted measures as suggested by Cheville et al. (1998) and correlated it with bison populations for the northern and central herds as from 1970-1993 presented in Taper et al. (2000:Table A1).

The population trend of the northern and central herds between 1970 and 1997 shows that the bison population had a strong growth rate. The only years in which the annual increment was below the regression line were severe winters (Figure 4.4). Cheville et al (1998:64) illustrate a similar trend for the entire YNP population from 1970 to 1997. They calculate an absolute annual increase of 145 bison. What this illustrates is that the northern and central bison herds are largely undisturbed by management, and the population can be used as a test of the impact of winter severity. Meagher et al. (2000) provides additional arguments to support this assumption.

Figure 4.4. Population trends from 1970 through 1997 of YNP combined northern and central bison herds (Taper et al. 2000: Table A1). Hollow triangles represent severe winters.

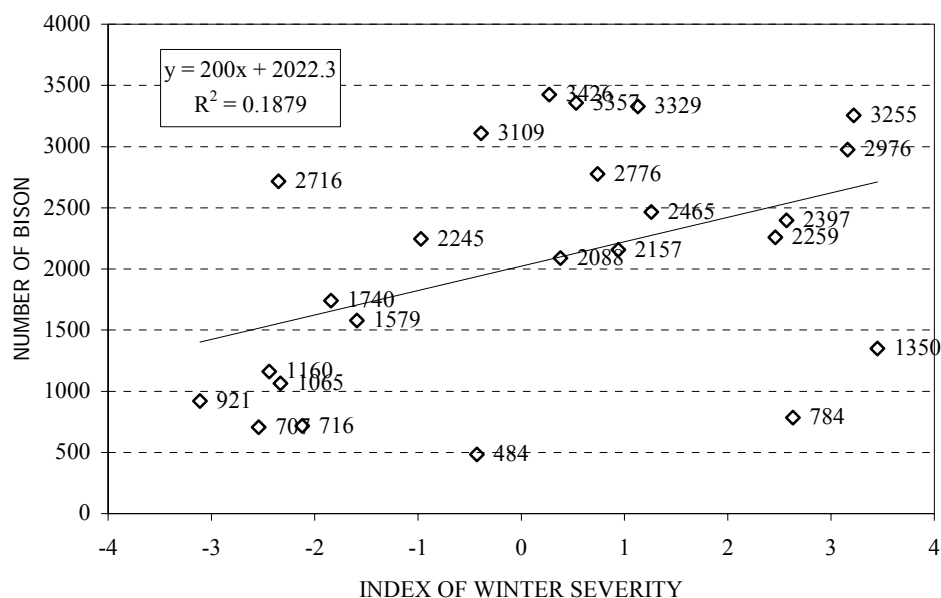


A linear regression analysis of the combined YNP northern and central herds against Farne's severe winter index indicates a rather weak correlation (Figure 4.5; $r^2=0.1879$). Further analysis of the bison populations using the adjusted population size, which includes the number of removals, illustrates a weaker correlation (Figure 4.6; $r^2=0.1657$). Cheville et al. (1998:58) analyses produced a similar pattern in which "[n]one of the weather variables or indexes shows a significant correlation with bison." They further suggest that population size may be a more critical factor in which the response to winter conditions would be greater in large populations due to increased competition (Cheville et al. 1998:59). More recent analyses by Taper et al. (2000) and Meagher et al. (2002) provide additional support for this argument.

Conditions on the winter range have been demonstrated by Meagher et al. (2002) and Taper et al. (2000) for interior bison herds in YNP. With the severe winter (above average snowfall) of 1981-82, interior bison populations (Mary Mountain and Pelican Valley) surpassed winter range ecological carrying capacity, which culminated in an estimated 20% population loss. As populations approached carrying capacity, interior bison herds began to migrate into areas with consistently lower snow depths. As bison migrated out of Pelican Valley, they came in

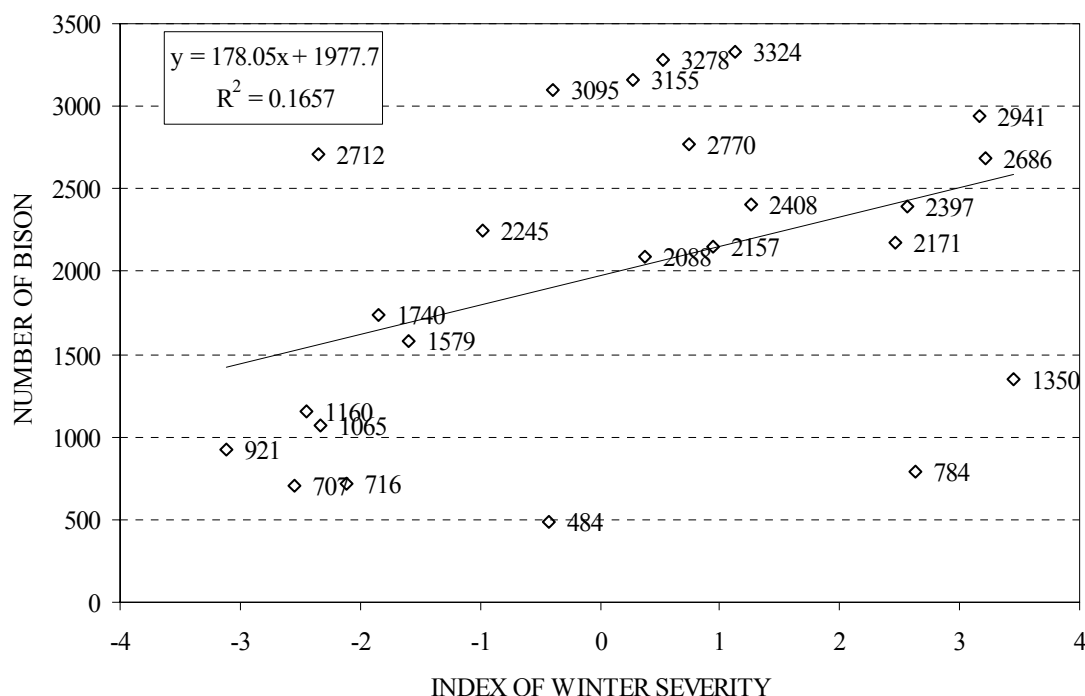
contact with the Mary Mountain herd, which caused a “domino effect”, forcing a range expansion to the north and west (Meagher et al. 2002:144).

Figure 4.5. Combined YNP northern and central bison herds from Taper et al. (2000:Table A1). Bison population size is plotted against Farnes (1996) winter severity index and illustrates a weak correlation.



Migration to more conducive winter range appears to be the preferred strategy of bison in order to maintain social bonds. However, while bison can survive by breaking social bonds by scattering into smaller groups to seek out areas of limited resources (e.g., geothermal areas), they preferentially move to maintain a higher level of aggregation (Meagher et al. 2002). If the area they are moving into is unoccupied, they will be able to survive largely intact. If the area is occupied, the migrating herd will either displace the resident herd or cause additional expansion of winter range. Migrate or die seems to be a fairly accurate way to define bison behavior in relation to winter severity.

Figure 4.6. Combined YNP northern and central bison herds from Taper et al. (2000:Table A1). Numbers reflect adjusted population size, N_t , which is defined as the maximum count minus management removals for the winter (following Taper et al. 2005).



Summary

What is apparent from this short review of the effect of weather on bison is that it is a complicated issue based not only on the severity of winter, but also physiological conditions of the bison going into the winter, population size, and the ability of bison to migrate to more amenable habitats. Short-term severe weather conditions appear to play a role in bison population dynamics as illustrated in Figure 4.4 for the northern and central herds throughout the 1970s, when severe winters were common (Appendix A).

A more sophisticated analysis of the effect of weather on bison could be constructed using a range of bison populations, such as the Canadian herds in Woods Buffalo National Park, which was not subjected to management until recently (Gates et al. 2001), plus bison herds in Badlands, South Dakota and Tallgrass Prairie, Kansas. These populations would be subjected to a

range of weather conditions, including severe winters and drought, and could provide a more robust analysis of the effect of weather on bison.

The information derived from this larger analysis might provide a better understanding of bison adaptations that can be applied to the prehistoric record. What is clear is that bison are a very robust herbivore that adapt to a variety of habitats and climatic conditions. Their effect on the ecosystem is profound and maybe a key to understanding the evolution of the GYE and beyond to surrounding grassland ecosystems, such as the Great Plains, over the course of the Holocene. Understanding this relationship will take interdisciplinary research that includes, but not limited to, palynology, limnology, geochemistry, and population studies of bison. In the following chapter I provide a discussion of the study set used to assess the relationship between past climate change and bison using carbon and oxygen isotope signatures from individual bison teeth.

Chapter V

The Study Set

Introduction

The role of bison in the GYE pre-Park ecosystem has been debated by biologists (Meagher 1973; Daubenmire 1985; Kay 1994), historians (Schullery and Whittlesey 2006), and archeologists (Wright 1984; Cannon 1992) over the past four decades. A range of views has been presented from Wright's (1984:28) that "bison were relatively rare" to Meagher's (1973:14) that there were "substantial numbers of bison." More recently, the Montana novelist Peter Bowen (1997) expressed the extreme position that "[n]either elk nor bison are native to the Park. They were installed there. They are the unmitigated disaster for the fragile plateau country." While both the historical and archeological record are problematic in their incomplete portrayal of the past, each has value when used with the understanding of their biases. Attempting to understand the limits and biases of the archeological record is important and may largely be the result of the local geomorphic conditions.

Soil conditions in the mountainous environment of the GYE are not typically conducive to long term preservation. Soils tend to be shallow, coarse-grained, and acidic with bioturbation from rodents common (Rodman et al. 1996; Table 5.1). With these characteristics, organic material is subjected both to chemical and mechanical breakdown. However, there are sites that have unique characteristics of preservation (soil pH slightly acidic to slightly alkaline) that have allowed specimens to be preserved (e.g., Goetz site). It is at these key locales that the largest assemblages of bison from the region have been recovered (Table 5.2).

While the characteristics of soils are important factors influencing bone preservation, other natural and cultural factors are equally as important. Understanding these taphonomic processes, such as processing of the carcass, rate of burial, postdepositional scavenging, has been a productive area of research for archeologists over the past three decades (Behrensmeyer and Kidwell 1985; Todd 1987; Lyman 1994; Burgett 1999; Todd and Rapson 1999; Enloe 2004). The

taphonomic studies that have been conducted in the region, specifically Todd's (1987) ground-breaking study of the Horner II assemblage, indicate that minimal disarticulation and rapid burial are important factors in bison bone preservation.

Table 5.1. Selected soil pH from archeological site investigations in the GYE.

Site	Range of pH	Presence of Fauna	Reference
48TE509, Lawrence Creek Section II	6.0-6.3	Very limited, fragmentary, unidentifiable.	Frison et al. 1988
48TE509, Lawrence Creek Section III	5.3-6.5	Very limited, fragmentary, unidentifiable.	Frison et al. 1988
48TE1071	6.4-7.6	None recovered	Frison et al. 1988
48TE1099	5.5-7.1	Limited, fragmentary.	Frison et al. 1988
48TE1103	5.4-6.3	None recovered.	Frison et al. 1988
48TE455	6.26-8.32	Large, well preserved assemblage.	Cannon, unpublished data
48TE1077	6.49-7.38	Limited, microfauna.	Cannon et al. 2001
48TE1079, Block B	5.75-7.56	Limited, microfauna.	Cannon et al. 2001
48TE1079, Block E	5.84-8.22	Limited, microfauna	Cannon et al. 2001
48TE1374, Block C	5.00-6.56	Very limited, microfauna.	Cannon et al. 2001
48YE697		Well preserved.	Cannon et al. 1997.

Bison remains from eight sites within the GYE were selected for this study (Figure 5.1).

Several criteria were used in selecting the sites and the bison assemblage:

1. Sites within the Greater Yellowstone Ecosystem, but from a variety of environmental contexts.
2. Well-dated context.
3. An assemblage that had well-preserved mandibular or maxillary teeth of aged individuals.
4. An assemblage that was accessible for study.

The eight sites include: the Rock Springs site (10OA210), a late Holocene primary kill and butchery site in Oneida County, Idaho; the Horner site (48PA29), an early Holocene primary kill location in Park County, Wyoming; four late Holocene sites from the upper Snake River Delta in Teton County, Wyoming that were inundated by Jackson Lake (48TE1090, 48TE1101, 48TE1102, 48TE1114); the Goetz site (48TE455) a late Holocene kill and butchery site in Teton County, Wyoming; and the Windy Bison site (48YE697) a late Holocene single bull bison kill along the north shore of Yellowstone Lake, Yellowstone National Park, Wyoming. Modern, control samples were obtained from Yellowstone National Park, Wyoming and the Henry Mountains, Utah. All sites are within the Mountain Grassland community, with the exception of the Rock Springs site which is within the Northwest Bunchgrass community (Sims et al. 1978). Each of the communities is dominated by cool-season grasses. The following section provides a discussion of each of the site assemblages, and the environmental context, age, and results of analysis concerning the method of procurement.

Characteristics of the bison mandibles and isolated teeth were measured following Todd (1987). Age and sex of the individual are based upon published data, but in the case of specimens with unknown age, descriptions published by Todd and Hofman (1987) were used in age determination. Sex of the individual was determined based on metrically comparing with bison of known gender (Figure 5.2). Unfortunately, based upon this limited sample, there is no discrete separation between cows and bulls based upon teeth measurements. Therefore other characteristics of the skull and mandible (e.g., robustness and general size) were used to discern sex of the individuals.

The Rock Springs Site (10OA210)

The Rock Springs site is a multi-component bison kill and processing camp in the Curlew Valley of Oneida County, southeastern Idaho. The site lies in the extreme southwestern edge of the GYE in the rolling hills east of the Sublette Mountains within the terraces formed by drainage from Rock Springs. The “finger-like” ridges of the drainage form a natural funnel through which

the bison were driven, dispatched and butchered (Figure 5.3). This is one of the few excavated sites in this generally unknown archeological region (Arkush 2002).

Figure 5.1. Regional map of precontact sites with recovered bison remains and location of bison specimens used in study.

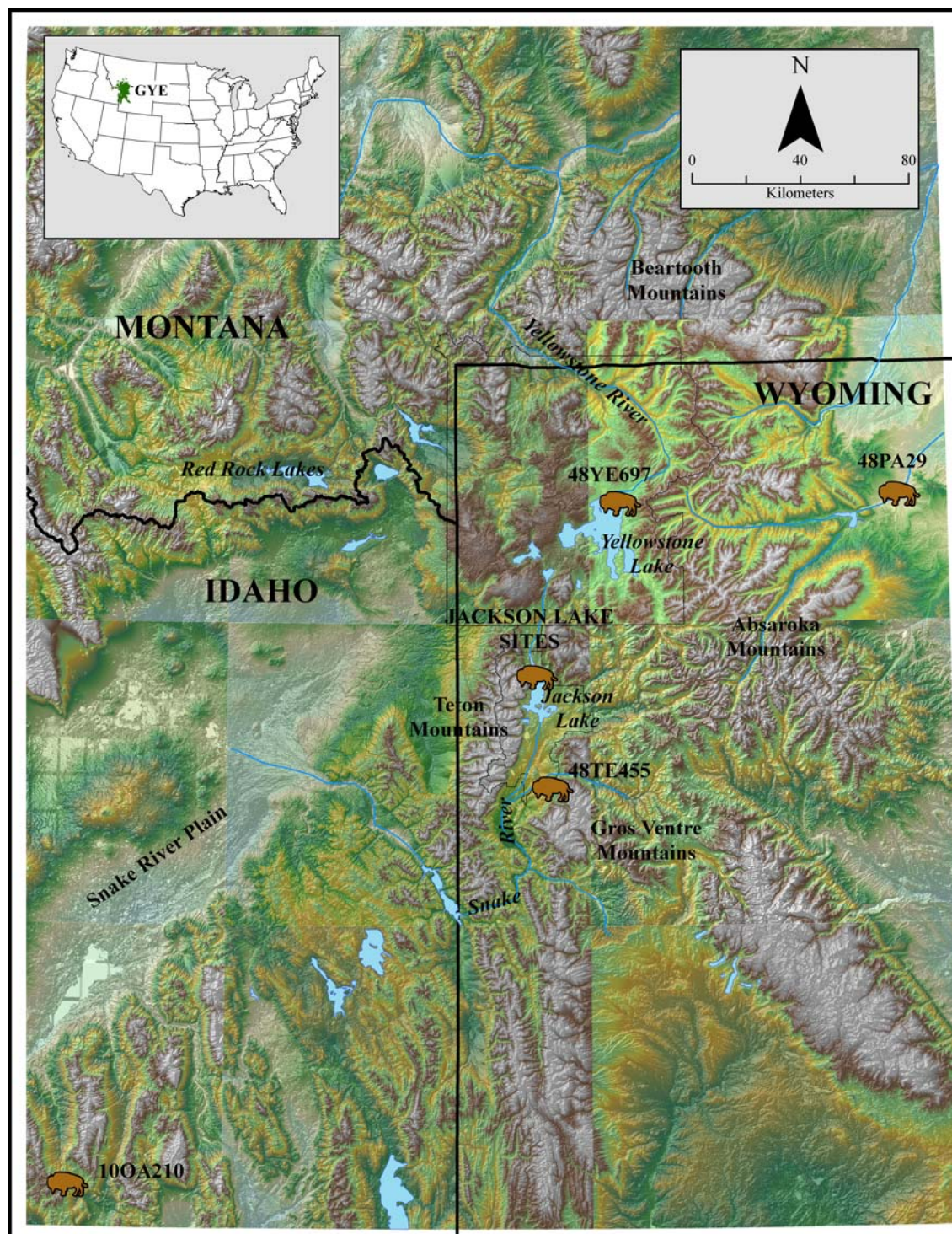


Table 5.2. Characteristics of sites used in study.

Site	Elevation m/ft AMSL	Soil Type or Name ¹	Soil Texture	Vegetation Community ²	Age	Bison MNI	Method of Procurement
10OA210	1664/5490	Raldrige gravelly loam	Gravelly loam	Sagebrush- grassland (C ₃)	AD 1450- 1650	3	Drive or ambush
					AD 1100- 1200	3	
48PA29	1476/4843	Aeric Calciaquoll	Silty clay loam to clay	Mixed grassland with short grass species dominant (C ₃)	9677- 9238 BC	65	Primary kill location, possible encounter kill.
48TE455	2092/6863	Starley-Tetonia Association	Silt loam	Moist grassland with sagebrush and aspen near spring. (C ₃)	AD 1480, AD 1175- 1285	4	Primary kill location, possible encounter kill.
48TE1090	2054/6740			C ₃	AD 1175- 1285	17	Primary kill location, possible encounter kill
48TE1101	2054/6740			C ₃	AD 655- 1345	6	Primary kill location, possible encounter kill
48TE1102	2054/6740			C ₃	AD 450- 860	8	Primary kill location, possible encounter kill
48TE1114	2053/6735			C ₃	AD 75- 640	4	Primary kill location, possible encounter kill

48YE697	2359/7740	Shook Family and McCort Family and Shadow Family Undifferentiated Group	Medium to coarse eolian sands	Subalpine Fir/Western Meadowrue Habitat Type (C ₃)	AD 1185- 1275	1	Encounter
¹ Soil type or name is generated from NRCS soil survey maps (where available) and site reports: 100A210 description is from the NRCS soil survey report; 48PA29 is from site report description Reider 1987; 48TE1090-1114 from geomorphic investigations by Frison et al. 1988; 48TE455 from NRCS soil survey data; 48YE697 from Rodman et al. 1996. ² Description of vegetation community is from site report.							

Figure 5.2. Plot of archeological lower third molar length and width against modern specimens of known gender.

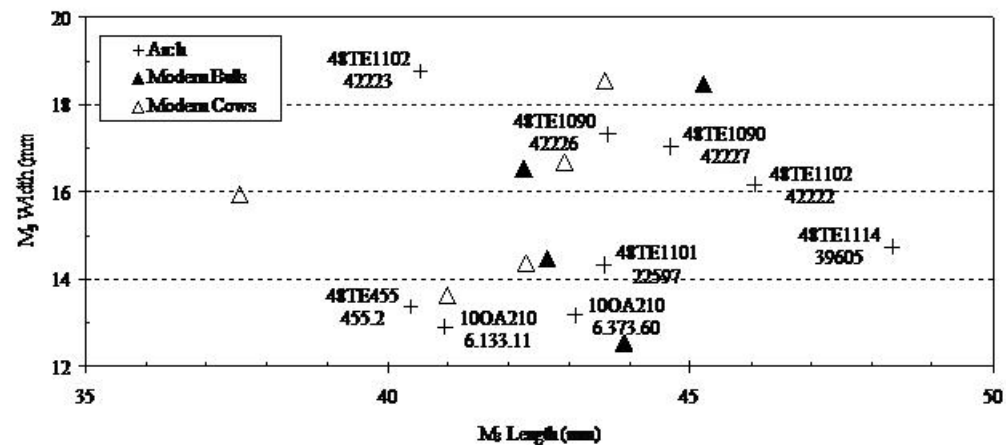
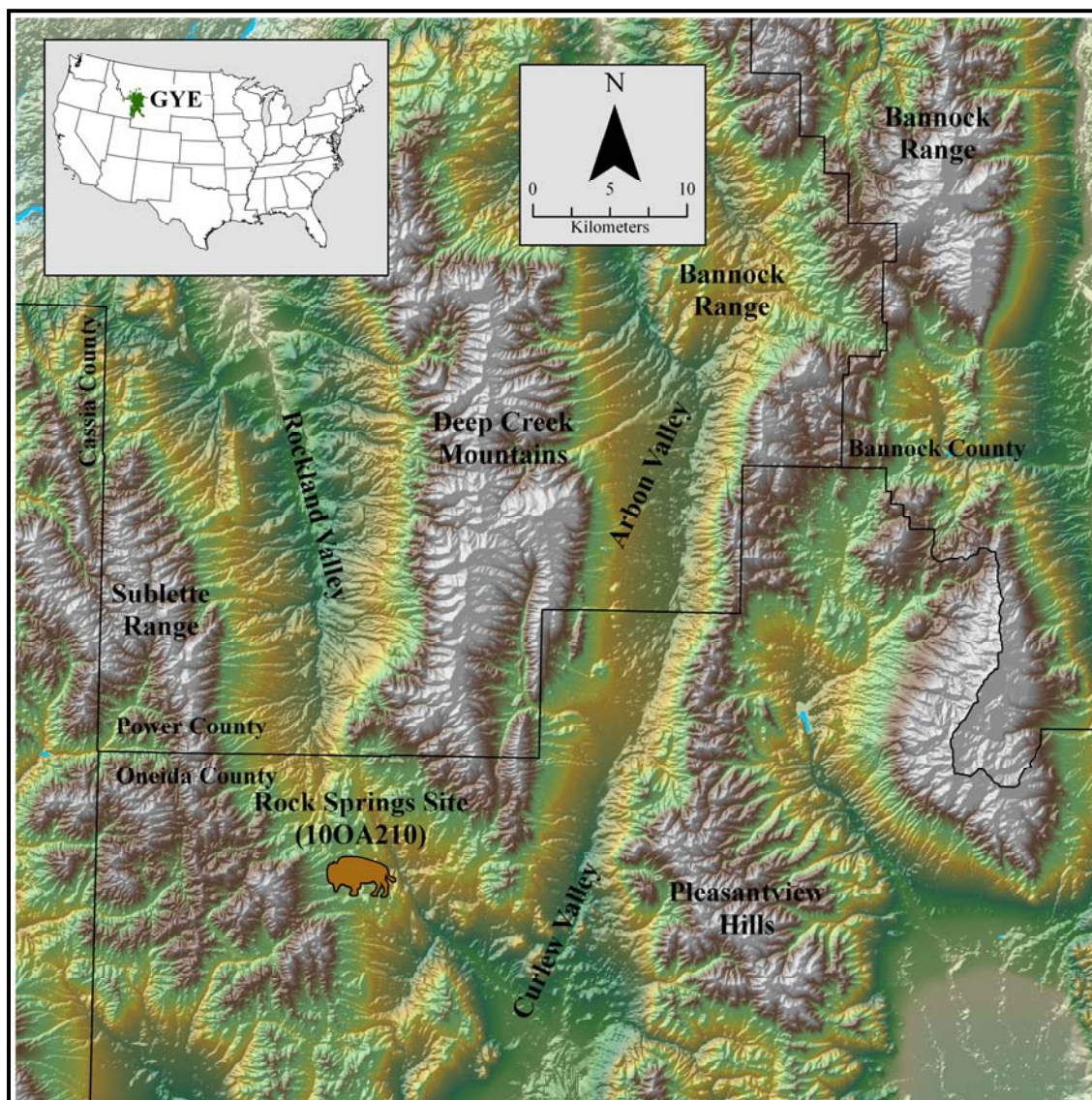


Figure 5.3. General location of the Rock Springs site (10OA210).



The site lies at an elevation of 1664 m (5490 ft) AMSL within a riparian setting of the Sagebrush Grassland Zone of the northern Bonneville Basin. Important vegetative species include big sagebrush (*Artemisia tridentata*), black sagebrush (*Artemisia nova*), rabbitbrush (*Chrysothamnus* sp.), willow (*Salix* sp.), golden currant (*Ribes aureum*), western serviceberry (*Amelanchier alnifolia*), goosefoot (*Chenopodium* sp.), Indian paintbrush (*Castilleja chromosa*), prickly pear (*Opuntia* sp.), Indian rice grass (*Oryzopsis hymenoides*), bluebunch wheatgrass

(*Agropyron spicatum*), and Great Basin wild rye (*Elymys cinereus*). All of the major grasses and browse species have the C₃ photosynthetic pathway. Sims et al. (1978) characterize the vegetation community as Northwest Bunchgrass dominated by cool-season grasses (C₃), such as *Agropyron spicatum*, and *Poa secunda*. *Artemisia tridentata* is also characteristic of this community. The site deposits are within the Raldrige gravelly loam soil series. Precipitation in the Curlew Valley falls mostly as snow, with average annual totals of about 35.56 cm (14 inches). Average January temperatures are -4.4°C (24°F) with a July average temperature of 21°C (70°F; Arkush 2002).

Arkush initially discovered the site in 1994 during a pedestrian survey within the Curlew National Grasslands. Between 1994 and 1997, Arkush, along with students of the Weber State University Archeological Field School, conducted investigations at the site. Key research questions poised by Arkush (2002:9) included the age of the kill episodes, the season of the bison kills, how the bison were hunted and butchered, and how the lithic technology was structured at the site.

A large assemblage of faunal material was recovered from the site and analyzed by Walker (2002). The Rock Springs Local Fauna consists of one gastropod, one fish, one snake, six avian, and 24 mammalian taxa. Seventeen adult bison (*Bison bison*) were recovered during the four years of excavation at the site. The remains were recovered from various excavation units and all identified seven cultural levels. Season of the kill(s) is suggested by the recovery of a fetal distal humerus (Level 4), a thoracic vertebra spine (Level 2), and a radius shaft fragment (Level 1). Based upon size comparison with known fetal material, Walker (2002:130) indicates the elements were from fetal bison one to two months short of full term, potentially placing three of the kill events in the early spring. These include the kill events of cal AD 1675-1750 (Bone Bed 1), cal AD 1600-1700 (Bone Bed 2), and cal AD 1200-1400 (Bone Bed 4). Based upon metric analysis of postcranial material, Walker (2002) demonstrates that the Rock Springs bison represent both mature bulls and cows. This pattern indicates individuals may have been hunted, as compared with deliberate hunting of cow-calf herds.

Radiocarbon ages for the site were derived from charcoal and bison bone collagen (Arkush 2002:Table 1). Based upon these ages and the site taphonomy, Arkush indicates that at least seven episodes of bison kills and processing occurred between cal AD 1050 and cal AD 1750 (Table 5.3). These seven small-scale bison drives over the span of 700 years suggest reuse of the area every 50 to 250 years (Arkush 2002:30).

Table 5.3. Accepted radiocarbon ages from the Rock Springs site (10OA210) as reported by Arkush (2002:Table 1).

Laboratory Number	Sample Material	Age	$\delta^{13}\text{C}$ Value	Calibrated Age (2 sigma)	Bone Bed
Beta-79031	Bison femur	50 \pm 60	-20.6	AD 1680-1755, AD 1805-1940	1
WSU-4956	Charcoal	289 \pm 60	-27.2	AD 1585-1705	2
Beta-79030	Bison scapula	370 \pm 50	-20.1	AD 1435-1650	3
Beta-79032	Bison humerus	730 \pm 70	-19.0	AD 1195-1400	4
Beta-136189	Bison long bone fragments	820 \pm 40	-20.0	AD 1160-1275	5-6
Beta-136190	Bison long bone fragments	840 \pm 40	-19.8	AD 1055-1085, AD 1150-1270	7

Despite the large assemblage (NISP= 983) of bison bone recovered from the excavations, only two mandible specimens were in adequate condition to be analyzed for this study (Table 5.4). These include a left mandible fragment (6.113.11) with the first through third molars intact and a mostly complete left mandible with most of the molar teeth intact (6.373.60). The first mandible was recovered in 1995 from Level 6 of Unit 0N/12W and dates to between cal AD 1100 and 1200 (Bone Bed 5-6). The second mandible was recovered from Level 3 (Bone Bed 3) of 29S/95W in 1997 and dated to cal AD 1450-1650 (Walker 2002:Table 6). The age of this individual at death was approximately 6.6 years. Each of the specimens is likely from cows.

Table 5.4. Specimens used in study.

SITE	SPECIMEN NO.	TOOTH	AGE GROUP	SIDE	Sex	AGE
10OA210	6.373.60	m3	6.6	L	F	AD 1450-1650
10OA210	6.133.11	m3		L	F	AD 1100-1200
48PA29	1233H	m3	2.6	L	M	8351-8278 BC
	2548H	m3	3.6	R	F	
	1181H	m3	4.6	R	F	

48TE1090	42226	m3	9.6	R	F?	AD 1175-1285
	42227	m3	8.6	L	M	
48TE1101	22597	m3	5.6-7.6	R	F?	AD 655-1345
48TE1102	42222	m3	6.6	R	M	AD 450-860
	42223	m3	9.6	L	F	
48TE1114	39605	m3	5.6-6.6	R	M	AD 75-640
48TE455	455.1	M3		R	M?	AD 1175-1285
	455.2	m3	4.6	R	F	AD 1480
48YE697	697.1	M3	4.0	L	M	AD 1185-1275
Hayden Valley, YNP	YELL.2000.HV.003	m3	2.6	R	F	Died Spring 1999
	YELL.2000.HV.002	m3	8.6	R	F	Spring 2000
Pelican Valley, YNP	94KC1	m3	10.6	R	M	Summer 94
Henry Mtns, Utah	12	m3	3.6-4.6	R	M	29-May-78
	768	m3	6.6	L	M	10-Sep-97

Analysis of the $\delta^{13}\text{C}$ values from bulk collagen samples derived during radiocarbon dating indicates a diet for all bison heavily dependent on C_3 or cool season vegetation (Figures 5.4 and 5.5). This is consistent with the present vegetation of the region. However, there is some variability between the initial and later occupations. This variability may be the result of the different herds' use of variable ranges. Diachronic changes in community structure may produce these results and should not be unexpected considering the several hundred years that separate the herds. Another explanation may be found in the differences in range size between bulls and cows. For example, bulls tend to move more widely during the season than cows in cow-calf herds, and thereby potentially sample a wider range of plants (Meagher 1973).

Figure 5. 4. Accepted radiocarbon ages against $\delta^{13}\text{C}$ values derived from bison bones (Arkush 2002: Table 1).

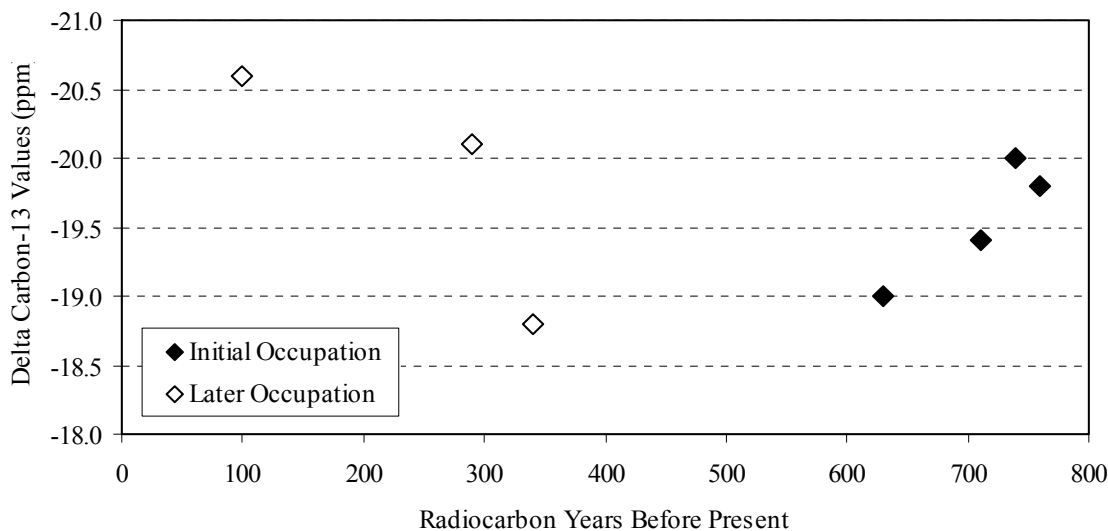
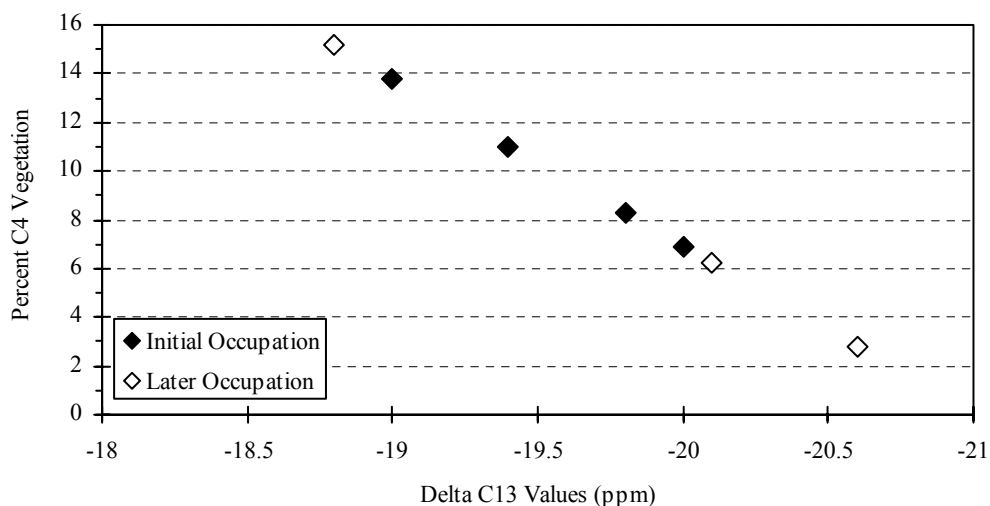


Figure 5.5. Percentage of C_4 vegetation in diet of bison from the Rock Springs site. Data was derived from radiocarbon dated specimens listed in Arkush (2002:Table 1). Calculations of percentage of C_4 vegetation is based upon Brooks (1995:76-77).

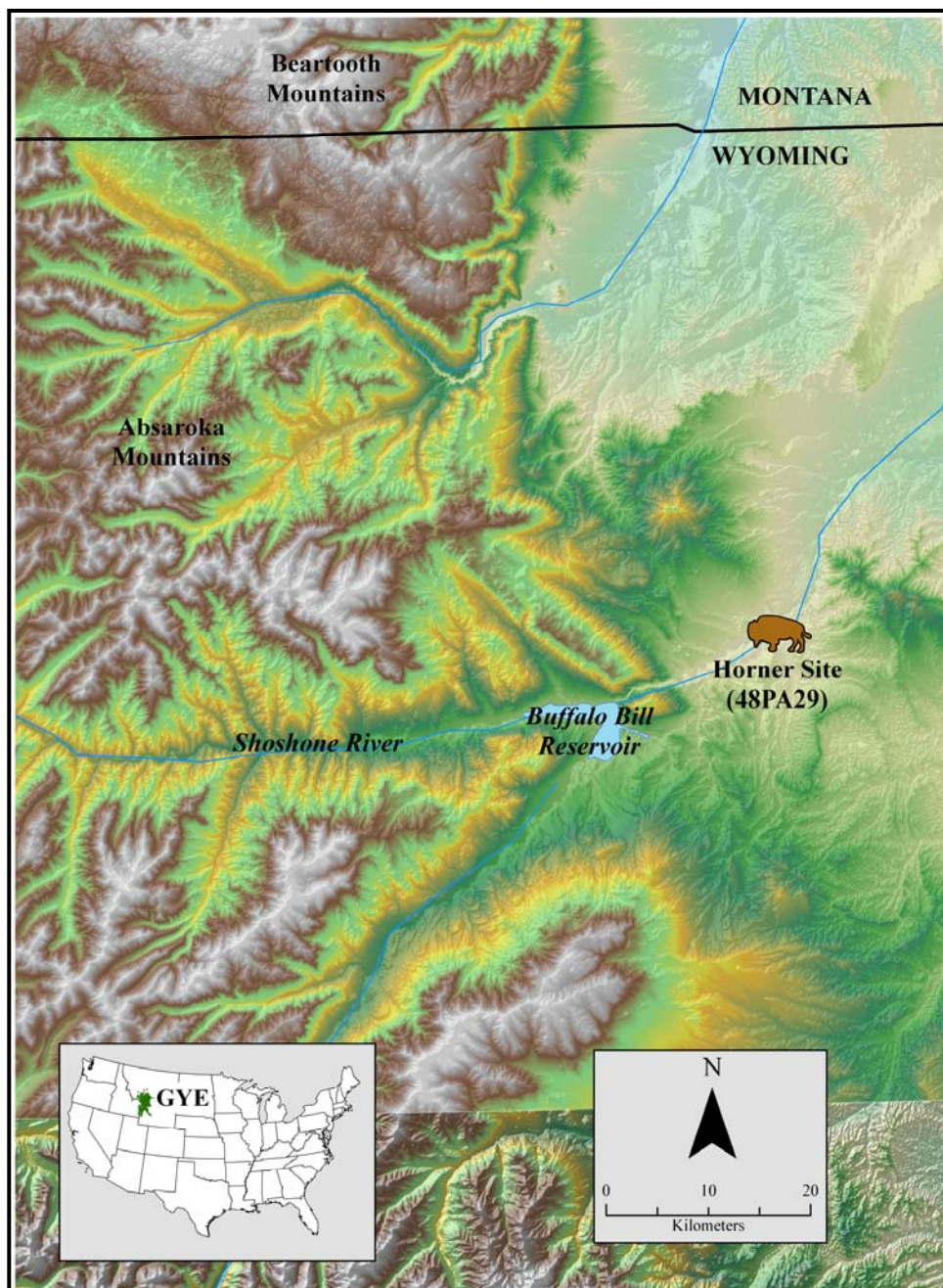


The Horner Site (48PA29)

To the east of the Yellowstone Plateau lies the Bighorn Basin, a large intermontane basin. The area lies within the rain shadow of the high plateau, and mountains of the GYE make the area relatively arid. Within this modern arid, shortgrass environment, bison were hunted 10,000 years ago during a period when the climate was probably more humid and cooler (Figure 5.6). Today

the mean annual temperature is 7.7°C (45.8°F) with a January mean of -4.3°C (24.3°F) and a July mean of 20.9°C (69.9°F). Precipitation averages about 25.3 cm (9.97 in) per year and is distributed rather evenly throughout the year, with a slight increase in June probably due to convection storms (www.wcc.dri.edu).

Figure 5.6. General location of the Horner site (48PA29).



James Allen, a collector living in Cody, Wyoming, originally discovered the Horner site (48PA29) in 1939. In 1949 Glenn Jepsen the Sinclair Professor of Vertebrate Paleontology and Curator of Vertebrate Paleontology at the Princeton Museum of Natural History undertook professional investigations of the site. The Princeton excavations continued until 1951. In 1952 Waldo Wedel took over the direction of the joint Princeton University and the Smithsonian Institution research investigations (Wedel 1987). Jepsen (1953:11) described the faunal remains from the Horner site:

Among the remains excavated in the “bone layer” are parts of poorly preserved skeletons of about 200 buffalo, apparently all belonging to the modern species, and a few bones of deer, antelope, wolves, rabbit, turtles, and birds. No complete skeletons have been found; the carcasses were thoroughly dismembered and the parts were scattered. Many bones were broken, probably for access to marrow. In places the bones were piled up to several layers thick.

Based upon these early excavations, the Horner site became the type site of the Cody Cultural Complex. This archeological complex dates to about 9000 years before present and is characterized by large, stemmed projectile points with parallel-oblique flaking patterns along the blade. A distinctive tanged knife, the Cody knife, is also a key part of the assemblage and is recognizable by its triangular blade with a transverse or oblique cutting edge (Wedel 1961).

The initial Princeton-Smithsonian excavations were in a mixed component of Cody Complex and Alberta-Cody origin. Excavations recorded a bone bed or beds and several features. However, due to the shallowness of the deposits bone preservation was relatively poor. Jepsen’s (1953:11) original interpretation that the animals “were all killed within a period of a month or so in the autumn or early winter, or they may represent the accretion of many kills made annually at that time of the year,” has been largely supported by more recent analysis (Frison and Todd 1987).

Under the direction of George Frison, the University of Wyoming returned to the Horner site in 1977 and 1978. In addition to work on the original Princeton-Smithsonian bone bed (Horner I), they uncovered a separate component (Horner II) that was nearly 1000 years older.

While the Princeton-Smithsonian bone bed was just below the surface and poorly preserved, the Horner II bone bed was buried under nearly two meters of sediments and well preserved (Frison and Todd 1987).

The Horner II assemblage consists of a minimum of 65 bison that were killed in the late fall or early winter. The bison remains were analyzed by Walker (1987b:338) who describes them as being of the extinct late Pleistocene-early Holocene genus *Bison* cf. *antiquus*. The bone bed lies within a shallow depression formed by a low gradient, intermittent stream and probably represents the primary kill location. Hunting of the bison likely occurred during their annual migration between the Oregon Basin and the Horner site area. The exact method of the kill is unknown, but may have involved the modification of a natural trap, such as the intermittent stream. Very few elements were removed from the kill site, and processing of the bison carcasses appears to have been minimal and focused on the hind limbs (Frison et al. 1987). The age of the Horner II bone bed is based upon two radiocarbon ages from charcoal (Table 5.5). The radiocarbon ages are statistically the same at the 95% confidence interval with an average age of 9899 ± 79 yrs BP ($T=0.615$; $X^2_{(0.05)}=3.84$). Taphonomic analysis, and limited weathering of the bones, indicate it was not subjected to extensive periods of exposure and was probably buried rapidly. Weathering of the bones is limited and suggests a rapid postdepositional burial.

Table 5.5. Radiocarbon ages of the Horner II bone bed (Frison 1987: Table 4.1). Calibration of radiocarbon ages was conducted using CALIB 5.0 and are reported at the 2-sigma level.

Laboratory Number	Material	Radiocarbon Age	Calibrated Age
SI-4851A	Charcoal	9875 ± 85	9680-9210 BC
I-10900	Charcoal	10060 ± 220	10,456-9133 BC
Average Age		9899 ± 79	9677-9238 BC

Phytoliths (microscopic silica bodies formed during the maturation process of plants) were collected from the Horner I and II profiles. A phytolith sample was recovered from the south wall profile of the 1977 University of Wyoming excavations of Horner II. The bone bed sample (Sample 1) reflected a mixed grass environment with short grasses dominant. Additional

samples were collected from the rib area of two butchered bison and reflected a similar grass community. Lewis (1987) interpreted the results from the profile and the bison rib areas as reflecting the community structure where the bison were grazing, and not necessarily the local Horner site vegetative community. Today this community is classified as Mountain Grassland with cool-season grasses dominant (Sims et al. 1978).

Soils on the site are described by Reider (1987) as *Aeric Calcicquoll*. These soils are commonly formed in depressions that are wet during part of the year. At other Paleoindian age sites, these soils formed in wet arroyo bottoms under sedges, grasses, rushes, and possibly some woodlands. In addition to the characteristics of the soil associated with the bone, other paleoenvironmental proxy data support the presence of periodic ponding of water and a more humid and cool climate. These data include the presence of gastropod shells, greater pine pollen in relation to sagebrush in the bone bed, and greater chenopod percentages (possible salt brush, *Atriplex*) in the bone bed in comparison to the modern surface (Reider 1987:354-356).

As previously stated, the Horner II assemblage dates to between 9677 and 9238 cal BC and consists of a kill of more than 65 individuals during the late fall or early winter. Three mandibles were selected from the material curated at the University of Wyoming Archaeological Repository (Table 5.4). I choose these specimens based upon their relatively good condition and also their ages. Todd and Hofman (1987) aged each of the specimens during the initial analysis of the Horner material. Because each specimen is a year apart in age it may potentially provide a view, albeit limited, into how the individuals may have used the landscape during different years, and by extension how the herd migrated. Specimen 1233H is the left mandible of a 2.6 year old bull, specimen 2548H is the right mandible from a 3.6 year old cow, and specimen 1181 H is also a cow, but 4.6 years old. Although the sample is limited, it may provide evidence for future analysis into how herds move through the ecosystem on an annual basis, as well as potentially examining differences between cow and bull land use.

The Snake River Delta Sites

The complex of archeological deposits that represent the Snake River Delta sites were excavated in 1987 and 1988 by the Midwest Archeological Center during a period of low water and drawdown of Jackson Lake to its prereservoir levels (elevation approximately 2052.2 m [6733 ft] AMSL). This work was part of the data recovery effort funded by the Bureau of Reclamation as part of the reconstruction of Jackson Lake dam (Connor et al. 1991).

The four sites (48TE1090, 48TE1101, 48TE1102, and 48TE114) represent prehistoric encampments along the Snake River north of Jackson Lake (Figure 5.7). The area is referred to as the Snake River Delta due to its progradation (building or accumulating sediments) into areas previously occupied by Jackson Lake. The Snake River has prograded approximately 20 km (12 miles) since deglaciation (Pierce 1987). The sediments of the delta area produced evidence of archeological materials that were previously buried, but erosional action of the reservoir has generally removed most of the overlying deposits, leaving previously vertically stratified deposits on the same surface. The deflation of these surfaces has confounded interpretation of the cultural deposits and their historical relationship.

The sites used in this study are all from the southern portion of the delta and are either within the area described by Pierce et al. (1998) as the “Meander Belt Sites” (48TE1090, 48TE114) or within “Beach Set B” (48TE1101 and 48TE1102). All of these landforms became stable during the last 2000-3000 years (Table 5.6). Inundation of the Snake River Delta sites precluded any systematic study and characterization of the sediments and vegetation community. This information is largely reconstructed by geomorphic work by Frison et al. (1988) and Pierce et al. (1998), with the vegetation community compiled from historic maps (Figure 5.8) and paleovegetation studies (Cummings 1991a, 1991b).

Figure 5.7. Map illustrating location of Snake River Delta sites in relation to important surficial geologic features (adapted from Pierce et al. 1998). Sites depicted have been inundated by construction of Jackson Lake dam.

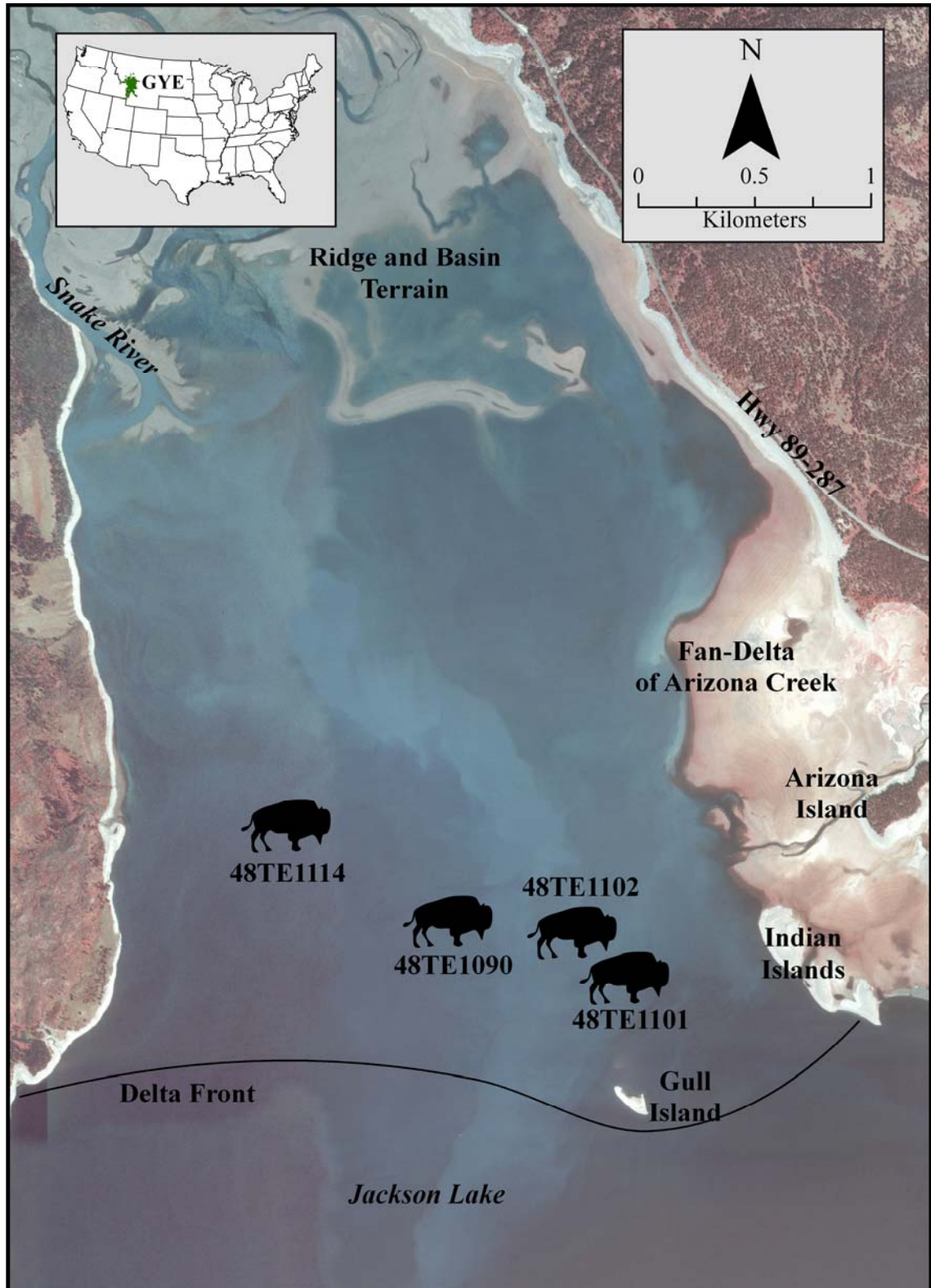


Figure 5. 8. Vegetation map of area around Jackson Lake (modified from Connor 1998 based upon map by Brandegee [1898: Plate XLIII]).

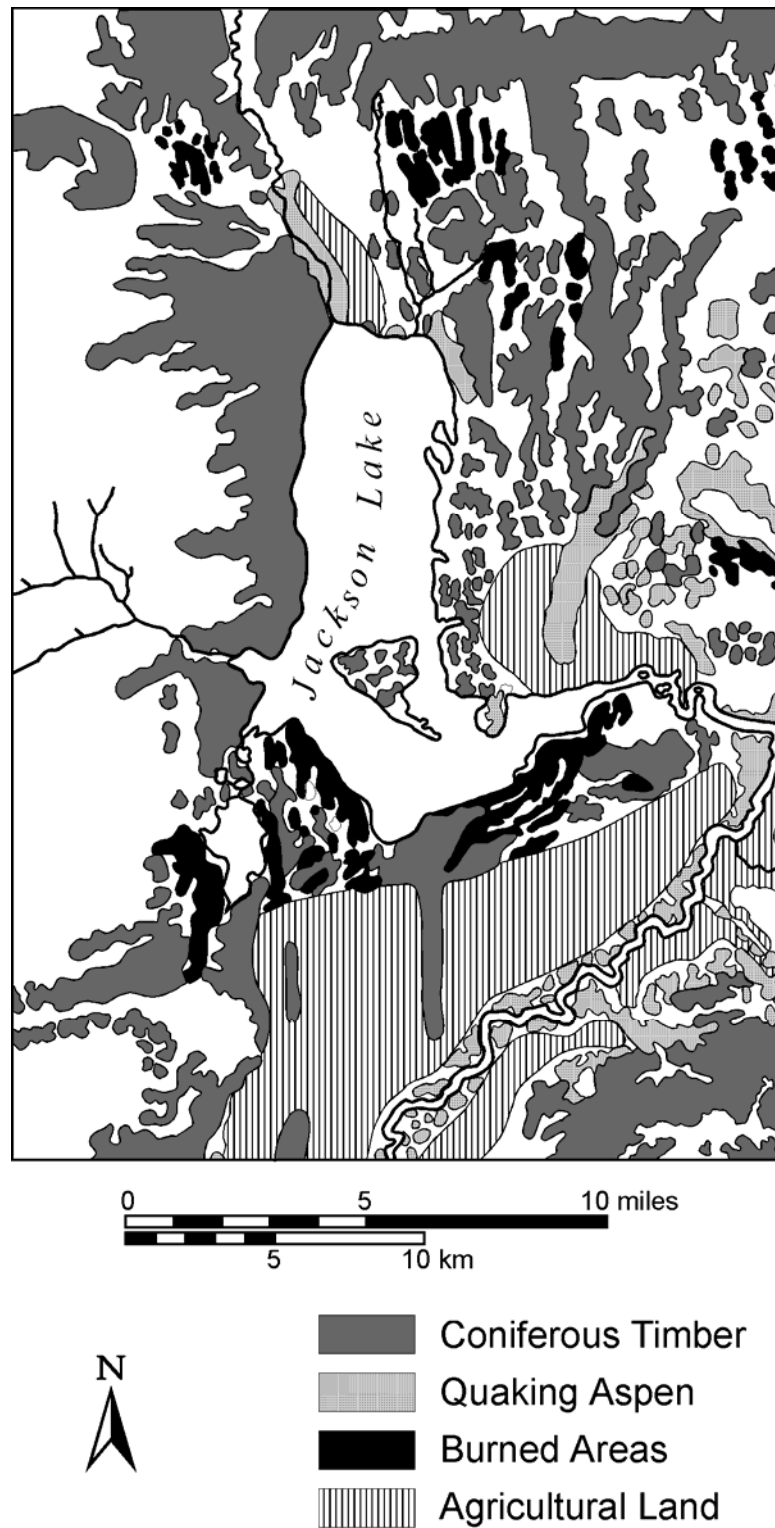


Table 5.6. Radiocarbon ages from Snake River Delta sites used in study.

Site Number	Provenience	Sample Material	Age	Calibrated Age (2 sigma)*
48TE1090	Feature 1	Charcoal	830 ± 100	AD 1015-1310
	Feature 3	Charcoal	1100 ± 90	AD 762-1052
	Feature 5	Charcoal	1320 ± 70	AD 605-879
	Feature 6	Charcoal	190 ± 70	
	Bison Block I	Unburned bone	770 ± 80	AD 1146-1321
48TE1101	Feature 1	Charcoal	1640 ± 60	AD 311-548
	Feature 2	Charcoal	1390 ± 90	AD 526-784
48TE1102	Bison Block I	Unburned bone	1380 ± 80	AD 533-831
48TE1114	Feature 1	Charcoal	1440 ± 60	AD 530-682
	Feature 2	Charcoal	1620 ± 70	AD 313-584
	Feature 3	Charcoal	1650 ± 100	AD 208-603
	Feature 7	Charcoal	1630 ± 100	AD 213-638
*Radiocarbon ages calibrated using CALIB 5.0.				

Cummings collected stratigraphic columns of pollen from the University of Wyoming backhoe trenches in 1987. The high level of sagebrush (*Artemisia* sp.) suggests an open sagebrush-steppe community. However, the lack of pine (*Pinus* sp.) pollen in these samples is in contrast to high levels of pine pollen from regional lake samples (Whitlock 1991). Cummings (1991a) has suggested that the physical degradation of the pine pollen may influence the interpretation. In 1988 more samples were collected. These samples illustrate a community dominated by pine pollen of local forests, together with *Abies* (fir), *Juniperus* (juniper), and *Picea* (spruce) members. Riparian species are also represented in the record and include *Alnus* (alder), *Salix* (willow), and Betulaceae (birch family). Areas of open sagebrush-steppe is suggested by relatively abundant *Artemisia* pollen.

Frison et al. (1987) provide potential contemporary vegetation communities based upon their soil analyses and correlation with regional vegetation mapping. Based upon their models, the Snake River floodplain probably had a wetland range type Engelmann spruce (*Picea Engelmann*) series. Potentially important species are listed in Table 5.7.

Table 5.7. Potentially important plant species associated with Jackson Lake sites (after Frison et al. 1987:Table 34).

Species	Common Name	Species	Common Name
<i>Carex</i> sp.	Sedge	<i>Osmorhiza</i> sp.	Sweetroot
<i>Ribes</i> sp.	Currant	<i>Prunus</i> sp.	Chokecherry

<i>Elymus cinereus</i>	Basin wildrye	<i>Balsamorhiza</i> sp.	Balsamroot
<i>Poa</i> sp.	Bluegrass	Cruciferae	Mustard
<i>Glycyrrhiza</i> sp.	American licorice	<i>Amelanchier</i> sp.	Serviceberry
<i>Heracleum lamatum</i>	Cow Parsnip		

Site 48TE1090

Site 48TE1090 was initially documented in September 1986 during a survey of the north shore of Jackson Lake, when the reservoir reached an approximate elevation of 2052.8 m (6735 ft) AMSL. The site lies within the inside of a meander loop of the modern (pre-inundation) course of the Snake River. The site area was probably a stable landform within the last 2000 years. Remaining stumps represent the prereservoir overstory community of large cottonwoods. Exposure of their roots suggests at least one meter of sediment loss since inundation (Connor et al. 1991).

Field work was conducted at the site between 1986 and 1988. Investigations included the excavation of fired rock features and large block excavations over concentrations of surface material, including bone. Four radiocarbon ages were obtained from charcoal associated with fired rock features, and a fifth was obtained from bison bone (Table 5.6).

Members of the University of Wyoming field team collected surface distributions of isolated elements of bison, specifically skulls, mandibles and metapodials. Controlled excavations of seven concentrations of bison bone was conducted by the MWAC field team (Figure 5.9). An estimate of the minimum number of individual bison from the controlled excavation is nine. Radiocarbon dated bison ribs from Bison Block I yielded an age of 770 ± 80 yrs BP (Figure 5.10; Cannon 1991).

Two specimens from site 48TE1090 were selected for analysis. These include specimen 42226, the right lower third molar from a 9.6 year old probable cow, and 42227, the left lower third molar from an 8.6 year old bull. Both of the specimens were isolated finds collected by the University of Wyoming and were not directly dated, but assuming they are associated with the human occupations of the site, they probably range date between cal AD 605 and cal AD 1321.

Figure 5.9. Annotated aerial photo of geomorphic context of site 48TE1090 following Connor et al. (1991). Aerial photos was taken on 7 October 1987. Please refer to Figure 5.7 for general site location. Exact location of site can not be revealed due to wishes of the National Park Service to protect the site.

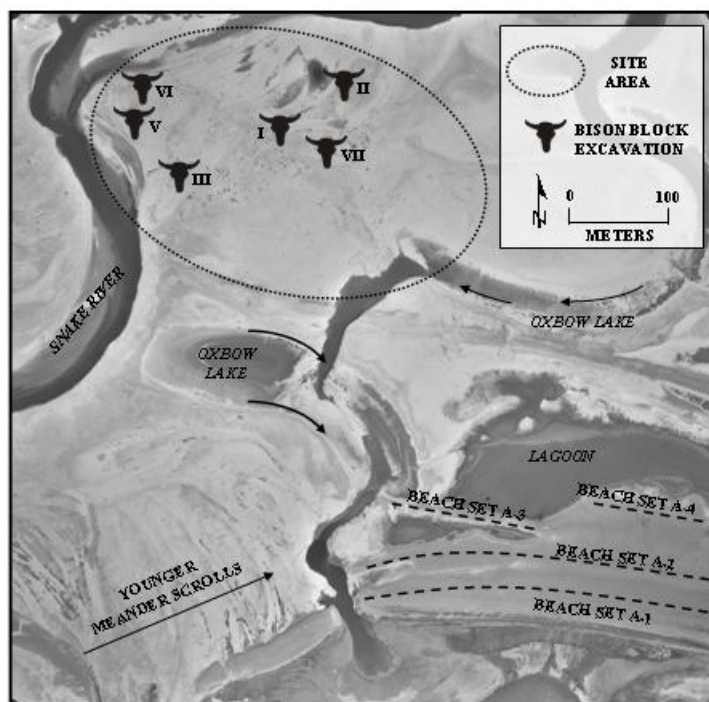
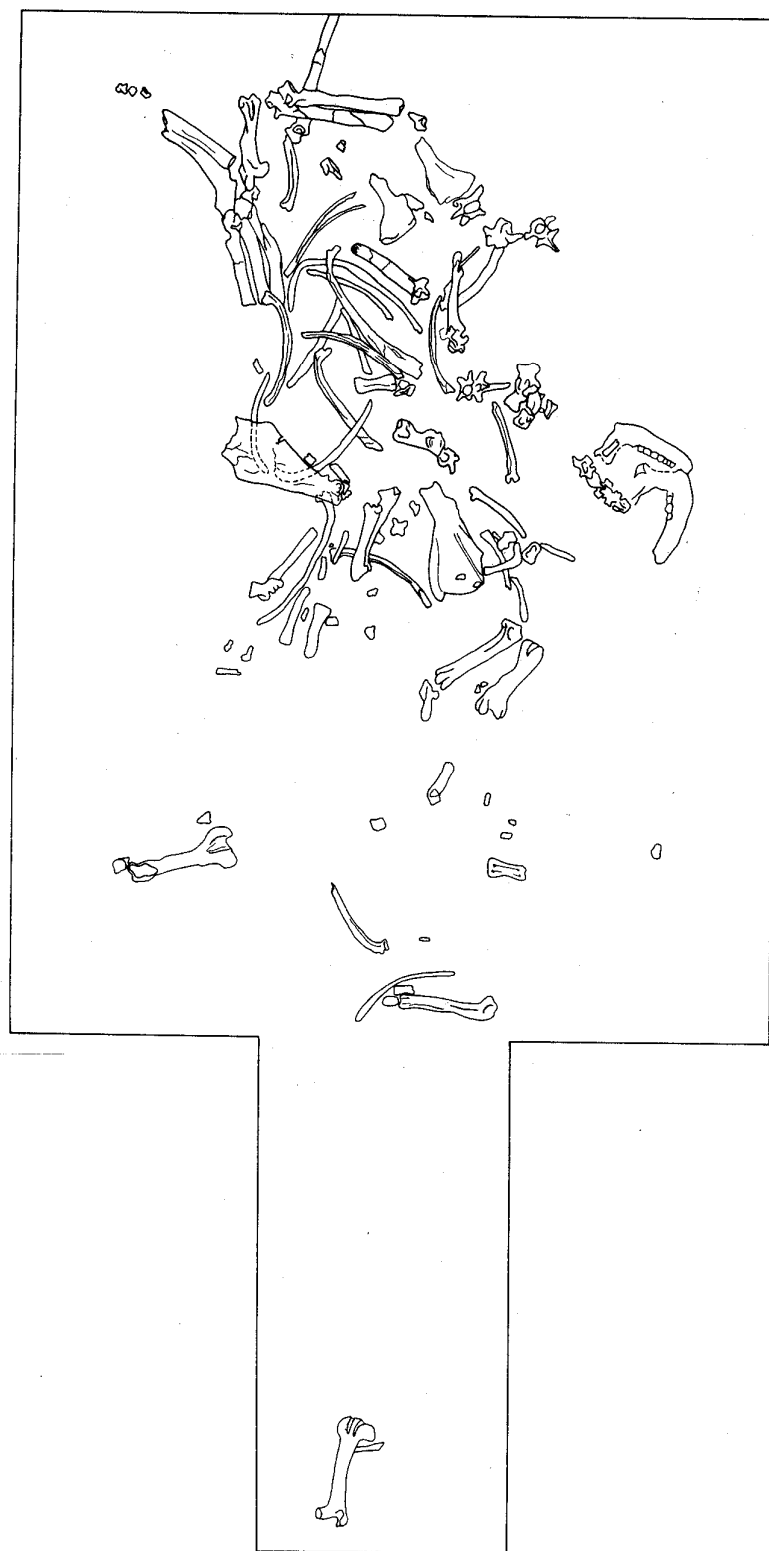


Figure 5.10. Plan view of Bison Block I excavation, site 48TE1090 (modified from Connor et al. 1991).



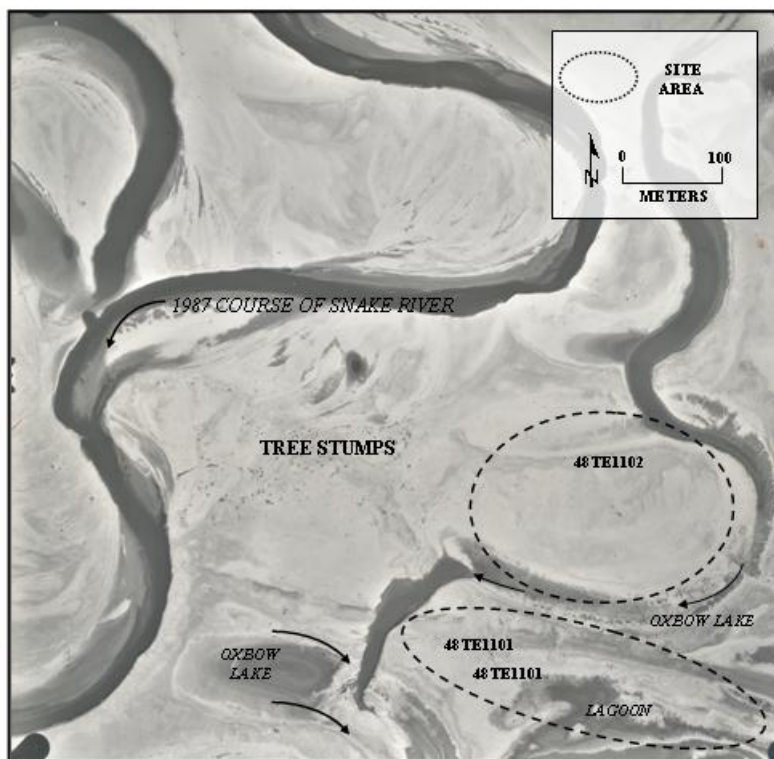
Site 48TE1101

Site 48TE1101 was initially documented in the fall of 1987 and lies along the northernmost beach ridge of Jackson Lake. This landform represents the oldest of a series of beach deposits formed near the delta front of the Snake River by lacustrine (lake) wave action. Subsequent meandering of the Snake River truncated and eroded the western portion of the ridge (Figure 5.11). Radiocarbon-dated archeological deposits suggest the ridge was probably forming between 2200 and 3000 years ago. The landform is oriented east-west and consists of a light scatter of fired rock, lithic artifacts, and isolated artiodactyl skeletons (Connor et al. 1991). Radiocarbon ages were obtained from charcoal in two fired rock features. The ages range from cal AD 311-784.

During the 1987 and 1988 field seasons, concentrations of bison bone were excavated. A single one-meter square unit was excavated over a concentration of bison bone in 1987. However, the material was in extremely poor condition. The material consisted of two mandible fragments and two cervical vertebrae of a subadult (Cannon 1991).

A block excavation was placed over the remains of a single individual in 1988. The elements were extensively weathered and exfoliated. Most of the elements conform to Todd et al. (1987) weathering stages five and six. While a high percentage of the elements are present, including those of high nutritional value, butchering marks are limited except for a possible v-shaped chop mark on the distal end of the left humerus (Cannon 1991). Sixty-three elements representing six bison individuals were recovered from this site (Cannon 1991: Table 158). The right lower third molar from a 5.6-7.6 year old possible cow was selected for analysis.

Figure 5.11. Annotated aerial photo of geomorphic context of sites 48TE1101 and 48TE1102 following Connor et al. (1991). Aerial photo taken 7 October 1987. Please refer to Figure 5.7 for general site location. Exact location of site can not be revealed due to wishes of the National Park Service to protect the site.



Site 48TE1102

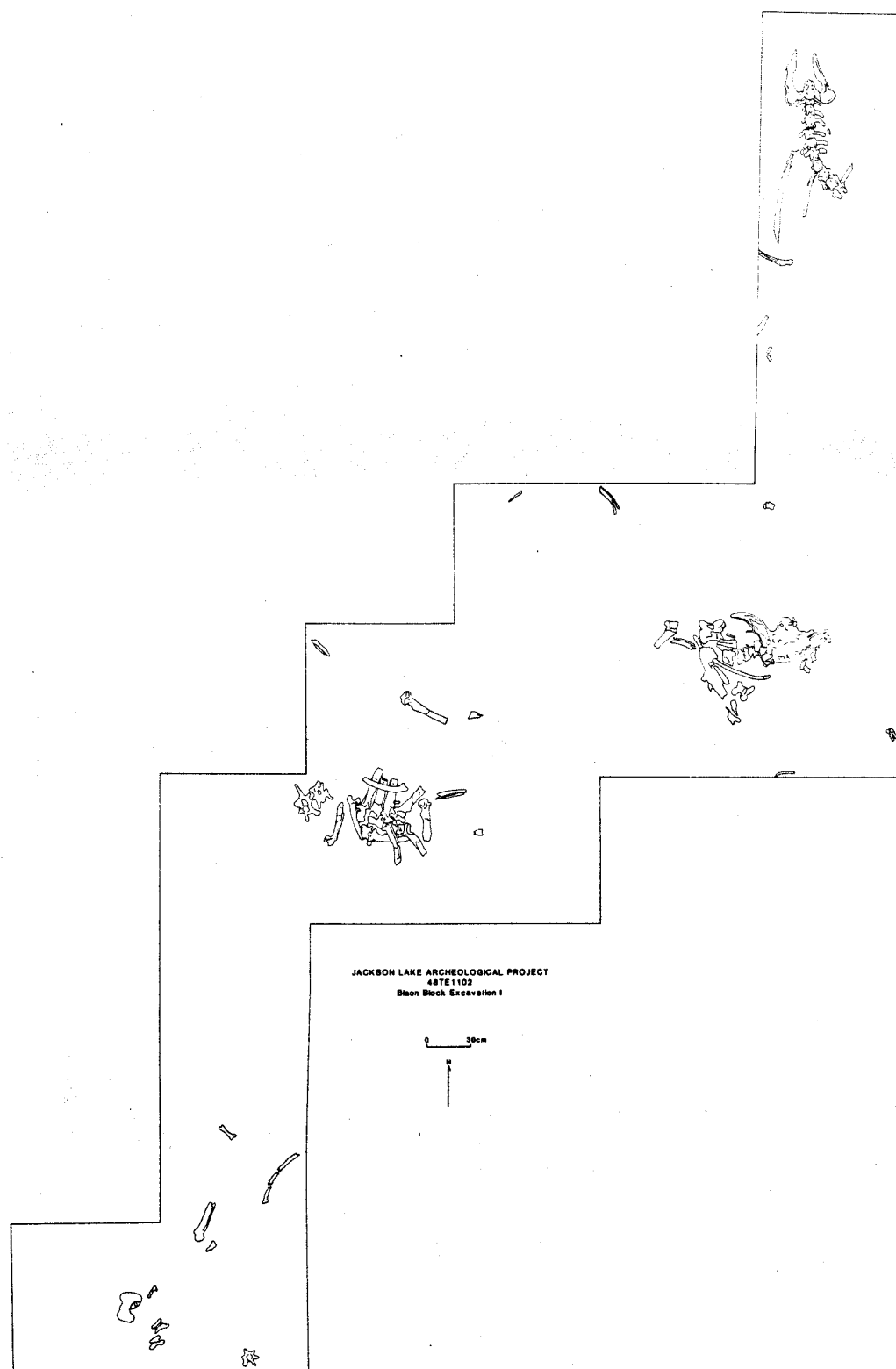
Site 48TE1102 lies north of site 48TE1101 on a low rise on the inside bend of an abandoned meander of the Snake River. Surface deposits of lithic artifacts, fired rock features, and bison bone were identified during the initial documentation of the site in 1987 (Connor et al. 1991).

The site deposits lie along a relict point bar deposit formed by the eastward migration of the Snake River (Figure 5.11). Sediments include reservoir muds, fluvial mud, and fluvial sands. Several organic and charcoal zones were also recorded in the sediments and probably represent natural fires (Frison et al. 1988). Deflation and erosion of the archeological deposits are present in the site area, but may not be as dramatic as in other portions of the delta.

Excavations in 1988 were focused upon two concentrations of bison bones. Bison Block I was initially identified by the University of Wyoming field crew with subsequent excavation being conducted by the Midwest Archeological Center crew. Four distinct concentrations of bone were present in the block (Figure 5.12). Three represent articulated, or semi-articulated, portions of a single individual, while the fourth is the axial skeleton of a second individual. Long bones are absent and may suggest human selection of the high utility (or meat-bearing) elements. Additional evidence of processing is suggested by score marks on the dorsal spines of two thoracic vertebrae (Cannon 1991).

Dating of the bison came from two sources. The base of a corner-notched projectile point was recovered from the southern bone concentration. Rib bones from the northern concentration were submitted for radiocarbon assay and produced an age of 1380 ± 80 yrs BP. Both the projectile point and radiocarbon age are consistent (Connor et al. 1991).

Figure 5.12. Plan view of Bison Block I excavation, site 48TE1102 (modified from Connor et al. 1991).



A second block excavation of bison bone was conducted after bone was uncovered during backhoe trenching by the University of Wyoming. A minimum of two individuals is indicated by the presence of two atlas vertebrae from this block. The association of fired rock, flaking debris, and the possible butchering marks on the acetabulum of the right pelvis indicate this bison is the result of human predation (Cannon 1991).

A total of 107 bison elements were recovered from site 48TE1102 for a minimum number of eight individuals. Radiocarbon ages from the site indicate human occupation between cal AD 533-AD 831. Two specimens, the right lower third molar of a 6.6 year old bull and the left lower third molar from a 9.6 year old cow, were selected for analysis.

48TE1114

The fourth of the Jackson Lake sites is 48TE1114 which was also recorded during the 1987 survey by the Midwest Archeological Center. The site consists of concentrations of fired rock features, lithic debris, and bison bone on an eroded surface dissected by several abandoned meanders of the Snake River. One-half to a meter of erosion has occurred, as indicated by the exposed roots of cottonwood stumps on site (Connor et al. 1991).

Large mammal bones are scattered across the site's surface. The bone is extremely weathered, exhibiting exfoliation of the pericortical surface. Excavations at the site were conducted in 1987 and 1988. Four blocks were excavated in 1988, three of which focused on concentrations of bison bone (Figure 5.13). Eight-hundred and twenty-nine bone specimens were recovered, of which 79 were bison.

Bison Block I was excavated in the extremely eroded southern portion of the site. Twenty-seven bison elements representing the upper torso, including a horn core and mandible, of a single individual were recovered. Fifteen bison elements, including a bison mandible, were recovered from Bison Block II. Score marks are present on a tibia. Bison Block III produced 187 bone specimens, 37 of which were identified as bison. Three individuals are represented (Cannon 1991).

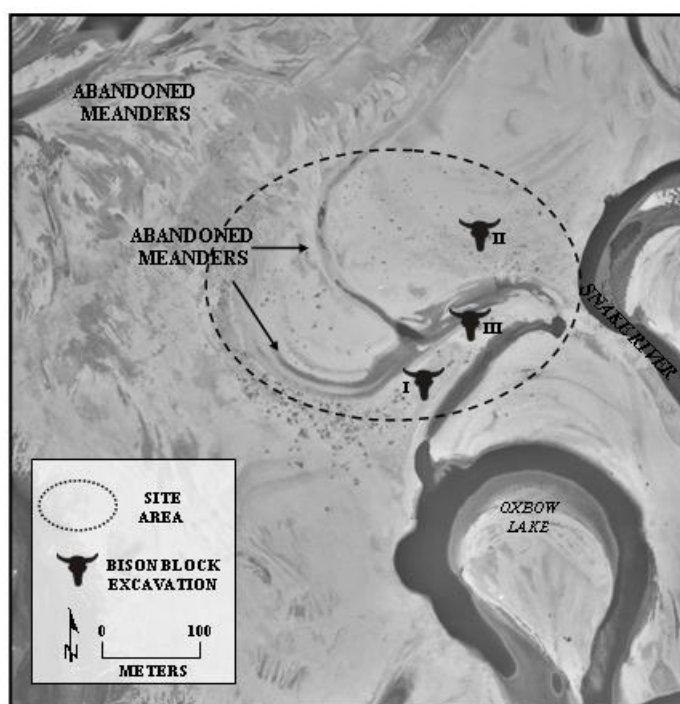
Four radiocarbon ages were obtained from charcoal recovered from fired rock features.

The ages have a pooled mean of 1552 yrs BP and are statistically the same at the 95% level

($T=5.99$, $X^2_{.05}=7.81$) indicating a narrow period of occupation between cal AD 208-AD 682. The

right lower third molar from a 5.6-6.6 year old bull was selected for analysis.

Figure 5.13. Annotated aerial photo of geomorphic context of site 48TE1114 following Connor et al. (1991). Aerial photo taken 7 October 1987. Please refer to Figure 5.7 for general site location. Exact location of site can not be revealed due to wishes of the National Park Service to protect the site.



The Goetz Site (48TE455)

The Goetz site is located in a narrow drainage in the northeastern portion of the National Elk Refuge that heads on the flanks of Sheep Mountain in the Gros Ventre Wilderness (Figure 5.14). The site lies at an elevation of 2092 m (6863 ft) AMSL. The southwest facing mouth of the drainage opens onto Long Hollow, a sagebrush-grassland underlain by loess. The walls of the valley contain lag deposits of glacial boulders and may easily have served as a natural bison trap. The valley is probably Bull Lake in age, with an inset bench of late Pleistocene Pinedale age. Holocene eolian and colluvial deposits overlie the older Pleistocene deposits and contain the archeological material (Kenneth Pierce, personal communication 2003). Soils are defined as the Starley-Tetonia association. The Tetonia soil is a silt loam that is slightly acidic to slightly alkaline, but which becomes strongly alkaline with depth. The potential vegetation on these soils include spike-fescue (*Leucopoa kingii*), Columbia needlegrass (*Achnatherum nelsonii*), mountain brome grass (*Bromus carinatus*), and antelope bitterbrush (*Purshia tridentata* [United States Department of Agriculture 1982]). Plant species identified on site are listed in Table 5.8.

The Goetz site material used in this study are from the original 1971 University of Wyoming investigations. Trying to reconstruct the original 1971 investigations has been difficult, and no original documentation (e.g., field notes and excavation maps) has been located so far. However, this is what is known. According to the annual report of the National Elk Refuge manager between August 19 and 22, 1971, Dr. George Frison (University of Wyoming) conducted “a preliminary exploration” of the site (Redfearn 1971:32). The investigation was in response to a dragline operation to increase flow at a nearby spring. A second season of excavation in 1972 was also proposed, but probably was never conducted.

Figure 5.14. General site location for the Goetz site, Teton County, Wyoming.

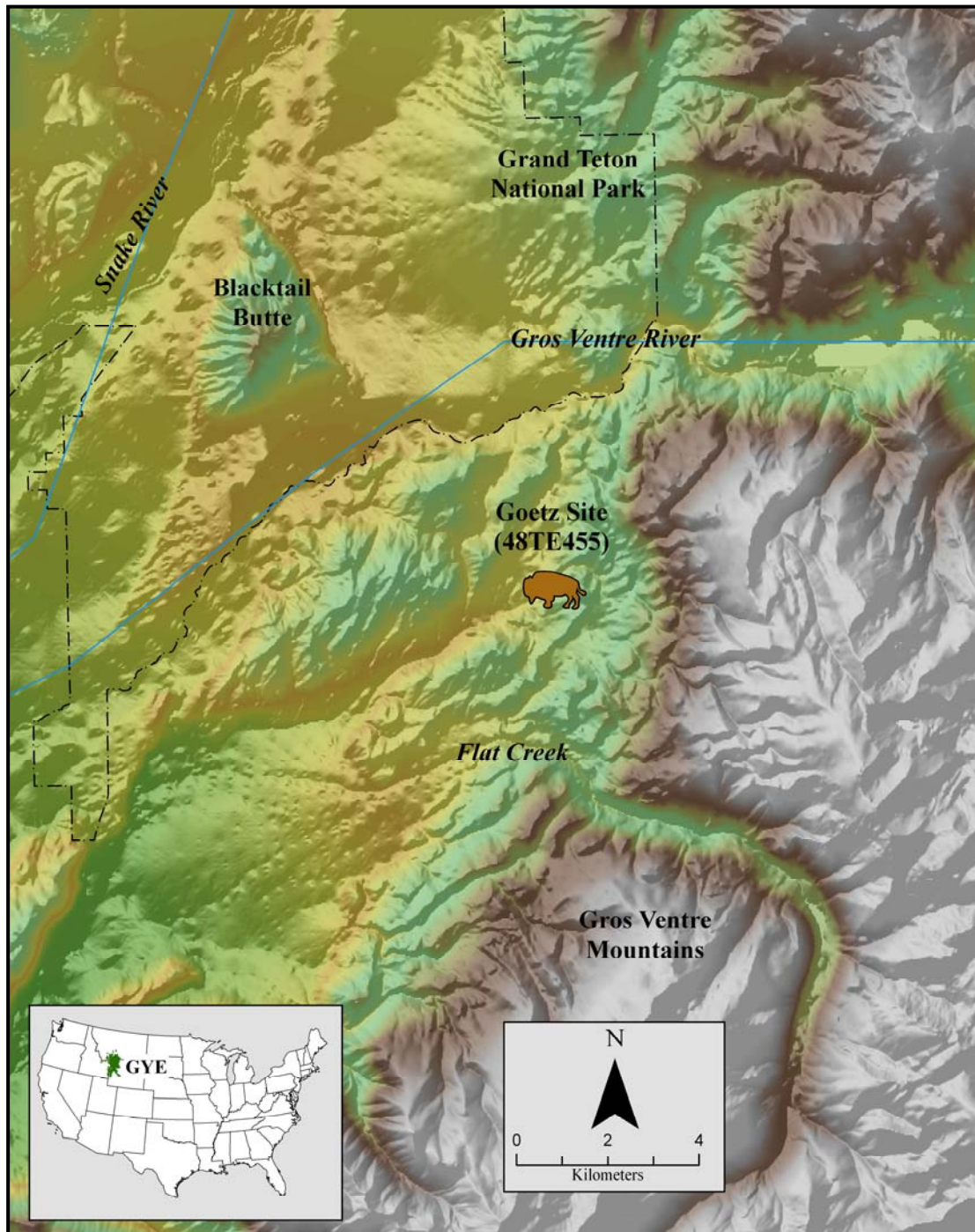


Table 5.8. Plants identified at the Goetz site.

Common Name	Scientific Name	Common Name	Scientific Name
Arrowleaf Groundsel	<i>Senecio trianularis</i>	Oblongleaf Bluebells	<i>Mertensia oblongifolia</i>
Big Sage	<i>Artemisia tridentata</i>	Prairie Smoke	<i>Geum triflorum</i>
Bristly Black Currant	<i>Ribes lacustre</i>	Rabbitbush	<i>Chrysothamnus nauseosus</i>
Dandelion	<i>Teraxacum officinale</i>	Silvery Lupine	<i>Lupinus argenteus</i>
Death Camas	<i>Zigadenus nuttallii</i>	Skyrocket	<i>Ipomopsis aggregata</i>
Goldfields	<i>Lasthenia chrysostoma</i>	Sticky Geranium	<i>Geranium viscosissimum</i>
Grouseberry	<i>Vaccinium scoparium</i>	Sulphur Buckwheat	<i>Eriogonum umbellatum</i>
Hairy Golden Aster	<i>Chrysopsis camporum</i>	Trembling Aspen	<i>Populus tremuloides</i>
Harebell	<i>Campanula rotundifolia</i>	Twinberry	<i>Lonicera involucrata</i>
Limber Pine	<i>Pinus flexilis</i>	Wasatch Penstemon	<i>Penstemon cyananthus</i>
Mountain Brome	<i>Bromus carinatus</i>	Wild Blue Flax	<i>Linum perenne</i>
Mountain Lover 'Oregon Boxwood'	<i>Paxistima myrsinites</i>	Wood's Rose	<i>Rosa woodsii</i>
Needle-and-Thread	<i>Stipa comata</i>	Yampah	<i>Perideridia gairdneri</i>
Northern Sweetvetch Crazyweed	<i>Oxytropis lambertii</i>	Yarrow	<i>Achillea millefolium</i>
Nuttal's Pussytoes	<i>Antennaria parvifolia</i>	Yellow Goatsbeard	<i>Tragopogon dubius</i>
Sego Lily	<i>Calochortus nuttallii</i>		

Love (1972:69-71; underlining in original), in his master's thesis entitled *An*

Archaeological Survey of the Jackson Hole Region, Wyoming, provides the following narrative of the investigations:

A dragline operation to open up the spring brought up quantities of butchered bison bone and flake materials. An incomplete bear mandible was recovered from this site in an earlier test hole. A 5 by 10 foot test pit into an undisturbed portion revealed the scattered remains of three separate butchered bison as well as numerous flakes, choppers, bifacial fragments, and projectile point pieces.

Over twenty pounds of flakes, core pieces, scrapers, and chopper or knife-like bifaces were obtained from the single test pit...A thin layer of carbon at a depth of approximately 9 inches was collected and subsequently dated at A.D. 1560 ± 115...At this level and below were found a reworked obsidian edge-ground lanceolate point, a thin straight edged, square-based, unnotched brown chert point, a piece of obsidian corner notched point, and what appears to be a McKean-like stem base of an obsidian point...A great deal of fire-cracked rock was distributed throughout the test pit as well as other undiagnostic tools...Possibly two layers of bone and materials are present, though a specific dividing line between them could not be drawn.

According To Dr. Frison, the excavation was salvage in nature (personal communication, October 1999). The relationship of the bone and the cultural material is difficult to assess, and Love's radiocarbon age of AD 1560 should be considered minimum.

In May 1999, I obtained the recovered bone from Western Wyoming College (WWC) for analysis. My intentions were to conduct an inventory of the bone and its condition for taphonomic interpretations. The condition of the bison bone is generally good. Most bones are fairly well preserved, although exfoliation has occurred on a number of specimens. Some of the damage probably occurred following recovery, as indicated by the difference in color of the cortical bone and the periosteum. The state of the bones suggests burial relatively soon after site abandonment, although there is variability. Some specimens show more advanced stages of weathering and associated cracking, splitting, and exfoliation. Variations in weathering may be associated with the different aged deposits that Love alluded to, but at this time, it is difficult to assess. A minimum of four bison are represented in the Goetz assemblage based upon the presence of four distal left femorae, left crania, and sacrum.

The right metatarsal (FS455.1.49) was submitted to Beta Analytic for radiocarbon assay. A small sample of bone was removed from the element and processed using the AMS technique. Processing produced good quality collagen and analytical steps proceeded normally. An age of 800 ± 40 yrs BP (Beta-133690; $\delta^{13}\text{C} = -21.0\text{‰}$) was returned on the specimen. The two-sigma calibrated range is cal AD 1175 to 1285. This age is approximately 400 years earlier than the age reported by Love (1972).

A second age from the 1972 University of Wyoming material was obtained from the roots of bison lower third molar. The age, 370 ± 40 yrs BP (Beta-241894; $\delta^{13}\text{C} = -18.8\text{‰}$), indicates a more complex history to the site. Both dates are earlier than the minimum age presented by Love (1972) and suggest periodic encounter hunting of bison.

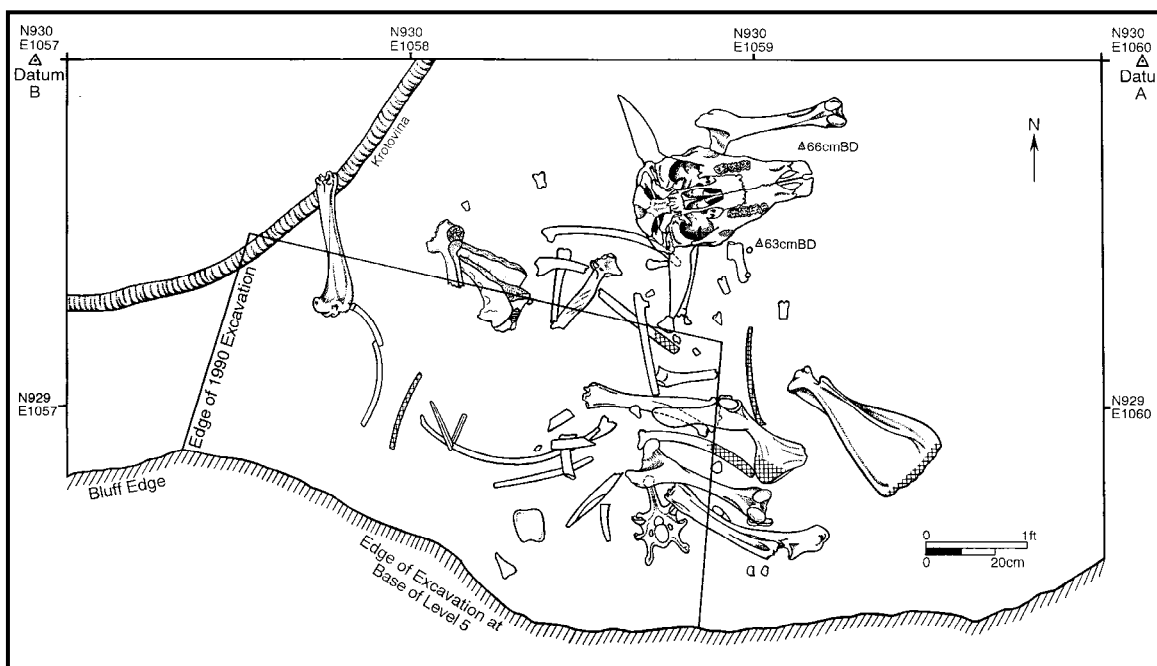
There were no complete mandibles recovered from the 1971 excavations, so two isolated bison third molars were selected for analysis. The specimens include the upper right third molar

(455.1) of a mature bull(?) and the lower right third molar of a mature cow (455.2). Based upon wear patterns described for the Horner material by Todd and Hofman (1987) the cow was approximately 4.6 years old at the time of death.

The Windy Bison Site (48YE697)

The Windy Bison site (48YE697) represents a probable encounter-type kill of a single bull (Figure 5.15). A survey crew from the Midwest Archeological Center discovered the skeletal remains of the bison eroding from the bluff face in 1989 (Cannon 1990). Excavation of the site occurred in 1993 and 1994 as part of the data recovery investigations in response to the reconstruction of the East Entrance Road (Cannon et al. 1997).

Figure 5.15. Plan view drawing of the Windy Bison site excavation that revealed the remains of a single bull bison.

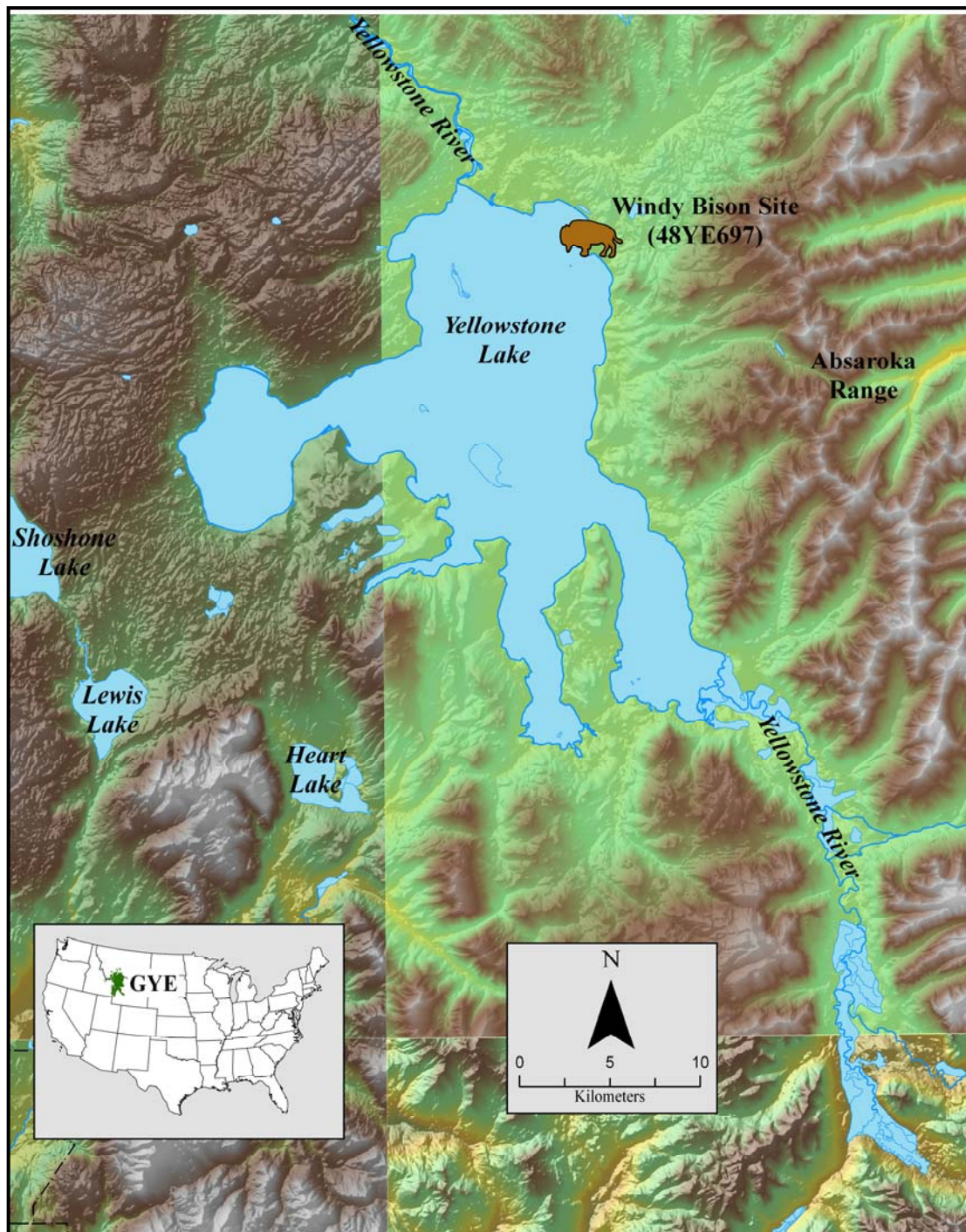


The site lies within Holocene-aged lacustrine deposits of eolian coarse to medium sands about 30 m above Yellowstone Lake along the western edge of Sedge Bay (Figure 5.16). The sands tend to be poorly sorted and have probably undergone mixing by rodent burrowing, as suggested by the general lack of internal stratification. The soils are mapped as Shook Family and McCort Family and Shadow Family Undifferentiated group. These mollisols form on glaciofluvial terraces and are derived from rhyolite and rhyolitic ashflow tuff (Rodman et al. 1996).

On site investigations identified and dated two paleosols during the 1990 investigations (Cannon et al. 1997). A distinct organic layer is present at about 1.9 m below surface. This clay loam deposit (Stratum VI) is about 10 cm thick and dark grayish brown (10YR 4/2) in color. A bulk soil sample produced a mean residence age of 4260 ± 60 yrs BP. A second organic layer, or paleosol, is present about 1.6 to 1.75 m below surface (Stratum IV). This clay loam deposit is also dark grayish brown (10YR 4/2) in color. A bulk soil sample provided a mean residence age of 1620 ± 50 yrs BP. Between these two paleosols is a brown (10YR 5/3) sandy clay loam disconformity that may represent a period of erosion or limited deposition (Cannon et al. 1997).

Climatic change is usually the mechanism driving landform stability and the development of soils; however, at the Windy Bison site, lake level change may be a more important factor in driving this system. When the lake is high, constant wave-lapping and periodic storm surges act to maintain an unstable cutbank that cannot support vegetation. As wave action continues to undercut the bank, winds pick up the sediments and redeposit them on the beach surface. This type of lake regime provides a ready source of depositional material that produces rapid buildup. At the opposite extreme, when the lake is at a low stand, wave action is reduced and the bank remains stable. During this time, deposition is limited and soils have an opportunity to form (Kenneth L. Pierce, personal communication 1990, as cited in Cannon et al. 1997).

Figure 5.16. General site location of Windy Bison site, 48YE697.



The role of hydrothermal activity in the geomorphic process is also important. Deposits of altered and angular rock, tentatively identified as hydrothermal ejecta, have been mapped and described across the site. A subaqueous vent is present at the western portion of the site and visible during late summer when the lake level is low. Hydrothermal input (e.g., increasing temperature with depth) has also been detected by soil temperature probes placed on the site for obsidian hydration dating. Ground heating may have been an attraction for game in the past, as it is today around Steamboat Springs and Beach Springs, and other thermal areas in YNP (Meagher 1973:98).

The open meadow of the site area ends abruptly upslope where a subalpine forest community is encroaching on the meadow. Jakobus and Romme (1993) attribute the tree invasion of dry meadows to regional climatic shift towards warmer and wetter growing season since the end of the Little Ice Age (ca. AD 1870). Despain (1990) describes the community as Subalpine Fir/Western Meadowrue Habitat Type (*Abies lasiocarpa*/*Thalictrum occidentale*). Common species of this habitat type include lodgepole pine, subalpine fir, Engelmann spruce, horsetail, bluejoint reedgrass, trapper's tea, twisted stalk, arrowleaf groundsel, and a variety of wet-site mosses. An on-site vegetation survey indicates a mesic meadow becoming more xeric lakeward. Grasses of the Poaceae family are common, as well as herbaceous plants (Table 5.9). Marmots are common on the site and large game (bison, mule, deer, and moose) were observed in the area during the period of investigation.

Fifty-seven elements identified as bison were recovered from the site excavations. Rib bones were submitted for radiocarbon assay and returned an age of 800 ± 60 yrs BP. The elements consist of almost the complete skeleton of a young bull bison in association with obsidian flaking debris. The most notable elements missing are the mandibles, which may have eroded into the lake. Although the bison appears to have been minimally butchered based on the general articulation of the elements, score marks, possibly the result of butchering, are present on the anterior portion of the humerus diaphysis, the hyoid, and the distal-lateral surface of the tibial

crest of the left tibia. Gender of the bull bison was determined by comparing the size of the metapodials with those of known modern bison and characteristics of the skull. Based upon incomplete fusion of the humerus the age of the bison was judged to be approximately four years old at the time of death (Cannon et al. 1997). The left upper third molar was selected for analysis.

Table 5.9. Identified vegetation on the Windy Bison site (48YE697).

Common Name	Species	Common Name	Species
Pussytoes	<i>Antennaria</i> sp.	Dandelion	<i>Taraxacum</i> sp.
Wild Rose	<i>Rosa</i> sp.	Yarrow	<i>Achillea</i> sp.
Sagebrush	<i>Artemisia</i> sp.	Buttercup	<i>Ranunculus</i> sp.
Mustard	Brassicaceae	Sticky geranium	<i>Geranium viscosissimum</i>
Larkspur	<i>Delphinium</i> sp.	Richardson's geranium	<i>Geranium richardsonii</i>
Lupine	<i>Lupinus</i> sp.	Chickweed	<i>Stellaria</i> sp.
Clover	<i>Trifolium</i> sp.		

Modern Samples

Modern bison samples from Yellowstone National Park and the Henry Mountains of Utah were obtained as control samples with which the archeological specimens can be compared. The modern samples are excellent controls, because they are from well-documented vegetation communities and their movements are restricted within management boundaries. A list of the potential plant species from each of the study areas and their photosynthetic pathway is presented in Appendix B.

Hayden Valley, Yellowstone National Park, Wyoming

Dr. Peter Gogan of Montana State University provided me with modern bison specimens he collected from natural winter deaths in Hayden Valley, Yellowstone National Park. Hayden Valley is a large grassland in the central portion of the Yellowstone Plateau that extends from the Grand Canyon of the Yellowstone south to Mud Volcano and west to Mary Mountain (Figure 5.17). The valley is drained by Trout and Alum Creeks, and includes Cygnet Lakes in the north and Beach and Dryad lakes to the south. The area is rolling with an average elevation of about 2400 m (7874 ft) AMSL.

Figure 5.17. Central portion of Yellowstone National Park, Wyoming detailing Hayden and Pelican Valleys.



Soils include alluvial silts along the creeks with lacustrine deposits above the alluvial terraces. Lodgepole pine dominates the surrounding slopes with stands of Engelmann spruce, subalpine fir, and Douglas fir interspersed. Wet meadows occur along the rivers with sedges (*Carex* spp.), and marsh reedgrass (*Calamagrostis* spp.) common. Areas of geothermal features are also common. The drier meadows are dominated by cool season grasses (*Festuca idahoensis*, *Poa* spp.), and sagebrush (*Artemisia* spp.). Despain (1990) describes the vegetation communities as the Silver Sage/Idaho Fescue (*Artemisia cana*/*Festuca idahoensis*) and the Big Sagebrush/Idaho Fescue-Sticky Geranium Phase (*Artemisia tridentata*/*Festuca idahoensis*/*Geranium viscosissimum*).

Bison are the dominant large mammal in the valley during the summer. The Central or Mary Mountain Herd migrates to the lower elevations of the Madison-Firehole-Gibbon region to spend the winter. The Mary Mountain herd is well studied, initially based upon Meagher's (1973) dissertation work, along with her subsequent study and more recent studies (Gogan et al. 2001). Meagher (1973:Table 2) compiled historic records of bison sightings and counts prior to 1915. These records indicate the area may have served as a refuge from poaching for a small number of bison. As Meagher notes (1973:17):

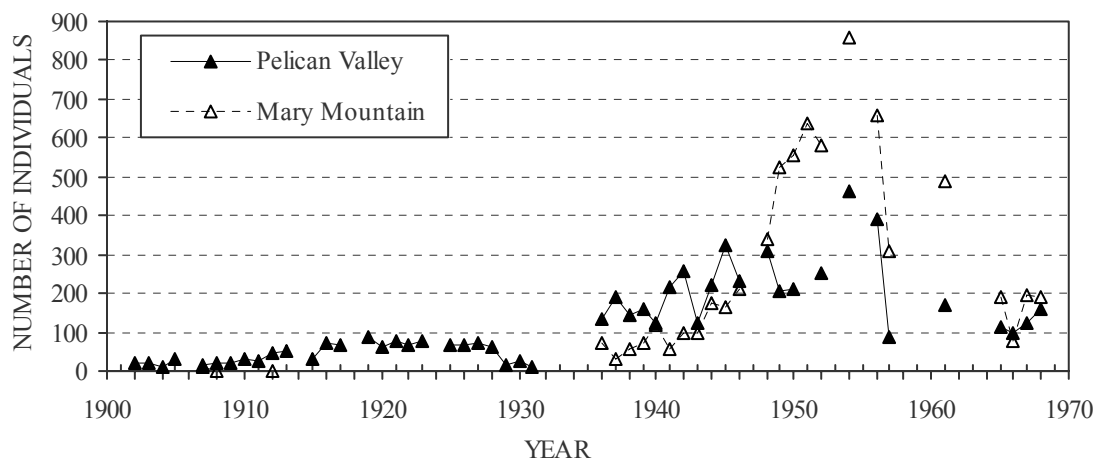
Natural losses, coupled with scattering of the few remaining animals, left a minimal breeding population in the most remote places of the Pelican-Mirror-Upper Lamar country.

Historically, the use of Hayden Valley is not well understood. Bison mixed herds (cows and calves, with some mature bulls) wintered in the valley, with movement west to the Madison Plateau in summer. Historic trails between Hayden Valley and the Firehole River are documented by early writers and visitors to the Park (Meagher 1973).

During the twentieth century efforts were made by YNP management to protect and rebuild the bison herd. Management efforts did not focus on the recreation of "a natural, wild bison population," but instead concentrated their efforts on ensuring a viable population

(Meagher 1973:29). Prior to 1936, efforts to reestablish the YNP herd were concentrated on the Mirror Plateau and Upper Lamar regions, with numbers in Hayden Valley being unknown and presumed absent. Meagher (1973) does note that a 1946 file report indicates some bison were present in Hayden Valley in 1930-31. In 1936, bison were trucked to the Hayden and Firehole valleys and released. As the numbers increased, movement between the two valleys increased and they have since been referred to as the Mary Mountain herd. Bison populations have steadily increased, although losses (mainly culling) have occurred (Figure 5.18).

Figure 5.18. Yellowstone National Park bison counts for the Pelican Valley and Mary Mountain herds from 1902-1968. Numbers are actual counts presented in Meagher (1970: Appendix IV). Breaks in lines indicate years when no counts were available.



The specimens used in the study include YELL2000.HV.002, the lower right third molar from an 8.6 year old cow. The second specimen, YELL2000.HV.003, is the lower right third molar of a 2.6 year old cow. The specimens were probably both winter deaths and were collected in the spring of 1999 and 2000, respectively. After collection the mandibles were defleshed by soaking in bleach.

Twenty-two rumen samples were collected by Meagher (1973:90). Half of the samples were collected in the winter, with the rest being collected throughout the other seasons.

Approximately two-thirds of the samples were collected from adult bulls. Grasses and grasslike

plants formed the vast majority of the diet, with sedges a main source during all seasons, but averaging more than half of the diet during the winter (Meagher 1973; Table 5.10).

Table 5.10. Food habits from fecal remains from 22 seasonal samples (after Meagher 1973:Table 17). Numbers indicate percent of sample composition.

Species		Winter (n=11)	Spring (n=4)	Summer (n=4)	Fall (n=3)	Total (n=22)
Grasses and grass-like plants		99	96	91	99	96
<i>Carex</i> sp.	Sedge	56	49	50	37	51
Grasses		34	46	32	30	35
<i>Juncus</i>	Wire rush	9	1	8	32	10
<i>Carex</i>	Spike-sedge	-	-	1	-	T
Forbs		T	3	6	T	2
<i>Phlox</i> sp.	Phlox	T	2	T	-	1
<i>Potentilla</i>	Northwest cinquefoil	-	T	6	-	1
<i>Eriogonum umbellatum</i>	Sulfur eriogoum (buckwheat)	T	T	T	T	T
<i>Taraxacum</i> sp.	Dandelion	T	-	T	T	T
<i>Antennaria</i> sp.	Pussytoes	-	T	-	-	T
<i>Senecio</i> spp.	Groundsel	-	-	T	-	T
<i>Potentilla fruticosa</i>	Shrubby cinquefoil	T	-	-	-	T
<i>Trifolium</i> sp.	Clover (introduced)	-	-	T	-	T
<i>Allium</i> sp.	Onion	-	-	T	-	T
<i>Collinsia</i> sp.	Blue-eyed Mary	-	-	-	T	T
Unidentified		-	T	T	T	T
Browse		1	T	2	T	1
<i>Artemisia tridentate</i>	Big sagebrush	1	T	-	-	1
<i>Cornus stolonifera</i>	Red dogwood	T	T	-	-	T
<i>Rubus</i> sp.	Raspberry	T	-	T	-	T
<i>Vaccinium caesoitosum</i>	Dwarf huckleberry	-	-	2	-	T
<i>Amelanchier</i> sp.	Serviceberry	-	-	-	T	T
<i>Amelachier</i> sp.	Fringed sagebrush	T	-	-	-	T
Unidentified		T	T	-	T	T
<i>Pinus contorta</i>	Lodgepole pine	T	T	T	T	T
<i>Equisetum</i> sp.	Horsetail	T	T	T	-	T
<i>Cassiope</i> sp.	Moss	T	-	T	T	T
	Lichen	T	T	-	-	T
Unidentified		T	T	T	T	T

T=trace amount.

Pelican Valley, Yellowstone National Park

I collected an associated skull and mandibles (94KC1) during the summer of 1994 along Pelican Creek in Yellowstone National Park. The skull is in good condition and had probably

been exposed on the surface for less than three years. The cow probably succumbed during the winter and, based upon the tooth wear, was probably 10.6 years of age. The third lower molar was submitted for analysis.

Pelican Valley is an important wintering area for bison and is one of the major study areas for understanding bison ecology (Meagher 1973). The valley begins in the east where Raven Creek leaves the high country of the Absoroka Mountains to the mouth of Pelican Creek at Mary Bay on the north shore of Yellowstone Lake (Figure 5.17). The valley sits at an elevation of approximately 2377 m (7800 ft) AMSL and is one of the few open grasslands on the Yellowstone Plateau. The remoteness of Pelican Valley probably helped protect the few remaining original Yellowstone bison from extinction in the late 19th and early 20th century (Meagher 1973).

Landforms of Pelican Valley consist largely of fluvial and glaciofluvial deposits with gentle slopes and limited relief (Shovic 1996). Soils tend to be mollisols and inceptisols (Rodman et al . 1996). Despain (1990) identifies two nonforested habitat types in the valley, sedge marshes and silver sage/Idaho fescue. Sedge marshes include areas where standing water occurs during most of the growing season. Dominant species include water sedge and inflated sedge. These are important winter forage for bison, who dig through the snow to access the dead sedge leaves.

Nonforested communities on the Yellowstone Plateau are typically restricted to the areas underlain by andesite and sedimentary rocks. The soils derived from these deposits are finer and richer in nutrients and organic matter. On the rhyolitic plateaus, nonforested or grassland communities are restricted to areas where geologic events have deposited significant amounts of fine particles, such as in Pelican and Hayden valleys. Each of these valleys has soils derived from Pleistocene lake sediments when ice dammed the Yellowstone River and increased the depth of Yellowstone Lake by 90 meters (Despain 1990).

The Big sagebrush/Idaho fescue habitat type is present along the shore of Mary Bay, as well as being distributed throughout the park at varying elevations, and provides both winter and summer range to large ungulates. Common species include big sagebrush (*Artemisia tridentata*),

Idaho fescue (*Festuca idahoensis*), junegrass (*Koeleria cristata*), occasionally bluebunch wheatgrass (*Agropyron spicatum*), rabbitbrush (*Chrysothamnus* sp.), fringed sagebrush (*Artemisia frigida*), and prairie smoke (*Geum triflorum* [Despain 1990]).

The Tufted hairgrass/sedge habitat grows in drainages where silts and organic matter have accumulated. This community is scattered throughout the Park and at low elevations provides important winter range. Characteristic species include tufted hairgrass (*Deschampsia cespitosa*), black-and-white called sedge (*Carex albonigra*), slender-beaked sedge (*Carex athrostachya*), American bistort (*Polygonum bistortoides*), meadow pussytoes (*Antennaria corymbosa*), and graceful cinquefoil (*Potentilla gracilis*).

An additionally important nonforested community present in Pelican Valley is the Silver sage/Idaho fescue habitat type. This community is associated with areas of high water table, such as stream banks, seeps, or areas of perched water tables in old lake sediments. Important species include silver sage (*Artemisia cana*), Idaho fescue, tufted hairgrass, various sedges, and shrubby cinquefoil (*Potentilla fruticosa* [Despain 1990]).

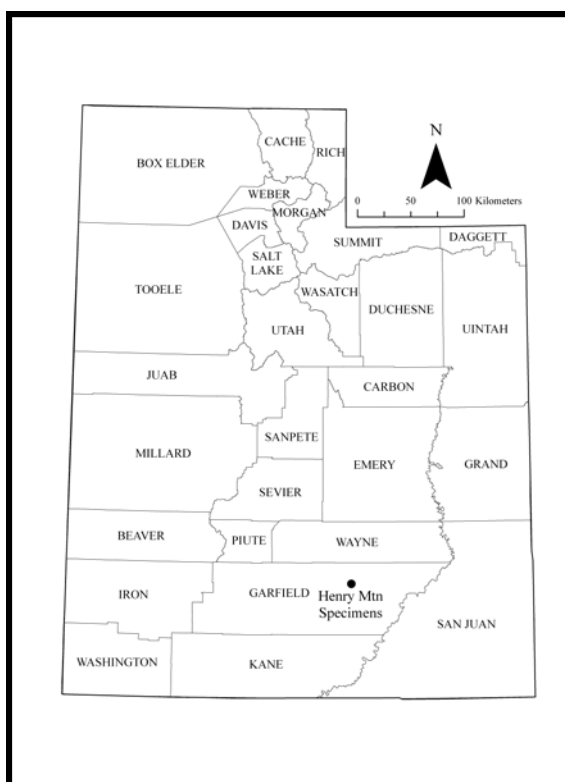
Henry Mountains, Utah

Dr. Dirk Van Vuren of the University of California-Davis supplied two modern bison mandibles. The specimens were collected during his research concerning the ecology of the introduced herd of the Henry Mountains, Utah. The samples include Specimen 12, the lower right third molar from a bull aged between 3.6-4.6 years. The specimen was collected in May 1978 from the west slope of Mount Ellen at an elevation of approximately 2682 m AMSL. The second specimen, Specimen 768, was also collected from the west slope of Mount Ellen at an approximate elevation of 2804 m AMSL in September 1997. This specimen is the lower left third molar from a 6.6 year old bull.

The Henry Mountains are located in Wayne and Garfield counties in southeastern Utah (Figure 5.19). These high islands in the desert represent important moisture traps within the arid Colorado Plateau. Osborn (1993) has noted that these upland areas, or “moisture islands”, were

important resource areas for hunter-gatherers and their ungulate prey species in the American Southwest. The terrain is rugged and steep with elevation ranges from 1500 m (4921 ft) in the surrounding deserts to 3540 m (11,614 ft) at the summit of Mount Ellen. As is typical of other mountainous terrain, average annual precipitation increases with elevation, from about 15 cm (5.9 in) at the base of the range to 50 cm (19.7 in) on the upper slopes. There is also an altitudinal change in vegetation. Extensive pinion pine (*Pinus edulis*)-juniper (*Juniperus* sp.) woodlands are present on the lower slopes (1500-2500 m). Introduced species, primarily crested wheatgrass (*Agropyron desertorum*) and alfalfa (*Medicago sativa*), have been seeded in cleared woodlands areas. Above 2500 m (8200 ft), the slopes are interspersed with Douglas fir and spruce forest, groves of quaking aspen, and shrub-steppe openings dominated by sagebrush, snowberry (*Symphoricarpos* sp.), forbs (*Penstemon* sp., *Oxytropis lambertii*, *Astragalus* sp., and *Potentilla* sp.), and perennial grasses (*Poa* sp., *Festuca* sp., *Stipa* sp., *Koeleria cristata*, *Sitanion hystrix* [Van Vuren and Bray 1986]).

Figure 5.19. General location of the Henry Mountains' specimens



The bison population was established in 1941-42 with the introduction of 15 cows and 8 bulls from Yellowstone National Park to the San Rafael Desert about 50 km northeast of the mountains. Within a few years the herd moved southeast and established a seasonal pattern of spending summers on the upper slopes of Mount Ellen and wintering in the desert to the east and northeast. In a seven-year study beginning in 1997, Van Vuren and Bray (1985) found that productivity was nonlinearly correlated with precipitation and was lower than other herds, a possible result of sparse vegetation. However, the herd has been increasing exponentially since its establishment despite the low forage production, annual hunts, and possible competition with domestic cattle. The researchers found that during the wet years following the 1977 drought the herd growth was particularly rapid.

In several other studies on the comparative ecology of bison and cattle in the Henry Mountains, Van Vuren and Bray (1983) and Van Vuren (1982, 1984) found that bison movements were correlated with preferred forage in comparison to cattle, which were limited by slope, horizontal distance and vertical distance to water. These bison also preferred grasses and sedges (Table 5.11).

Summary

Bison mandibles from eight prehistoric sites in the GYE were selected for this study and represent a variety of time periods and environmental contexts. Modern samples from Yellowstone National Park, Wyoming and the Henry Mountains, Utah also were selected as controls against which the prehistoric samples could be compared.

In the following chapter, I will discuss the scientific application of stable isotope analysis to questions of bison diet, migration, and possible avenues for understanding past climate change.

Table 5.11. Percent plant composition of bison in a shrub-steppe and seeded area in the Henry Mountains, Utah (Van Vuren and Bray 1983; Van Vuren 1984).

Forage	Percent Composition	
	Shrub-Steppe	Seeded
Grasses and sedges		
<i>Agropyron</i> spp.	2	86
<i>Bromus ciliatus</i>	3	Trace
<i>Carex</i> sp.	3	Trace
<i>Festuca</i> spp.	10	-
<i>Koeleria cristata</i>	13	-
<i>Oryzopsis hymenoides</i>	Trace	1
<i>Poa</i> spp.	66	2
<i>Sitanion hystrix</i>	Trace	6
<i>Stipa</i> spp.	1	-
Total grasses and sedges	99	96
Forbs		
<i>Astragalus</i> spp., <i>Oxytropis</i> spp.	Trace	-
<i>Lesquerella</i> spp.	-	1
<i>Medicago sativa</i>	-	3
<i>Senecio</i> spp.	-	Trace
Other forbs	1	-
Total forbs	1	4
Shrubs		
<i>Artemisia</i> spp.	Trace	Trace
<i>Symphoricarpos</i> spp.	Trace	Trace
<i>Quercus gambelii</i>	-	Trace
<i>Shepherdia rotundifolia</i>	-	Trace
Total shrubs	Trace	1

Chapter VI

Stable Isotopes and Their Application to Bison Ecology

Introduction

The application of stable isotope analysis to questions of changes in diet, migration, and the effect of shifting climatic patterns on plant distributions has been an evolving technique within a number of interdisciplinary sciences (Rundel et al. 1988; Ambrose and Katzenberg 2000; Ehrlinger and Cerling 2001; Ehrlinger, et al. 2005). Currently, it is widely used for the reconstruction of dietary preferences, and related issues, of mammals at archeological (Widga 2006) and geologic time-scales (Passey et al. 2005). Studies applying stable carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), and oxygen ($\delta^{18}\text{O}$) have been highly successful in reconstructing life histories of extinct (Hoppe 2006), extirpated (Cannon 2007), and extant mammals (Hobson 1999). In the initial portion of this section, I will review the science and application of these stable isotopes and the context in which they will be applied to the bison recovered in the GYE. Following this review, I present the results of my study on bison teeth and its implications for understanding trends in bison ecology during the Holocene.

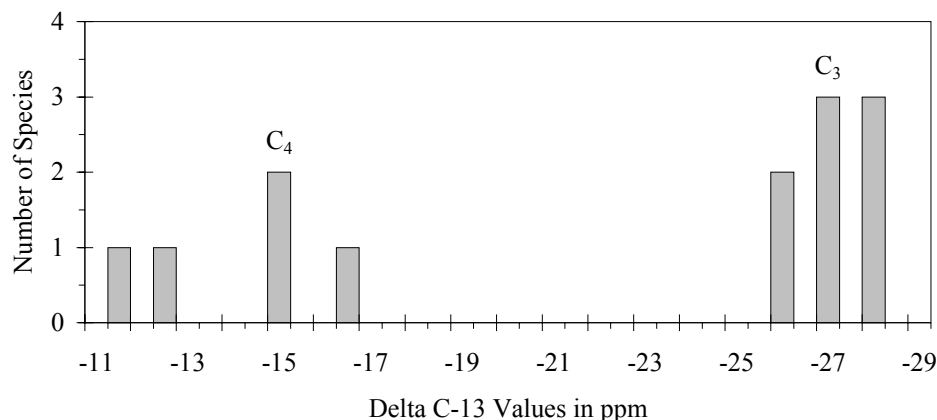
Stable Carbon Isotope ($\delta^{13}\text{C}$)

The application of carbon isotope analysis to ecological studies became apparent with the publication of an article by Bender (1968), which described a systematic relationship between the photosynthetic pathways (C_3 and C_4) and the stable isotopic ratios of carbon in grasses (Tieszen 1994:261). The dietary application of carbon isotope studies involves the quantification of ratios of $^{13}\text{C}/^{12}\text{C}$ isotopic abundance in bone collagen, which is linked through the food web to the primary producers of carbon—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 (Figure 6.1). The C_3 plants represent about 90% of all plants and include all trees and herbaceous plants from cold and temperate climates. Their $\delta^{13}\text{C}$ values range between -23‰ and -32‰, with

an average of about -26‰. These plants probably evolved earlier than the C₄ plants during periods of lower atmospheric CO₂ concentrations. Some warm weather and tropical herbaceous plants, such as maize, sugar cane and millet, are classified as C₄ and have a $\delta^{13}\text{C}$ value between -9 and -16‰, averaging around -13‰ (Smith and Brown 1973:505; Bocherens et al. 1994:214). C₄ plants probably evolved during the Tertiary and are more competitive than C₃ plants during periods of stress, specifically under conditions of high temporary light, intensity and moisture stress. These plants are more efficient in capturing CO₂ at high leaf temperatures and low stomatal conductance. Patterns of C₄ diversity in North America indicate a strong positive relationship with growing season temperature. On the Great Plains, both relative and absolute C₄ grass abundances correlate with mean annual temperature (MAT) and mean annual precipitation (MAP). In contrast, C₃ grass abundance decreases with MAT and summer precipitation. Because C₃ plants do most of their growing in the spring and early summer, ideal conditions for productivity are cool temperatures with adequate winter precipitation. Warm summers accompanied by summer precipitation favor C₄ grasses. With this understanding of the $\delta^{13}\text{C}$ values, the amount of C₃ and C₄ plants consumed by herbivores can be quantified and applied to various biogeographic questions.

Figure 6.1. $\delta^{13}\text{C}$ values in parts per million for common graminoids and forbs for the Niobrara Valley Preserve, Nebraska (from Steuter et al. 1995: Table 2). This graph illustrates the strong bimodal distribution of values for the two photosynthetic pathways. Cool season C₃ plants average -26‰ and warm season C₄ plants average around -13‰.



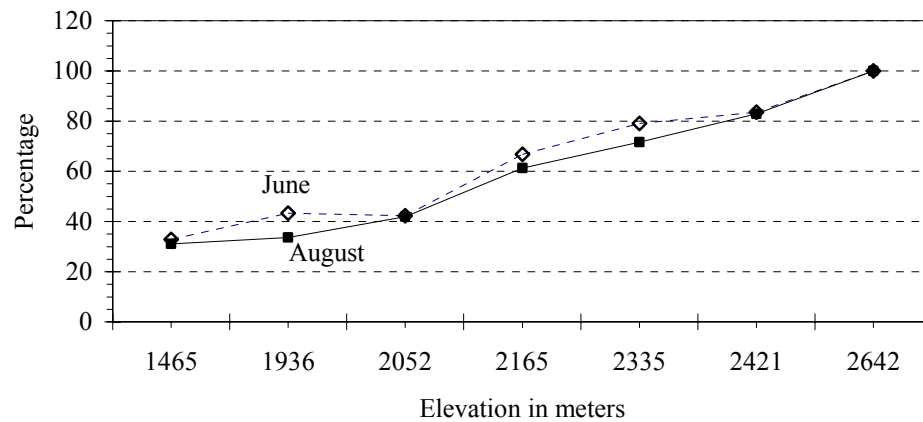
A third group of plants uses the crassulacian acid metabolism photosynthetic pathway (CAM) and includes succulents, such as cactus. These plants are probably not relevant to bison or other herbivores as forage and are not included in this discussion.

An important aspect in using carbon isotope analysis in reconstructing diets is that atmospheric values of $\delta^{13}\text{C}$ have varied in predictable ways through time, and under different environmental conditions. In systems where the respiratory release of CO_2 does not mix freely with the atmosphere, such 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). An example from the Amazonian forests measured $\delta^{13}\text{C}$ values as negative as -37‰. In comparison, open habitats of C_3 grasses average about -26.5‰ (van der Merwe and Medina 1991:250). This depletion is transferred to other trophic levels and must be taken into account when considering diet for forest-dwelling herbivores, as well as humans (Tieszen 1994:264).

The anthropogenic addition of CO_2 to the atmosphere over the past two centuries through the burning of fossil fuels has depleted atmospheric CO_2 of $\delta^{13}\text{C}$. This input has also enhanced decomposition associated with agriculture and deforestation. Preindustrial $\delta^{13}\text{C}$ values of -6.45‰ have been measured from Antarctica ice cores, compared with modern conservative estimates at -8.0‰. Based on this knowledge, significant adjustments must be made in the reconstruction of past diets and paleoecological interpretations due to the addition of CO_2 to the atmosphere from fossil fuel burning. Therefore, an adjustment of about 1.5‰ must be made to Holocene samples dating to before A.D. 1800 in comparison to modern values (Tieszen 1994:264).

In a study from southeast Wyoming, Boutton et al. (1980) demonstrated that the percentage of C_3 biomass increased with elevation (Figure 6.2). Regressions of relative biomass abundance of C_3 and C_4 plants on climatic variables illustrated that both mean annual temperature and mean annual precipitation were equally reliable predictors. Temperature was the factor the authors felt strongly influenced the ratios.

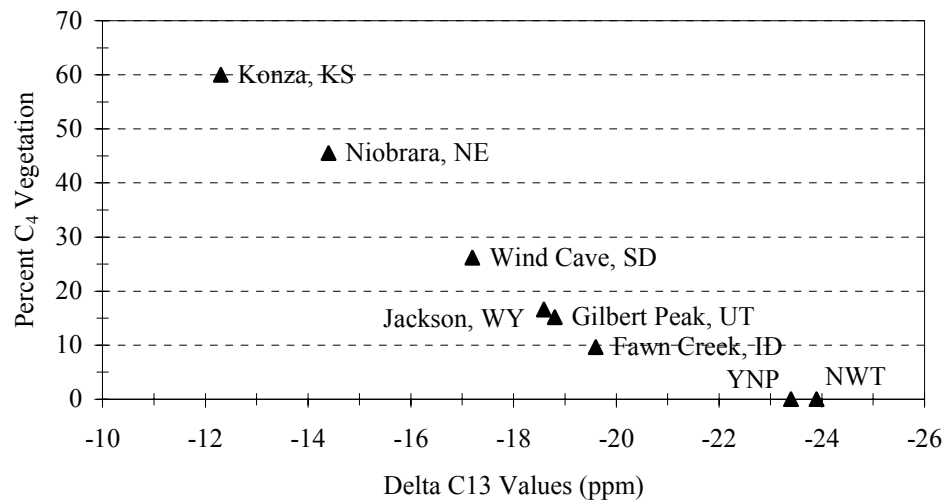
Figure 6.2. Percent of C_3 vegetation at various altitudes along transect in southeast Wyoming (following Boutton et al. 1980: Table 1). Percentage is based upon mean total grams/0.5 m². The graph clearly illustrates the increasing percentage of cool season C_3 plants with elevation.



On the Great Plains, an increase in C_3 grasses is correlated with increasing latitude. In south and southwest Texas, C_4 grasses are represented at 68 and 82 percent, respectively. C_4 grasses decrease to 35 percent in South Dakota. Browse species, such as sedges, do not show as clear a temperature dependent distribution as grasses. *Carex*, a common genus of sedge in the mountains, is C_3 (Tieszen 1994:265).

It is therefore expected that generalist consumers of grass biomass should have a modern isotopic signal that reflects the mixture of C_3 and C_4 species in the utilized environment. Figure 6.3 illustrates the decreasing percentage of C_4 vegetation in the diet of bison with increasing latitude and longitude. However, because climatic changes have been demonstrated for various periods during the course of the Holocene, vegetation values should be expected to reflect these climatic shifts (e.g., Whitlock 1993). This temporal variable is another complicating factor involved in the interpretation of isotopic signals from paleosamples (Tieszen 1994:166).

Figure 6.3. Percent C_4 vegetation in individual bison diet based upon $\delta^{13}C$ values as computed by Brooks (1995:77). Samples are arranged from south (left) to north (right). Figure is modified from Cannon (2007). Abbreviations are YNP=Yellowstone National Park and NWT=Northwest Territories, Canada.



Connin and colleagues (1998) sought to apply stable isotope ratios extracted from herbivore teeth to test the current model of LGM climate and vegetation for the southwestern United States. Community Climate Model (CCM) simulations and plant macrofossil data, primarily from packrat middens, indicate a pattern of cooler temperatures and winter-dominated precipitation. This climatic regime would favor communities dominated by C_3 plants. Their sample consisted of five genera of megaherbivores dating from 40 to 10 ka and recovered from various contexts in Arizona, California, Nevada, and New Mexico. The taxa represented include *Mammuthus* sp., *Bison* spp., *Equus* spp., *Camelops* spp., and Antilocaprids. They argue that this suite of herbivores provides a better sampling of the regional vegetation, because of their physiology and behavior, particularly their seasonal migration. For example, bison and mammoth are preferential, but not obligate grazers, and subsist on the most abundant plant species; camels and horses are browsers, as well as antelope. These species provide a much more rigorous assessment of vegetation communities than do packrats, which tend to sample only local, rocky upland environments. The results of their study indicate a substantial eastward increase in C_4 plant consumption by the herbivores, with some local patterns of C_4 -dominated grazing. Connin

and colleagues (1998) argue that these data imply a pattern of significant availability of C₄ plants, and a pattern of significant summer rainfall in parts of southern Arizona and New Mexico throughout the last glaciation.

The science of the relationship between the stable carbon isotopic signature of mammal bone and diet is well established (e.g., Tieszen 1994). In general, the stable carbon isotopic signature indicates the relative abundance of C₄ vegetation in a herbivore's diet (Wang et al. 1993), and can provide information on the paleoecology (Cerling et al. 1993). Bison in the GYE should reflect a feeding strategy, and corresponding $\delta^{13}\text{C}$ values, that are dominated by C₃ vegetation. The exception would be samples from the Horner site that are from the east side of the GYE in the rain shadow of the Absaroka Mountains and more arid. These specimens should reflect a diet that is more mixed reflecting the presence of C₄ vegetation.

Stable Nitrogen Isotope ($\delta^{15}\text{N}$)

Another stable isotope that is linked to trophic level and potentially important for investigating diet and herbivore migration is $\delta^{15}\text{N}$. Nitrogen is an important component of life, with its primary source from atmospheric nitrogen (N₂). Nitrogen enters the soil through the atmosphere, by precipitation, or from parent rock decomposition. Once in the system, nitrogen is taken up by plants and moves up through the food chain, where it progressively becomes enriched by 2-5‰ through each trophic level (Ambrose 1991; Bocherens et al. 1994). Nitrogen isotopes have been most widely applied to discerning the contribution of marine and terrestrial foods in human diets (e.g., Ambrose 1991).

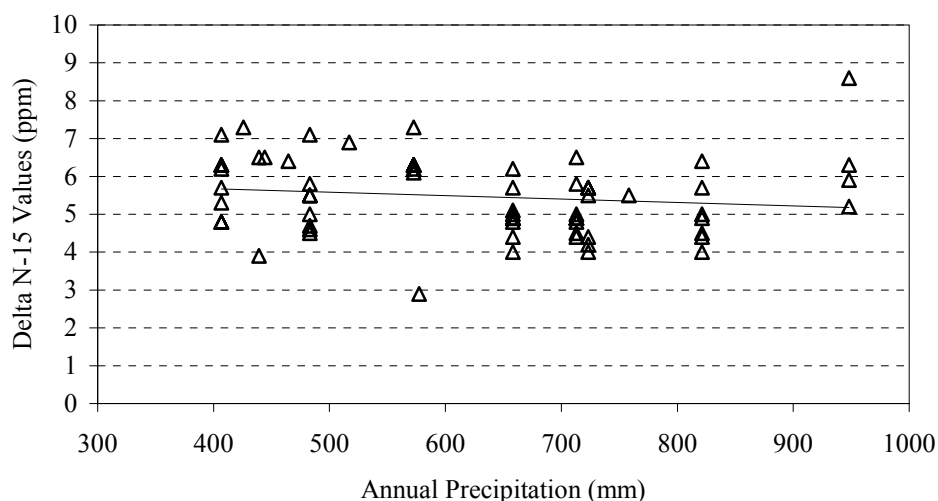
The potential of dietary stress can also be assessed by examining $\delta^{15}\text{N}$ values. In examining horn sheath annuli of bison from the Central Plains, Tieszen and colleagues (1996) identified a change in $\delta^{13}\text{C}$ values accompanied by changes in $\delta^{15}\text{N}$ that they interpreted as a large degree of stress undergone by these individuals with shifts in diet. The researchers did not

identify the specific cause of the dietary stress, but suggested it may have been related to illness or water stress (i.e., drought).

Ambrose and DeNiro (1986) noted a strong correlation between annual rainfall and herbivore $\delta^{15}\text{N}$ ratios. They suggest enrichment may be caused by physiological adaptations to water stress and low-protein diets in arid habitats. For example, when drought-tolerant mammals are water stressed they will concentrate ^{15}N in their tissues and eliminate ^{14}N in urea, producing greater isotopic variability and more tolerant values than obligate drinkers. In arid, or saline environments (<400 mm of precipitation), these herbivores are more depleted than browsers living in the same environment (Ambrose and DeNiro 1986; Heaton et al. 1986).

In a sample of bison from North America, $\delta^{15}\text{N}$ ratios show a negligible correlation to precipitation (Figure 6.4). However, there is also variability among individuals from the same deposits that could be reflective of individual health, mobility, and dietary stress. The effect of drought on bison may not occur until they are faced with conditions that are considered extreme (<400 mm of precipitation). Ambrose and DeNiro (1989) interpreted shifts in herbivore $\delta^{15}\text{N}$ values as evidence of decreasing precipitation patterns from the early to late Holocene in the Kenya Rift Valley. North American attempts to study the relationship between precipitation and herbivore $\delta^{15}\text{N}$ values have been frustrated by the use of nitrogen fertilizers, which masks natural variability (Koch 1998). Cormie and Schwarcz (1996) found a negative correlation between rainfall abundance and $\delta^{15}\text{N}$ values in deer consuming a large amount of C_4 grass. Tieszen (1994) found no evidence for significant variation in $\delta^{15}\text{N}$ values among Great Plains bison during the Holocene.

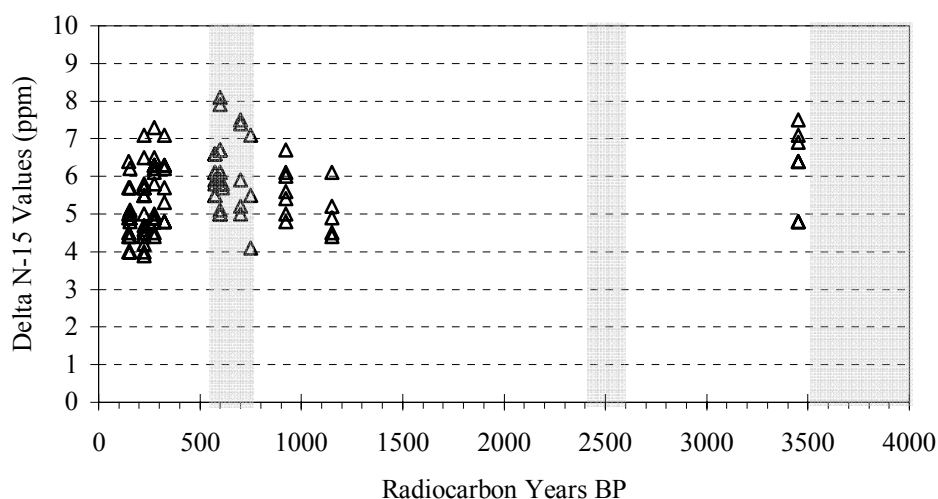
Figure 6.4. North American bison $\delta^{15}\text{N}$ values (Bozell et al. 1997; Tieszen et al. 1997) plotted against modern precipitation. Mean annual precipitation (MAP) is derived from local weather stations (<http://www.wrcc.dri.edu/>). All specimens are less than 500 years in age and may reflect individual variability since there does not appear to be a significant correlation between $\delta^{15}\text{N}$ values and precipitation ($r^2=0.0197$).



To further explore the potential relationship between $\delta^{15}\text{N}$ values and precipitation, I plotted $\delta^{15}\text{N}$ values for deer and bison (Bozell et al. 1997; Tieszen et al. 1997) against years before present to see if there were significant variations during the Holocene in comparison to paleoenvironmental conditions derived from lake sediments (Figure 6.5). While the record is skewed towards the Late Holocene, there are interesting patterns during this time period. Most apparent is the amount of variability in these samples, which may reflect natural variation in bison, as suggested by Tieszen (1994), or variability in precipitation. Mason et al. (2004) and Miao et al. (2007; see also Miao et al. 2005) have reconstructed drought cycles for the Central Great Plains based upon dune activity from the Sand Hills region of Nebraska. High resolution dating of dune movement by radiocarbon and optical dating indicates periods of dry climate that may be linked to larger cycles, such as El Niño events. The results indicate periodic dry phases over the past 10,000 years. Their results suggest maxima of loess accumulation centered on ~700, 2500, and 3800 yrs BP. Drier than present conditions are also suggested by a period of sustained rapid loess accumulation from ~9400 to 6500 yrs BP (Miao et al. 2007). These events correlate well

with regional events recorded in lake sediments and described by Laird et al. (1996) and Fritz et al. (2000).

Figure 6.5. Bivariate plot of Nebraska bison $\delta^{15}\text{N}$ values against age with periods of drought from Miao et al. (2007) as indicated by shading. Drought data is compiled from eolian dune activity in the Sand Hills region of Nebraska. Eolian records from the Sand Hills by Mason et al. (2004) provide additional evidence of dry climates between 1000 and 700 years ago. Data are from Bozell et al. (1997) and Tieszen et al. (1997).



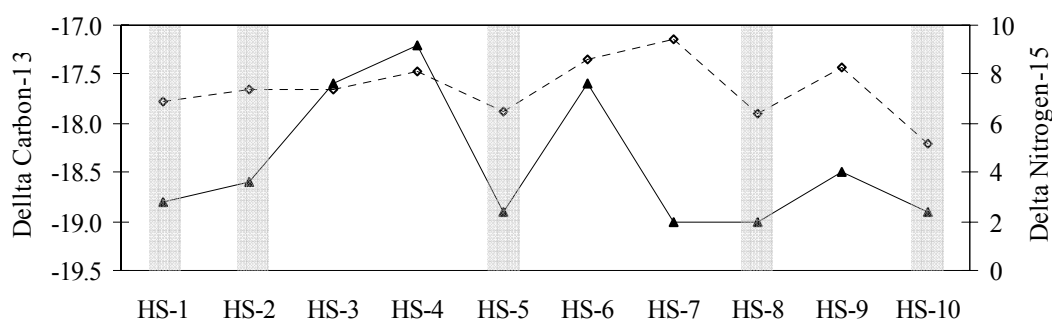
The correlation of the higher $\delta^{15}\text{N}$ values with periods of drought is weak, although some of the higher values correlate with the 570-770 yrs BP drought episode and are within the range of radiocarbon ages of the samples. While there may be some problem with correlating different data sets, it may not be possible to recognize these patterns without large sample and tightly controlled samples. Tieszen (1994) has suggested that sample sizes need to be robust enough to recognize the variability inherent in herd structure and among individuals in order to begin to understand the relationship between climate and biological response as provided by $\delta^{15}\text{N}$ values.

In comparing the $\delta^{15}\text{N}$ values with respect to $\delta^{13}\text{C}$ values from modern specimens, Tieszen et al. (1996) found that shifts in values were correlated in the Konza, Kansas and Niobrara, Nebraska specimens and suggest a shift in diet may have been accompanied by a large degree of stress. However, the circumstances surrounding the diet changes are unknown and may

have involved the individuals being physically moved to different preserves, which may also account for the stress.

In a recent study, Cannon (2007) removed 10 samples from horn sheath growth rings or cones from a 150 ± 40 yr BP bull bison recovered from near Gilbert Peak in the Uinta Mountains of Utah. The pattern of change in $\delta^{15}\text{N}$ values of the Gilbert Peak bison tends to follow that of $\delta^{13}\text{C}$ values. In general, as $\delta^{15}\text{N}$ values increase the $\delta^{13}\text{C}$ values become less negative. Hughes (2003) noted a similar pattern with bighorn sheep and suggested higher (enriched) $\delta^{15}\text{N}$ values were an indication of use of lower elevation range. The depleted (lower) values of the Late Holocene and modern bighorn sheep were interpreted by Hughes (2003) as reflecting a shift to high-altitude winter range in nitrogen depleted environments. Bighorn sheep today are excluded from nitrogen-enriched environments (i.e., valley bottoms) and forced to higher elevations where soils are thin, young, and subject to colder temperatures. In the Gilbert Peak bison sample, relatively depleted values $\delta^{15}\text{N}$ values correspond to depleted $\delta^{13}\text{C}$ values and may reflect periods of high altitude use (Figure 6.6).

Figure 6.6. Results of stable carbon and nitrogen analyses performed on horn sheath cones of Gilbert Peak bison. Results are oriented from oldest (HS-1) on the left to youngest (HS-10) on the right. Upper dotted line is $\delta^{15}\text{N}$ values. $\delta^{13}\text{C}$ values have been adjusted for keratin enrichment of 3.1‰ (modified from Cannon 2007). Shaded areas illustrate cones with depleted $\delta^{14}\text{C}$ and $\delta^{15}\text{N}$ values.



Another possible explanation involves nitrogen waste through urine. Steele and Daniel (1978) have found that in herbivorous mammals, urea is the main form of nitrogen waste, and the ^{15}N isotopic composition in urine is lower than the ^{15}N isotopic composition of the vegetation they subsist on. With the elimination of urea, collagen $\delta^{15}\text{N}$ values are elevated. As

Fizet et al. (1995) relate, protein quality also has an effect of lower $\delta^{15}\text{N}$ values in herbivores due to less urea in the urine. Ambrose and DeNiro (1986) demonstrated that modern East African herbivorous mammals living in arid areas have increasingly higher $\delta^{15}\text{N}$ values. These higher levels are related to the excretion of urine highly concentrated in urea, a strategy for water conservation. Based upon this information, Fizet et al. (1995) argue that higher $\delta^{15}\text{N}$ values of mammal collagen from the French Pleistocene Marillac cave layer #7 was related to an episode of aridity between 45,000 and 40,000 years BP. Other paleoclimatic proxy data support this interpretation. The elevated levels of $\delta^{15}\text{N}$ values for the Gilbert Peak bison may reflect periods of increased aridity at periods during its life and may provide evidence of short-term climate shifts. Local tree-ring records from the Uinta Basin indicate “the most intense dry regime in the proxy record [A.D. 1226-2000] occurred during the late 18th century from 1772 through 1786” (Gray et al. 2004:953). While this was not an exceptionally long drought, it did encompass four of the driest years (1773, 1774, 1780, and 1786) in the entire record. Earlier in the 18th century, decade-long droughts are also present. These periods of drought overlap with the radiocarbon age obtained from the Gilbert Peak bison and may provide an explanation for elevated $\delta^{15}\text{N}$ values and the rather large percentage of C_4 vegetation (13.79-26.21%) of this high altitude specimen. Another explanation is that the bison was not living at high elevations, but the skull was transported to the high country by humans (Cannon 2007). Bison from the high altitudes moving into lower elevation grasslands of the surrounding basins should illustrate similar patterns: low $\delta^{15}\text{N}$ values for high elevation grasslands and high $\delta^{15}\text{N}$ values for low elevation grasslands.

As is apparent from the preceding discussion, interpretation of $\delta^{15}\text{N}$ values is problematic and can be related to a number of environmental, behavioral, and physiological factors. What may be best to keep in mind when comparing $\delta^{15}\text{N}$ values is that they need to be understood within the context of other data, particularly in relation to their environmental context and in relation to other stable isotope values.

Stable Oxygen Isotope ($\delta^{18}\text{O}$)

Oxygen isotopic analysis of bones also can be used to elucidate bison ecology. As Shikha et al. (2004) have argued, bovid (including bison) teeth are an archive of paleoclimatic information. Experimental studies have demonstrated a strong linear relationship between $\delta^{18}\text{O}$ values and temperature, proving value for paleoclimatic reconstruction (Fricke and O'Neil 1996; Schoeninger et al. 2000), and tooth enamel is considered to be a better reservoir of oxygen isotope signatures than any of the other oxygen-bearing hard tissues (Fricke et al. 1998). Obligate-drinking herbivores (i.e. dependent on drinking water), in contrast to non-water-dependent animals (i.e. animals that get the majority of water primarily from food sources), display average $\delta^{18}\text{O}$ values that are closely correlated with the average $\delta^{18}\text{O}$ values of local precipitation (Hoppe 2006). As meteoric water is ingested, either through surface water sources or vegetation, the oxygen isotopic composition is reflected in the enamel apatite. While most studies of oxygen isotopes are focused on paleoclimatic changes, the signals preserved in bison teeth will also provide information on seasonal migration. For example, bison should be drinking water from wetlands and lakes that experience evaporation and will have an isotopically enriched signature. If they are exclusively drinking from streams and rivers filled by snow runoff, there should be less seasonal variation and the signature should be isotopically depleted.

In order to more fully understand this relationship and the practicality of using bison $\delta^{18}\text{O}$ values as a proxy for paleoclimate, Hoppe (2006) measured oxygen isotope ratios of tooth enamel carbonate from 64 North American bison from 11 locations. These $\delta^{18}\text{O}$ values were then compared with $\delta^{18}\text{O}$ values of local surface waters and precipitation. Her results indicate that bison tooth enamel can be used as a quantitative proxy for reconstructing the isotopic values for surface waters and in turn paleoclimatic conditions.

Summary

Stable isotope analysis has evolved over the last 20 years to be an important method for the study of range of behavioral and environmental questions. The preceding review provides the

background of the science of carbon, nitrogen, and oxygen stable isotope analyses. In the following section I will present the methods and results of carbon and oxygen stable isotope analysis to Holocene bison teeth from the GYE.

Chapter VII

Results of Analysis

Introduction

In the preceding section I have discussed the role of carbon, nitrogen, and oxygen stable isotope analysis to understanding the ecology of mammals and the paleoclimatic conditions in which they lived. The science of isotopic studies is mature and is being applied to a variety of topics. Specific issues, such as reconstructing the past using modern mammals as proxies (e.g., Hoppe 2006), and the explicit integration of paleoclimatic modeling into these topics (e.g., Koch 1998), are being addressed. With this section as a background, the ecology and paleoenvironmental context of prehistoric bison from the GYE can be explored.

Over the past decade a relatively new application of geochemical techniques had provided another group of data to bear upon the problem of paleoecological reconstruction (McFadden and Cerling 1996)—analysis of stable isotope signatures of herbivore bone and teeth. Herbivores are particularly relevant to the study of paleoecological reconstruction for a number of physiological and ecological reasons (Cannon 2007):

1. Herbivores, particularly bison (*Bison* sp.), are widespread worldwide and are a common component of fossil and subfossil assemblages (Guthrie 1990).
2. Bison were a major component of Great Plains post-glacial ecosystems and a major prey species of native groups prior to Euroamerican contact (e.g., Frison 1991; Fisher and Roll 1998).
3. Depending upon their particular dietary requirements, herbivore grazing will reflect the relative abundance of vegetation in a particular ecosystem (Tieszen 1991). For example, bison are relatively nonselective grazers due to their requirement of large volumes of forage. This requirement limits their ability to be selective (Pedon 1976). In contrast, antelope are highly selective herbivores, subsisting almost exclusively on sagebrush (Schwartz and Ellis 1981).

4. Stable isotope analysis is an effective tool in determining photosynthetic pathways (Bender 1968). It has also been applied to the tissue of primary consumers in determining their diet (DeNiro and Epstein 1981). As Chisholm et al. (1986) noted in their initial study, if bison (as well as other migratory animals) are moving through various ecosystems during their annual migrations, and if these environments have different food resources, it should be evident in the bison's diet, as expressed by stable carbon isotope signatures. Specifically, bison $\delta^{13}\text{C}$ values should correlate with the mean $\delta^{13}\text{C}$ values of the local grasslands due to their selective feeding of >90% graminoids (Tieszen 1994).
5. As tissues develop, they incorporate carbon, and the isotopic value of these tissues reflects the relative amounts of the ingested carbon. Bone, which is commonly preserved in fossil and subfossil contexts, is a likely candidate for analysis, but because bone is constantly in a state of growth and modification the isotopic values reflect an aggregate or averaged record of the individual's diet over an extended period of time (Larson et al. 2001). Studies by Chiholm (1989) and Tieszen (1994) indicate that complete bone replacement occurs over a period of about 10 years.
6. Teeth, in contrast to bone, preserve a detailed record of an individual's foraging history through incremental growth of the tooth enamel. By sampling the third molar, which mineralizes from the 9th to the 24th month of life and is not affected by isotopic offsets caused by nursing (Bryant et al. 1994), a geochemical record reflecting the individuals foraging history can be extracted at the resolution of seasonal or subannual (Gadbury et al. 2000; Larson et al. 2001; Widga 2006).

Prehistoric bison remains from sites in the Greater Yellowstone Ecosystem were selected in order to explore their potential as a proxy for paleoenvironmental conditions and to assess land use patterns in comparison to modern populations that are limited in their range.

Materials and Methods

Fourteen third molar teeth of prehistoric bison from eight sites in the GYE were selected for analysis (Table 7.1). Five modern specimens from Yellowstone National Park and the Henry Mountains, Utah were also included in the analysis as controls. The prehistoric specimens were selected based on several criteria:

1. The sites were within the Greater Yellowstone Ecosystem, but from a variety of environmental contexts and time periods.
2. They were from well-dated contexts.
3. The assemblage had well-preserved mandibular or maxillary teeth of aged individuals.
4. The assemblage was accessible for study.

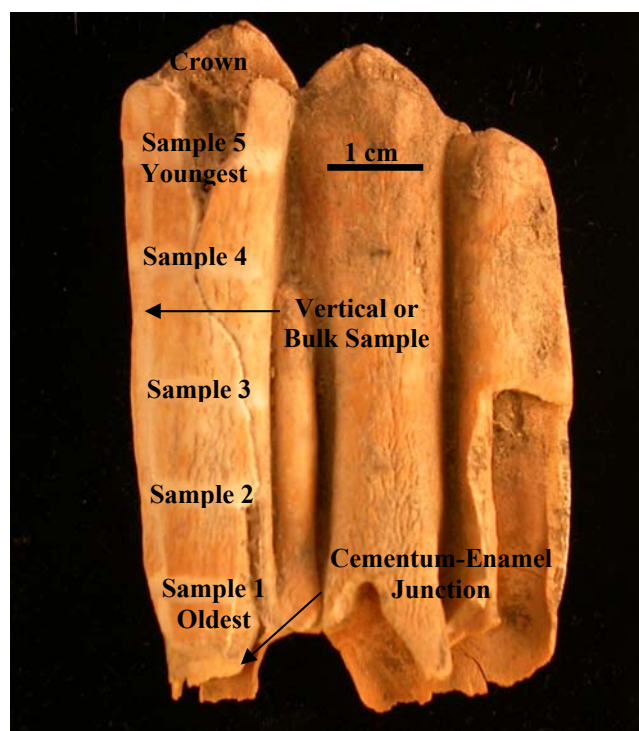
Table 7.1. Specimens sampled for study.

SITE	SPECIMEN NO.	TOOTH	AGE GROUP	SIDE	SEX	NUMBER OF SAMPLES
100A210	6.373.60	m3	6.6	L	F	5
100A210	6.133.11	m3		L	F	6
48PA29	1233H	m3	2.6	L	M	6
	2548H	m3	3.6	R	F	6
	1181H	m3	4.6	R	F	6
48TE455	455.1	M3		R	M?	4
	455.2	m3	4.6	R	F	6
48TE1090	42226	m3	9.6	R	F?	3
	42227	m3	8.6	L	M	4
48TE1101	22597	m3	5.6-7.6	R	F?	5
48TE1102	42222	m3	6.6	R	M	5
	42223	m3	9.6	L	F	3
48TE1114	39605	m3	5.6-6.6	R	M	6
48YE697	697.1	M3	4.0	L	M	6
Hayden Valley, YNP	YELL.2000.HV.003	m3	2.6	R	F	6
	YELL.2000.HV.002	m3	8.6	R	F	2
Pelican Valley, YNP	94KC1	m3	10.6	R	M	3
Henry Mtns, Utah	12	m3	3.6-4.6	R	M	6
	768	m3	6.6	L	M	4

Susan Hughes (Seattle, Washington) conducted the initial processing of the teeth following the protocol established by Balasse et al. (1999). Dr. Hughes removed each of the enamel sections with a dremel tool. The sampling consisted of down-tooth samples for intra-

individual variability and a vertical sample that can be used to compare between individuals. The number of samples per tooth was dictated by the condition of the tooth and the maximum length (Figure 7.1). For example, younger animals have more of their tooth remaining so more samples can be removed. Data sheets for each of the teeth are presented in Appendix C. After processing, approximately 10 grams of powdered tooth enamel per sample were submitted to Dr. David Dettman in the Department of Geosciences at the University of Arizona for analysis. $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of tooth enamel carbonate were measured using an automated carbonate preparation device (KIEL-III) coupled to a gas-ratio mass spectrometer (Finnigan MAT 252). Powdered samples were reacted with dehydrated phosphoric acid under vacuum at 70°C in the presence of silver foil. The isotope ratio measurement is calibrated based on repeated measurements of NBS-19 and NBS-18 and precision is $\pm 0.1 \text{ ‰}$ for ^{18}O and $\pm 0.06 \text{ ‰}$ for $\delta^{13}\text{C}$ (1σ). The carbonate – CO_2 fractionation for the acid extraction is assumed to be identical to calcite.

Figure 7.1. Buccal side of left M3 (Specimen 48PA29/1233H) from the Horner site illustrating location of intra-individual samples were removed for isotopic analysis. A vertical or bulk sample was also removed from the metaconid. Distance from the maximum length (crown of tooth) represents an age proxy with the oldest portion of the tooth at the bottom (Sample 1).



Values are reported in permil (‰) units relative to PDB (^{13}C) and SMOW (^{18}O) standards. Standard deviation in $\delta^{13}\text{O}$ and $\delta^{18}\text{O}$ values associated with triplicate measurements on a single sample is also presented. A total of 99 samples were submitted (Table 7.2).

The basis for this study is the understanding that mammalian tooth enamel forms continuously over several years (Hillson 1990). In bison the tooth grows from the top of the crown to the cementum-enamel junction. Enamel is biomineralized daily and is not remetabolized like other elements, such as bone collagen, allowing for a discrete record to be sampled and analyzed. This results in a high-resolution ‘down-tooth’ record of changing body $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values driven by seasonal changes in carbon (i.e., vegetation) and water intake (Gadbury et al. 2000).

Because bison exhibit reproductive synchronicity, with all births occurring in the spring in a tightly constrained and predictable manner, isotopic data from the same tooth of different individuals of the same biological age will likely reflect similar seasonal patterns (Berger and Cunningham 1994; Gadbury et al. 2000). Unfortunately, this data set is not from a single site or kill event, which complicates comparisons. With the exception of the Horner individuals, each of the GYE bison sampled are not from the same breeding population. In contrast to other studies trying to understand paleoenvironmental conditions at the time of herd death (e.g., Gadbury et al. 2000), this study is focused on comparing behavior of prehistoric bison with modern bison.

Bison are non-selective grazers and will subsist on vegetation as it is available. The difference in the $\delta^{13}\text{C}$ values of the C_3 and C_4 grasses allows the bison diet to be a means to determine paleoenvironmental conditions. Laboratory analyses have determined that the observed $\delta^{13}\text{C}$ value of tooth enamel is ~12‰ more positive than the animal’s dietary intake (Wang et al. 1994; Morgan et al. 1994).

The $\delta^{18}\text{O}$ value of body water of animals is determined by the isotopic composition of oxygen into and out of the body, with the most important source for oxygen being ingested water, both as liquid and plant water. (Gadbury et al. 2000). Studies show that animals that are water-

dependent, or get the majority of their water through drinking, display average $\delta^{18}\text{O}$ values that are closely correlated with the average $\delta^{18}\text{O}$ values of local precipitation (Ayliffe, et al. 1992). Hoppe (2006) has demonstrated a strong correlation between mean enamel oxygen isotope ratios with the mean annual oxygen isotope ratios of local surface waters and precipitation. These results demonstrate that oxygen isotope values from bison enamel can be used as a quantitative proxy for reconstructing the values of surface water, and potentially paleoclimatic information.

Table 7.2. Results of carbon and oxygen stable isotope analysis. All values are reported in permil (‰) units relative to PDB ($\delta^{13}\text{C}$) and SMOW ($\delta^{18}\text{O}$) standard.

SAMPLE ID	$\delta^{13}\text{C}$	C STD DEV	$\delta^{18}\text{O}$	O STD DEV	DISTANCE FROM MAX LENGTH (mm)	SITE AND CATALOG NUMBER
KC02.1	-9.09	0.017	18.77	0.096	53.98	100A210/6.133.11
KC02.2	-9.62	0.062	20.30	0.082	42.37	100A210/6.133.11
KC02.3	-9.57	0.022	20.11	0.030	30.80	100A210/6.133.11
KC02.3	-9.70	0.027	19.66	0.055	30.80	100A210/6.133.11
KC02.4	-9.19	0.035	17.67	0.040	20.67	100A210/6.133.11
KC02.5	-8.97	0.012	17.53	0.026	9.25	100A210/6.133.11
KC02.6	-8.83	0.051	20.19	0.041	Vertical	100A210/6.133.11
KC10.1	-9.38	0.025	20.90	0.039	45.63	100A210/6.373.60
KC10.2	-9.25	0.021	19.61	0.045	33.46	100A210/6.373.60
KC10.3	-8.61	0.035	18.41	0.013	21.89	100A210/6.373.60
KC10.4	-8.46	0.022	18.87	0.066	9.88	100A210/6.373.60
KC10.5	-8.60	0.035	19.89	0.079	Vertical	100A210/6.373.60
KC06.1	-11.48	0.023	18.83	0.028	28.47	2000.HV.002
KC06.2	-11.59	0.036	18.77	0.070	Vertical	2000.HV.002
KC07.1	-11.04	0.029	15.49	0.058	53.57	2000.HV.003
KC07.1	-11.04	0.012	15.14	0.050	53.57	2000.HV.003
KC07.2	-11.33	0.033	17.16	0.022	43.27	2000.HV.003
KC07.3	-11.80	0.030	14.84	0.057	31.80	2000.HV.003
KC07.4	-11.68	0.023	14.58	0.079	19.74	2000.HV.003
KC07.5	-11.41	0.027	16.82	0.060	7.23	2000.HV.003
KC07.6	-11.20	0.015	14.98	0.053	Vertical	2000.HV.003
KC03.1	-6.21	0.032	19.91	0.042	59.90	48PA29/1181H
KC03.2	-6.57	0.023	23.06	0.076	47.87	48PA29/1181H
KC03.3	-7.55	0.030	19.56	0.056	34.13	48PA29/1181H
KC03.4	-7.98	0.019	19.89	0.041	22.74	48PA29/1181H
KC03.5	-7.78	0.034	19.81	0.060	12.58	48PA29/1181H
KC03.6	-6.78	0.033	20.99	0.038	Vertical	48PA29/1181H
KC04.1	-7.52	0.165	19.97	0.104	58.41	48PA29/1233H
KC04.2	-7.03	0.041	22.90	0.051	49.20	48PA29/1233H
KC04.3	-5.00	0.027	23.19	0.016	39.02	48PA29/1233H
KC04.4	-2.80	0.028	21.03	0.081	27.73	48PA29/1233H
KC04.5	-2.82	0.068	21.85	0.039	16.52	48PA29/1233H

SAMPLE ID	$\delta^{13}\text{C}$	C STD DEV	$\delta^{18}\text{O}$	O STD DEV	DISTANCE FROM MAX LENGTH (mm)	SITE AND CATALOG NUMBER
KC04.6	-4.50	0.030	21.75	0.060	Vertical	48PA29/1233H
KC08.1	-7.37	0.033	17.69	0.069	55.68	48PA29/2548H
KC08.2	-6.85	0.017	22.23	0.051	44.48	48PA29/2548H
KC08.3	-7.38	0.014	21.48	0.065	35.50	48PA29/2548H
KC08.4	-7.64	0.021	21.00	0.050	23.68	48PA29/2548H
KC08.5	-7.81	0.029	19.61	0.031	12.83	48PA29/2548H
KC08.6	-7.18	0.019	20.69	0.017	Vertical	48PA29/2548H
KC14.1	-9.06	0.029	17.69	0.076	21.78	48TE1090/42226
KC14.2	-9.62	0.036	18.00	0.074	8.26	48TE1090/42226
KC14.3	-9.18	0.016	19.06	0.026	Vertical	48TE1090/42226
KC16.1	-9.51	0.025	16.43	0.023	32.90	48TE1090/42227
KC16.2	-9.80	0.033	19.59	0.095	19.57	48TE1090/42227
KC16.3	-9.82	0.052	20.27	0.060	6.53	48TE1090/42227
KC16.4	-9.73	0.021	18.18	0.058	Vertical	48TE1090/42227
KC11.1	-8.09	0.038	16.63	0.078	44.31	48TE1101/22597
KC11.2	-8.19	0.033	20.13	0.076	35.33	48TE1101/22597
KC11.3	-8.11	0.031	17.53	0.038	25.14	48TE1101/22597
KC11.4	-7.71	0.012	15.64	0.083	13.49	48TE1101/22597
KC11.5	-7.81	0.030	17.85	0.069	Vertical	48TE1101/22597
KC13.1	-6.94	0.030	17.40	0.030	48.23	48TE1102/42222
KC13.2	-7.39	0.038	19.48	0.049	36.82	48TE1102/42222
KC13.3	-7.76	0.0029	19.38	0.087	25.75	48TE1102/42222
KC13.4	-7.97	0.026	17.04	0.046	14.48	48TE1102/42222
KC13.5	-7.38	0.021	19.16	0.049	Vertical	48TE1102/42222
KC15.1	-9.06	0.015	19.90	0.086	25.25	48TE1102/42223
KC15.2	-9.53	0.036	20.54	0.075	15.03	48TE1102/42223
KC15.3	-9.21	0.024	20.04	0.051	Vertical	48TE1102/42223
KC12.1	-9.44	0.012	18.04	0.068	51.31	48TE1114/39605
KC12.2	-10.05	0.022	19.42	0.086	39.15	48TE1114/39605
KC12.3	-9.23	0.009	18.17	0.047	28.85	48TE1114/39605
KC12.4	-8.36	0.053	15.98	0.057	17.16	48TE1114/39605
KC12.5	-8.01	0.012	17.19	0.035	6.28	48TE1114/39605
KC12.6	-8.89	0.053	17.01	0.041	Vertical	48TE1114/39605
KC05.1	-10.03	0.023	20.98	0.022	28.59	48TE455/455.1

SAMPLE ID	$\delta^{13}\text{C}$	C STD DEV	$\delta^{18}\text{O}$	O STD DEV	DISTANCE FROM MAX LENGTH (mm)	SITE AND CATALOG NUMBER
KC05.1	-10.15	0.038	20.75	0.064	28.59	48TE455/455.1
KC05.2	-9.64	0.043	19.01	0.044	18.91	48TE455/455.1
KC05.3	-10.01	0.029	21.45	0.048	6.72	48TE455/455.1
KC05.4	-9.53	0.027	20.40	0.061	Vertical	48TE455/455.1
KC01.1	-8.27	0.018	20.32	0.042	50.63	48TE455/455.2
KC01.2	-8.47	0.031	17.79	0.020	40.04	48TE455/455.2
KC01.3	-8.15	0.051	17.09	0.051	29.14	48TE455/455.2
KC01.4	-8.21	0.015	17.49	0.074	18.44	48TE455/455.2
KC01.5	-8.74	0.025	19.45	0.039	8.28	48TE455/455.2
KC01.6	-7.98	0.008	17.31	0.075	Vertical	48TE455/455.2
KC09.1	-7.41	0.037	17.03	0.038	46.49	48YE697/697.1
KC09.2	-8.64	0.029	18.44	0.025	36.77	48YE697/697.1
KC09.3	-9.27	0.013	19.99	0.031	25.71	48YE697/697.1
KC09.3	-9.09	0.013	19.92	0.049	25.71	48YE697/697.1
KC09.4	-9.71	0.044	18.42	0.059	14.79	48YE697/697.1
KC09.5	-9.96	0.007	19.01	0.058	5.92	48YE697/697.1
KC09.5	-9.59	0.025	18.77	0.057	5.92	48YE697/697.1
KC09.6	-9.25	0.027	18.76	0.091	Vertical	48YE697/697.1
KC20.1	-8.10	0.012	23.32	0.091	43.00	HM/12
KC20.2	-8.63	0.011	21.40	0.056	34.00	HM/12
KC20.3	-7.36	0.019	20.40	0.054	25.00	HM/12
KC20.4	-7.58	0.036	21.51	0.061	16.00	HM/12
KC20.5	-8.85	0.028	23.79	0.043	8.00	HM/12
KC20.6	-7.76	0.018	22.19	0.052	Vertical	HM/12
KC18.1	-4.93	0.034	22.08	0.023	38.10	HM/768
KC18.2	-7.64	0.039	25.58	0.078	23.90	HM/768
KC18.3	-5.80	0.007	23.21	0.059	10.76	HM/768
KC18.4	-6.16	0.032	24.17	0.108	Vertical	HM/768
KC19.1	-9.88	0.022	17.82	0.058	38.18	YNP/94KC1
KC19.2	-10.29	0.009	16.89	0.044	28.62	YNP/94KC1
KC19.3	-10.77	0.023	14.70	0.030	16.57	YNP/94KC1
KC19.4	-10.46	0.016	15.41	0.073	Vertical	YNP/94KC1

The specimens for this study consist of either upper or lower third molars (Table 5.1). This molar is of particular importance, because it forms between nine months and around two years of age and is therefore not influenced by the mother's milk consumption (Gadbury et al. 2000).

Results of Analysis

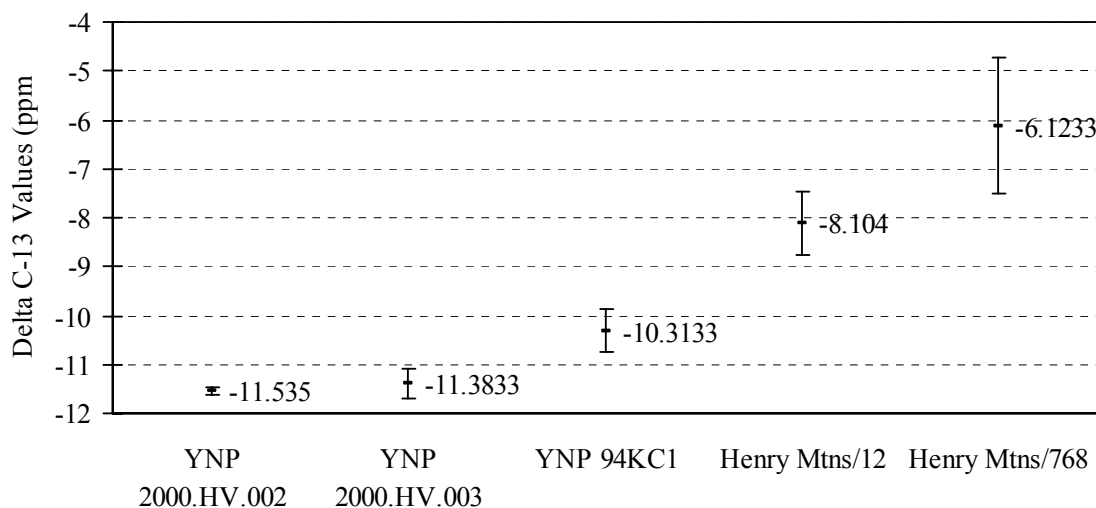
Five modern bison from YNP and the Henry Mountains in Utah that died of natural causes were sampled and represent controls. The sample consists of four right and one left lower third molar from individuals aged from ca. 2.6 to 10.6 years at the time of death (Table 5.1). Twenty-three samples were obtained from the individual teeth. The individuals were selected as good isotopic proxies for modern ecological conditions, because of their ability to range in high altitude open country. While the YNP bison are considered free-ranging, their movements are restricted to the YNP boundaries and a C₃-dominated ecosystem (Feranec 2007). The individuals from the Henry Mountains are important because they migrate seasonally from high altitude grasslands in the summer to low elevation winter ranges which provides them an opportunity to graze in a variety of ecosystems. Table 7.3 provides a descriptive summary of the analysis of these individuals analyzed for isotopic composition.

As would be expected, the YNP samples illustrate limited variability in the $\delta^{13}\text{C}$ values, with a range of only 1.92‰ between the three individuals (Figure 7.2). The limited range and standard deviation of individual YNP2000.HV.002 may be due to the small number of down-tooth samples (n=2). However, the limited range in the $\delta^{13}\text{C}$ values is consistent with observations by Meagher (1973) and Singer and Norland (1994) that bison have a more restricted resource use than other large herbivores in YNP. Feranec 's (2007) $\delta^{13}\text{C}_{\text{enamel}}$ values confirm these observations (range=2.91‰). The Henry Mountains' sample illustrates greater variability reflective of their greater seasonal altitudinal migration.

Table 7.3. Summary statistics for stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotope analysis. All values are reported in permil (‰) units relative to PDB ($\delta^{13}\text{C}$) and SMOW ($\delta^{18}\text{O}$) standard. Summary statistics are presented only for the downturn samples and do not include the single vertical slice.

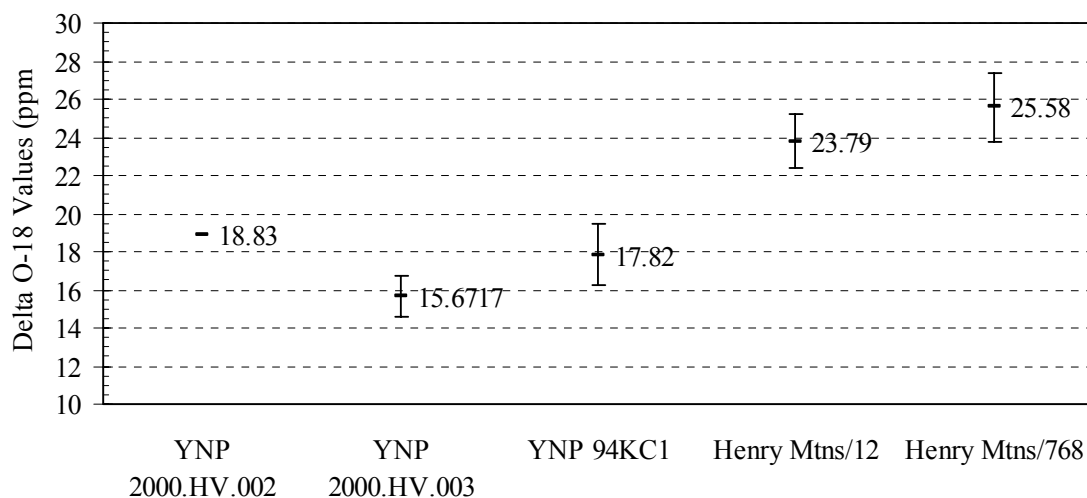
SITE AND CATALOG NUMBER	VALUE	N	MEAN	RANGE	MIN VALUE	MAX VALUE	σ	σ^2
Archeological Specimens								
100A210/6.113.11	$\delta^{13}\text{C}$	6	-9.3567	0.73	-9.70	-8.97	0.31020	0.96
	$\delta^{18}\text{O}$	6	19.0067	2.77	17.53	20.30	1.21162	1.468
100A210/6.373.60	$\delta^{13}\text{C}$	4	-8.9250	0.92	-9.38	-8.46	0.45757	0.209
	$\delta^{18}\text{O}$	4	19.4475	2.49	18.41	20.90	1.08721	1.182
48PA29/1181H	$\delta^{13}\text{C}$	5	-7.2180	1.77	-7.98	-6.21	0.78145	0.611
	$\delta^{18}\text{O}$	5	20.4400	3.50	19.56	23.06	1.47080	2.163
48PA29/1233H	$\delta^{13}\text{C}$	5	-5.0340	4.72	-7.52	-2.80	2.23930	5.014
	$\delta^{18}\text{O}$	5	21.7880	3.22	19.97	23.19	1.33095	1.771
48PA29/2548H	$\delta^{13}\text{C}$	5	-7.4100	0.96	-7.81	-6.85	0.36366	0.132
	$\delta^{18}\text{O}$	5	20.4020	4.54	17.69	22.23	1.79189	3.211
48TE1090/42226	$\delta^{13}\text{C}$	2	-9.3400	0.56	-9.62	-9.06	0.39598	0.157
	$\delta^{18}\text{O}$	2	17.8450	0.31	17.69	18.00	0.21920	0.048
48TE1090/42227	$\delta^{13}\text{C}$	3	-9.7100	0.31	-9.82	-9.51	0.17349	0.030
	$\delta^{18}\text{O}$	3	18.7633	3.84	16.43	20.27	2.04913	4.199
48TE1101/22597	$\delta^{13}\text{C}$	4	-8.0250	0.48	-8.19	-7.71	0.21440	0.046
	$\delta^{18}\text{O}$	4	17.4825	4.49	15.64	20.13	1.92640	3.711
48TE1102/42222	$\delta^{13}\text{C}$	4	-7.5150	1.03	-7.97	-6.94	0.45214	0.204
	$\delta^{18}\text{O}$	4	18.3250	2.44	17.04	19.48	1.28503	1.651
48TE1102/42223	$\delta^{13}\text{C}$	2	-9.2950	0.47	-9.53	-9.06	0.33234	0.110
	$\delta^{18}\text{O}$	2	20.2200	0.64	19.90	20.54	0.45255	0.205
48TE1114/39605	$\delta^{13}\text{C}$	5	-8.01	2.04	-10.05	-8.01	0.82721	0.684
	$\delta^{18}\text{O}$	5	19.42	3.44	15.98	19.42	1.27430	1.624
48TE455/455.1	$\delta^{13}\text{C}$	4	-9.64	0.51	-10.15	-9.64	0.22051	0.049
	$\delta^{18}\text{O}$	4	21.45	2.44	19.01	21.45	1.06559	1.135
48TE455/455.2	$\delta^{13}\text{C}$	5	-8.15	0.59	-8.74	-8.15	0.24025	0.058
	$\delta^{18}\text{O}$	5	20.32	3.23	17.09	20.32	1.38756	1.925
48YE697/697.1	$\delta^{13}\text{C}$	7	-7.41	2.55	-9.96	-7.41	0.86104	0.741
	$\delta^{18}\text{O}$	7	19.99	2.96	17.03	19.99	1.01014	1.020
Modern Specimens								
Henry Mtns/12	$\delta^{13}\text{C}$	5	-7.36	1.49	-8.85	-7.36	0.64446	0.415
	$\delta^{18}\text{O}$	5	23.79	3.39	20.40	23.79	1.42050	2.018
Henry Mtns/768	$\delta^{13}\text{C}$	3	-4.93	2.71	-7.64	-6.1233	1.38363	1.914
	$\delta^{18}\text{O}$	3	25.58	3.50	22.08	23.6233	1.78623	3.191
YNP 94KC1	$\delta^{13}\text{C}$	3	-9.88	0.89	-10.77	-10.3133	0.44546	0.198
	$\delta^{18}\text{O}$	3	17.82	3.12	14.70	16.4700	1.60184	2.566
YNP 2000.HV.002	$\delta^{13}\text{C}$	1	-11.48	-	-	-	0.023	-
	$\delta^{18}\text{O}$	1	18.83	-	-	-	0.028	-
YNP 2000.HV.003	$\delta^{13}\text{C}$	6	-11.3833	0.76	-11.80	-11.04	0.31652	0.100
	$\delta^{18}\text{O}$	6	15.6717	2.58	14.58	17.16	1.07078	1.147
All Samples	$\delta^{13}\text{C}$	78	-	-	-	-	-	-
	$\delta^{18}\text{O}$	78	-	-	-	-	-	-

Figure 7.2 . Plot of mean and one standard deviation of $\delta^{13}\text{C}$ values from modern YNP and Henry Mountains individuals based upon down-tooth samples. The mean $\delta^{13}\text{C}$ value for each individual is provided. Modern YNP individuals have limited variability in $\delta^{13}\text{C}$ values due to their restriction to the boundaries of the Park, a C_3 -dominated ecosystem. In contrast, the Henry Mountain individuals have a wide elevational range which is reflected in the more variable $\delta^{13}\text{C}$ values



The oxygen isotope data indicate a significant difference between YNP individuals and the Henry Mountains' individuals (Figure 7.3). The YNP specimens range from -10.31 to -11.80‰ while the Henry Mountains individuals are more positive with a range of -6.12 to -8.85‰. This difference is important and demonstrates that bison $\delta^{18}\text{O}$ values reflect variations in environmental conditions (Hoppe 2006). The intra-individual range in the YNP bison extends from a minimum of 2.58‰ to 3.12‰. These values are within the range (-10.78‰ to -16.02‰) reported for other modern YNP bison individuals (Feranec 2004). The Henry Mountains' intra-individual range is from 3.39‰ to 3.50‰. The large oxygen isotope variation in these individuals suggests a seasonal range in the $\delta^{18}\text{O}$ dietary waters and would be consistent with the natural seasonal water trends that would be reflected in free-ranging animals (Gadbury et al. 2000). Hughes (2003) collected data from five studies that illustrate higher variation within single teeth for migratory species.

Figure 7.3 Plot of mean and one standard deviation of $\delta^{18}\text{O}$ values from modern YNP and Henry Mountains individuals based upon down-tooth samples. The mean $\delta^{18}\text{O}$ value for each individual is provided.



As moisture off the ocean evaporates, the lighter isotope (^{16}O) is preferentially released into the atmosphere where it forms clouds. These moisture-laden clouds move inland with the heavier isotope (^{18}O) being precipitated more rapidly. Therefore, as these storm clouds move inland they become more depleted in $\delta^{18}\text{O}$. Studies have shown that fractionation of the ^{16}O and ^{18}O isotopes are temperature dependent, with greater fractionation occurring at lower temperatures (Gat 1980; Burk and Stuiver 1981). This contributes to further depletion of ^{18}O at higher latitudes and elevations (-0.5‰ per degree of latitude and -0.15 to -0.5‰ per 100 meters in elevation), with precipitation as snow being the most isotopically depleted. Therefore, waters in the GYE, which are largely derived from cold, isotopically light winter precipitation (Kharaka et al. 2002), should exhibit limited seasonal variability (Table 7.4). Hughes' (2005: personal communication) analysis of water and snow samples from the North Fork of the Shoshone River (east of YNP) show highly depleted values (-19 to -20‰) that reflect the great distance clouds travel before they precipitate over the region.

Isotopic values from the Henry Mountain samples are enriched in comparison to Yellowstone samples. Surface waters from the Delores River near Cisco (~162 km from Henry Mountains) are also enriched in comparison to GYE surface water values (Table 7.4). Prevailing westerlies in the region would track storms from the Pacific Ocean in winter and would be expected to be highly depleted since these storms have first traversed the Sierra Nevada and Cascade ranges. However, in the eastern part of the state summer storms originating in the Gulf of Mexico would be a closer source and not nearly as depleted (Climate of Utah, <http://www.wrcc.dri.edu/narratives/UTAH.htm>). However, research by Evans (2005) in the Middle Bowl drainage in the northern Wasatch Range suggests more complexity to the system. In sampling snow following individual storms he found $\delta^{18}\text{O}$ enrichment with elevation (0.1 per mil/100 m) on the leeward side which differs other studies which indicate depletion with elevation. This pattern may explain the enriched values obtained from the Henry Mountain samples.

Table 7.4. Location of GYE and Henry Mountains* water collection sites (Coplen and Kendall 2000) with associated mean annual temperature (MAT), precipitation (MAP) and mean $\delta^{18}\text{O}$ values of local environmental waters. Climate data is from the Western Regional Climate Center (www.wrcc.dr.edu). With the exception of the Dolores River, limited seasonal variability of $\delta^{18}\text{O}$ is apparent in these local waters.

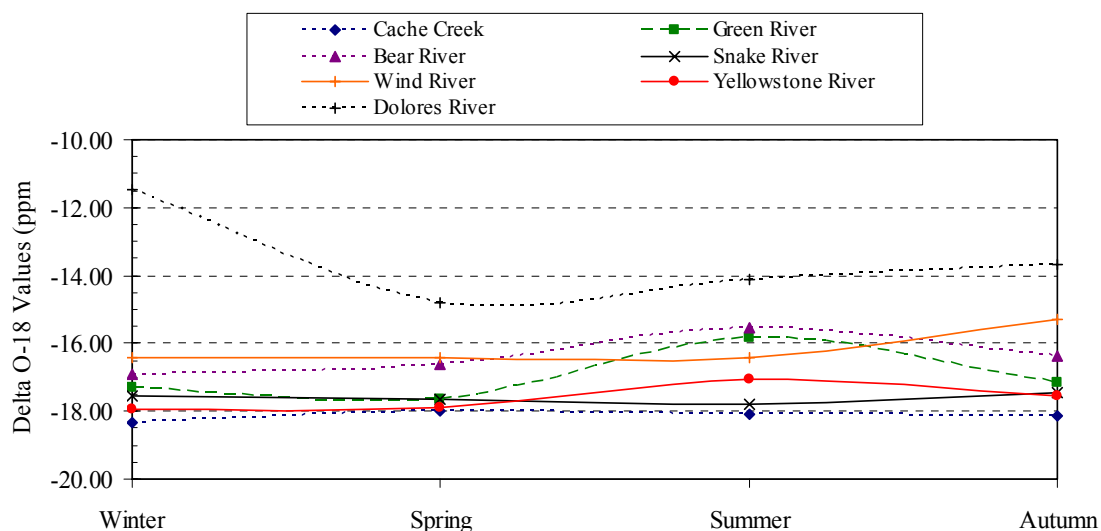
Locality	Elevation (m)	$\delta^{18}\text{O}$ H ₂ O VSMOW (‰)	Seasonal Variability (‰)	MAT (°C)	MAP (mm)
Bear River, Border, Wyoming	1844.5	-16.30 ± 0.69	2.63	3.39	343.66
Cache Creek, Jackson, Wyoming	2057.4	-18.11 ± 0.22	1.00	3.68	403.86
Green River, La Barge, Wyoming	1987.3	-17.05 ± 0.69	1.78	3.61	204.22
Snake River, Heise, Idaho	1528.7	-17.58 ± 0.21	0.68	7.50	311.66
Wind River below Boysen Reservoir, Wyoming	1404.69	-16.34 ± 0.55	1.89	8.38	243.84
Yellowstone River, Livingston, Montana	1387.6	-17.70 ± 0.49	1.90	7.17	416.05
Dolores River, near Cisco, Utah*	1270.4	-13.74 ± 0.47	9.38	12.8	204

While bison are obligatory drinkers, additional body water may be obtained through grasses. Grasses and forbs growing at higher elevations may be substantially

enriched. Spring and summer rains coming from the south contribute to the growth of grasses and forbs in foothill areas, while winter snowmelt sustains mountain vegetation growth. Elevation variability in $\delta^{18}\text{O}$ vegetation can be expected. Therefore, as bison migrate between elevationally different ranges, the $\delta^{18}\text{O}$ values of plants and meteoric water may vary as well (Hughes 2003). Hoope's (2006) data from modern bison further confirm this pattern.

The seasonal variability in these waters, while not extreme, does provide some patterns that can be used to interpret the bison tooth enamel $\delta^{18}\text{O}$ values (Figure 7.4). The patterns indicate enriched values in summer and autumn when evaporation is most important. This is especially true of the drainages at lower elevations (e.g., Green River, Bear River, and Wind River).

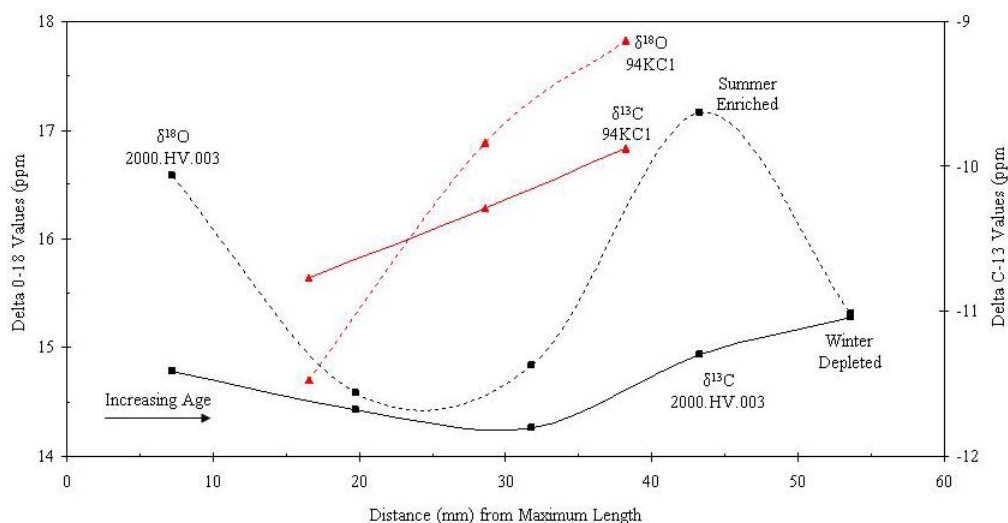
Figure 7.4. Seasonal plot of mean values for drainages in the Greater Yellowstone Ecosystem and Dolores River, Utah. Enrichment (or less negative values) in summer and autumn reflect evaporation. Depleted values in winter and spring are reflective of moisture falling as snow. Smaller drainages, such as Cache Creek, exhibit limited variability reflecting relative continuity of source from snow and melting snow pack. Colorado River discharge data from http://pubs.usgs.gov/wdr/2004/wdr-ut-04/PDF/2Colorado_River.pdf.



The detailed down-tooth variability of the modern bison provides evidence of seasonal use of vegetative and water resources which reflect migration patterns (Figure

7.5). Individual YNP 2000.HV.003 provides the best record of seasonal variability in water intake with a range of 2.51‰. While this bison was restricted to the Yellowstone Plateau, it does display the sinusoidal pattern of ratios expected of tooth mineralization across winter and summer seasons (Balasse et al. 2003). The third molar forms between the 9th and 24th month after birth, so the initial value should reflect a winter signal of highly depleted precipitation in the form of snow. Moving into the summer months there is a pattern of enrichment (less negative $\delta^{18}\text{O}$ values) that may be reflective of the use of smaller water sources, such as lakes or ponds, which may be more effected by evaporation. Coplen and Kendall's (2000:199) data for the Yellowstone River indicate slight enrichment during summer months.

Figure 7.5 Plot of down-tooth samples from modern YNP bison. Due to the limited number of samples (n=2) for individual YNP 2000.HV.002, it was excluded from the plot. The oldest portion of the tooth would be on the right side of graph moving left and younger. The $\delta^{13}\text{C}$ values show little variability reflecting the C_3 dominated ecosystem of the Yellowstone Plateau.



Stable carbon isotope signatures are important, but the real value lies in the ability to reconstruct the composition of the vegetation community that bison were grazing upon. Hoppe et al. (2006) provide an equation for reconstructing percentage of C_4 vegetation in the diet of bison based upon $\delta^{13}\text{C}$ values for tooth enamel. The equation is:

$$\%C_4 = [9.16(\pm 0.94) * \text{mean } \delta^{13}\text{C}_{\text{enamel}}] + 112.80(\pm 0.80)$$

Solving for the $\delta^{13}\text{C}$ values for each individual provides a better understanding of grassland vegetation used by each of the bison (Table 7.5). For the modern YNP bison (Figure 7.5) the calculated percentage of C_4 vegetation in the diet ranges from 22.31 to 14.14% ($\Delta 8.17\%$) for specimen 94KC1 and 4.75 to 11.66% ($\Delta 6.91\%$) for specimen 2000.HV.003. Both heavily reliant on cool season, or C_3 vegetation.

Table 7.5. Calculated percentage of C_3 and C_4 vegetation based upon equation provided by Hoppe et al. (2006). Vertical specimens represent average values for each individual tooth. Corrected value for $\delta^{13}\text{C}$ is based on -1.5‰ adjustment based to pre-19th century samples due to fossil fuel burning (Tieszen 1994). $\delta^{13}\text{C}$ values are presented in parts per mil (‰).

Specimen	Downtooth Distance (mm)	$\delta^{13}\text{C}$	$\delta^{13}\text{C}$ Corrected	$\%C_4$	$\%C_3$
HM/12	43.00	-8.10		38.60	61.40
HM/12	34.00	-8.63		33.77	66.23
HM/12	25.00	-7.36		45.37	54.63
HM/12	16.00	-7.58		43.37	56.63
HM/12	8.00	-8.85		31.77	68.23
HM/12	Vertical	-7.76		41.73	58.27
HM/768	38.10	-4.93		67.60	32.40
HM/768	23.90	-7.64		42.79	57.21
HM/768	10.76	-5.80		59.67	40.33
HM/768	Vertical	-6.16		56.40	43.60
2000.HV.002	28.47	-11.48		7.61	92.39
2000.HV.002	Vertical	-11.59		6.60	93.40
2000.HV.003	53.57	-11.04		11.66	88.34
2000.HV.003	53.57	-11.04		11.64	88.36
2000.HV.003	43.27	-11.33		9.01	90.99
2000.HV.003	31.80	-11.80		4.75	95.25
2000.HV.003	19.74	-11.68		5.85	94.15
2000.HV.003	7.23	-11.41		8.27	91.73
YNP/94KC1	38.18	-9.88		22.31	77.69
YNP/94KC1	28.62	-10.29		18.53	81.47
YNP/94KC1	16.57	-10.77		14.14	85.86
YNP/94KC1	Vertical	-10.46		16.96	83.04
48YE697/697.1	46.49	-7.41	-8.91	31.23	68.77
48YE697/697.1	36.77	-8.64	-10.14	19.93	80.07
48YE697/697.1	25.71	-9.27	-10.77	14.15	85.85
48YE697/697.1	25.71	-9.09	-10.59	15.78	84.22
48YE697/697.1	14.79	-9.71	-11.21	10.10	89.90
48YE697/697.1	5.92	-9.96	-11.46	7.85	92.15
48YE697/697.1	5.92	-9.59	-11.09	11.26	88.74
10OA210/6.133.11	53.98	-9.09	-10.59	15.82	84.18

Specimen	Downtooth Distance (mm)	$\delta^{13}\text{C}$	$\delta^{13}\text{C}$ Corrected	%C ₄	%C ₃
100A210/6.133.11	42.37	-9.62	-11.12	10.93	89.07
100A210/6.133.11	30.80	-9.57	-11.07	11.37	88.63
100A210/6.133.11	30.80	-9.70	-11.20	10.25	89.75
100A210/6.133.11	20.67	-9.19	-10.69	14.84	85.16
100A210/6.133.11	9.25	-8.97	-10.47	16.88	83.12
100A210/6.133.11	Vertical	-8.83	-10.33	18.21	81.79
100A210/6.373.60	45.63	-9.38	-10.88	13.10	86.90
100A210/6.373.60	33.46	-9.25	-10.75	14.29	85.71
100A210/6.373.60	21.89	-8.61	-10.11	20.22	79.78
100A210/6.373.60	9.88	-8.46	-9.96	21.53	78.47
100A210/6.373.60	Vertical	-8.60	-10.10	20.30	79.70
48PA29/1181H	59.90	-6.21	-7.71	42.17	57.83
48PA29/1181H	47.87	-6.57	-8.07	38.88	61.12
48PA29/1181H	34.13	-7.55	-9.05	29.92	70.08
48PA29/1181H	22.74	-7.98	-9.48	26.01	73.99
48PA29/1181H	12.58	-7.78	-9.28	27.83	72.17
48PA29/1181H	Vertical	-6.78	-8.28	37.00	63.00
48PA29/1233H	58.41	-7.52	-9.02	30.18	69.82
48PA29/1233H	49.20	-7.03	-8.53	34.67	65.33
48PA29/1233H	39.02	-5.00	-6.50	53.26	46.74
48PA29/1233H	27.73	-2.80	-4.30	73.41	26.59
48PA29/1233H	16.52	-2.82	-4.32	73.23	26.77
48PA29/1233H	Vertical	-4.50	-6.00	57.84	42.16
48PA29/2548H	55.68	-7.37	-8.87	31.57	68.43
48PA29/2548H	44.48	-6.85	-8.35	36.36	63.64
48PA29/2548H	35.50	-7.38	-8.88	31.44	68.56
48PA29/2548H	23.68	-7.64	-9.14	29.06	70.94
48PA29/2548H	12.83	-7.81	-9.31	27.54	72.46
48PA29/2548H	Vertical	-7.18	-8.68	33.29	66.71
48TE1090/42226	21.78	-9.06	-10.56	16.06	83.94
48TE1090/42226	8.26	-9.62	-11.12	10.96	89.04
48TE1090/42226	Vertical	-9.18	-10.68	14.94	85.06
48TE1090/42227	32.90	-9.51	-11.01	11.95	88.05
48TE1090/42227	19.57	-9.80	-11.30	9.28	90.72
48TE1090/42227	6.53	-9.82	-11.32	9.12	90.88
48TE1090/42227	Vertical	-9.73	-11.23	9.90	90.10
48TE1101/22597	44.31	-8.09	-9.59	24.99	75.01
48TE1101/22597	35.33	-8.19	-9.69	24.05	75.95
48TE1101/22597	25.14	-8.11	-9.61	24.74	75.26
48TE1101/22597	13.49	-7.71	-9.21	28.39	71.61
48TE1101/22597	Vertical	-7.81	-9.31	27.48	72.52
48TE1102/42222	48.23	-6.94	-8.44	35.52	64.48
48TE1102/42222	36.82	-7.39	-8.89	31.36	68.64
48TE1102/42222	25.75	-7.76	-9.26	27.98	72.02
48TE1102/42222	14.48	-7.97	-9.47	26.05	73.95
48TE1102/42222	Vertical	-7.38	-8.88	31.46	68.54

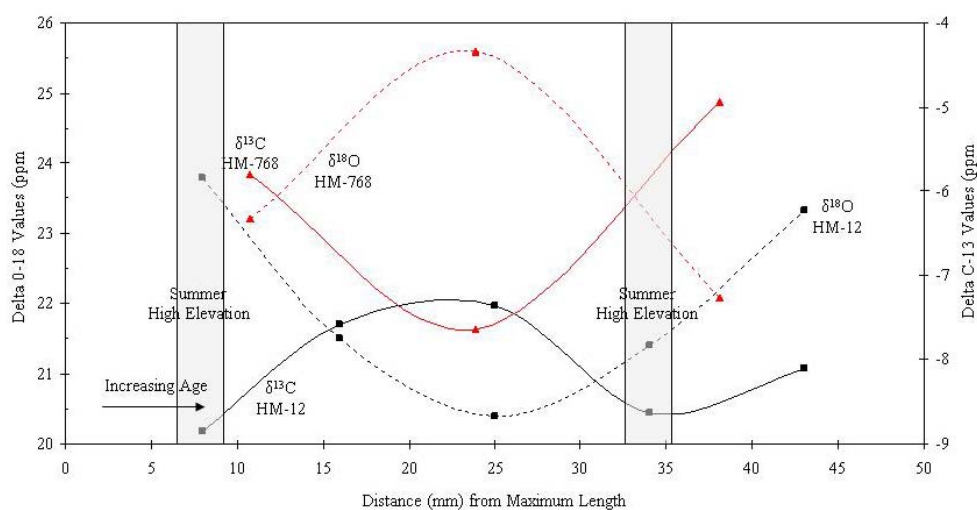
Specimen	Downtooth Distance (mm)	$\delta^{13}\text{C}$	$\delta^{13}\text{C}$ Corrected	%C ₄	%C ₃
48TE1102/42223	25.25	-9.06	-10.56	16.08	83.92
48TE1102/42223	15.03	-9.53	-11.03	11.78	88.22
48TE1102/42223	Vertical	-9.21	-10.71	14.72	85.28
48TE1114/39605	51.31	-9.44	-10.94	12.63	87.37
48TE1114/39605	39.15	-10.05	-11.55	6.99	93.01
48TE1114/39605	28.85	-9.23	-10.73	14.48	85.52
48TE1114/39605	17.16	-8.36	-9.86	22.49	77.51
48TE1114/39605	6.28	-8.01	-9.51	25.68	74.32
48TE1114/39605	Vertical	-8.89	-10.39	17.61	82.39
48TE455/455.1	28.59	-10.03	-11.53	7.17	92.83
48TE455/455.1	28.59	-10.15	-11.65	6.05	93.95
48TE455/455.1	18.91	-9.64	-11.14	10.71	89.29
48TE455/455.1	6.72	-10.01	-11.51	7.33	92.67
48TE455/455.1	Vertical	-9.53	-11.03	11.80	88.20
48TE455/455.2	50.63	-8.27	-9.77	23.34	76.66
48TE455/455.2	40.04	-8.47	-9.97	21.44	78.56
48TE455/455.2	29.14	-8.15	-9.65	24.43	75.57
48TE455/455.2	18.44	-8.21	-9.71	23.82	76.18
48TE455/455.2	8.28	-8.74	-10.24	19.00	81.00
48TE455/455.2	Vertical	-7.98	-9.48	26.00	74.00
48YE697/697.1	46.49	-7.41	-8.91	31.23	68.77
48YE697/697.1	36.77	-8.64	-10.14	19.93	80.07
48YE697/697.1	25.71	-9.27	-10.77	14.15	85.85
48YE697/697.1	25.71	-9.09	-10.59	15.78	84.22
48YE697/697.1	14.79	-9.71	-11.21	10.10	89.90
48YE697/697.1	5.92	-9.96	-11.46	7.85	92.15
48YE697/697.1	5.92	-9.59	-11.09	11.26	88.74
48YE697/697.1	Vertical	-9.25	-10.75	14.31	85.69

The Henry Mountains' specimens display a similar seasonal pattern in both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values (Figure 7.6). However, the two individuals display exactly opposite patterns. Individual 12 displays an expected sinusoidal pattern for both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values. As would be expected, the summer months spent at higher elevations would be illustrated by more negative $\delta^{13}\text{C}$ values (>C₃ vegetation use) and less negative $\delta^{18}\text{O}$ values, because of enrichment from evaporation. Individual 768 displays a $\delta^{13}\text{C}$ pattern of low elevation C₄ plant use with movement to higher elevations in summer illustrated by more negative $\delta^{13}\text{C}$ values and lower C₄ plant usage. Calculated percentage of C₄

vegetation indicates a more substantial dependence on warm season vegetation than the YNP individuals. This would be consistent with the local vegetation of this more southern and arid region. Individual 12 ranges from 31.77 to 43.37% ($\Delta 11.6\%$) and Individual 768 illustrates a more C_4 -dependent diet with a range of 42.79 to 67.60% ($\Delta 24.81\%$). Water use, as inferred from $\delta^{18}\text{O}$ values, illustrates depleted values in winter with enrichment in summer due to evaporation.

The modern samples from both YNP and the Henry Mountains show very distinct patterns, which are linked to local conditions; the important aspect is that the patterns within each of the individuals seems to be consistent. This suggests that bison are creatures of habitat and follow similar migration patterns throughout their lives, or at least the portion of their lives depicted by these samples.

Figure 7.6. Plot of down-tooth samples from modern Henry Mountains bison. The oldest portion of the tooth would be on the right side of graph moving left and younger. Seasonal patterns for HM-12 conform to expected patterns (grey bar). Summer months would be spent at higher elevations illustrated by more negative $\delta^{13}\text{C}$ values and depleted $\delta^{18}\text{O}$ values because of enrichment from evaporation.



In the modern samples, it is apparent that a multi-year seasonal record of migration and landscape use is present. The modern YNP specimens provide a pattern that is relatively flat with respect to vegetation intake (YNP 2000.HV.003 range=0.76). The calculated percentage of C_4 vegetation ranges from 4.75 to 11.66% ($\Delta 6.91\%$). This is not unexpected considering that these

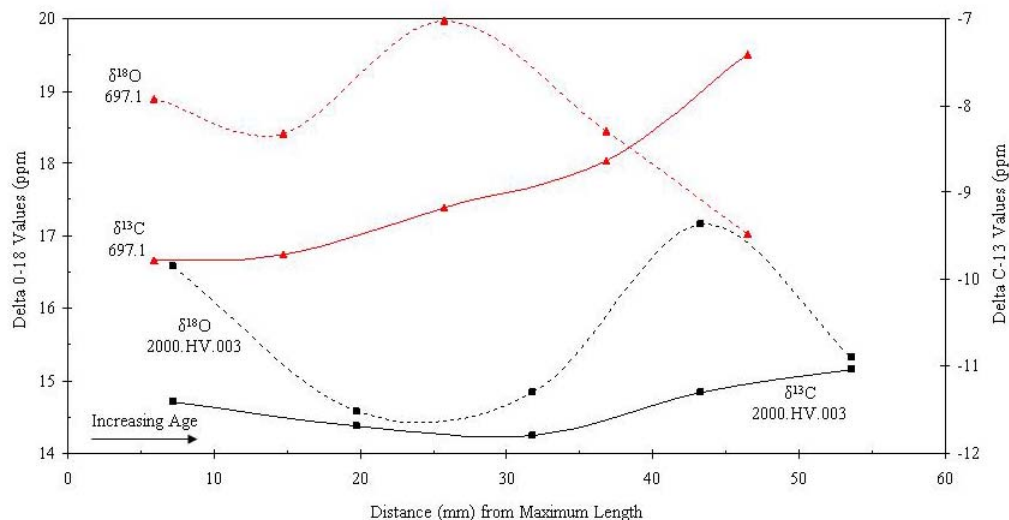
animals, while they are considered free-ranging, are restricted to movement within the Park, a C₃-dominated ecosystem. Based upon this individual bison's pattern and relevant hydrologic information, some testable scenarios for prehistoric bison can now be developed.

1. Bison that have a migration pattern that includes the high elevation areas of the GYE and the surrounding low elevation valleys will have marked seasonal differences in both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values. Summer values of $\delta^{13}\text{C}$ will be relatively more negative, reflecting C₃-dominated vegetation. The summer $\delta^{18}\text{O}$ values should be enriched (greater value) if bison are drinking from wetlands and lakes that experience evaporation. Meagher's (1973) observations indicate that bison tend towards lush meadows and wetlands in the open valleys of Hayden, Pelican, and Lamar. However, if they are drinking from larger streams and rivers that are filled primarily with snow runoff, there will be little seasonal variability and $\delta^{18}\text{O}$ values will be depleted (lower value).
2. Winters will reflect migration downslope to areas where C₄ vegetation may be present. Therefore $\delta^{13}\text{C}$ values should be more positive, with $\delta^{18}\text{O}$ values being less depleted as with lower elevation (Gat 1980; Burke and Stuiver 1981). Waters at lower elevation in the GYE also tend to be less (for example Bear River and Wind River in Table 7.4).

Comparison of down-tooth values of individual 697.1, a mature bull that died about 800 years ago along the north shore of Yellowstone Lake, with modern YNP individual 2000.HV.003, a mature female that died in the Hayden Valley reveals some similarity in patterns (Figure 7.7). In particular, the oldest $\delta^{18}\text{O}$ values are significantly depleted, indicating potential use of snow or snow melt as a water source followed by increased enrichment (summer evaporation), followed by slight depletion, and again, slight enrichment. Interestingly, the range of the values for both the archeological and modern bison do not differ greatly, (2.87‰ and 2.51‰), corresponding to the limited variability in isotopic values for the region's precipitation (see Table 5.3; Hoppe 2006).

The $\delta^{13}\text{C}$ pattern of the modern bison (2000.HV.003) is relatively flat with a range of 0.76‰. As stated above, this pattern is consistent with modern YNP bison, which are restricted to the C_3 -dominated ecosystem of YNP. Calculated percentage of C_4 vegetation range from 4.75 to 11.66‰ ($\Delta 6.91\%$). The archeological specimen, a bull, displays a greater range of values (2.55‰) with more positive values corresponding to the depleted $\delta^{18}\text{O}$ values. The more positive $\delta^{13}\text{C}$ values reflect greater reliance on C_4 vegetation (7.85 to 31.23%, $\Delta 23.38\%$), possibly at lower elevations. However, pattern of the $\delta^{13}\text{C}$ values does not replicate, but continues to become more negative. The contribution of vegetation around thermal areas has not been evaluated and may be responsible for the relatively high percentage of C_4 vegetation.

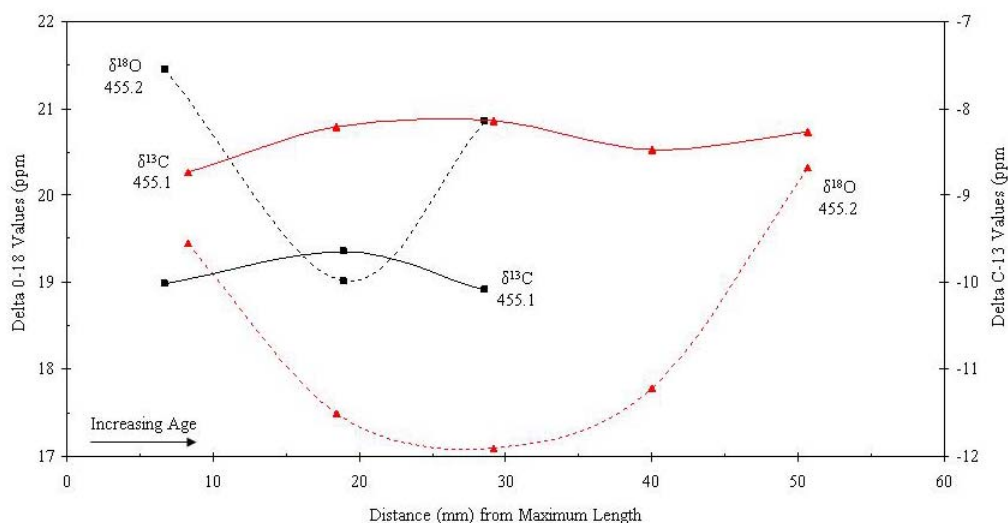
Figure 7.7. Plot of down-tooth samples of modern YNP (2000.HV.003) and archeological (697.1) specimens. The oldest portion of the tooth would be on the right side of graph moving left and younger. Archeological specimen (697.1), a bull, has much greater variability in the use of vegetation ($\Delta 23.38\%$) implying wider range than the modern bison which is restricted to the C_3 -dominated Yellowstone National Park. Both exhibit variability in water intake.



Two specimens from the Goetz site (48TE455) in Jackson Hole also were sampled. Both specimens were recovered in 1971 by University of Wyoming excavations. Specimen 455.1 is undated, but presumed to be associated with the age AD 1175-1285 obtained from the 1971 bison metatarsal. The second sample, 455.2, was directly dated to AD 1480 (Figure 7.8). The specimens illustrate similar patterns of variability, particularly in $\delta^{18}\text{O}$ values, which reflect seasonal migration. The range of $\delta^{13}\text{C}$ values is limited (0.51‰ and 0.59‰) and reflects a diet dominated

by C_3 vegetation. The calculated values for percentage of C_4 vegetation ranges from 6.61 to 10.71% ($\Delta 4.1\%$) for specimen 455.1 and 19.00 to 24.43% ($\Delta 5.43$) for specimen 455.2. The $\delta^{18}O$ values are quite variable (2.36‰ and 3.13‰) and reflect migratory patterns on the order ($>3\%$) described by Hughes (2003). However, the $\delta^{18}O$ patterns reflect enrichment during what is presumed to be a winter signal. These specimens may reflect migration from the south where surface water values are more enriched (see for example Bear River values in Table 5.3). The relatively higher values for C_4 vegetation usage and the more enriched $\delta^{18}O$ values indicates possible seasonal migration to warmer and more arid ecosystems. Of interest is the patterns clearly depict variability among bulls, which tend to move over greater distances during the year and would therefore be in contact with a variety of vegetation suites and water sources.

Figure 7.8. Plot of down-tooth samples of archeological specimens recovered from the Goetz site (48TE455) in Jackson Hole, Wyoming. The oldest portion of the tooth is on the right side of graph. Calculated values for percentage of C_4 vegetation ranges from 6.61 to 10.71% for specimen 455.1 and 19.00 to 24.43% for specimen 455.2. The highly variable $\delta^{18}O$ values for both are on the order of migratory animals described by Hughes (2003). Each of the data sets suggests possible seasonal migration to areas that have increased C_4 vegetation and higher evaporation rates.



Additional specimens from Jackson Hole were sampled. Each of these specimens was recovered from the Snake River delta during excavations in 1987-88 by the MWAC. They are late Holocene in age. The specimens from site 48TE1090 are limited due to the age of the individuals (Figure 7.9). The $\delta^{13}C$ values are limited in range, but illustrate

bison subsisting on predominantly C₃ vegetation (Table 5.5). The $\delta^{18}\text{O}$ values of specimen 42227 record a shift from highly depleted to enriched, a pattern that is most likely the result of migration. Patterns from sites 48TE1101, 48TE1102, and 48TE114 provide additional evidence of the value of bison teeth for tracking seasonal migrations given that the teeth are large enough to sample a significant portion of the individual's life (Figures 7.10-7.12).

Lower elevation specimens from within the GYE were also sampled. Two specimens from the Rock Springs site (10OA21) in southeastern Idaho were sampled (Figure 7.13). Specimen 6.373.11 is from deposits dating ca. AD 1100-1200, while specimen 6.373.60 is from younger deposits dating ca. AD 1450-1650. The $\delta^{13}\text{C}$ values of both specimens reflect reliance on C₃ vegetation with little variability (0.73‰ and 0.92‰). Calculated values for C₄ vegetation ranges are 10.81 to 16.88% ($\Delta 6.07\%$) for specimen 6.133.11 and 13.10 to 21.53% ($\Delta 8.43\%$) for specimen 6.373.60 (Table 6.5). The values indicate a slight variability in C₄ vegetation usage that may suggest limited variability in the ecosystem vegetation within the seasonal round. The $\delta^{18}\text{O}$ values illustrate a sinusoidal pattern that reflects changes in water intake on a seasonal basis. The $\delta^{18}\text{O}$ values are enriched compared to other bison sampled, which probably reflects the warmer annual temperatures at lower elevations. While the $\delta^{18}\text{O}$ values illustrate a seasonal pattern of water use, the values are significantly enriched ($>4\%$) in comparison to modern YNP bison. These values would suggest these bison were probably not migrating very far east into the higher elevations of the GYE.

Figure 7.9. Plot of down-tooth samples of archeological specimens recovered from site 48TE1090 in Jackson Hole, Wyoming. The oldest portion of the tooth is on the right side of graph. Calculated values for percentage of C_4 vegetation ranges from 10.96 to 16.06% for specimen 42226 and 9.12 to 11.95% for specimen 42227. Increased use of C_4 vegetation is correlated with depleted $\delta^{18}O$ values which may indicate a seasonal shift to ecosystems with slightly more warm season vegetation and winter-depleted precipitation values.

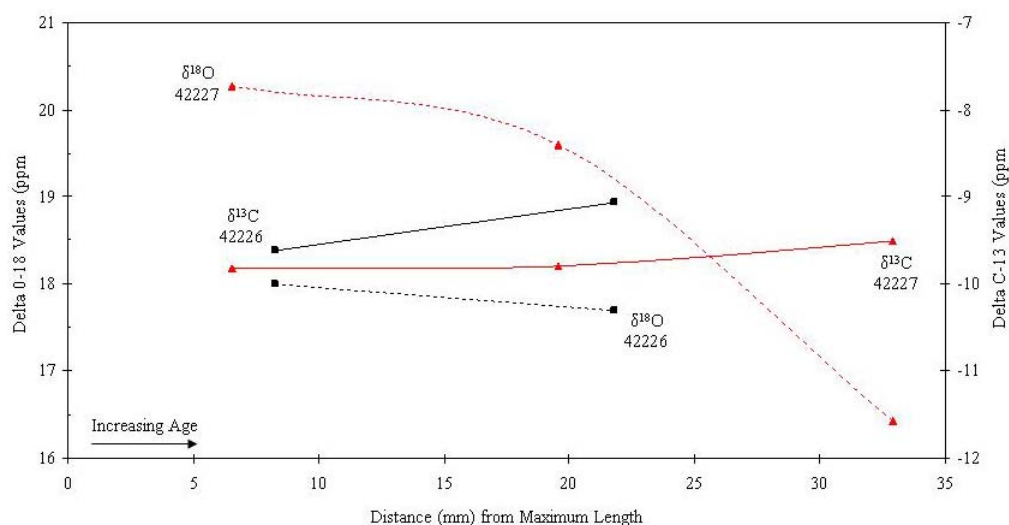


Figure 7.10. Plot of down-tooth samples of archeological specimen recovered from site 48TE1101 in Jackson Hole, Wyoming. The oldest portion of the tooth is on the right side of graph. Calculated values for percentage of C_4 vegetation are relatively high from 24.05 to 28.39%. The range of the $\delta^{18}O$ values suggests a seasonal shift between depleted and enriched values, a possible migratory shift. The relatively high use of C_4 vegetation is not consistent with vegetation in Jackson Hole.

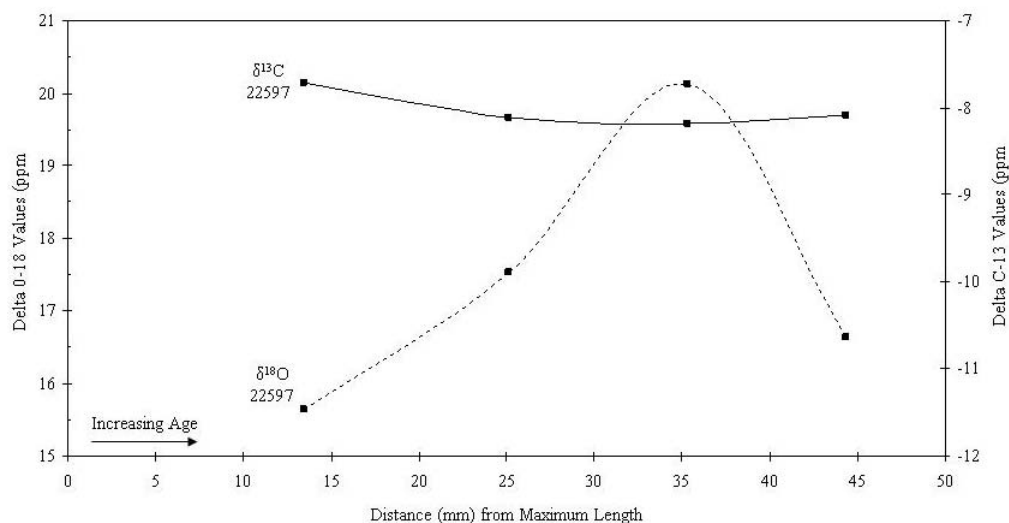


Figure 7.11. Plot of down-tooth samples of archeological specimens recovered from site 48TE1102 in Jackson Hole, Wyoming. The samples are very limited due to the advanced age of the individuals. The oldest portion of the tooth is on the right side of graph. Calculated values for percentage of C_4 vegetation ranges are relatively high from 11.78 to 16.08% for specimen 42223 and 31.36 to 35.52% for specimen 42222. The range of the $\delta^{18}O$ values suggests a seasonal shift between depleted and enriched values, a possible migratory shift. The relatively high use of C_4 vegetation is not consistent with vegetation in Jackson Hole.

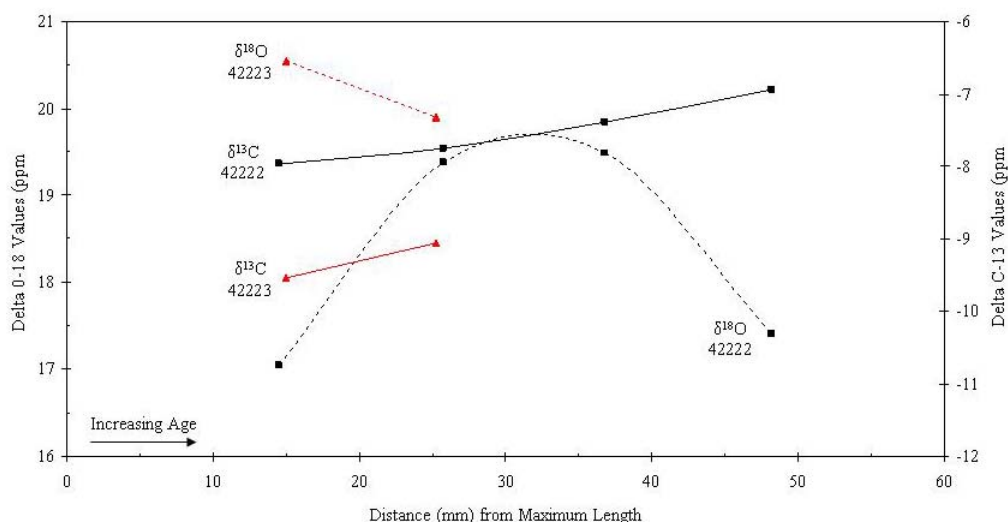


Figure 7.12. Plot of down-tooth samples of archeological specimen recovered from the site 48TE1114 in Jackson Hole, Wyoming. The oldest portion of the tooth is on the right side of graph. Variability in both $\delta^{13}C$ and $\delta^{18}O$ values suggest a seasonal pattern. Calculated values for percentage of C_4 vegetation ranges suggest a seasonal migratory pattern in C_3 -dominated ecosystems (6.99%) to areas with significant C_4 vegetation (25.68%). The range of the $\delta^{18}O$ values suggests a seasonal shift between depleted and enriched values, a possible migratory shift. The relatively high use of C_4 vegetation is not consistent with vegetation in Jackson Hole.

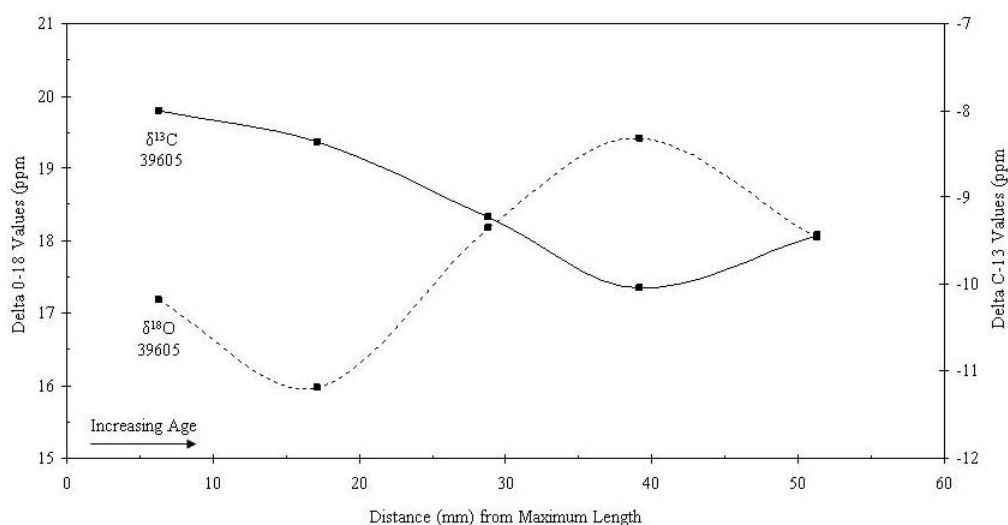
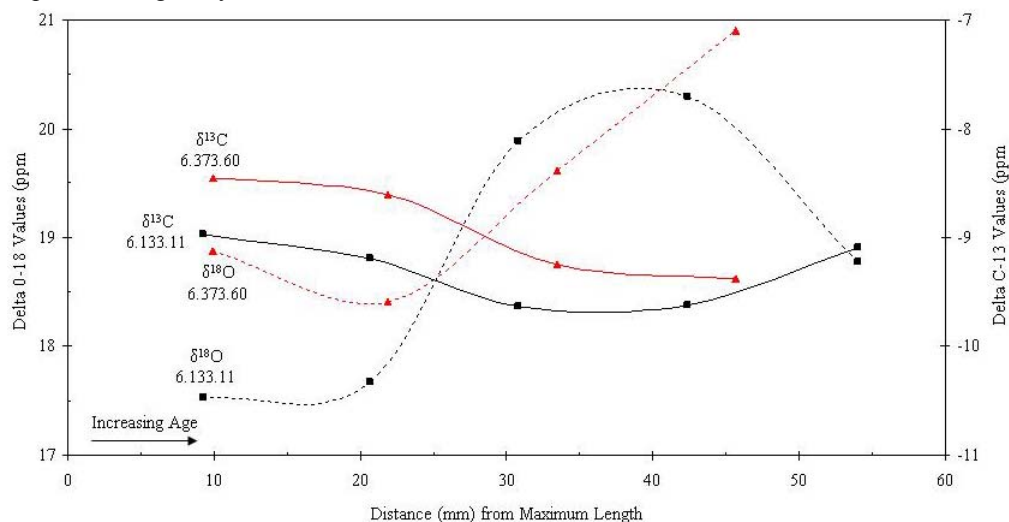


Figure 7.13. Plot of down-tooth samples of archeological specimens recovered from the site 100A210, Oneida County, Idaho. The oldest portion of the tooth is on the right side of graph. Variability in both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values suggest a seasonal pattern. Calculated values for percentage of C_4 vegetation ranges suggest a seasonal migratory pattern in C_3 -dominated ecosystems, although significant C_4 vegetation is available. Specimen 6.373.60 has a much higher percentage of C_4 vegetation with a range from 13.10 to 21.53 % ($\Delta 8.43\%$). The range of the $\delta^{18}\text{O}$ values suggests a seasonal shift between depleted and enriched values, a possible migratory shift.



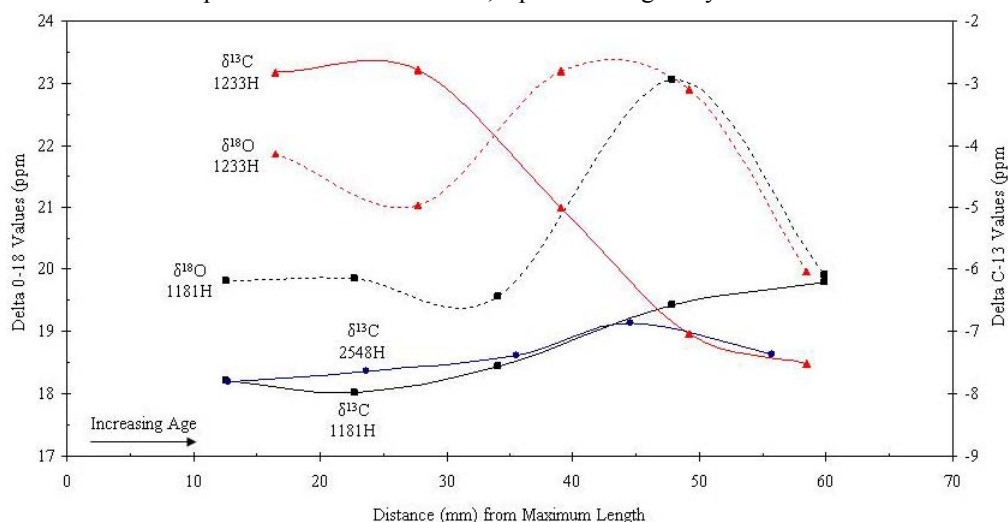
Three samples from the Early Holocene Horner site (48PA29) were also sampled.

The Horner site is located to the east of the Yellowstone Plateau in a more xeric environment due to the rainshadow effect of the Absaroka Mountains. The paleoclimate record developed from pollen by Whitlock and Bartlein (1993) for southern YNP indicates warmer and drier than present conditions. The Horner specimens are represented by two cows aged 3.6 years (2548H) and 4.6 years (1181H) at death, and a probable young bull aged 2.6 years (1233H). Therefore, they represent three members of the same herd but different age cohorts and can provide information on herd movement over the course of three generations.

In general, the patterns reflect seasonal shifts in $\delta^{18}\text{O}$ values from winter depletion to summer enrichment (Figure 7.14). However, what is striking is the mean values from the vertical samples are significantly enriched (21.75 for Horner 2548H) in comparison to modern YNP specimen 2000.HV.003 (14.98; Table 6.2). This enrichment probably

reflects the greater effect of evaporation during the warmer and drier early Holocene as reflected in Whitlock and Bartlein's (1993) pollen data. The $\delta^{13}\text{C}$ values, while the two display limited variability (1.77‰ and 0.96‰), are significantly more positive than the other GYE specimens and reflect a greater reliance on C_4 vegetation. The third specimen (1233H) has a much greater variability than the other two (4.72‰). Calculated percent of C_4 vegetation for the three specimens range from 26.01 to 42.07 % ($\Delta 16.16\%$) for specimen 1181H to 30.18 to 73.4% ($\Delta 43.23\%$) for specimen 1233H. (Table 6.5). The $\delta^{13}\text{C}$ values of the three individuals are significantly different ($t=-14.937$, $p=0.000$) indicating that they grazed in areas where vegetation was similar. The $\delta^{18}\text{O}$ values are more variable ($t=51.251$, $p=0.000$) and suggest the use of different water sources during their lifetimes and the possible use of slightly different habitats.

Figure 7.14. Plot of down-tooth samples of archeological specimens recovered from the Horner site (48PA29), Park County, Wyoming. The oldest portion of the tooth is on the right side of graph. Calculated values for percentage of C_4 vegetation ranges suggest a seasonal migratory pattern within a mixed ecosystem with significant C_4 vegetation is available. $\delta^{13}\text{C}$ values for the two individuals are not significantly different and suggest continuity in vegetation. The range of the $\delta^{18}\text{O}$ values suggests a seasonal shift between depleted and enriched values, a possible migratory shift.

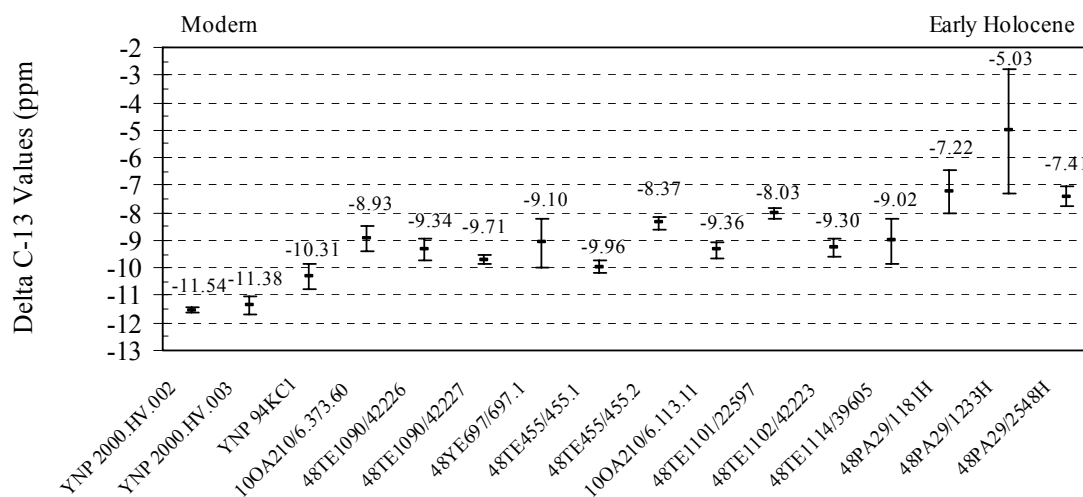


Summary

The preceding discussion has demonstrated the value of down-tooth sampling to illustrate meaningful patterns of land use by bison from different portions of the GYE. The range and

variability in the values is greater than the modern YNP specimens, but this should not be a surprise because prehistoric herds were not constrained by artificial management boundaries. Unfortunately, the samples are limited in size and only provide a glimpse at how herds used the landscape during different climatic periods. Figure 7.15 depicts the $\delta^{13}\text{C}$ values based upon time period with the youngest (modern) samples on the left. The early Holocene Horner site specimens reflect a greater reliance on C_4 vegetation than any of the late Holocene specimens, as predicted by the Whitlock and Bartlein (1993) pollen record for southern YNP. Unfortunately, the sample analyzed does not include specimens from the mid-Holocene and the northern YNP area that may be used in further testing the pollen record of Whitlock and Bartlein (1993) that shows increased warmth and aridity.

Figure 7.15 Plot of mean and standard error for $\delta^{13}\text{C}$ values for all samples arranged by time period with youngest (or modern) samples on the left. Mean values are also provided. The range of the values for the prehistoric specimens suggests use of more varied ecosystems. The Horner specimens have the least negative values indicating greater reliance on C_4 vegetation.



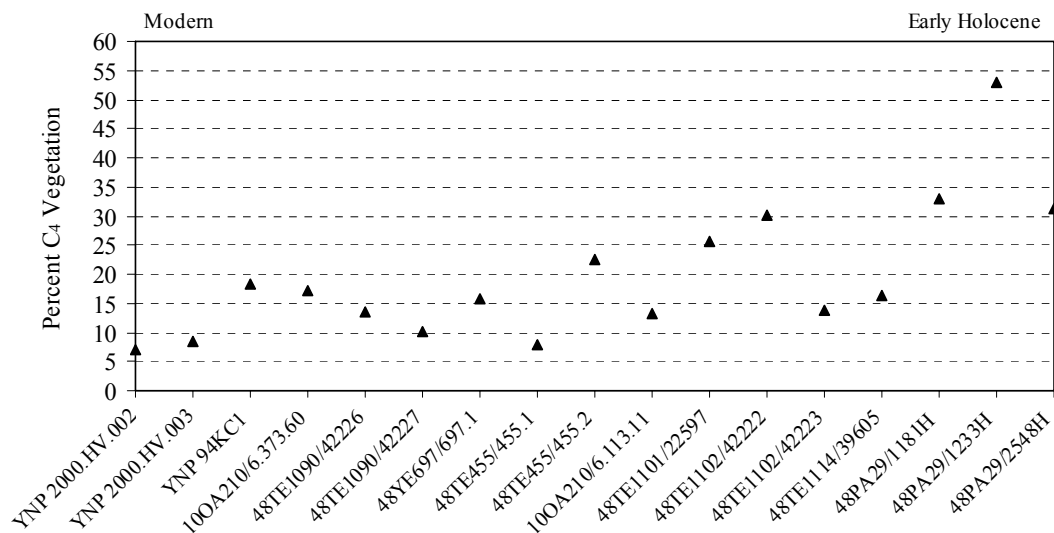
Solving for the mean of each of the individuals using Hoppe et al.'s (2006) equation provides a better understanding of grassland vegetation used by each of the bison (Table 7.6). Figure 7.16 illustrates the percentage of calculated C_4 vegetation in each of the individual's diet. As expected, the higher altitude bison from the Yellowstone Plateau and Jackson Hole have the least amount of the warm season vegetation. The bison from the early Holocene Horner site

(48PA29) on the east side of the GYE subsisted on the highest percentage of warm season vegetation. This pattern is consistent with Whitlock and Bartlein's (1993) paleoclimatic data and the paleoenvironmental work in association with the Horner site investigations (Frison and Todd 1987). An unexpected pattern is provided by the two individuals represented by the Goetz site specimens (48TE455.1 and 48TE455.2). These individuals represent almost 15% difference in their use of C₄ vegetation.

Table 7.6. Calculated percentage of C₄ vegetation in diet of GYE samples based upon Hoppe et al.'s (2006) equation 1. Mean values used in calculation are adjusted for prehistoric specimens by 1.5‰ because of $\delta^{13}\text{C}$ value of atmospheric CO₂ due to burning of fossil fuels (Tieszen et al. 1996).

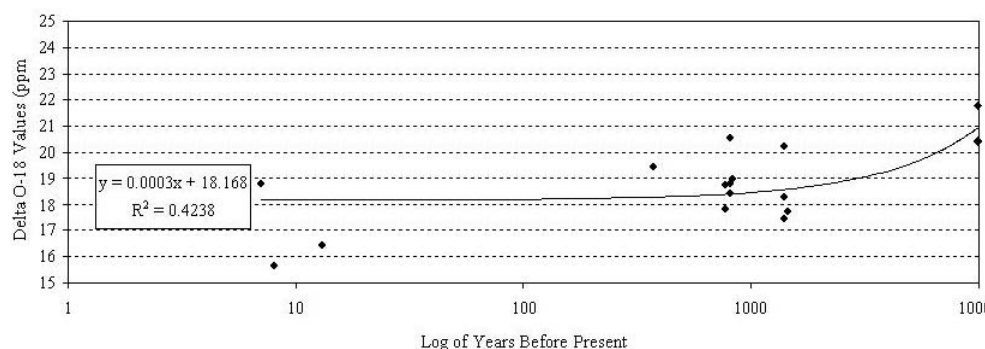
SITE AND CATALOG NUMBER	N	MEAN	ADJUSTED VALUE	% C ₄ VEGETATION	% C ₃ VEGETATION
100A210/6.113.11	6	-9.3567	-10.86	13.35	86.65
100A210/6.373.60	4	-8.9250	-10.42	17.31	82.69
YNP 2000.HV.002	2	-11.5350		7.14	92.86
YNP 2000.HV.003	6	-11.3833		8.53	91.47
48PA29/1181H	5	-7.2180	-8.72	32.94	67.06
48PA29/1233H	5	-5.0340	-6.53	52.95	47.05
48PA29/2548H	5	-7.4100	-8.91	31.18	68.82
48TE1090/42226	2	-9.3400	-10.84	13.51	86.49
48TE1090/42227	3	-9.7100	-11.21	10.12	89.88
48TE1101/22597	4	-8.0250	-9.52	25.55	74.45
48TE1102/42222	4	-7.5150	-9.02	30.22	69.78
48TE1102/42223	2	-9.2950	-10.79	13.92	86.08
48TE1114/39605	5	-9.0180	-10.52	16.46	83.54
48TE455/455.1	4	-9.9575	-11.46	7.85	92.15
48TE455/455.2	5	-8.3680	-9.87	22.41	77.59
48YE697/697.1	7	-9.0957	-10.59	15.74	84.26
Henry Mtns/12	5	-8.1040		38.57	61.43
Henry Mtns/768	3	-6.1233		56.71	43.29
YNP 94KC1	3	-10.3133		18.33	81.67

Figure 7.16. Calculated percentage of C₄ vegetation based upon mean $\delta^{13}\text{C}$ values for individual bison. Bison are arranged by time with the youngest (or modern) specimens on the left and the early Holocene specimens (48PA29) on the right. Bison from the Yellowstone Plateau and Jackson Hole indicate the lowest use of C₄ vegetation, while the Horner bison (48PA29) indicate the highest percentage of use.



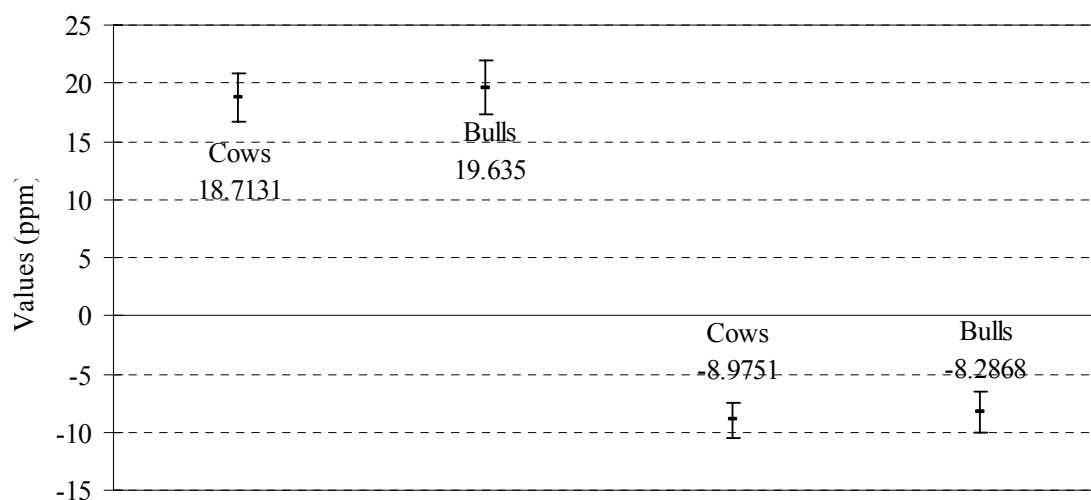
In general, the $\delta^{18}\text{O}$ values indicate a slight correlation through time (Figure 7.17). A plot of the values against the log of years before present illustrate a pattern of enriched values occurring at around 1000 years ago and again during the early Holocene values for the Horner samples. The more enriched samples are supported by warmer and more arid conditions when evaporation would be enhanced. Some of the other enriched samples come from Jackson Hole, which may suggest migration of these species between Jackson Hole and more southern wintering areas.

Figure 7.17 Plot of mean $\delta^{18}\text{O}$ values against log of years before present indicates enriched values through time. The enriched (less negative) values suggest periods of increased evaporation during periods of warmer and drier conditions. Another possible conclusion is that the enriched values reflect dependence on water sources that have significant seasonal evaporation.



Other behavioral patterns that can be explored include the variability in isotope values for bulls and cows. Bulls typically are not tied to herds after they mature and wander more widely than cows in nursery herds (Meagher 1973). Therefore, bulls will be sampling a wider range of environments and have greater variability in their isotopic signatures. The predicted pattern does not occur in these samples, but instead indicates overlap between bull and cows for both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values (Figure 7.18). It is possible that some of the individuals were not properly assigned to gender, or that the sample size is too small for each group to detect within herd patterning, or that behavioral differences are minimal and they do not affect ultimate dietary composition.

Figure 7.18 Plot of mean and standard deviation for $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values based upon sex. The plot indicates no difference between bulls and cows in their migration patterns as indicated by variability in the stable isotope values. Values plotted are means for each sample.



While the results of this study indicate that valuable information can be obtained from down-tooth sampling of bison teeth, a number of problems need to be resolved to truly provide a detailed picture of bison herd migration and land use patterns through time:

1. Selection of teeth of known age and known sex individuals that have high confidence level. Determination of the sex of the teeth for this study was based upon metric analysis for which there was no discrete separation. Separation into gender was based on metric analysis and other information from the skull (e.g., robustness) if available. Additional information from other characteristics of the individuals can be used to more confidently assign sex. Therefore, some of the individuals may have been misidentified to gender.
2. More detailed sampling per tooth. Balasse et al. (2003) analyzed oxygen isotope values of Late Stone Age domestic sheep from South Africa at a much finer scale and was able to detect seasonal cycles in the record.
3. Larger samples of individual teeth. Tieszen (1994) recommends a large number of replicates for short time periods to derive an acceptable mean for the population. Hoppe (2006) suggests a minimum of four to five individuals are necessary to derive a robust mean and standard deviation of a population.
4. Samples from a single herd in which cohort age can be assigned and sampled. This will allow a more detailed understanding of herd structure and behavior to be detected (Gadbury et al. 2000). The Horner site population is an ideal group for this type of study.

Despite the limitations, the results of this case study do provide important evidence concerning bison ecology during the Holocene in comparison with modern bison of Yellowstone National Park and Jackson Hole. Specifically, the downtooth samples indicate seasonal patterns of water intake ($\delta^{18}\text{O}$) and vegetation consumption ($\delta^{13}\text{C}$) can be derived from prehistoric specimens. The variability can inform us on how bison used the landscape, and potentially, how climate and vegetation may have shifted through time. The Rocky Mountains in general, and the GYE in particular, show considerable spatial variability in the present and the past (Whitlock and

Bartlein 1993). Understanding how bison reacted to those temporal and spatial shifts is possible as demonstrated by this limited dataset. However, a much larger sample of individuals from temporally controlled sites can yield information on these patterns.

Chapter VIII

Conclusions

The primary objective of this study was to provide an ecological and historic context for bison within a prescribed spatial setting by applying various descriptive and metric analyses that compare the biogeography of Holocene bison and modern bison from the GYE. Biogeography in its broadest sense involves not only the study of the distribution of a species, both past and present (Brown and Gibson 1983), but has expanded to include all aspects of an individual's life history within the context of contemporary issues of wildland management and climate change (e.g., Grayson 2005). This case study has examined a sample of precontact bison from the GYE within the broad context of historical biogeography.

Bison are the largest land mammals in North America, and because of their size and nutritional requirements have evolved to become efficient consumers of grass, with sedges, forbs, and browse as minor components of the diet under normal circumstances. Part of their dietary strategy involves foraging and moving over large areas to acquire adequate food and a digestive system that allows them to subsist under circumstances of limited supply. A major component of this strategy is to consume seasonally nutritious grasses. Cool season (C_3) grasses are consumed in the late fall into the late spring, followed by warm season (C_4) grasses that become available in the late spring increasingly through summer and into early fall. These seasonal changes in feeding chronology are recorded the stable carbon isotope values in their tissues. Skeletal material is an important component in the study of fossil and subfossil specimens, because bone collagen extract is the only organic tissue that is reliably preserved in sufficient quantity for analysis. Unfortunately, bone collagen turnover is slow with complete replacement taking at least 10 years. Therefore, these measurements provide only an average of the seasonal contribution of C_3 and C_4 vegetation (Chisholm 1989). To overcome this problem of 'averaging' and develop a dataset that is more detailed, downturn samples can be analyzed. By sampling downturn it is possible to

develop a record of the individual bison throughout its life, and depending on the scale of sampling, a subannual or seasonal record can be obtained.

This case study provides that record. Specimens of bison teeth were obtained from both high elevation (YNP) and lower elevation sites (Horner and Rock Springs) that span the Holocene. Results from downturn sampling indicate that a subannual record of bison foraging and water intake is present and interpretable. The results also indicate that prehistoric bison have a much greater range of $\delta^{13}\text{C}$ values than modern YNP individuals likely reflect larger and more varied home ranges. All bison sampled indicate a predominance of C_3 vegetation in the diet, although the grazing of C_4 vegetation is also recorded and variable, with the highest proportion illustrated by the early Holocene Horner site individuals.

Understanding the influence of climate on bison has been an important subject for North American archeologists in the context of Native American subsistence patterns (e.g., Bamforth 1988; Bozell 1995). Data from modern bison in YNP indicate winter severity has an impact on modern populations. Specifically, the YNP data indicate that if bison are at the carrying capacity of the ecosystem, severe winter weather will force them to migrate to areas where forage can be obtained. If other bison are occupying adjacent territories, competition can result, and herds may not be able to maintain their integrity. In pre-park times, seasonal migration out of the high country was probably a typical pattern, and bison would have spent winters at lower elevations. While drought has always been assumed to be a more limiting factor for bison, severe winters would also have impacted individual animals, particularly young individuals that will not be able to travel in deep snows, and older individuals already stressed.

In the GYE it is difficult to assess the effect of climate on bison due to the limited nature of the faunal record. Most of the sites have little or no faunal remains preserved, and those that are preserved come from single component deposits of late Holocene age. Regionally, there are some multi-component sites that may provide a better view of the effect of climate on bison availability.

Whitlock and Bartlein (1993) found was that at 9000 yrs BP the summers were warmer and drier than today in the summer-dry region because of intensification of the Pacific subtropical high. Conversely, the summer-wet region was wetter (see Figure 4.1). This pattern is reflected in the regional pollen record, but how does the regional faunal record compare? Because bison are grass eaters, the expectation is that bison would increase in size and numbers with increasing available moisture and, hence, more grass production.

In a review of bison-bearing archeological deposits from eastern and central Idaho, I indicated that reliance on bison was a more significant part of the precontact economy in the wider valleys of central Idaho with an increase in dependence through time. In more mountainous regions other ungulates, particularly sheep (*Ovis canadensis*) and mule deer (*Odocoileus hemionus*), were of more importance. In referring to the high mountain plateau regions I suggested:

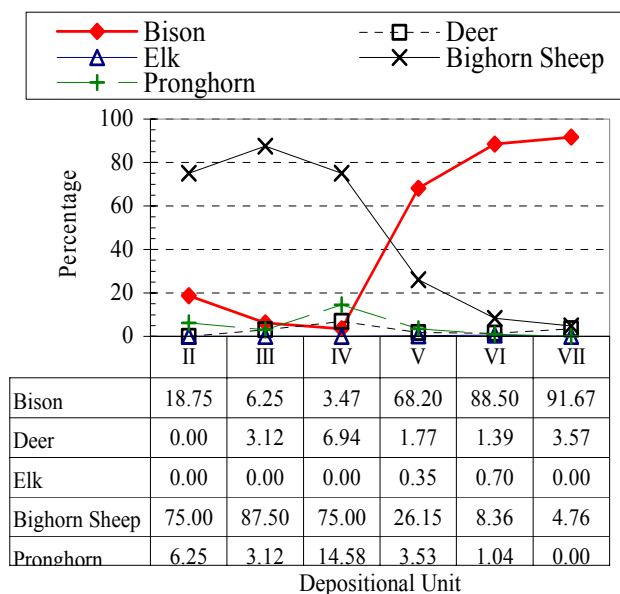
Bison populations in the mountains are probably of lower density and more dispersed. This pattern may have facilitated a different hunting strategy than the massive drives and traps that appear on the plains, and presumably in the wider valleys (e.g., the Snake River Plain). Evidence from Yellowstone and Grand Teton National Parks suggests hunting of bison was probably practiced by small groups of hunters either stalking individual animals or trapping small groups in a conducive topographic setting (e.g., bluff edge or marshy area [Cannon 1991]). This pattern has also been documented in the Northern Rockies by Reeves (1978). Butler (1978:111) also relates how small hunting bands of Shoshone on snowshoes would chase bison into deep snow where they could be easily killed with bow and arrow, butchered, and packed back to camp” (Cannon 1997:20).

In two recent articles, Henrickson (2003,2004) has looked at the presence of bison on the Snake River Plain of Idaho and its relative importance in the regional precontact diet. Using a prey choice model to orient her investigation, she concludes that “bison were probably always taken when encountered” (Henrickson 2003:283), but that the sagebrush steppe environment of the Snake River Plain would have supported a much reduced population in comparison to the short-grass prairies of the Great Plains (Henrickson 2004:914).

Henrickson's analysis further supports Lupo and Schmitt (1997) who assert that bison populations were climatically limited, but when they were available, as during Fremont times (after AD 1300), they were an important resource. The inability of the sagebrush- steppe of the Intermountain West to support large herds of bison has also been argued by Mack and Thompson (1982) and Daubenmire (1985).

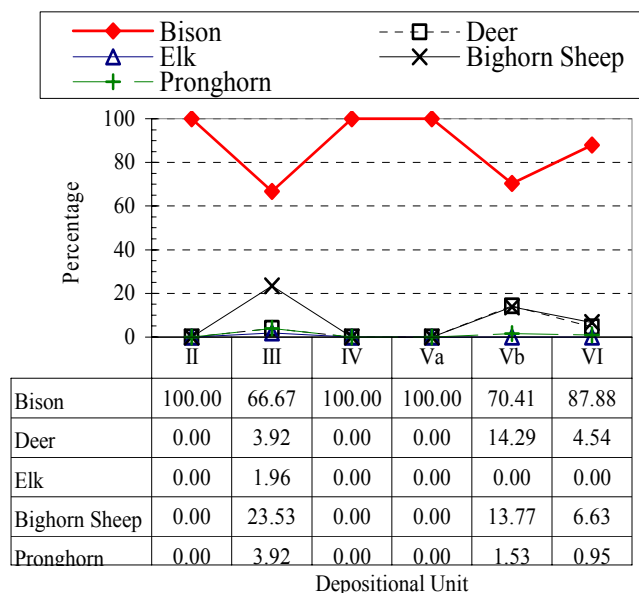
At Veratic (10CL3) and Bison (10CL10) rockshelters in Clark County, Idaho excavations by Earl Swanson (1972) in the 1960s revealed well-stratified deposits with large faunal assemblages. These sites lie within the modern summer-wet regime (www.wrcc.dri.edu), and Whitlock and Bartlein's (1993) model would predict wetter conditions in the early Holocene and becoming drier later. While criticism has been leveled at Swanson's methods, particularly his excavation methods, which did not distinguish between natural and cultural levels (Lohse and Sammons 1994), the record does provide important insights into Holocene fauna. At Veratic Rockshelter we see selection in the early Holocene for bighorn sheep with increasing reliance on bison (Figure 8.1).

Figure 8.1. Percentage of large herbivores from Veratic Rockshelter (10CL3), Clark County, Idaho. Age of the deposits goes from oldest (left) to youngest. Radiocarbon ages are: Depositional Unit III-6030 \pm 190 and 6282 \pm 229 yrs BP; Depositional Unit IV-3995 \pm 470, 4500 \pm 170, 5670 \pm 120, 5870 \pm 120 yrs BP; Depositional Unit V-1580 \pm 80, 2920 \pm 120 yrs BP; and Depositional Unit VII-370 \pm 80 yrs BP.



At Bison Rockshelter (Figure 8.2) the pattern is obscured by the overwhelming percentage of bison. However, the pattern of exclusive bison selection in the early Holocene followed by an increase in bighorn sheep selection. An increase in bighorn sheep selection also occurs in the late Holocene. While Bison Rockshelter, in general, conforms closer to the expectations of the Whitlock and Bartlein (1993) model the assumption that humans are selecting based upon the availability of game (a climatic influence) may not completely explain the patterns. Shifts to upland game (bighorn sheep) away from valleys (bison) may also reflect other decision-making processes not tied to availability, such as prey preference, season of use, shifts in settlement patterns. Another confounding factor is the significantly long periods of time represented in each Depositional Unit that would mask more meaningful trends.

Figure 8.2. Percentage of large herbivores from Bison Rockshelter (10CL10), Clark County, Idaho. Age of the deposits goes from oldest (left) to youngest. Radiocarbon ages are: Depositional Unit II-6925 \pm 200 and 10,340 \pm 830 yrs BP; Depositional Unit Va-2960 \pm 100; 3360 \pm 100, yrs BP; Depositional Unit Va-948 \pm 75; 2350 \pm 120 yrs BP.



Lubinski (2000) examined 93 radiocarbon dated faunal assemblages from 58 sites in the Wyoming Basin of southwestern Wyoming. In this study Lubinski found, through a variety of measures, that bison were a dominant genera along with *Antilocapra*, *Spermophilus*, *Sylvilagus*, and *Lepus*. In examining the dietary selection of bison and antelope (bison prefer grasses while

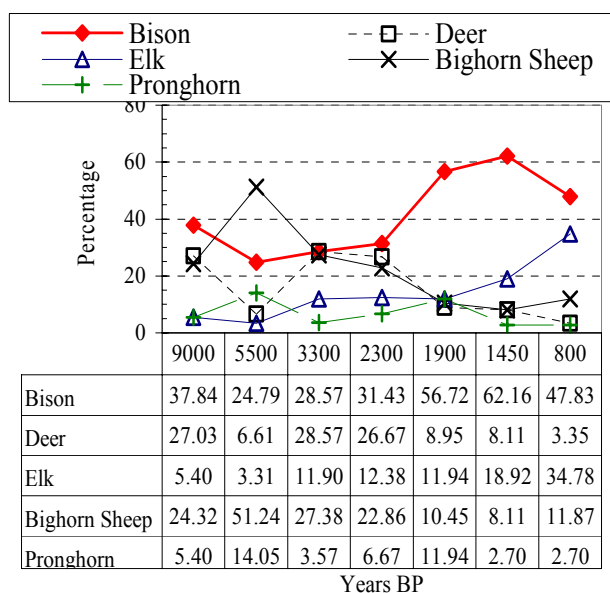
antelope browse primarily on sagebrush), climatic conditions may influence the relative availability of these two species. For example, during moist phases grasses will be more common and support relatively more bison, while during more xeric times antelope will be more prevalent due to an increase in sagebrush.

Lubinski's (2000:184) analysis, based upon climatic reconstruction by Eckerle and Obey (1995), indicates bison were more prevalent during the moist earliest Holocene (10,000-9000 yrs BP), the moist middle Neoglacial (3500-1800 yrs BP), and the moist Little Ice Age (500-150 yrs BP). Although Lubinski (2000:184) indicates that understanding subsistence and climate in the Wyoming Basin is still in "its infancy", his work does provide an initial step in bringing together a large dataset in the resolution of this issue.

The Myers-Hindman site (24PA504) is located in the upper Yellowstone River valley. The site lies within the floodplain of Dry Creek at an elevation of 1571.93 m (5157.24 ft) in the Mountain Flank Zone, an ecosystem that consists of grasslands intermingled with sagebrush, aspen, and coniferous trees (Lahren 1976). This site is within the modern summer-wet regime. The site was excavated in 1969 and 1970 as part of Lahren's doctoral research and represents one of the few stratified sites in the region that have been excavated. The cultural deposits are rich and provide well-preserved faunal remains that extend back approximately 9000 years.

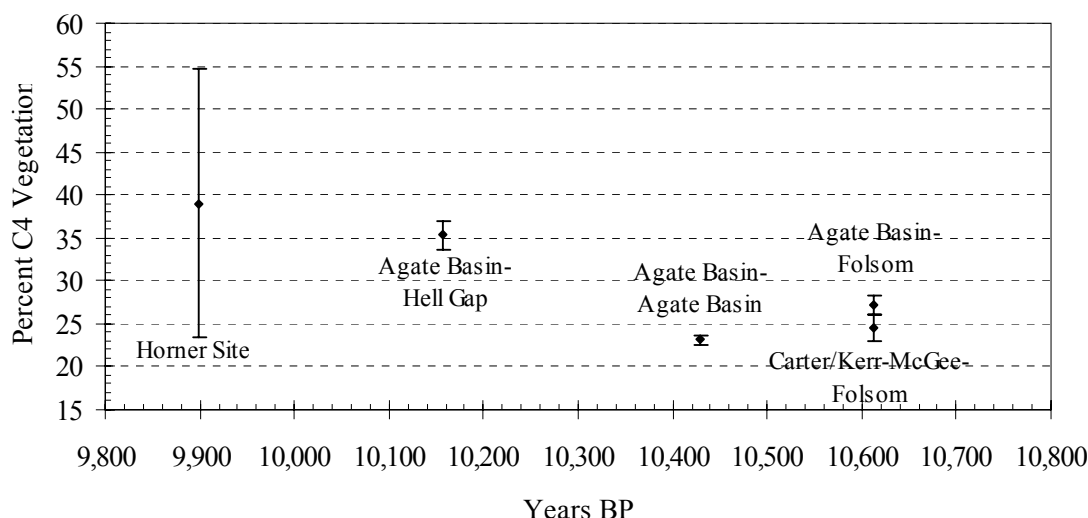
The resolution and control of the deposits is much higher than the Veratic and Bison Rockshelters. Based upon the Whitlock and Bartlein (1993) model, the early Holocene should be wetter with increased aridity in the late Holocene. In the early Holocene deposits, bison are more common, but then drop off around 5500 yrs BP when bighorn sheep and pronghorn selection increases followed by a steady increase in bison until about 800 yrs ago (Figure 8.3). The descriptive analysis of each of these stratified sites indicates a more complex pattern of ungulate selection and presumed availability based upon the predicted climatic regimes.

Figure 8.3. Percentage of large herbivores from the Myers-Hindman (24PA504) site located north of YNP in Park County, Montana. Values are based on NISP (number of identified specimens) and represent relative abundance (percentage) per Settlement Unit. Radiocarbon age for Settlement Unit and faunal counts are from Lahren (1976).



A final comparison can be made with the Horner site specimens to other late Pleistocene-early Holocene bison samples. The Horner site is located within the summer-wet regime, which Whitlock and Bartlein (1993) predict would have been wetter than present during the early Holocene. Calculated percentage of C_4 vegetation suggests a wide range, possibly indicating increased home range (Figure 8.4). However, the values suggest the greatest reliance on C_4 vegetation than any of the early populations, reflecting the rainshadow effect of the Absaroka Mountains. These specimens also have enriched $\delta^{18}O$ values, which suggest warmer winter temperatures, a pattern Hughes (2003) found in her bighorn sheep samples from Mummy Cave.

Figure 8.4. Comparison of Horner site calculated C_4 vegetation with other Wyoming Late Pleistocene-Early Holocene bison from Wyoming. Horner values are based upon mean downtown $\delta^{13}C$ values for two specimens ($n=12$). Values for other Wyoming bison are from Brooks (1995: Table 4.2). Time is presented as radiocarbon years before present and is the average value for the assemblage. The Horner specimens show overlap with other Wyoming specimens and suggests an ecosystem in which C_4 vegetation was common, a reflection of early Holocene aridity and potential variability. Horner specimens also have enriched $\delta^{18}O$ values which reflect warmer winter temperatures.



Obviously, the influence of the two climate regimes that are present in the GYE are important for understanding vegetation responses and the impact on animal populations, which ultimately affected human subsistence patterns. The opening of forests and the increased frequency of fire may have had a positive effect on ungulate populations (Despain 1990; Cannon 1996), while increased moisture would have potentially provided greater biomass. However, the timing of precipitation, in concert with temperature, have important implications for spring calving. The ideal conditions for ungulate reproduction would be for heavy spring precipitation (snow or rain) followed by warm days that produce large quantities of nutritious grasses. Hot, dry springs would be adverse for grass production (cf. Frison 1991).

These shifts in the influencing climatic regimes may have had significant implications for ungulate fecundity, but it would also have caused shifts in calving areas. As Whitlock and Millspaugh (1994) note, early Holocene winters were likely colder than today, and although snow accumulations may have been comparable, the decrease in the number of thaw days may have made the high country undesirable for overwintering by ungulates and humans. What may be

most compelling about the data are its implications for understanding mammal response and human economies within variable climatic and vegetative patterns across relatively small areas.

The purpose of this research was to explore the record of bison in the Greater Yellowstone Ecosystem and the applicability of downturn stable isotope analysis for investigating the ecology of prehistoric bison in comparison to modern bison from Yellowstone National Park. Metric analysis of bison suggests possible geographic isolation of mountain populations that may be reflected genetically. The regional record of climatic influence on bison populations is complex and does not necessarily follow predictions made by Whitlock and Bartlein (1993). However, they also acknowledge the complex nature of the area's topography, and increasing warmth and aridity may not necessarily negatively impact grassland production. Pollen records from the Northern Region (summer-wet) illustrate increased production of grasses. Pollen influx data from the Powder River Basin of Wyoming also provides evidence of greater grassland productivity as the region became drier and warmer in the last 5000 years (Whitlock and Bartlein 1993:235).

While the data are nonclusive, they do illustrate the potential value of these methods to address the complex issues of mammal biogeography in the region in relation to Holocene climate change. Testable hypotheses concerning bison response to climate change can be addressed with greater resolution of the downturn record and samples from well-documented assemblages, such as the Horner site. Hypotheses such as those articulated by Bamforth (1988):

- poor forage quality due to drought conditions will produce low population density, small herds, greater mobility within a larger home range; conversely
- high forage quality will create high population density, large herds, less mobility and smaller home range

are easily accessible through the application of the technique described here. Reanalysis of older collections also can be an important tool for a more complete understanding of bison ecology. By

applying contemporary methods of analysis, exciting new insight and information can be accessed (Cannon and Cannon 2003).

What is clear is that current understanding of the response of mammal communities to climate change in the Greater Yellowstone Ecosystem is still very limited. Considerably more interdisciplinary studies of paleoclimate, archeology, and mammal paleoecology are imperative. Research should emphasize collection of data at the highest resolution possible at sites that have the potential to yield high resolution records, such as rockshelters. The research will not only allow us to understand how these communities evolved over the course of the Holocene but may also help us understand how they will evolve in relation to future climate change (Cannon and Cannon 2004).

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Appendix A
Cranimetric Data for Modern and Archeological
Bison Used in Comparative Study

Table A1. Summary of male skull biometrics following McDonald (1981a). All measurements are presented in millimeters. Data for *Bison occidentalis* are from McDonald (1981a:Table 25), *Bison bison athabasca* represent pre-1929 adults and are presumed to be pure breed individuals from McDonald (1981b:575-579), *Bison bison bison* are Central Great Plains specimens from McDonald (1981b:538-546), and high altitude bison are from McDonald (1981b:550-553), Wilson (1974: Table III), Cannon (2006). Bison included in high altitude population are from sites above 2100 m AMSL and are listed in Table A.4

Measurement*	<i>Bison antiquus occidentalis</i>				<i>Bison bison athabasca</i>				<i>Bison bison bison</i>				High Altitude Bison			
	N	Mean	Range	σ	N	Mean	Range	σ	N	Mean	Range	σ	N	Mean	Range	σ
Spread of horn core, tip to tip (SHTT).	77	779.3 \pm 8.8	626-1055	76.9	9	681.2 \pm 30.7	542-848	92.0	128	603.9 \pm 3.9	510-778	44.7	19	608.8 \pm 12.84	508-719	55.9
Horn core length, tip to burr (CLUC).	86	277.8 \pm 4.2	186-392	39.1	9	235.1 \pm 14.7	165-323	43.9	134	190.7 \pm 2.1	124-270	24.7	20	191.0 \pm 7.5	140-295	33.6
Straight line distance, tip to burr, dorsal horn core (TB).	81	248.1 \pm 3.5	175-350	31.8	9	207.0 \pm 11.5	154-277	34.4	132	172.4 \pm 1.9	120-243	21.4	20	173.7 \pm 5.3	127-216	23.6
Dorso-ventral diameter, horn core base (VD).	85	94.6 \pm 0.9	70-114	8.4	9	91.5 \pm 2.9	81-106	8.7	139	81.9 \pm 0.5	69-99	6.4	24	85.0 \pm 1.9	69-105	9.4
Minimum circumference, horn core base (CHC).	89	300.3 \pm 2.9	237-355	27.7	9	289.1 \pm 7.7	254-322	22.9	142	255.4 \pm 1.6	199-324	19.5	23	261.0 \pm 4.4	228-305	21.0
Width of occipital at auditory openings (GWA).	61	262.0 \pm 1.7	238-294	13.2	10	273.6 \pm 4.8	243-298	15.3	120	243.9 \pm 0.9	220-270	9.7	18	251.1 \pm 3.4	228-281.2	14.4
Width of occipital condyles (CW).	71	135.0 \pm 0.9	111-151	7.7	11	130.2 \pm 1.9	118-139	6.4	122	126.6 \pm 0.5	111-140	5.7	19	122.4 \pm 2.1	106-138	9.0
Depth, nuchal line to dorsal margin of foramen magnum (DEP).	57	104.0 \pm 0.9	89-120	7.0	10	99.6 \pm 2.1	92-114	6.6	112	98.7 \pm 0.6	81-115	6.2	17	99.7 \pm 2.1	88-121	5.6
Antero-posterior diameter, horn core base (TD).	91	98.8 \pm 1.1	77-120	10.1	9	97.2 \pm 3.1	83-109	9.5	142	83.4 \pm 0.5	67-103	6.3	27	85.1 \pm 1.3	74-97	7.0
Least width of frontals, between	74	296.6 \pm 2.0	261-348	16.8	10	293.4 \pm 3.3	273-313	10.5	135	271.1 \pm 1.1	237-318	12.6	24	272.2 \pm 2.5	248-294	12.1

Measurement*	<i>Bison antiquus occidentalis</i>				<i>Bison bison athabascaae</i>				<i>Bison bison bison</i>				High Altitude Bison			
	N	Mean	Range	σ	N	Mean	Range	σ	N	Mean	Range	σ	N	Mean	Range	σ
horn cores and orbits (WHCO).																
Greatest width of frontals at orbits (GPW).	64	348.0 \pm 2.1	311-394	16.7	10	354.0 \pm 4.7	326-384	14.8	117	324.6 \pm 1.2	289-356	12.9	19	323.1 \pm 4.2	280-356	18.1
M1-M3, inclusive of alveolar length.	3	97.3 \pm 3.7	90-102	6.4	1	91.7	-	-	22	90.6 \pm 0.9	81.8-97.9	4.4	2	90.5 \pm 2.5	88-93	3.5
M3, maximum width, anterior cusp.	2	28.4 \pm 0.7	27.8	29.1	1	27.9	-	-	22	27.7 \pm 0.3	22.3-31.4	1.6	-	-	-	-
Distance, nuchal line to tip of premaxillae (OP).	25	564.3 \pm 5.0	511-606	24.8	7	578.6 \pm 5.7	562-604	15.2	56	535.2 \pm 2.3	500-583	17.0	8	459.5 \pm 21.3	397-568	60.3
Distance, nuchal line of nasal-frontal suture (ON).	57	259.8 \pm 1.6	233-287	12.3	9	256.0 \pm 4.4	240-276	13.4	106	245.7 \pm 1.2	214-279	12.2	15	243.1 \pm 5.8	206-279	22.4
Angle of divergence of horn cores, forward from sagittal (AHC).	62	72.1° \pm 0.7°	63°-83°	5.2°	6	71.0° \pm 2.0°	63°-77°	5.0°	124	67.7° \pm 0.4°	58°-79°	4.4°	16	67.8° \pm 1.2°	62°-79°	5.0°
Angle between foramen magnum and occipital planes (OF).	57	129.6° \pm 1.0°	110°-142°	7.3°	9	129.4° \pm 2.9°	119°-144°	8.8°	115	133.8° \pm 0.7°	118°-159°	7.6°	10	138.1° \pm 2.3°	128°-153°	7.3°
Angle between foramen magnum and basioccipital planes (BF).	56	113.4° \pm 0.7°	98°-126°	5.6°	9	113.8° \pm 2.2°	106°-125°	6.6°	115	110.5° \pm 0.5°	100°-129°	5.0°	10	108.8° \pm 1.1°	102°-113°	3.6°

Table A2. Summary of female skull biometrics following McDonald (1981a). All measurements are presented in millimeters. Data on *Bison occidentalis* are from McDonald (1981a:Table 25), *Bison bison athabasca* from McDonald (1981a:Table 34), *Bison bison bison* from McDonald (1981a:Table 29), and high altitude bison are from McDonald (1981b:550-553) and Wilson (1974: Table III).

Measurement*	<i>Bison antiquus occidentalis</i>				<i>Bison bison athabasca</i>				<i>Bison bison bison</i>			
	N	Mean	Range	σ	N	Mean	Range	σ	N	Mean	Range	σ
Spread of horn core, tip to tip (SHTT).	13	614.4 ± 14.2	556-749	51.3	-	-	-	-	28	451.0 ± 6.6	397-514	34.7
Horn core length, tip to burr (CLUC).	19	197.1 ± 4.4	165-235	19.0	-	-	-	-	34	124.1 ± 3.0	93-177	17.5
Straight line distance, tip to burr, dorsal horn core (TB).	16	182.9 ± 3.5	154-212	14.0	-	-	-	-	33	117.1 ± 2.7	92-161	15.3
Dorso-ventral diameter, horn core base (VD).	25	60.4 \pm 1.0	54-71	4.8	-	-	-	-	37	51.2 \pm 0.6	43-59	3.9
Minimum circumference, horn core base (CHC).	24	191.5 ± 2.7	168-219	13.4	-	-	-	-	37	162.1 ± 1.9	136-191	11.5
Width of occipital at auditory openings (GWA).	11	217.3 ± 2.4	208-237	8.0	-	-	-	-	26	201.3 ± 1.5	187-219	7.7
Width of occipital condyles (CW).	12	126.8 ± 2.0	115-140	7.0	-	-	-	-	27	115.7 ± 0.9	111-129	4.6
Depth, nuchal line to dorsal margin of foramen magnum (DEP).	11	86.9 \pm 1.8	78-99	5.9	-	-	-	-	26	84.6 \pm 1.2	74-98	5.9
Antero-posterior diameter, horn core base (TD).	27	60.3 \pm 1.1	52-73	5.7	-	-	-	-	38	51.5 \pm 0.6	44-61	3.9
Least width of frontals, between horn cores and orbits (WHCO).	19	238.2 ± 2.8	214-262	12.3	-	-	-	-	27	216.7 ± 1.7	198-233	8.6

Measurement*	<i>Bison antiquus occidentalis</i>				<i>Bison bison athabasca</i>				<i>Bison bison bison</i>			
	N	Mean	Range	σ	N	Mean	Range	σ	N	Mean	Range	σ
Greatest width of frontals at orbits (GPW).	12	292.3 \pm 3.2	276-210	10.9	-	-	-	-	25	267.5 \pm 2.0	248-291	10.0
M1-M3, inclusive of alveolar length.	4	97.3 \pm 1.4	95-101	2.9	-	-	-	-	2	82.0 \pm 6.0	760-880	8.4
M3, maximum width, anterior cusp.	4	24.3 \pm 1.3	22.4-28.1	2.6	-	-	-	-	2	26.0 \pm 0.0	25.9-26.0	0.1
Distance, nuchal line to tip of premaxillae (OP).	8	523.5 \pm 6.3	503-557	17.8	-	-	-	-	19	484.7 \pm 3.2	464-516	13.9
Distance, nuchal line to nasal-frontal suture (ON).	15	227.3 \pm 3.5	200-246	13.7	-	-	-	-	24	212.4 \pm 1.6	195-228	7.8
Angle of divergence of horn cores, forward from sagittal (AHC).	15	75.0° \pm 1.1°	68°-84°	4.4	-	-	-	-	21	66.0° \pm 0.8°	60°-72°	3.7°
Angle between foramen magnum and occipital planes (OF).	9	131.7° \pm 2.4°	122°-140°	7.1	-	-	-	-	24	131.8° \pm 1.5°	115°-144°	7.3°
Angle between foramen magnum and basioccipital planes (BF).	9	110° \pm 1.8°	103°-109°	5.4	-	-	-	-	25	109.7° \pm 1.0°	101°-119°	4.9°

Table A3. Summary of Grand Teton and Yellowstone skull biometrics following McDonald (1981a). All measurements are presented in millimeters.

Measurement*	Males				Females			
	N	Mean	Range	σ	N	Mean	Range	σ
Spread of horn core, tip to tip (SHTT).	5	621.4 ± 14.8	588.3- 670.0	33.1	1	452.0	452.0	-
Horn core length, tip to burr (CLUC).	5	187.2 ± 8.0	166.0- 214.0	17.9	2	127.0 ± 20.0	107.0- 147.0	28.3
Straight line distance, tip to burr, dorsal horn core (TB).	5	172.0 ± 7.7	154.0- 195.0	17.2	2	101.0 ± 19.5	101.0- 140.0	27.6
Dorso-ventral diameter, horn core base (VD).	3	79.3 \pm 4.8	73.7- 88.8	8.3	2	54.0 \pm 2.6	51.3- 56.63	3.7
Minimum circumference, horn core base (CHC).	3	244.5 ± 2.1	241.0- 248.0	3.69	2	178.0 ± 13.0	165.0- 191.0	18.4
Width of occipital at auditory openings (GWA).	1	260.8	260.8	-	0	-	-	-
Width of occipital condyles (CW).	2	120.9 ± 3.5	117.4- 124.4	4.9	0	-	-	-
Depth, nuchal line to dorsal margin of foramen magnum (DEP).	1	92.6	92.6	-	0	-	-	-
Antero-posterior diameter, horn core base (TD).	6	82.6 \pm 1.4	76.9- 87.8	1.4	2	54.6	48.9- 60.2	8.0
Least width of frontals, between horn cores and orbits (WHCO).	2	281.7 ± 7.1	274.6- 288.7	10.0	1	219.9	219.9	-
Greatest width of frontals at orbits (GPW).	0	-	-	-	1	269.6	269.6	-
M1-M3, inclusive of alveolar length.	3	94.7 \pm 1.4	92.89- 97.37	2.4	0	-	-	-
M3, maximum width, anterior cusp.	6	22.1 \pm 1.0	19.5- 26.8	2.6	0	-	-	-
Distance, nuchal line to tip of premaxillae (OP).	0	-	-	-	0	-	-	-
Distance, nuchal line to nasal-frontal suture (ON).	1	263.9	263.9	-	0	-	-	-
Angle of divergence of horn cores, forward from sagittal (AHC).	4	88.8 \pm 12.8	60.0- 115.0	25.6	0	-	-	-
Angle between	0	-	-	-	0	-	-	-

Measurement*	Males				Females			
	N	Mean	Range	σ	N	Mean	Range	σ
foramen magnum and occipital planes (OF).								
Angle between foramen magnum and basioccipital planes (BF).	0	-	-	-	0	-	-	-

Table A4. Provenience of comparative high altitude bison specimens from western North American.

Specimen Number ¹	Provenience	Elevation (meters) ²	Reference
Male Specimens			
AMNH M1399937	Sheep Mountain, Wyoming	2921	McDonald 1981b:550-553
CoMNH 1846	Near Pagoda, Colorado	2004	McDonald 1981b:550-553
UCy A(K)	Crowsnest Pass (DjPp-8), Alberta		McDonald 1981b:550-553
UCy A(L)	Crowsnest Pass (DjPp-8), Alberta		McDonald 1981b:550-553
UCM G:S29G	15 mi SE from Walden, Colorado	2469	McDonald 1981:550-553b
UCM G:S66	Mt. Audubon, Colorado	3438	McDonald 1981b:550-553
UCM G:4278	Near Leadville, Colorado	3094	McDonald 1981b:550-553
UCM G(A)	Near Ward, Colorado	2792	McDonald 1981b:550-553
UM Z5461	Yogo Peak, Montana	2683	McDonald 1981b:550-553
UM Z5462	Beartooth Plateau, Wyoming-Montana	3042	McDonald 1981b:550-553
UM Z13251	Beartooth Plateau, Wyoming	3042	McDonald 1981b:550-553
USGS (A)	Barger Gulch, Colorado	2225	McDonald 1981b:550-553
USNM M168816	Big Horn Mountains, Wyoming	-	McDonald 1981b:550-553
UWy (B)	Union Pass, Wyoming	2807	McDonald 1981b:550-553
UWy (C)	Big Horn Mountains, Wyoming	-	McDonald 1981b:550-553
UWy (D)	Wind River Mountains, Wyoming	-	McDonald 1981b:550-553
FC-1	Fawn Creek, Salmon River Mountains, Idaho	2256	Cannon 1997:Table 3
BH-1	Bighorn Mountains, Wyoming	-	Wilson 1974:Table III
BH-2	Bighorn Mountains, Wyoming	-	Wilson 1974:Table III 4
BH-3	Bighorn Mountains, Wyoming	-	Wilson 197:Table III 4
BH-4	Bighorn Mountains, Wyoming	-	Wilson 1974:Table III
BH-5	Bighorn Mountains, Wyoming	-	Wilson 1974:Table III
BH-6	Bighorn Mountains, Wyoming	-	Wilson 1974:Table III
BH-7	Bighorn Mountains, Wyoming	-	Wilson 1974:Table III
BH-8	Bighorn Mountains, Wyoming	-	Wilson 1974:Table III
BH-9	Bighorn Mountains, Wyoming	-	Wilson 1974:Table III
BH-10	Bighorn Mountains, Wyoming	-	Wilson 1974:Table III
GP-1	Gilbert Peak, Utah	3840	Cannon 2007:Table 1
111083	48YE697, Yellowstone Lake, Yellowstone National Park, Wyoming	2380	This report
<p>1. Specimen number abbreviations: AMNH=American Museum of Natural History; CoMNH= Denver Museum of Nature and Science (formerly Colorado Museum of Natural Museum); UCy= University of Calgary; UCM= University of Colorado Museum; UM= University of Montana; USGS= United States Geological Survey; USNM= United States National Museum; UWy=University of Wyoming.</p> <p>2. Elevation was obtained through the USGS Place Name database (http://geonames.usgs.gov/) and should be considered approximate.</p>			

Table A5. Craniometric data of individual bison used in study. Specimen description is provided in Tables 1 and A4.

Specimen	Sex	SHTT	CLUC	TB	VD	CHC	TD	WHCO	GPW	ON	OP	GWA	CW	DEP	AHC	BF	OF
AMNH M1399937	M	630	192	178	84	269	88	279	331	239	530	253	134	94	62°	112°	145°
CoMNH 1846	M	667	205	193	94	287	97	281	330	248	-	235	138	106	63°	110°	140°
UCy A(K)	M	645	185	174	77	240	76	-	-	-	-	-	-	-	68°	-	-
UCy A(L)	M	-	-	-	83	258	81	-	-	-	-	-	-	-	-	-	-
UCM G:S29G	M	608	180	172	82	258	82	265	-	222	-	243	120	88	72°	109°	133°
UCM G:S66	M	555	179	169	76	244	82	254	-	-	-	-	-	-	-	104°	143°
UCM G:4278	M	-	-	-	-	-	79	258	314	-	-	249	111	-	-	102°	135°
UCM G(A)	M	-	221	209	99	297	97	286	327	262	-	-	-	-	71°	-	-
UM Z5461	M	543	154	139	69	237	78	262	326	-	-	-	-	-	64°	-	-
UM Z5462	M	589	166	148	-	-	-	-	-	-	-	-	125	98	79°	-	-
UM Z13251	M	591	214	184	84	255	82	273	321	235	-	-	-	-	64°	-	-
USGS (A)	M	667	200	183	92	288	94	287	343	279	-	251	120	109	62°	112°	135°
USNM M168816	M	648	175	166	85	264	87	294	351	251	568	257	138	104	67°	109°	128°
UWy (B)	M	-	-	-	77	232	74	260	-	-	-	245	124	90	71°	107°	153°
UWy (C)	M	-	-	-	-	-	-	272	326	-	-	249	131	101	69°	113°	133°
UWy (D)	M	624	198	187	89	257	81	262	313	-	-	233	114	97	64°	110°	136°
BH-1	M	576	186	167	89	254	83	270	324	-	429	264	121	105	-	-	-
BH-2	M	-	-	-	-	286	86	272	330	-	466	250	106	92	-	-	-
BH-3	M	-	190	162	86	248	92	-	-	-	-	-	-	-	-	-	-
BH-4	M	541	143	140	71	235	76	266	298	210	-	228	121	102	-	-	-
BH-5	M	-	-	-	76	-	83	267	280	206	-	-	-	105	-	-	-
BH-6	M	-	-	-	92	273	94	292	356	267	445	276	124	102	-	-	-
BH-7	M	-	-	-	-	-	78	-	-	-	-	248	124	-	-	-	-
BH-8	M	508	140	127	70	228	79	248	296	218	397	234	114	89	-	-	-
BH-9	M	576	197	181	92	265	95	270	319	232	403	264	128	92	-	-	-
BH-10	M	719	225	216	98	305	95	276	324	248	438	260	128	121	-	-	-
FC-1	M	554	175	170	82.4	257	85.5	270	330	265	-	-	-	-	64°	-	-
GRTE- 40535	M	602.01	179	168	-	-	84.01	-	-	-	-	-	-	-	60°		
GRTE- 41404	M	-	-	-	-	-	-	-	-	-	-	-	124.41	-	-	-	-

Specimen	Sex	SHTT	CLUC	TB	VD	CHC	TD	WHCO	GPW	ON	OP	GWA	CW	DEP	AHC	BF	OF
GRTE-41405	M	588.30	184	159	73.70	241	76.87	-	-	-	-	260.75	117.44	92.62	-	-	-
GRTE-41406	M	-	214	195	-	-	87.81	-	-	-	-	-	-	-	-	-	-
GRTE-42240	M	640	-	-	-	-	-	-	-	-	-	-	124.41	-	-	-	-
GRTE-42244	M	606.77	193	184	75.35	248	82.94	274.61	-	-	-	-	-	-	115°	-	-
GRTE-42247	M	-	166	154	88.78	246	-	-	-	-	-	-	-	-	105°	-	-
GRTE-42252	M	-	-	-	-	-	81.81	-	-	-	-	-	-	-	-	-	-
YELL 111083	M	670	-	-	-	-	82.32	288.72	-	263.85	-	-	-	-	75°		
AMNH M16322	F	408	125	113	51	161	48	218	272	214	431	202	120	88	66°	106°	138°
USNM M122672	F	500	122	122	56	165	51	218	264	216	484	197	114	83	70°	114°	115°
USNM M122685	F	419	129	121	45	146	47	225	262	211	574	205	123	81	62°	107°	142°
UWy C3071	F	502	129	128	59	191	61	227	272	199	-	205	113	76	70°	101°	144°
UWy C30	F	-	-	-	53	168	54	224	272	203	479	206	115	84	68°	118°	118°
USNM M248950	F	483	145	139	55	171	53	221	267	219	506	205	123	89	-	113°	134°
USNM M249844	F	438	123	117	51	157	51	213	268	216	491	199	112	78	-	107°	131°
USNM M249847	F	441	134	122	47	154	49	208	265	213	483	187	111	80	64°	107°	133°
USNM M249848	F	484	135	129	47	153	51	224	276	221	494	202	115	95	69°	109°	131°
USNM M249849	F	451	164	146	54	173	54	218	268	225	516	205	115	86	59°	119°	123°
USNM M250089	F	514	134	134	54	163	51	214	272	216	479	206	115	89	69°	110°	141°
USNM M250090	F	505	177	161	58	182	60	229	281	218	508	219	129	98	-	118°	127°
USNM M250091	F	441	135	124	52	163	52	218	287	210	486	203	114	88	65°	103°	135°
USNM	F	410	120	111	47	144	45	199	256	211	478	192	111	85	65°	111°	137°

Specimen	Sex	SHTT	CLUC	TB	VD	CHC	TD	WHCO	GPW	ON	OP	GWA	CW	DEP	AHC	BF	OF
M250095																	
GRTE-40555	F	452	107	101	51.34	165	48.90	219.93	269.56	-	-	-	-	-	-	-	-
GRTE-40553	F	-	147	140	56.63	191	60.20	-	-	-	-	-	-	-	-	-	-

Appendix B

Table B1. List of plants identified in bison from Yellowstone National Park (Meagher 1973:Table 17), Henry Mountains, Utah (Van Vuren 1984:Table 1), shortgrass plains of northeastern Colorado (Peden 1976:Table 1), northern mixed prairie of Badlands National Park, South Dakota (Plumb and Dodd 1993:Table 2). Mountain grassland sites in Montana list of potential plant species identified by (Sims et al. 1978). Pathway data provided by Sims et al. (1978), Brooks (1995: Table 3.3) and Larry Tieszen (1997: personal communication).

Species	Common Name	Pathway
Yellowstone National Park, Wyoming		
<i>Carex</i> sp.	Sedge	C ₃
<i>Juncus</i>	Wire rush	C ₃
<i>Carex</i>	Spike-sedge	C ₃
<i>Phlox</i> sp.	Phlox	C ₃
<i>Potentilla</i>	Northwest cinquefoil	C ₃
<i>Eriogonum umbellatum</i>	Sulfur eriogonum (buckwheat)	C ₃
<i>Taraxacum</i> sp.	Dandelion	C ₃
<i>Antennaria</i> sp.	Pussytoes	C ₃
<i>Potentilla fruticosa</i>	Shrubby cinquefoil	C ₃
<i>Trifolium</i> sp.	Clover (introduced)	C ₃
<i>Allium</i> sp.	Onion	C ₃
<i>Collinsia</i> sp.	Blue-eyed Mary	C ₃
<i>Artemisia tridentata</i>	Big sagebrush	C ₃
<i>Cornus stolonifera</i>	Red dogwood	C ₃
<i>Rubus</i> sp.	Raspberry	C ₃
<i>Vaccinium caesoitosum</i>	Dwarf huckleberry	C ₃
<i>Amelanchier</i> sp.	Serviceberry	C ₃
<i>Amelachier</i> sp.	Fringed sagebrush	C ₃
<i>Pinus contorta</i>	Lodgepole pine	C ₃
<i>Equisetum</i> sp.	Horsetail	C ₃
<i>Cassiope</i> sp.	Moss	C ₃
	Lichen	C ₃
<i>Festuca idahoensis</i>	Idaho fescue	C ₃
<i>Agropyron spicatum</i>	Wheatgrass	C ₃
Henry Mountains, Utah		
<i>Agropyron</i> spp.	Crested wheatgrass	C ₃
<i>Bromus ciliatus</i>	Brome grass	C ₃
<i>Carex</i> spp.	Sedge	C ₃
<i>Festuca</i> spp.	Fescue	C ₃
<i>Koeleria cristata</i>	Junegrass	C ₃
<i>Oryzopsis humneoides</i>	Indian ricegrass	C ₃
<i>Poa</i> spp.	Blue grass	C ₃
<i>Sitanion hystrix</i>	Squirreltail	C ₃
<i>Stipa</i> spp.	Needlegrass	C ₃
<i>Astragalus</i> spp.	Milk vetch	C ₃
<i>Oxytropis</i> spp.	Locoweed	C ₃
<i>Artemisia</i> spp.	Sagebrush	C ₃
<i>Symphoricarpos</i> spp.	Snowberry	C ₃
Northeastern Colorado		
<i>Agropyron smithii</i>	Crested wheatgrass	C ₃
<i>Aristida longeseta</i>	Red threeawn	C ₃
<i>Artemisia frigida</i>	Sagebrush	C ₃
<i>Bouteloua gracilis</i>	Blue grama	C ₄
<i>Carex heliophila</i>	Sedge	C ₃
<i>Eriogonum</i> sp.	Buckwheat	C ₃

Species	Common Name	Pathway
<i>Festuca octoflora</i>	Sheep fescue	C ₃
<i>Sphaeralcea crytandrus</i>	Sand Dropseed	
<i>Stipa commaua</i>	Needlegrass	C ₃
Badlands National Park, South Dakota		
<i>Agropyron cristata</i>	Crested wheatgrass	C ₃
<i>Agropyron repens</i>	Couch grass	C ₃
<i>Agropyron smithii</i>	Western wheatgrass	C ₃
<i>Bromus inermis</i>	Smooth brome	C ₃
<i>Bromus tectorum</i>	Cheatgrass	C ₃
<i>Carex lanuginose</i>	Sedge	C ₃
<i>Carex filifolia/eleocharis</i>	Needleleaf sedge	C ₃
<i>Hordeum jubatum</i>	Foxtail barley	C ₃
<i>Poa pratensis</i>	Kentucky bluegrass	C ₃
<i>Spartina pectinata</i>	Prairie cordgrass	C ₃
<i>Stipa comata</i>	Needle-and-thread grass	C ₃
<i>Stipa spartea</i>	Needlegrass	C ₃
<i>Stipa viridula</i>	Needlegrass	C ₃
<i>Andropogon gerardii</i>	Big bluestem	C ₄
<i>Bouteloua curtipendula</i>	Sideoats grama	C ₄
<i>Buchloe dactyloides</i>	Buffalo grass	C ₄
<i>Calamovilfa longifolia</i>	Prairie sandreed	C ₄
<i>Muhlenbergia cuspidate</i>	Stonyhills muhly	C ₄
<i>Panicum virgatum</i>	Switchgrass	C ₄
<i>Schizachyrium scoparium</i>	Little bluestem	C ₃
<i>Sorghastrum nutans</i>	Indiangrass	C ₃
<i>Ambrosia psilostachya</i>	Cuman ragweed	C ₄
<i>Astragalus crassicaupus</i>	Milkvetch	C ₄
<i>Mellilotus officianalis</i>	Yellow sweetclover	C ₄
<i>Medicago sativa</i>	Alfalfa	C ₄
<i>Psoralea argophylla</i>	Silverleaf scurf pea	C ₄
<i>Solidago canadensis</i>	Goldenrod	C ₄
<i>Sphaeralcea coccinea</i>	Scarlet globemallow	C ₄
<i>Tragopogon dubius</i>	Goatsbeard	C ₄
<i>Amorpha canescens</i>	Lead plant	C ₃
<i>Glychyrhizza lepidota</i>	American licorice	C ₄
Mountain Grassland, Bison and Bridger Sites, Montana		
<i>Bromus tectotum</i>	Cheat grass	C ₃
<i>Agropyron spicatum</i>	Bluebunch wheatgrass	C ₃
<i>Agropyron subsecundum</i>	Bearded wheatgrass	C ₃
<i>Danthnia intermedia</i>	Timber oatgrass	C ₃
<i>Festuca idahoensis</i>	Idaho fescue	C ₃
<i>Festuca scabrella</i>	Rough fescue	C ₃
<i>Koeleria cristata</i>	June grass	C ₃
<i>Poa pratensis</i>	Kentucky bluegrass	C ₃
<i>Stipa richardsonii</i>	Richardson's needlegrass	C ₃
<i>Achillea millefolium</i>	Common yarrow	C ₃
<i>Agoseris glauca</i>	Pale agoseris	C ₃
<i>Agoseris grandiflora</i>	Bigflower agoseris	C ₃
<i>Anaphalis margaritacea</i>	Pearly everlasting	C ₃
<i>Antennaria rosea</i>	Rosy pussytoes	C ₃
<i>Arnica fulgens</i>	Foothill arnica	C ₃
<i>Balsamorhiza sagittata</i>	Arrowleaf balsamroot	C ₃

Species	Common Name	Pathway
<i>Callirhoe leiocarpa</i>	Tall poppymallow	C ₃
<i>Castilleja sulphurea</i>	Sulphur Indian paintbrush	C ₃
<i>Cerastium arvense</i>	Field chickweed	C ₃
<i>Crepis acuminata</i>	Tall hawksbeard	C ₃
<i>Dodecatheon conjugens</i>	Slimpod shooting star	C ₃
<i>Erigeron speciosus</i>	Aspen fleabane	C ₃
<i>Fritillaria pudica</i>	Yellowbells	C ₃
<i>Galium boreale</i>	Northern bedstraw	C ₃
<i>Gaura coccinea</i>	Scarlet beeblossom	C ₃
<i>Geum triflorum</i>	Old man's whiskers	C ₃
<i>Heuchera cylindrica</i>	Roundleaf alumroot	C ₃
<i>Lithospermum ruderale</i>	Western stoneseed	C ₃
<i>Lupinus argenteus</i>	Silvery lupine	C ₃
<i>Lupinus sericeus</i>	Silky lupine	C ₃
<i>Microseris nutans</i>	Nodding microseris	C ₃
<i>Silene parryi</i>	Catchfly	C ₃
<i>Tragopogon dubius</i>	Goat's beard	C ₃
<i>Zigadenus paniculatus</i>	Foothill deathcamas	C ₃
<i>Asclepias pumila</i>	Plains milkweed	C ₄
<i>Aster falcatus</i>	White prairie aster	C ₄
<i>Cirsium arvense</i>	Canada thistle	C ₄
<i>Hieracium albertinum</i>	Western hawkweed	C ₄
<i>Lactuca tatarica</i>	Blue lettuce	C ₄
<i>Arenaria congesta</i>	Ball- head sandwort	C ₃
<i>Artemisia frigida</i>	Prairie sagewort	C ₃

Appendix C
Data Sheets for Stable Isotope Sample Collection
Data Forms Completed by Dr. Susan S. Hughes

Bone Documentation Form
(1/15/2006)

Sample No: KC2006.02 Catalogue No: 6.133.11
 Date: Jan. 30, 2006
 Project: Ken's bison
 Site Name/No: 10 OA 210
 Strata: _____ Provenience: _____

Taxon: Bison
 Element: M3 lower Prox: _____ Distal: _____ Shaft: _____
 Side: (L) R Unknown Sex: M F Unk
 Age: _____

How determined: stage 1-2

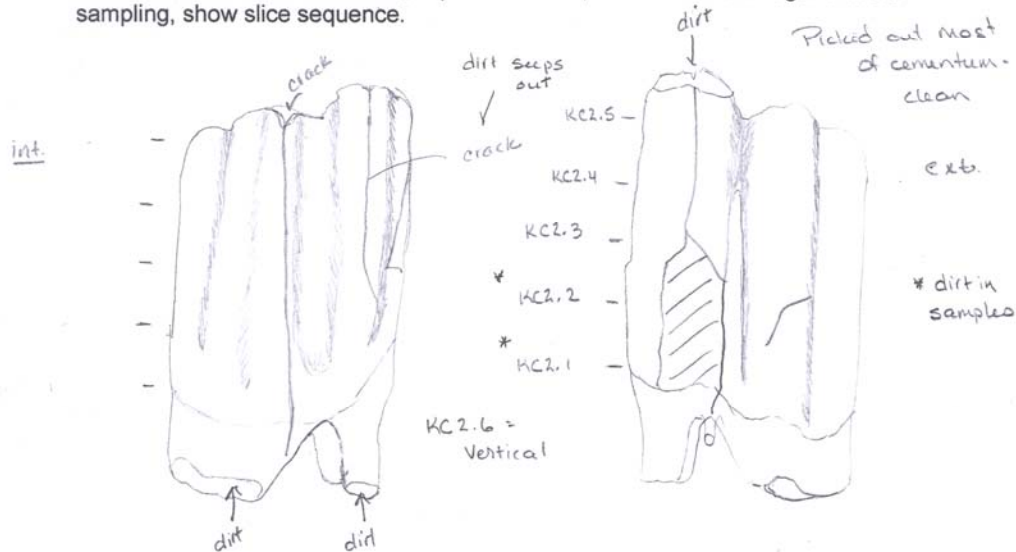
Behrensmeyer's Weathering Stage: 1 2 (3) 4 5

Comments on physical condition: Roots missing; cracking of enamel
Accompanied by bone-marrow. Dirt constantly drips out of base; was hard

Residues: 0 to separate from sample; may

Preservatives or glues: 0 contaminate.

Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.

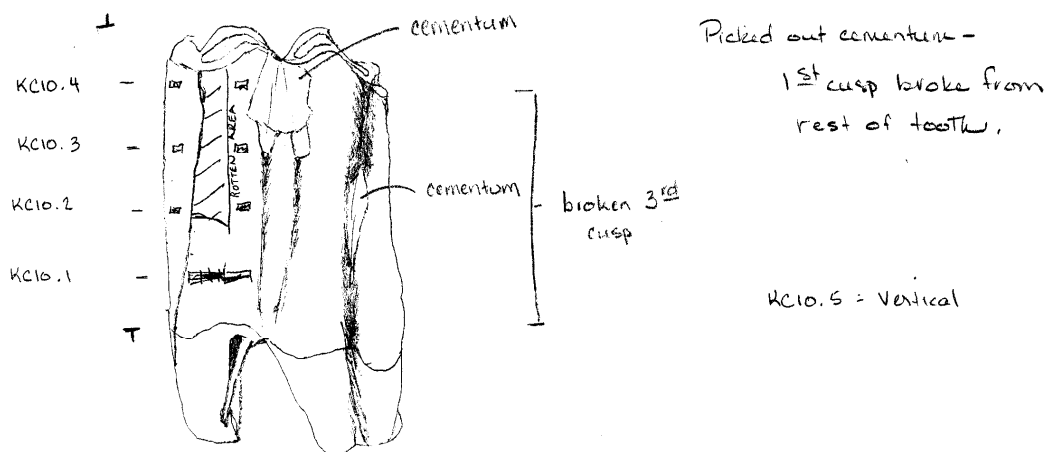


Maximum Dimensions: Length: 76.5 mm enamel 57.8 mm
 Width: 41.4 mm Weight: _____

Bone Documentation Form
(1/15/2006)

Sample No: KC06.10 Catalogue No: #6.373.60
 Date: 2/26/06
 Project: Ken's Bison
 Site Name/No: 10 CA 210
 Strata: ? Provenience: Idaho?
 Taxon: Bison
 Element: L M3 Prox: Distal Shaft
 Side: (L) R Unknown Sex: M F Unk
 Age: middle adult
 How determined: medium wear Stage 2
 Behrensmeyer's Weathering Stage: 1 (2) (3) 4 5
 Comments on physical condition: Some vertical cracks
Enamel flakes off vertical; sampling area was decomposing
 Residues: NO
 Preservatives or glues: NO

Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.



Maximum Dimensions: Length: 76.1 mm enamel: 48.4 mm
 Width: 43.54 mm Weight: _____

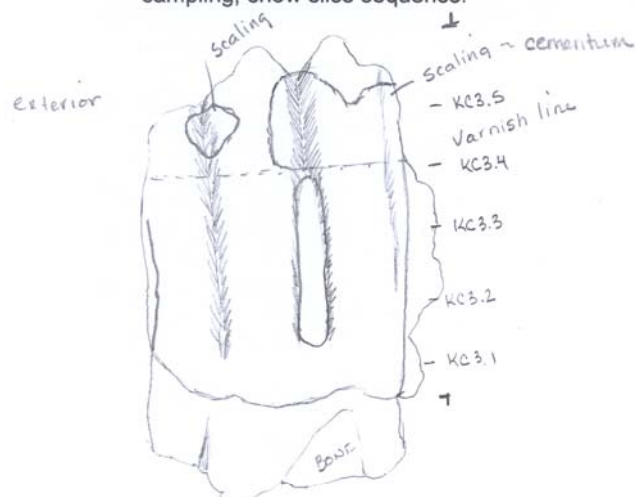
* Good One!

Bone Documentation Form (1/15/2006)

Sample No: KC2006.03 Catalogue No: # 1181 H
 Date: January 30, 2006
 Project: Ken's Bison
 Site Name/No: 4B PA 29
 Strata: _____ Provenience: Park

Taxon: Bison
 Element: M3 lower Prox _____ Distal _____ Shaft _____
 Side: L R Unknown Sex: _____ M _____ F Unk
 Age: Adult
 How determined: Stage 2
 Behrensmeyer's Weathering Stage: 1 2 3 4 5
 Comments on physical condition: minor cracking; top is scaling off
 Residues: _____
 Preservatives or glues: varnish on exterior surface; above gum line
on inside, Elmer's Glue

Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.



Picked out most of
cementum - clean

Bone was coated in Elmer's glue
KC3.6 = vertical

Removed cementum - bone - cleaned
up nicely

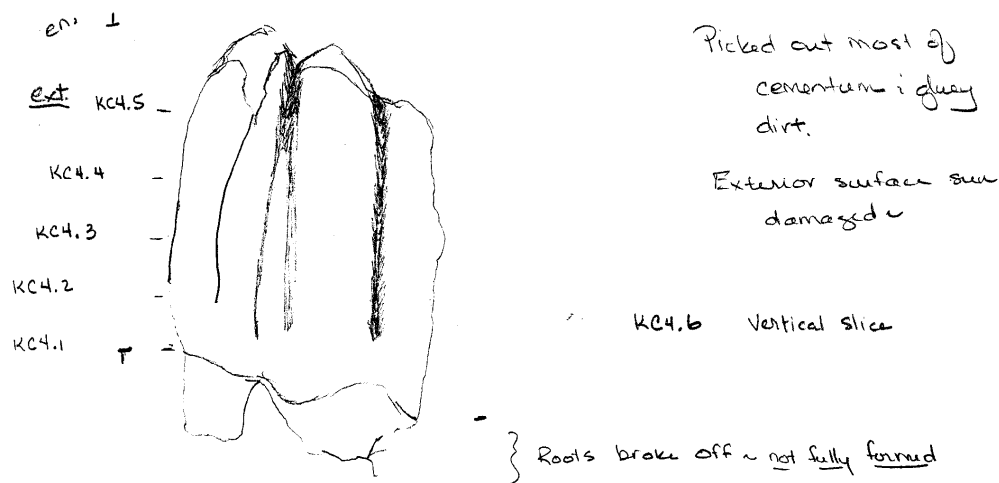
Maximum Dimensions: Length: 86.2 mm enamel: 59.9 mm
 Width: 47.14 mm Weight: _____

Bone Documentation Form
(1/15/2006)

Sample No: KC 2006.04 Catalogue No: # 1233 H
 Date: Jan. 30, 2006
 Project: Ken's bison
 Site Name/No: 48PA 29
 Strata: _____ Provenience: Park

Taxon: Bison
 Element: M3 lower Prox _____ Distal _____ Shaft _____
 Side: (L) R Unknown Sex: M F Unk
 Age: Adult ~ young; 3rd cusp unworn ~ newly erupted
 How determined: wear stage 1
 Behrensmeyer's Weathering Stage: 1 2 (3) 4 5
 Comments on physical condition: cracked; grooves in surface enamel ~ either
diagenesis or incomplete mineralization
 Residues: varnish over whole tooth (Elmer's Glue)
 Preservatives or glues: glues attaching bone to tooth

Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.



Maximum Dimensions: Length: 75.2 mm Enamel - 63.9 mm
 Width: 46.9 mm Weight: _____

Bone Documentation Form
(1/15/2006)

Sample No: KC06.08 Catalogue No: #2548H
 Date: 2/26/06
 Project: Ken's bison
 Site Name/No: 48 PAZ9
 Strata: _____ Provenience: Park City

Taxon: Bison
 Element: 3rd Molar lower Prox _____ Distal _____ Shaft _____
 Side: L (R) Unknown Sex: _____ M _____ F (Unk)
 Age: young

How determined: little wear stage 1 ~ Roots not completely formed

Behrensmeyer's Weathering Stage: 1 2 3 4 5

Comments on physical condition: Vertical cracks; not so good

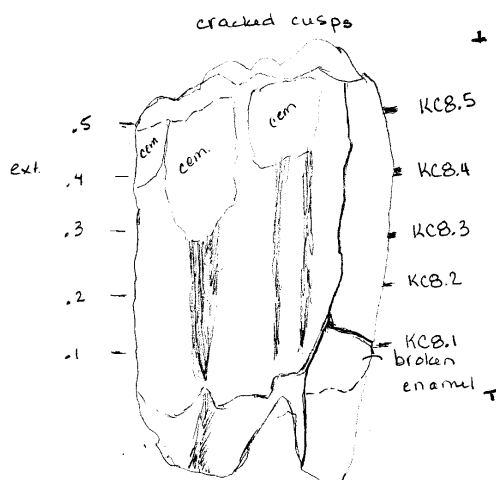
When wet tooth falls apart; 1st loph is in worst shape; enamel degraded & splits vertically

Residues: yes

Preservatives or glues: yes Elmer's Glue

BAD TOOTH!
Too fragile to clean properly.

Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.



All samples taken from 3rd loph.
 1st loph severely cracked w/ degraded enamel. Also released lots of dirt.
 3rd loph allowed cleaner work

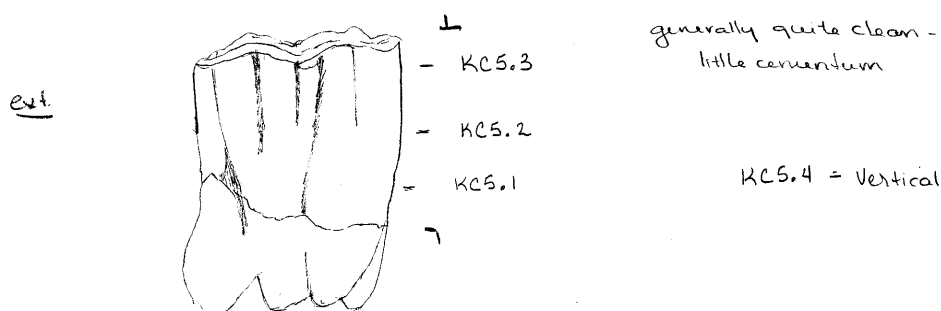
KCB.6 = Vertical

Maximum Dimensions: Length: 82.2 mm enamel: 64 mm
 Width: 46.9 mm Weight: _____

Bone Documentation Form
(1/15/2006)

Sample No: KC2006.5 Catalogue No: #455.1
 Date: _____
 Project: _____
 Site Name/No: 48TE455 ANBML1.56
 Strata: _____ Provenience: Teton
 Taxon: Bison
 Element: m³ - upper Prox: _____ Distal: _____ Shaft: _____
 Side: L (R) Unknown Sex: _____ M _____ F (Unk)
 Age: older
 How determined: well worn ~ stage 4
 Behrensmeyer's Weathering Stage: 1 (2) 3 4 5
 Comments on physical condition: minor cracks
 Residues: ∅
 Preservatives or glues: ∅

Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.

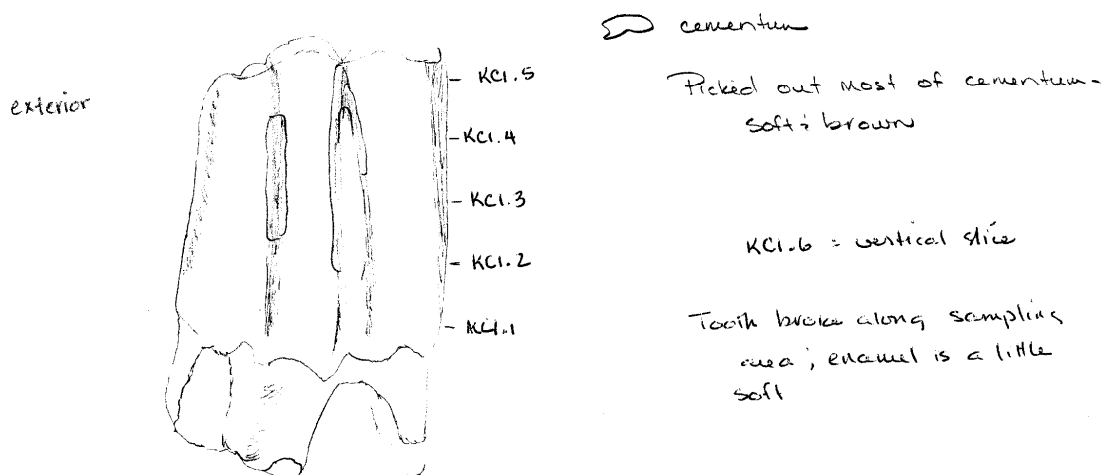


Maximum Dimensions: Length: 50.1 mm
 Width: 34.92 mm Weight: _____

Bone Documentation Form
(1/15/2006)

Sample No: KC2006.01 Catalogue No: # 455.2
 Date: Jan. 30, 2006
 Project: Ken's bison A48ML17
 Site Name/No: 48TE455
 Strata: ? Provenience: Teton Ck
 Taxon: Bison
 Element: Lower M3 Prox: Distal Shaft
 Side: L (R) Unknown Sex: M F (Unk)
 Age: Adult
 How determined: wear stage 2
 Behrensmeyer's Weathering Stage: 1 (2) (3) 4 5
 Comments on physical condition: Roots missing
 Residues: #
 Preservatives or glues: No

Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.



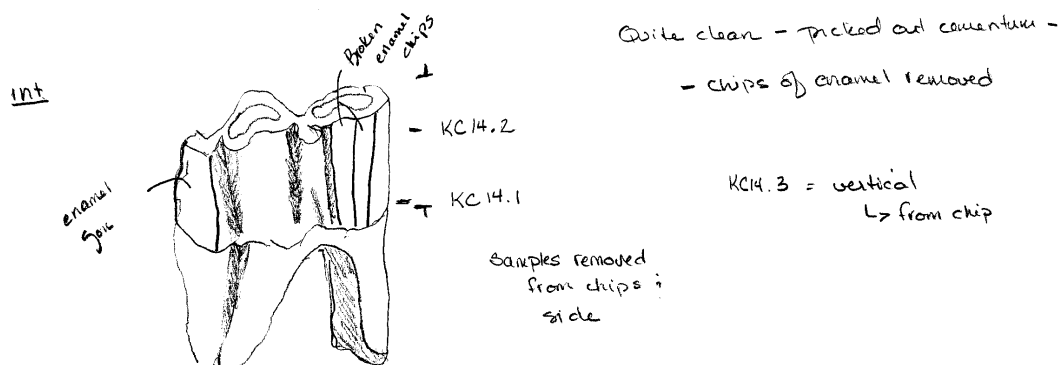
Maximum Dimensions: Length: 78.3 mm enamel: 58.5 mm
 Width: 43.6 mm Weight: _____

Bone Documentation Form
(1/15/2006)

Sample No: KC06.14 Catalogue No: FS 42226
 Date: 2/26/06
 Project: Ken's Bison
 Site Name/No: 48TF1090
 Strata: ? Provenience: Teton City

Taxon: Bison
 Element: Lower M3 Prox Distal Shaft
 Side: L (R) Unknown Sex: M F (Unk)
 Age: old
 How determined: well worn Age 4
 Behrensmeyer's Weathering Stage: 1 (2) (3) 4 5
 Comments on physical condition: good; enamel appears in good shape;
vertical cracks; substantial cracking
 Residues: NO
 Preservatives or glues: NO

Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.



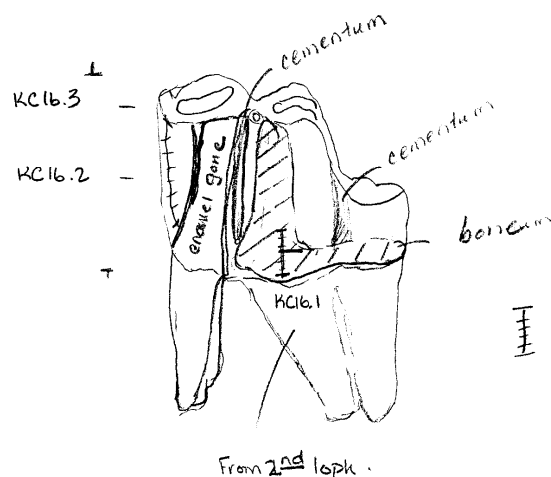
Maximum Dimensions: Length: 56.1 mm Enamel: 26.4 mm
 Width: 42.0 mm Weight: _____

Bone Documentation Form
(1/15/2006)

Sample No: KC06.16 Catalogue No: FS 42227
 Date: 2/26/06
 Project: Ken's Bison
 Site Name/No: 48TE 1090
 Strata: ? Provenience: Teton Cty.

Taxon: Bison
 Element: M2 lower Prox Distal Shaft
 Side: (L) R Unknown Sex: M F (Unk)
 Age: 3-4
 How determined: heavy wear
 Behrensmeier's Weathering Stage: 1 (2) (3) 4 5
 Comments on physical condition: enamel chip off;
heavy wear on 3rd cusp - unusual; vertical cracking of enamel
 Residues: no
 Preservatives or glues: no

Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.



Picked out most of
cementum - quite clean

Enamel chip present -
use this as sample

Bone removed in clearing

→ KC16.4 = vertical slice

Maximum Dimensions: Length: 64.2 mm Enamel: 36.0 mm
 Width: 44.4 mm Weight: _____

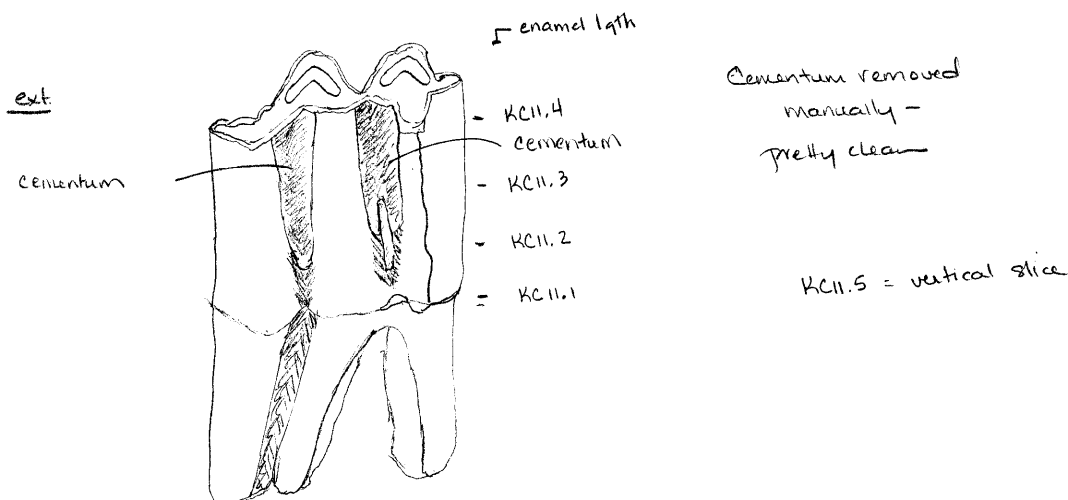
* Good ENAMEL

Bone Documentation Form
(1/15/2006)

Sample No: KC06.11 Catalogue No: FS 22597
 Date: 2/26/06
 Project: Ken's Bison
 Site Name/No: 48 TE 1101 MWAC - 260
 Strata: ? Provenience: Teton City

Taxon: Bison
 Element: 3rd m lower Prox: Distal Shaft
 Side: L (R) Unknown Sex: M F Unk
 Age: older adult
 How determined: moderately worn stage 3
 Behrensmeyer's Weathering Stage: 1 (2) 3 4 5
 Comments on physical condition: looks pretty good overall
vertical cracks
 Residues: NO
 Preservatives or glues: NO

Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.

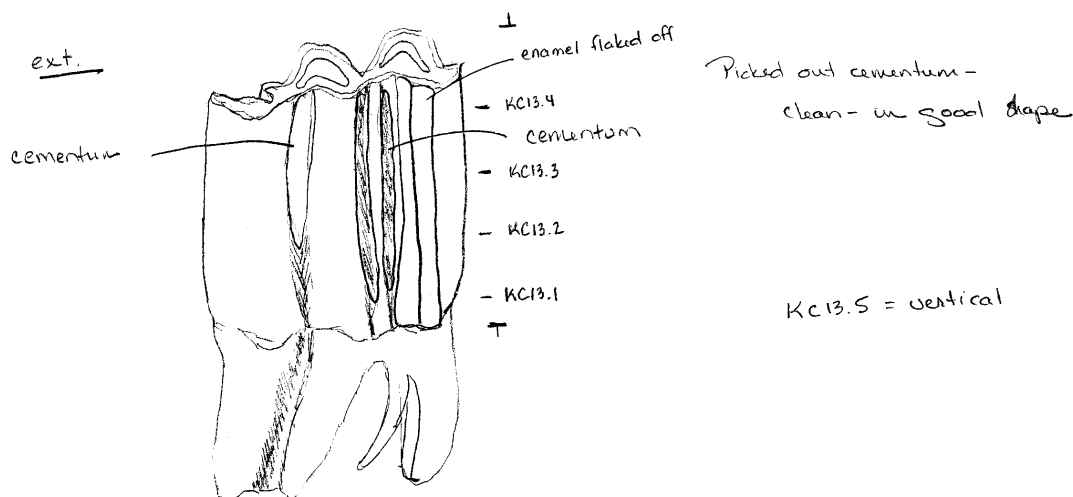


Maximum Dimensions: Length: 77.5 mm Enamel length 49.2 mm
 Width: 43.72 mm Weight: _____

Bone Documentation Form
(1/15/2006)

Sample No: KC06.13 Catalogue No: 42222
 Date: 2/26/06
 Project: Ken's Bison
 Site Name/No: 48TE1102 MWAC-286
 Strata: > Provenience: Teton Clay
 Taxon: Bison
 Element: 3rd M lower Prox: Distal Shaft
 Side: L (R) Unknown Sex: M F (Unk)
 Age: Age 2 ~ almost new
 How determined: wear S
 Behrensmeyer's Weathering Stage: 1 (2) (3) 4 5
 Comments on physical condition: good
vertical cracks in enamel; enamel breaking apart at top of 1st cusp
 Residues: No
 Preservatives or glues: NO

Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.

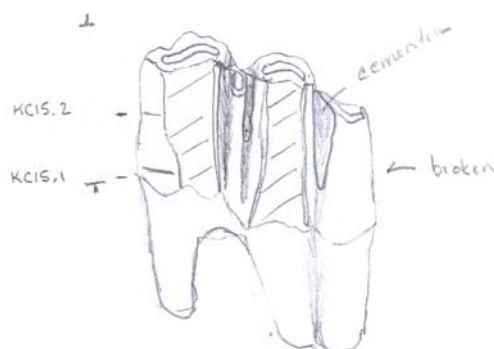


Maximum Dimensions: Length: 85.5 mm enamel: 53.5 mm
 Width: 46.11 mm Weight: _____

Bone Documentation Form
(1/15/2006)

Sample No: KC06.15 Catalogue No: 42223 MWAC - 286
 Date: 2/26/06
 Project: Kari's Bison
 Site Name/No: 48TE1102
 Strata: ? Provenience: Teton City
 Taxon: Bison
 Element: Lower M3 Prox: _____ Distal: _____ Shaft: Unk
 Side: (L) R Unknown Sex: _____ M F
 Age: Age 3-4 (middle adult)
 How determined: tooth wear
 Behrensmeier's Weathering Stage: 1 2 (3) 4 5
 Comments on physical condition: Vertical cracks; 3rd cusp is broken; very poor condition
 Residues: No
 Preservatives or glues: #1 nail polish M3 36 + 37

Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.



Picked out most of
cementum - quite clean

Broken enamel ~ vertical fractures

KCIS.3 : vertical slice
(fell apart ~ mixed sample)

 enamel gone

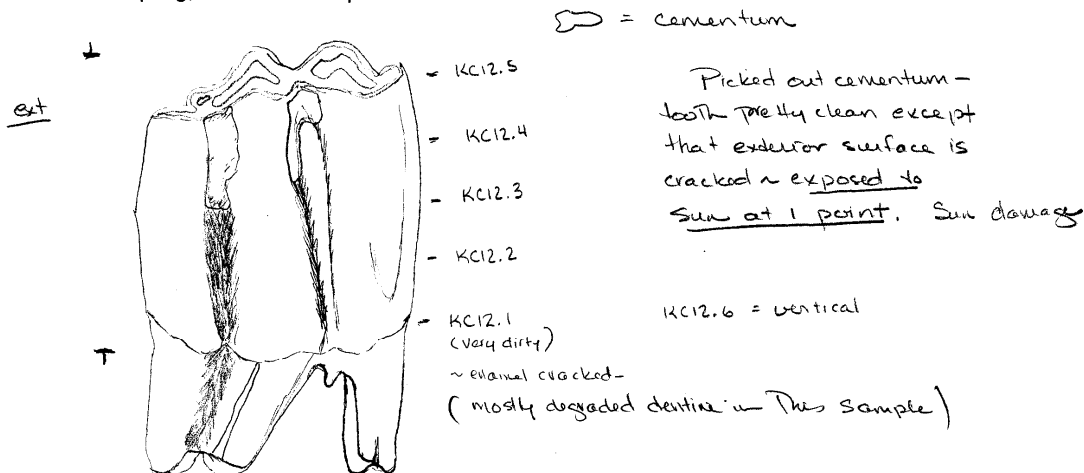
Maximum Dimensions: Length: 57.0 mm Enamel: 32.7 mm
 Width: 42.0 mm Weight: _____

Bone Documentation Form
(1/15/2006)

Sample No: KC06.12 Catalogue No: FS 39605
 Date: 2/26/06
 Project: Ken's Bison
 Site Name/No: 48 TE 1114
 Strata: ? Provenience: Teton Cty.

Taxon: Bison
 Element: M3 lower Prox: Distal Shaft
 Side: L (R) Unknown Sex: M F (Unk)
 Age: middle adult
 How determined: Wear not heavy stage 2
 Behrensmeier's Weathering Stage: 1 (2) (3) 4 5
 Comments on physical condition: good; Roots are cracked
enamel good (Not); enamel has vertical cracks & broke along face of
 Residues: No 1st loph
 Preservatives or glues: NO

Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.

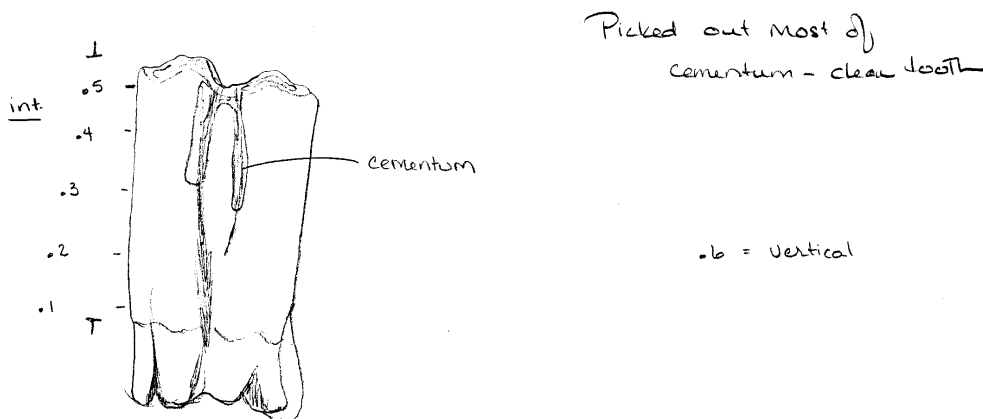


Maximum Dimensions: Length: 79.76 mm enamel: 55.0 mm
 Width: 50.6 mm Weight: _____

Bone Documentation Form
(1/15/2006)

Sample No: KC06.09 Catalogue No: # 697.1
 Date: 2/26/06
 Project: Ken's Bison
 Site Name/No: 484E697
 Strata: ~ Provenience: Yellowstone Park
 Taxon: Bison
 Element: upper M3 Prox _____ Distal _____ Shaft Unk
 Side: L (R) Unknown Sex: _____ M _____ F _____
 Age: Adult
 How determined: mid-weal stage 2-3
 Behrensmeyer's Weathering Stage: 1 (2) 3 4 5
 Comments on physical condition: excellent shape
 Residues: No
 Preservatives or glues: No

Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.



Maximum Dimensions: Length: 64.6 mm enamel: 54.6 mm
 Width: 31.6 mm Weight: _____

GOOD TOOTH

Bone Documentation Form
(1/15/2006)

Sample No: KC20.20 Catalogue No: Dirk Van Vuren #12
 Date: 4-12-06
 Project: Ken's Bison
 Site Name/No: Unknown
 Strata: Unknown Provenience: Unknown

Taxon: Bison

Element: Mandible ~ whole Prox: Distal Shaft
 Side: L (R) Unknown Sex: M F Unk

Age: young adult; P2 erupting ~ almost in; 3rd loph on M3 just erupted

How determined: Roots are not closed

Behrensmeyer's Weathering Stage: (1) (2) 3 4 5

Comments on physical condition: looks good; tooth is still in mandible w/ bone cut away on exterior side (closed side)

Residues: glues or other preservative; whitish like Elmer's Glue

Preservatives or glues: " Enamel general hard in good shape!

Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.

Not drawn because in mandible; several vertical cracks. Also some cementum

cleaning:

- 1) Used dental drill to remove surface of 1st loph
- 2) Washed tooth in mandible w/ tap H₂O.

5 slices: Sampled 3rd loph ~ exterior as all others

KC20.5 }
 KC20.4 } 8-9 mm apart
 KC20.3
 KC20.2
 KC20.1

KC20.6 = vertical

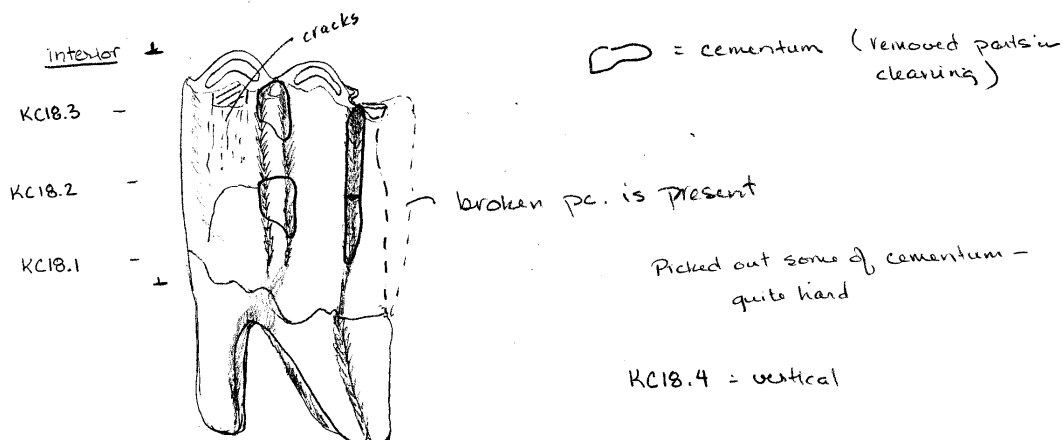
Maximum Dimensions: Length: 78 mm
 Width: 44 mm estimated Enamel Ht: 61 mm (base to top of int. cusp)
 this same msmt. on others

Bone Documentation Form
(1/15/2006)

Sample No: KC18.18 Catalogue No: FS 768
 Date: 3/3/06
 Project: Ken's Bison
 Site Name/No: ?
 Strata: ? Provenience: Henry Mts, Idaho

Taxon: Bison
 Element: 3rd M lower Prox: _____ Distal: _____ Shaft: _____
 Side: (L) R Unknown Sex: _____ M F (Unk)
 Age: Adult - wear stage 2-3
 How determined: wear
 Behrensmeyer's Weathering Stage: 1 (2) (3) 4 5
 Comments on physical condition: vertical cracks, stain bleaching; enamel in sampling area degraded
 Residues: no overall - enamel not as bad
 Preservatives or glues: no shape - not chipping

Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.



Maximum Dimensions: Length: 74.7 mm enamel: 45.5 mm
 Width: 37.6 mm - broken Weight: _____

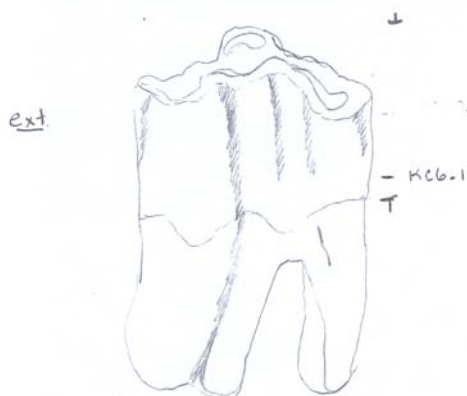
Bone Documentation Form
(1/15/2006)

Sample No: KC2006.06 Catalogue No: #YELL.2006.HV.002
 Date: Jan. 30, 2006
 Project: Ken's bison
 Site Name/No: Hayden Valley, UNP
 Strata: _____ Provenience: _____

Taxon: Bison
 Element: Lower M3 Prox _____ Distal _____ Shaft _____
 Side: L (R) Unknown Sex: M F (Unk)
 Age: old
 How determined: well worn stage 4
 Behrensmeyer's Weathering Stage: 1 2 3 (4) 5
 Comments on physical condition: Exterior enamel flaking off;
dissolved look; soaked in hot springs? Acidic? Whitened
 Residues: Ø (Enamel appears alkali ~ partially acid etched)
 Preservatives or glues: Ø

Includes mandible frag.

Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.



Cementum over entire tooth -
 John picked it away around
 Sampling area.

KCB.2 = Vertical

Not enough distance to collect
 another sample on tooth.

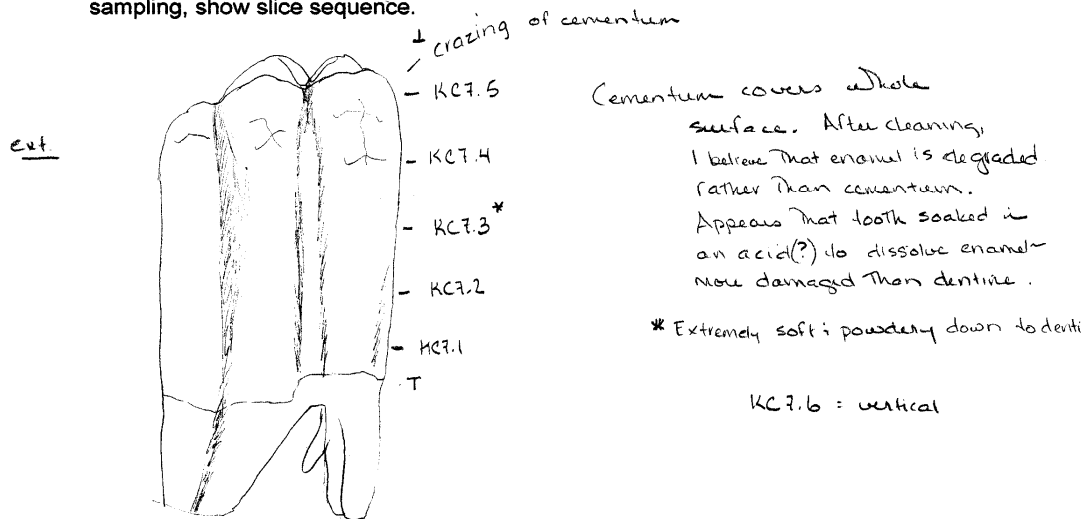
Maximum Dimensions: Length: 68.2 mm 29.1 mm
 Width: 43.4 mm Weight: _____

Bone Documentation Form
(1/15/2006)

Sample No: KC 2006.07 Catalogue No: #4EL L. 2000. HV.003
 Date: Jan. 30, 2006
 Project: Ken's bison
 Site Name/No: Houden Valley, YNP
 Strata: _____ Provenience: _____

Taxon: Bison
 Element: M3 - lower Prox _____ Distal _____ Shaft _____
 Side: L (R) Unknown Sex: M F (Unk)
 Age: younger adult
 How determined: little wear on 3rd cusp Stage 1
 Behrensmeier's Weathering Stage: 1 2 (3) 4 5
 Comments on physical condition: Enamel is cracked; whitened;
soaked - bleach? Prob acid as enamel is more degraded than dentine.
 Residues: Ø Doggy Tooth!
 Preservatives or glues: Ø

Associated mandible frags.
 Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.



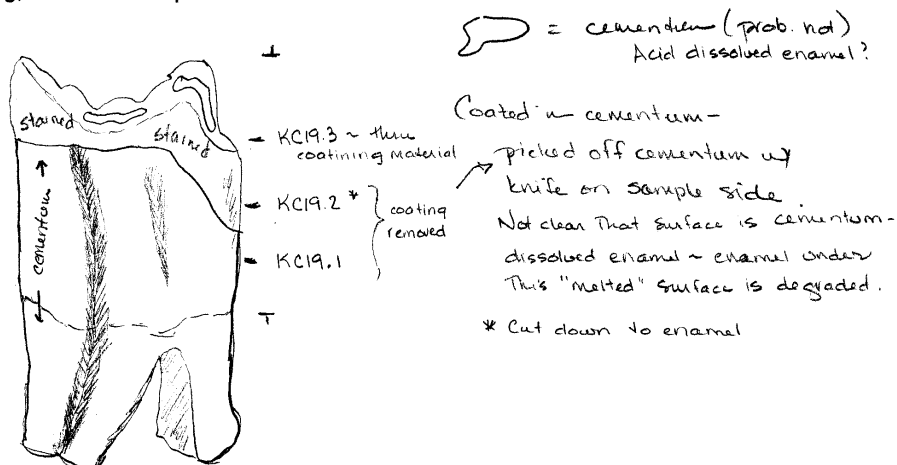
Maximum Dimensions: Length: 86.5 mm enamel: 61.6 mm
 Width: 43.3 mm Weight: _____

Bone Documentation Form
(1/15/2006)

Sample No: KC 06.19 Catalogue No: FS 94KC1
 Date: 3/3/06
 Project: Ken's Bison
 Site Name/No: ?
 Strata: ? Provenience: YNP

Taxon: Bison
 Element: 3rd M lower Prox: Distal
 Side: L (R) Unknown Sex: M F Shaft
 Age: Adult ~ age 3 Unk
 How determined: tooth wear
 Behrensmeier's Weathering Stage: 1 2 (3) 4 5
 Comments on physical condition: vertical cracks; sunbleach
lots of cementum ~ cracking; strange tooth wear Daddy Tooth!!
 Residues: No heavy staining above cementum
 Preservatives or glues: No

Specimen drawing with sampling portion indicated (to scale); also note modifications such as cutmarks, impact fractures, or carnivore damage. If micro-sampling, show slice sequence.



Maximum Dimensions: Length: 76.3 mm Enamel: 47.8 mm
 Width: 41.4 mm Weight: _____

