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**THE ANALYSIS OF A
LATE HOLOCENE BISON SKULL
FROM THE ASHLEY NATIONAL FOREST,
UTAH**



National Park Service - Midwest Archeological Center

**THE ANALYSIS OF A LATE HOLOCENE BISON SKULL
FROM THE ASHLEY NATIONAL FOREST, UTAH**

By

Kenneth P. Cannon

Report Prepared for
The Department of Agriculture
United States Forest Service
Ashley National Forest
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United States Department of the Interior
National Park Service
Midwest Archeological Center
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This report has been reviewed against the criteria contained in 43CFR Part 7, Subpart A, Section 7.18 (a) and (1) and, upon recommendation of the Midwest Regional Office and the Midwest Archeological Center, has been classified as

Available

Making the report available does not meet the criteria of 43CFR Part 7, Subpart A, Section 7.18 (a) (1).



Executive Summary

In 2003 a partial bison skull was recovered by Ashley National Forest archeologist Brian Storm from an elevation of 3840 m (12,600 ft) AMSL in the Uinta Mountains. The partial skull consists of a portion of the frontal, occipital region, and horn cores including horn sheaths. The presence of the horn sheaths is of particular interest for the ecological information they can provide. Through the analysis of the individual cones of the horn sheath a record of the animal's dietary and migration patterns can be obtained.

The skull was recovered downslope of Gilbert Peak in an alpine environment. Tundra vegetation characterizes the area. Downslope, and to the east, of the skull find is the headwaters area of the Uinta River. This boggy area is drained by Gilbert Creek with wet meadow vegetation and Engelmann spruce along the edge.

While high altitude bison remains have been discussed in the scientific literature periodically over the past 80 years they have not gone beyond the descriptive. The study of this specimen focuses on a more complete

understanding of bison ecology in the intermountain west. In addition to metric analysis of the skull, radiometric assay, and stable isotope analyses were applied.

The radiocarbon age of the specimen is 150 ± 40 yrs BP. The 2 sigma calibrated age is cal AD 1660 to 1950. Metric analysis of the skull indicates it was an adult male, at least 10 years of age, that compares well with *Bison bison athabasca* in size and is larger than either *Bison bison bison* specimens or other high altitude bison. However, it is probable this individual represents a member of the species *Bison bison bison*, but phenotypic characteristics (e.g., large horn size) may be the result of gene flow. More definitive taxonomic placement of the Gilbert Peak bison may not be resolved without genetic analysis.

Temporal and spatial gaps in the Holocene record of bison still exist and isolated skulls can help fill them. Detailed analyses of these specimens can provide an understanding of the history, the paleoecology, and evolution of the species. The results of this study begin to fill this gap.

Acknowledgements

To begin, I would like to express my gratitude to Dr. Byron Loosle, Heritage Program Leader for the Ashley National Forest (ANF), for supporting this research endeavor. I would also like to thank Clay Johnson (ANF) for providing supporting information and Brian Storm (ANF) for making the long hike to retrieve the skull. Also, thanks to Dr. Ralph Hartley of the Midwest Archeological Center (MWAC) for allowing me the opportunity to do the work.

A number of individuals have assisted me over the years in understanding the application of stable isotope analysis to mammal ecology. These individuals include Dr. Sheri Fritz, Dr. Alan Osborn, Dr. Larry Tieszen, and Dr. Susan Hughes. I would also like to thank Mary Anne Davis, Kristen Jensen, Dr.

Joel Janetski, and Mary Sullivan for providing information on bison site locales. Dr. Danny Walker, Dr. Jerry McDonald, Dr. Michael Wilson, and Dr. C.R. van Zyll de Jong also graciously provided me with information on bison and access to their databases.

Production of this manuscript is attributed to a number of individuals: Molly Boeka Cannon (MWAC) produced the ArcGIS maps used in the report and Alan Smith photographed the skull. I would also like to acknowledge John Andresen, Dawn Bringelson, and Molly Boeka Cannon (MWAC) for their editorial skills in helping to make this a more concise document. Even though a number of people worked on this project, the interpretations presented here are mine and any errors in the data reporting or interpretation are my burden.

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Introduction

"I doubt the bison had much respect for altitude, and I believe they went as high as they choose" (Warren 1927:61).

Documenting the range of mammalian species was an important aspect of biologists working in the late 19th and early 20th century, especially with respect to shrinking habitat from expanding settlement in the intermountain west. This was particularly true of the North American bison (*Bison bison*, Linnaeus 1758) which was reduced to a few hundred individuals at the beginning of the 20th century with their long-term preservation uncertain (Shell 2002:viii).

Altitudinal range, as well as latitudinal and longitudinal, were often reported in scientific journals. Fryxell (1926) reported on a number of bison specimens in the Medicine Bow Mountains of Wyoming at altitudes ranging from 2895 to 3658 m (9500 to 12,000 ft). In a later article Fryxell (1928) reports on high altitude bison records from Colorado, Wyoming, and Montana. High altitude bison citations in southern and northern Colorado are also reported by Cook (1930), Warren (1927), and Beidleman (1955). More recently, Wilson (1974) reported on bison remains from above timberline in the Bighorn Mountains of northern Wyoming. With possible climate-driven ice/snow-field melting in high altitude and latitude region, a new source of bison remains has been established (Lee et al. 2004).

Unfortunately, few high altitude records of bison have been reported in Utah. Madsen (2000) reports that 30 genera of late Quaternary fauna have been found in alpine settings. However, only two high altitude sites, Mastodon Sinkhole (3232 m [10,604 ft]) in Sanpete County (Gillette and Madsen 1993 citing W. Miller personal communication) and Huntington Canyon (2740 m [2743 ft]) near the crest of the Wasatch Plateau (Gillette and Madsen 1993; Madsen 2000), produced bison. The paucity of high altitude bison remains from Utah is therefore noteworthy (Table 1). While the Gilbert Peak

bison represents a single individual, it does contribute significantly to our knowledge of high elevation fauna.

This study takes its queue from Fryxell (1928:139), a statement which may be more imperative today:

It is now out of the question to turn bison loose on the plains. The only portions, if any, of the former range of the bison that could now possibly be restocked are certain uninhabited tracts in or adjacent to the mountains—within the national forests and national parks. Hence, obviously, the importance of preserving such scraps of information as can be obtained at this late period concerning the former range and life habits of the bison in our western mountains.

Therefore, it is the purpose of this study to provide some of these *scraps of information* using contemporary research techniques (e.g., Cannon 1997). These include radiometric dating, metric analysis of the specimen and its relationship to other intermountain and high altitude specimens, and stable isotope analyses. Stable carbon and nitrogen isotope analyses have the potential to yield information on the diet and ecology of an individual. Cool (C₃) and warm (C₄) season grasses have been demonstrated to have distinct ratios of ¹³C to atmospheric CO₂ due to their particular photosynthetic pathways. 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). Results of these techniques will provide a more complete understanding of the age and ecology of this particular individual, and how it compares with other late Quaternary bison.

As Walker (1992) explains there are still temporal and spatial gaps in the Holocene

record of bison and isolated skulls can help fill them. He goes on to further argue that isolated bison skulls can provide specific information for understanding the paleoecology and evolution of the species. Information derived from detailed study of isolated bison skulls can have implications for a number of social and ecological issues (Van Vuren 1987:65), such as the management and restoration of ecosystems (Lyman 1996; Lyman and Cannon 2004), zoogeography (Lyman and Livingstone 1983),

and ethnography (Bamforth 1988; Reeves and Peacock 2001).

While this study focuses on the results of various analyses conducted on the Gilbert Peak bison, the context of the study is regional in scope. This study, along with an earlier one (Cannon 1997), provide the initiation of a larger study to understand the biogeography of bison in the intermountain west within the context of long term climate change (Cannon 2001; Lyman 2004).

Table 1. High elevation fauna sites from Utah.

SITE	ELEVATION	COUNTY	AGES (yrs BP)	FAUNA	REFERENCE
Silver Creek	1950 m	Summit	> 40 ka	25 mammalian and non-mammalian species	Miller 1976
Mastodon Sinkhole	3232 m	Sanpete	7590 ± 100 7650 ± 100 <10,000*	<i>Mammuthus americanus</i>	Miller 1987
Blonquist Rockshelter	2125 m	Summit	5640 ± 260 7985 ± 480 9665 ± 550	Numerous small mammal species	Nelson 1988; Nelson et al. 1989
Huntington Canyon	2981 m	Sanpete	8430 ± 110 to 12,340 ± 85	<i>Arctodus simus</i> , <i>Mammuthus columbi</i> , <i>Equus</i> sp., <i>Bison</i> sp., <i>Camelops</i> sp.	Gillette and Madsen 1992, 1993; Madsen 2000
*Age determined by racemization analysis.					

Environmental Context

Introduction

Rising from the Wyoming and Uinta basins to the north and south, respectively, the Uinta Mountains form a distinct topographic unit in northeastern Utah that parallels the southern border of Wyoming. The Ashley National Forest (ANF) is generally coextensive with the Uinta Mountains. The Uinta Mountains have been further defined into three distinct subsections (Stokes 1986).

The Gilbert Peak skull was recovered in the area defined as the High Uintas Subsection which forms the crestal portion of the Uinta Mountains (Figure 1). The subsection includes the western half of the mountains and extends from approximately Mirror Lake in the west to Fox Lake in the east. The Uinta High Wilderness is generally coextensive with this geologic area (Stokes 1986).

The High Uintas include Utah's highest peak, Kings Peak (4123 m [13,528 ft]), as well as the headwaters of the Provo, Weber, Duchesne, Uinta, and Bear Rivers. Glaciation has produced gently sloping, semi-circular, flat-bottomed cirque valleys that are separated by steep-walled arêtes. The area is also known for the hundreds of rock-rimmed lakes that have been left by the glaciers. Modern timberline is 3505 m (Stokes 1986:245-246).

The growing season in this high elevation region is short with temperatures in the summer seldom above 26° C (80° F). Precipitation falls mostly as snow, totaling about 1016 mm (40 in). Climatic information from the Ashley National Forest web page (www.fs.fed.us/r4/ashley/).

Modern Environment

The Gilbert Peak bison skull was recovered from a ridge southwest of Gilbert Peak at an

elevation of 3840 m (12,600 ft) AMSL in Summit County along the boundary between the Ashley and Wasatch National Forests (Figure 2). Gunsight Pass between Gilbert Peak and Kings Peak is to the southwest (Figure 3). The area consists of alpine vegetation with surface cobbles common. Soils are shallow and well-drained. Tundra vegetation is present in the immediate area. Common species include perennial herbs (*Geum rossi*, *Silen acaulis*, *Paronychia pulvinata*, *Arenaria obtusiloba*, *Trifolium nanum*, *Kobresia myosuroides*, *Polygonum bistoroides*, *Eriophorum chamissonis*), perennial grasses (*Deschampsia caespitosa*, *Festuca ovina*, *Koeleria cristata*, *Trisetum spicatum*), sedges (*Carex* sp.), and willow (*Salix* sp.). Vegetation information is based upon Utah vegetation codes and cover types as defined by Edwards et al. (1995).

To the east the landscape slopes dramatically into a boggy area with an unnamed lake that is drained by Gilbert Creek. This area is part of the headwaters of the Uinta River. Engelmann spruce (*Picea engelmannii*) are present along the edge of the boggy area. The wet meadow vegetation consists mostly of grasses, forbs, sedges, and rushes (Figure 4).

Dietary studies of bison in the Henry Mountains of southeastern Utah (Van Vuren 1982: Table 1) and Yellowstone National Park (Meagher 1973: Table 17) indicate that grasses and sedges are highly preferred forage.

The skull was recovered from the steep gravel and boulder-covered slope on the southwest slope of Gilbert Peak (Figure 5). The find location is about 1900 m west of the headwaters of Gilbert Creek (see Figure 4).

Figure 1. Map of the Ashley National Forest and approximate find location of the Gilbert Peak bison skull.

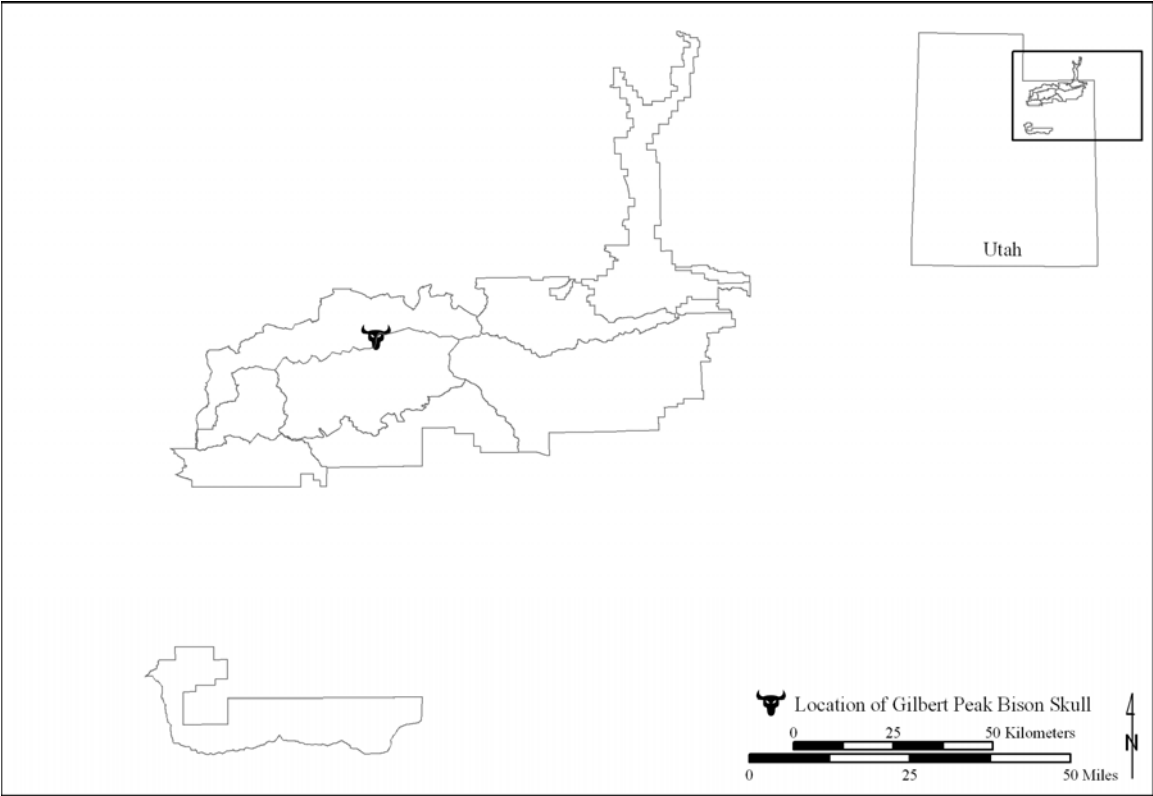


Figure 2. Find location of the Gilbert Peak bison skull as modified Kings Peak, Utah 7.5 minute topographic quadrangle.

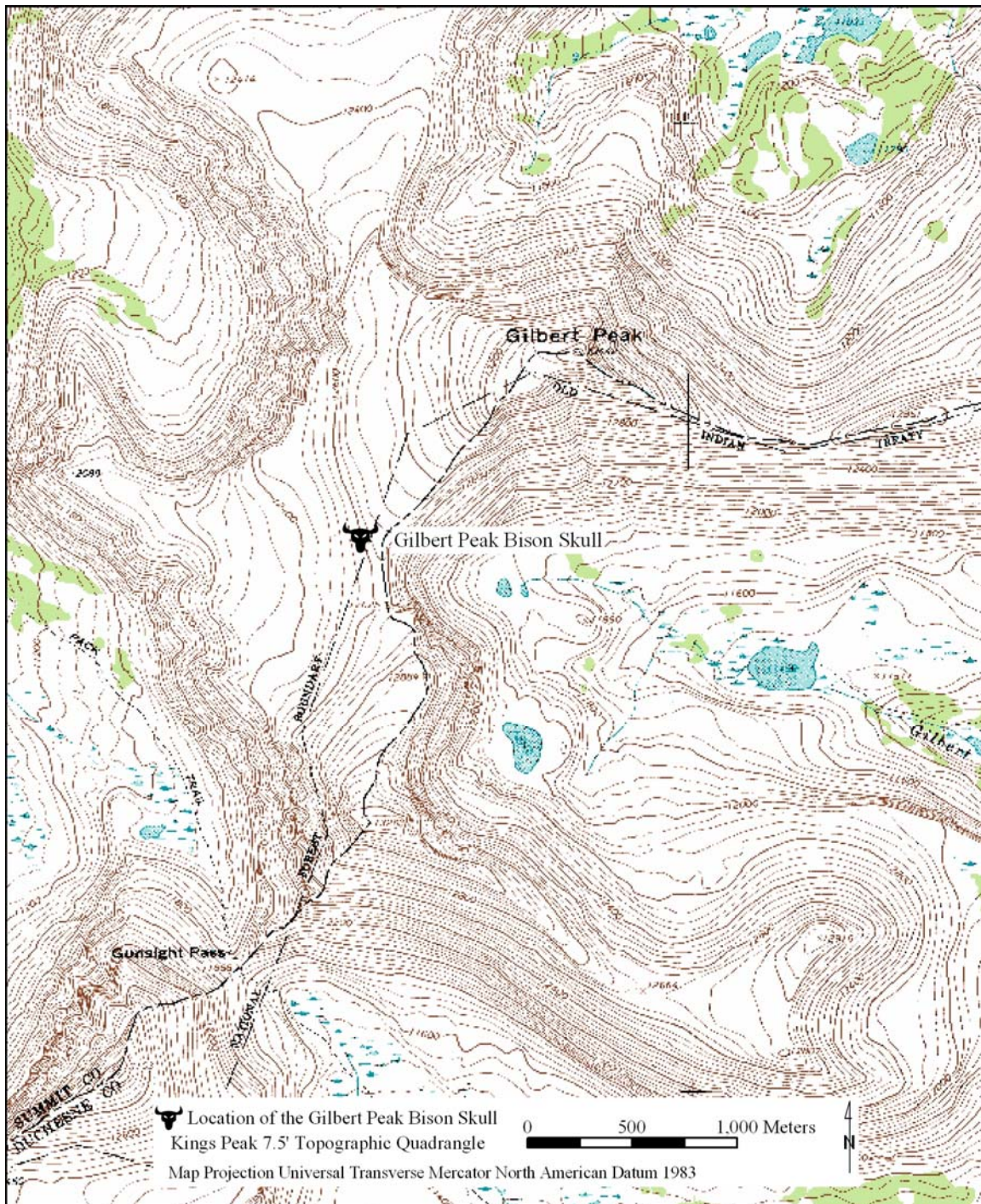


Figure 3. DOQQ of local environment from which Gilbert Peak bison skull was recovered.



Figure 4. View to north of Gilbert Creek basin area (1 October 2003; photo by Brian Storm ANF).



Figure 5. View to southeast of the collection area. Skull location is indicated by arrow (1 October 2003; photo by Brian Storm ANF).



Regional Evidence of Bison

Introduction

The record of bison remains from late Quaternary sites in the region is fairly extensive, and almost exclusively the result of human predation (Figure 6). The distribution in northern Utah, southeastern Idaho, and southwestern Wyoming indicates bison were present throughout the Holocene with population density fluctuating in relation to climate patterns (e.g., Lupo and Schmitt 1997). In compiling data on bison in the region the FAUNMAP database was initially consulted, but was supplemented by the regional literature. These include La Point (1987), Janetski and Madsen (1990), Thompson and Pastor (1995), Bruder et al. (1999), and Johnson and Loosle (2002). State site records were also reviewed. Mary Sullivan provided information from Colorado; Mary Anne Davis for Idaho; and Kristen Jensen and Joel Janetski provided information for Utah. A list of the counties included in the review is presented in Table 2 with a listing of the sites in Appendix A. While regional evidence of bison have been discussed elsewhere in greater detail the following section will present an overview of these studies.

Southeastern Idaho and the Northeastern Great Basin

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).

Table 2. Counties reviewed for evidence of precontact bison remains.

Colorado	Idaho
Eagle	Bannock
Garfield	Bear Lake
Jackson	Bingham
Lake	Bonneville
Moffat	Caribou
Pitkin	Cassia
Rio Blanco	Franklin
Rout	Oneida
Summit	Power
Utah	Wyoming
Cache	Lincoln
Daggett	Sweetwater
Davis	Uinta
Duchesne	
Morgan	
Rich	
Salt Lake	
Summit	
Wasatch	
Weber	
Uintah	
Utah	

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), 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).

High altitude bison remains in Utah are rare, as are high altitude local faunas in general (Gillette and Madsen 1993). Madsen (2000) has suggested a seasonal use of high altitude valleys in the Wasatch Plateau during post-glacial times by mammoth, mastodon, horse, camel, and bison. These patterns are similar to modern migrations of ungulates through multiple floristic zones, for example the seasonal migration of bison in the Henry Mountains of southeastern Utah (e.g., Van Vuren 1982). Meagher (1973) in her study of Yellowstone bison indicates that seasonal movements between elevation zones include seasonal changes in the vegetation, the rut, and biting insects.

Southwestern Wyoming

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, bison were found to be 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.

Colorado

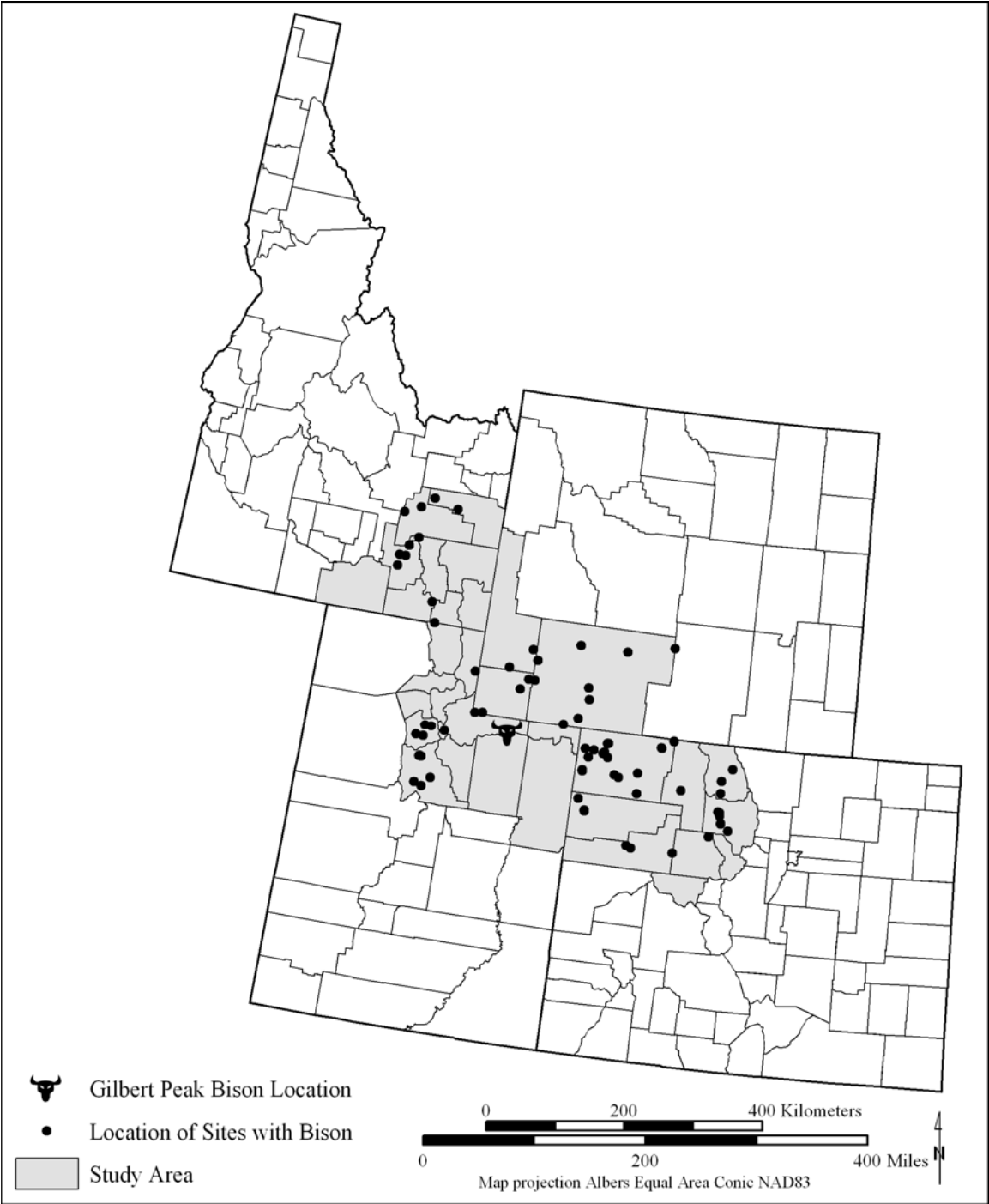
In an overview of the archaeology in the Gunnison Basin, Stiger (2001) indicates that bison were present prior to contact and were an occasional prey species, although there appears to be changes in prevalence of bison remains through time. However, faunal remains in general are typically not well-preserved which may influence interpretations.

While bison in Colorado were probably most common in the eastern grasslands, high elevation parks represented areas that appear to have been attractive to bison (Pitblado 2003:244-245). For example, Goshen occupations at Upper Twin Mountain site (5GA1513) has produced a bison bone bed (Kornfeld and Frison 2000).

Summary

Regional evidence of bison indicates they have been a consistent member of the Holocene mammalian community, although climate may have influenced herd numbers and the availability of bison as a human prey item.

Figure 6. Regional map illustrating location of precontact sites with bison remains.



Description and Examination of the Skull

Description

The Gilbert Peak bison skull is represented by the proximal portion of the cranium including the horn cores with preserved horn sheaths. A portion of the frontal bone is also preserved, while the occipital region is eroded with only the occipital condyles and the area around the foreman magnum present (Figure 7). Colonies of the lichen *Xanthoria elegans* are present on the horn sheaths and in the interior of the skull (Figure 8). This species of lichen is common on calcium-rich rocks, old bones, and old wood in alpine regions of the Rocky Mountains (Kershaw et al. 1998:344).

The incomplete nature of the specimen limits the number of measurements. All available skull measurements follow those defined by McDonald (1981a:43-47) which are based upon those originally defined by Skinner and Kaisen (1947). Measurements for the Gilbert Peak skull are presented in Table 3.

Sexing of the Gilbert Peak bison was based upon relative robustness of the skull and horn core morphology. Female skulls are typically smaller in size, and some features, such as horn cores and eye orbits, are less massive. Male horn cores have a distinct burr or rim at the dorsal base, while females typically do not have a distinct burr, and the horn core often blends with the neck and frontals (McDonald 1981a:44). The Gilbert Peak skull has distinct burrs at the base of the horn cores, suggesting it is a bull.

A less subjective means of assessing gender is the metric comparison of the Gilbert Peak skull with other skulls of known gender. Utilizing McDonald's (1981b) data for other western United States bison, the dorso-ventral diameter of the horn core was plotted against spread of the horn cores. The plot indicates that the Gilbert Peak bison skull is a large male (Figure 9).

Assessing age at death of archeological bison is typically conducted through wear patterns of mandible teeth (e.g., Frison and Reher 1970). Unfortunately, the teeth are not preserved in this specimen. Suture closure is another means of assessing relative age. McDonald (1981a:44) considered a skull mature:

If the sagittal frontal suture was completely fused posteriorly from about midway between the planes of the orbits and bases of the horn cores, and if the frontal-parietal sutures were completely fused from the sagittal origin laterally and ventrally to below the level of the ventral horn core bases.

McHugh (1958) and Fuller (1959) suggest that the size and shape of the horn can be used to determine age. While this can be used as a relative means for assessing age in populations, it is not of particular value.

Counting the number of growth rings on the horn sheath was also suggested by McHugh (1958:31) as a means of estimating age. However, he cautions that the determination should be increased by three years to allow for the juvenile period when no obvious rings are formed. Reynolds, et al. (1982) discount the counting of rings as a reliable estimate of age.

For the Gilbert Peak skull, the sagittal frontal suture appears to be almost completely fused (Figure 7a), suggesting an adult. In his master's thesis Wilson (1975: Figure 7 and 8) presented a preliminary study of age based upon allometric growth. Plotting two skull measurements against known ages he illustrated logarithmic curves for estimating age. Walker (1992) applied this technique in his study of isolated bison skull from the Seminoe Reservoir, Carbon County, Wyoming. For the Gilbert Peak bison skull only one skull measurement was available for study, least width of frontals.

Superimposing the Gilbert Peak measurement onto Walker's graph (1992: Figure 7

lower), an estimated age at death for the Gilbert Peak bison is 12 years (Figure 10).

Figure 7. Gilbert Peak bison skull views: (a) dorsal view; (b) nuchal view; and (c) basal view.

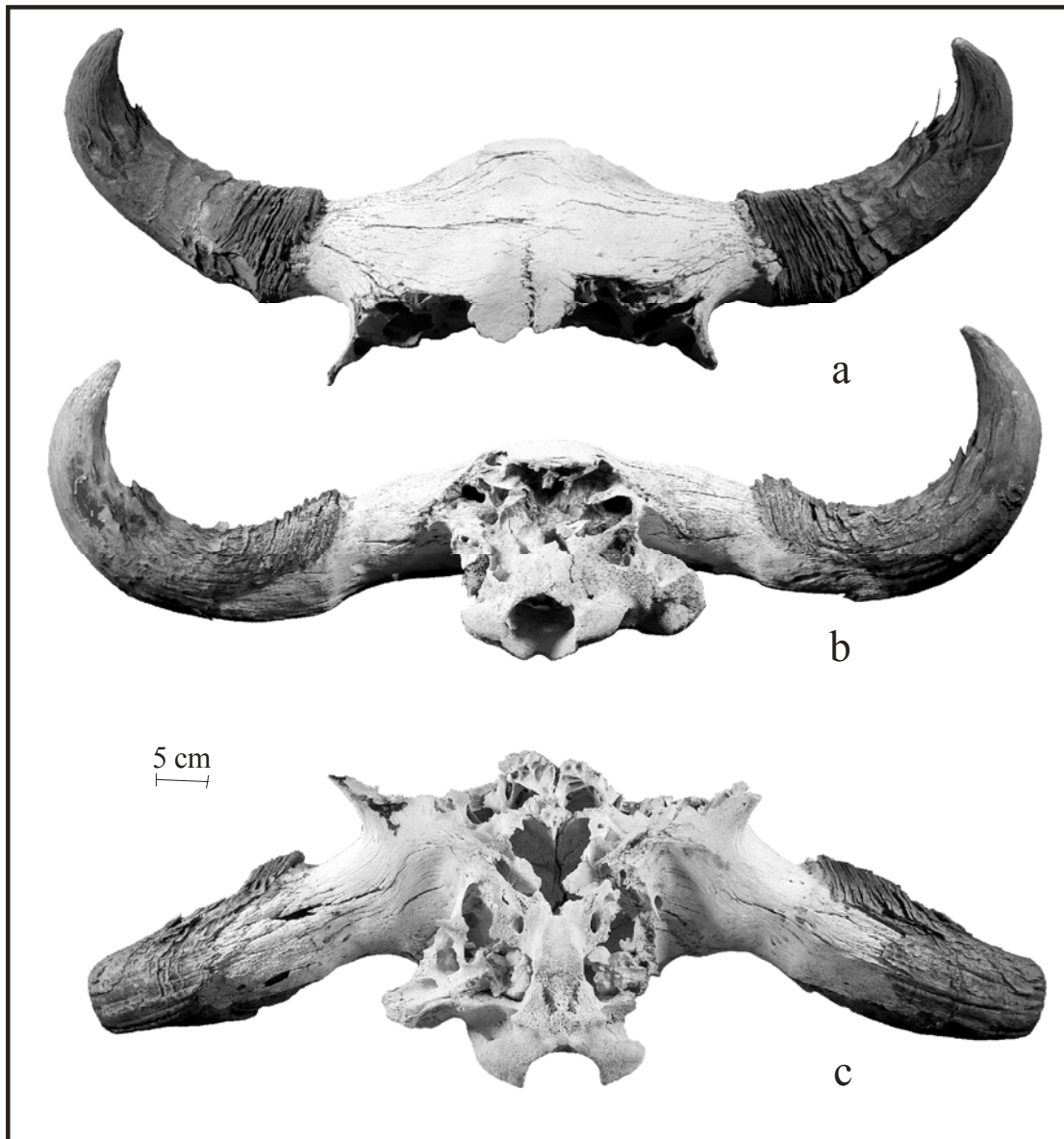


Table 3. Skull measurements following McDonald (1981a). All measurements are presented in millimeters. Data on *Bison occidentals* are from McDonald (1981a:Table 25), *Bison bison athabasca* from McDonald (1981a:Table 34), *Bison bison bison* from McDonald (1981a:Table 29), and high altitude bison are from McDonald (1981b:550-553) and Wilson (1974: Table III). All specimens used in analysis are males.

Measurement*	Gilbert Peak	<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).	657	77	779.3	626-1055	76.9	9	681.2	542-848	92.0	128	603.9	510-778	44.7	17	602.4	508-719	55.7
Horn core length, tip to burr (CLUC).	295	86	277.8	186-392	39.1	9	1235.1	165-323	43.9	134	190.7	124-270	24.7	19	185.5	140-225	23.7
Straight line distance, tip to burr, dorsal horn core (TB).	210	81	248.1	175-350	31.8	9	207.0	154-277	34.4	132	172.4	120-243	21.4	19	171.8	127-216	22.7
Dorso-ventral diameter, horn core base (VD).	105	85	94.6	70-114	8.4	9	91.5	81-106	8.7	139	81.9	69-99	6.4	23	84.2	69-99	8.6
Minimum circumference, horn core base (CHC).	266	89	300.3	237-355	27.7	9	289.1	254-322	22.9	142	255.4	199-324	19.5	22	260.8	228-305	21.5
Width of occipital at auditory openings (GWA).	281.2	61	262.0	238-294	13.2	10	273.6	243-298	15.3	120	243.9	220-270	9.7	17	249.3	228-276	12.6
Width of occipital condyles (CW).	110	71	135.0	111-151	7.7	11	130.1	118-139	6.4	122	126.6	111-140	5.7	18	123.1	106-138	8.7
Depth, nuchal line to dorsal margin of foramen magnum (DEP).	-	57	104.0	89-120	7.0	10	99.6	92-114	6.6	112	98.7	81-115	6.2	-	-	-	-
Antero-posterior diameter, horn core base (TD).	90.8	91	98.8	77-120	10.1	9	97.2	83-109	9.5	142	83.4	67-103	6.3	25	84.9	74-97	7.2
Least width of frontals, between horn cores and orbits (WHCO).	280	74	296.6	261-348	16.8	10	293.4	273-313	10.5	135	271.1	237-318	12.6	22	271.1	248-294	11.9

Measurement*	Gilbert Peak	<i>Bison antiquus occidentalis</i>				<i>Bison bison athabasca</i>				<i>Bison bison bison</i>				High Altitude Bison			
Greatest width of frontals at orbits (GPW).	-	64	348.0	311-394	16.7	10	354.0	326-384	14.8	117	324.6	289-356	12.9	19	232.1	280-356	18.1
M1-M3, inclusive of alveolar length.	-	3	97.3	90-102	6.4	1	91.7	-	-	22	90.6	81.8-97.9	4.4	-	-	-	-
M3, maximum width, anterior cusp.	-	2	28.4	27.8	29.1	1	27.9	-	-	22	27.7	22.3-31.4	1.6	-	-	-	-
Distance, nuchal line to tip of pre-maxillae (OP).	-	25	564.3	511-606	24.8	7	578.6	562-604	15.2	56	535.2	500-583	17.0	-	-	-	-
Distance, nuchal line of nasal-frontal suture (ON).	-	57	259.8	233-287	12.3	9	256.0	240-276	13.4	106	245.7	214-279	12.2	14	241.6	206-279	22.4
Angle of divergence of horn cores, forward from sagittal (AHC).	70°	62	72.1°	63°-83°	5.2°	6	71.0°	63°-77°	5.0°	124	67.7°	58°-79°	4.4°	-	-	-	-
Angle between foramen magnum and occipital planes (OF).	-	57	129.6°	110°-142°	7.3°	9	129.4°	119°-144°	8.8°	115	133.8°	118°-159°	7.6°	-	-	-	-
Angle between foramen magnum and basioccipital planes (BF).		56	113.4°	98°-126°	5.6°	9	113.8°	106°-125°	6.6°	115	110.5°	100°-129°	5.0°	-	-	-	-
*Abbreviations are those used in Figure 13.																	

Figure 8. Close-up of left horn sheath (nuchal view) illustrating colony of *Xanthoria elegans* and individual horn sheath cones sampled for stable isotope analysis.

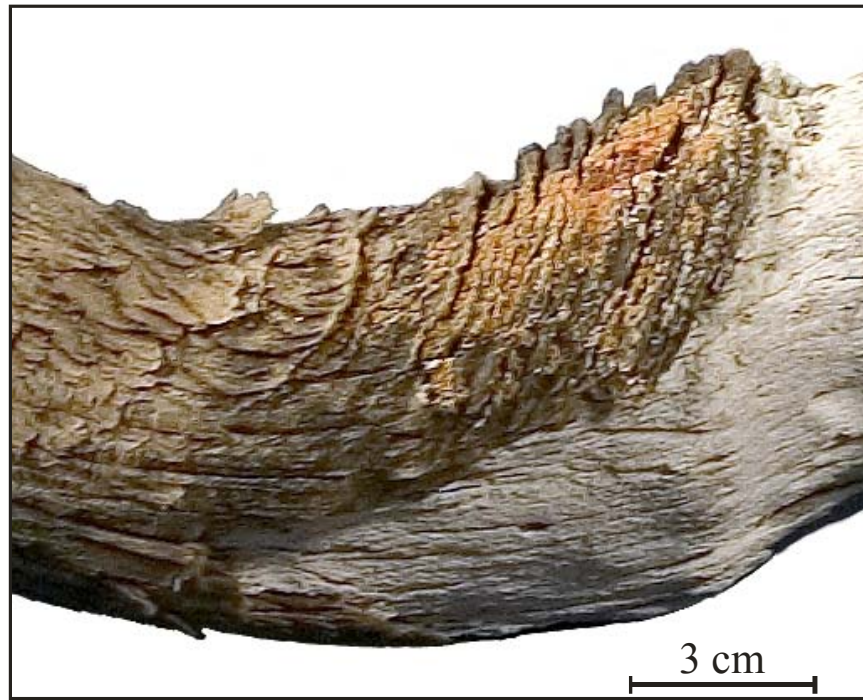
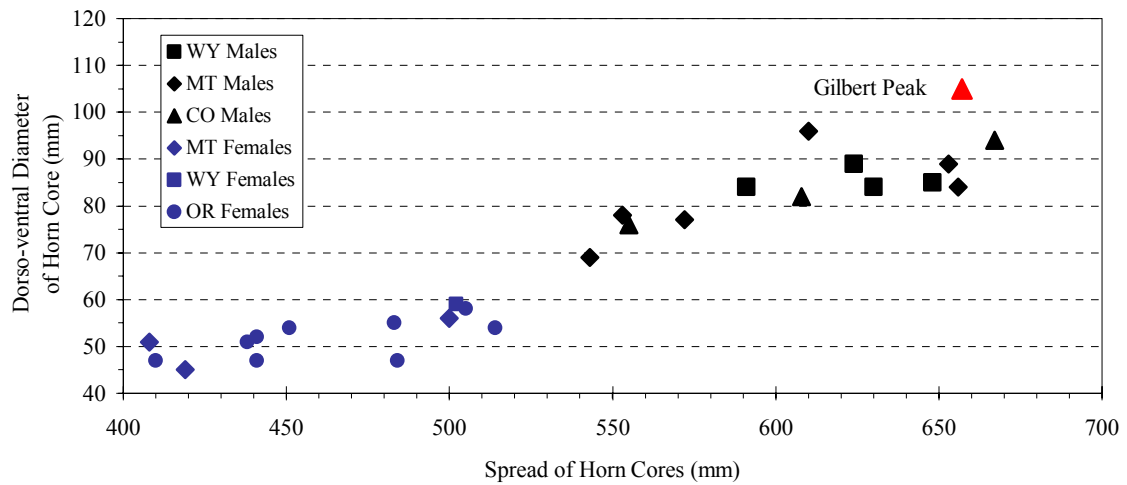


Figure 9. Plot of Gilbert Peak bison skull in relation to male bison skulls from western United States specimens. Data presented in Appendix C.



Preparation

As previously noted, the bison skull was recovered from the surface on the southwest slope of Gilbert Peak. The skull had been known for several years on the ANF prior to it being recovered. The skull was collected by ANF archeologist Brian Storm and transported to MWAC. No formal stabilization of the specimen was conducted, except for the removal of adhering sediments with a soft brush. A sample from the skull was cut from the basal portion of the occipital bone for radiocarbon assay (see below).

The horn sheath is a keratinized epidermis that covers the horn and consists of many periodically developed horn cones which tightly cling together (Bubenik 1990:5). It is these cones that were sampled for an annual record of the Gilbert Peak bison. Removal of the horn sheath samples was accomplished using a Dremel variable-speed rotary tool (Figure 11). After removal of the 10-x-4-cm section of the right horn sheath, it was

placed in distilled water for approximately eight hours (Figure 12). Rehydration of the sheath allowed for the separation of the individual horn cones. Ten cones were submitted to Beta Analytic for stable carbon and nitrogen analysis. The results are presented below.

Figure 11. Horn sheath being cut using Dremel variable-speed rotary tool.



Figure 10. Semi-log plot of least width of frontals to individual age in late Pleistocene and modern bison skulls (adapted from Walker 1992: Figure 7).

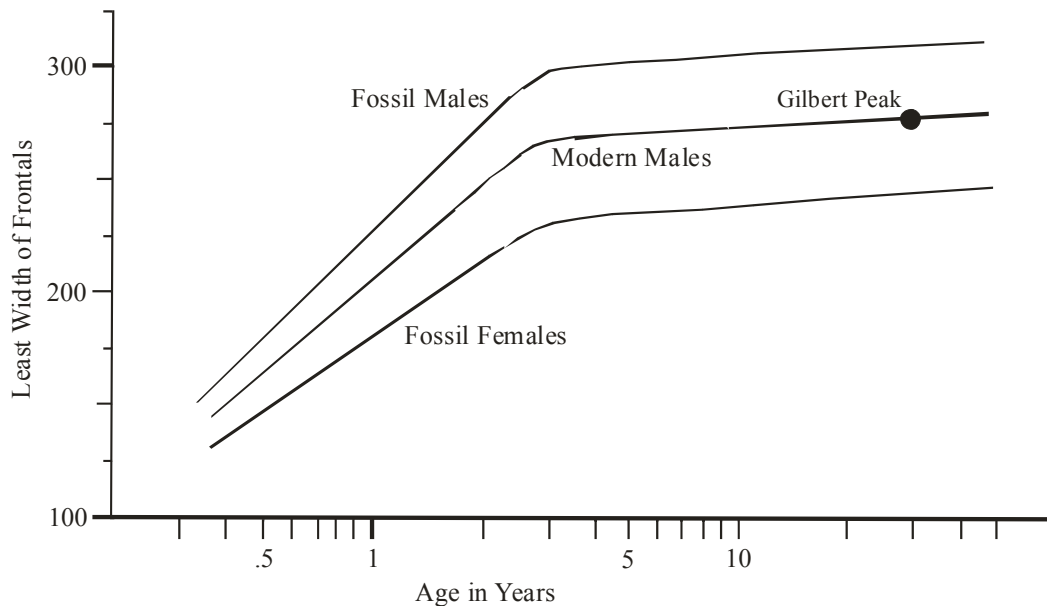
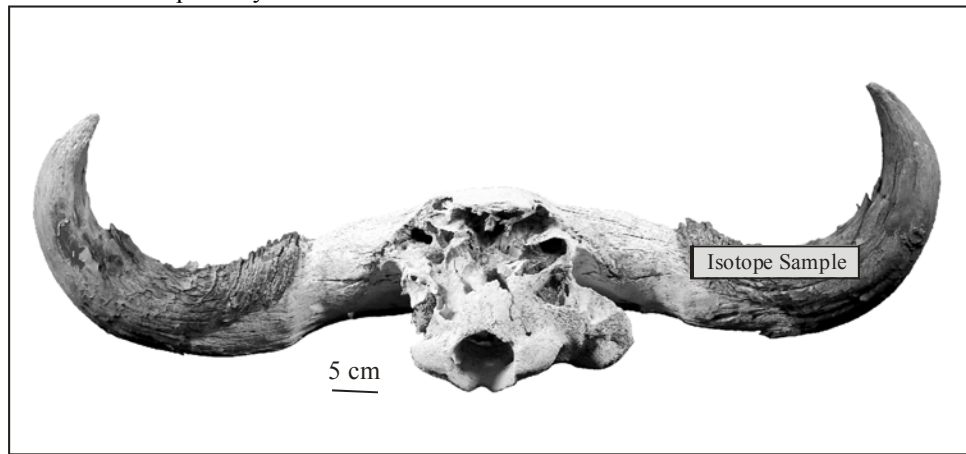


Figure 12. Dorsal view of Gilbert Peak bison skull. Hatched area illustrates portion of horn sheath removed for stable isotope analysis.



Radiocarbon Dating Results

In order to accurately place the specimen within a historical context, a 11.79-gram sample was collected from the skull and submitted to Beta Analytic for radiocarbon assay. The sample was removed from the basal portion of the occipital bone.

The sample was processed by Beta Analytic using the accelerator mass spectrometry (AMS) technique. Standard procedures for bone dating included collagen extraction with alkali. The protocol for collagen extraction specimens involved the initial assessment of the material for friability or softness. Specimens of very soft bone usually do not provide reliable ages. If a bone is judged to have sufficient collagen fraction, >5 percent original collagen remaining (Hedges and van Klinken 1992), it is washed in deionized water and gently crushed. Next, dilute, cold HCl acid is repeatedly applied and replenished until the mineral fraction (bone apatite) is eliminated. The collagen is then dissected and inspected for rootlets. If rootlets are found, they are also removed when replenishing the acid solutions. If a sufficient quantity of collagen is present (as was with this sample), NaOH is applied to ensure the absence of secondary organic acids (Hood 2004a). Hedges and van Klinken

(1992) review the treatment of bone for AMS dating. In their opinion, “the methods that date carefully extracted and purified [collagen] gelatin, and can demonstrate analytically that the material dated corresponds to the composition expected for gelatin, are adequate for the great majority of bones that have lost up to 95 percent of indigeneous protein” (Hedges and van Klinken 1992:290). Beta Analytic adheres to these standards.

Hedges and van Klinken (1992) warn that contamination must always be suspected for poor or intermediate preservation, and if the specimen lacks evidence of a recognizable collagen signature, there is no longer any support for believing that the extracted organic material is indigenous. Contamination can come from a number of sources depending upon the particular environment. However any, and probably all buried bone is liable to have incorporated exogenous soluble and insoluble organic materials, such as rootlets, soil humics, or other molecules mobilized in groundwater. Bone is particularly susceptible to absorption of these contaminants due to its high surface area ($10 \text{ m}^2 \text{ g}^{-1}$). Fortunately, the “humic” fraction is nearly always extractable from bone with alkali pretreatment (NaOH), and generally provides an accurate or younger date (Hedges and van Klinken 1992:284). With

surface materials, such as the Gilbert skull, weathering and leeching are most critical in the preservation of collagen. In a recent study by Trueman and colleagues (2004) in the arid grasslands of Amboseli National Park, Kenya, they found that surface exposed bone can act like the “wicking of a candle” during evaporative transport that may influence the geochemistry of the bone towards that of the groundwater. This may have implications of using bone geochemistry as environmental proxies.

The radiocarbon dating procedure proceeded normally and the sample contained adequate carbon for dating. The $^{13}\text{C}/^{12}\text{C}$ ratio was measured at -18.8‰, which is within the expected range for ungulates. This measurement indicates that sufficient collagen was present for an accurate radiocarbon age. The $^{15}\text{N}/^{14}\text{N}$ ratio was also measured for this specimen which produced a value of 7.3‰ (Hood 2004a). Published $\delta^{15}\text{N}$ values for bison range from 2.9‰ to 6.9‰ (Cannon 1997; Table 4; Figure 13).

The radiocarbon age obtained is 150 ± 40 yr BP (Beta-192144). The radiocarbon years before present are referenced to AD 1950 and calculated using the Libby ^{14}C half life of 5568 years. The radiocarbon age was calibrated using the Pretoria Calibration Procedure program based upon known-age tree rings of oak, sequoia, and fir. The procedure is described by Talma and Vogel (1993) and Stuiver et al. (1998). At the two-sigma level (95 percent) the calibrated results range from cal AD 1660 to 1950 with intercepts at cal AD 1680, 1740, 1810, 1930, and 1950 (Figure 14). The greatest areas under the probability distribution curves for the one-sigma and two-sigma calibrations occurs between cal AD 1725 to 1778 (0.362) and cal AD 1665 to 1784 (0.480), respectively (Table 5), and implies that the age of the bison’s death is statistically more likely to be of this age rather than the other calibrated ages. Based upon this information it is most likely that this bison died during the early to mid-eighteenth century.

Table 4. Results of stable isotope analysis of modern North American bison specimens. Alaska data from Bocherens et al. (1994:Table 4), Konza, Niobrara, Wood Buffalo, and Yellowstone data from Tieszen et al. (1996), Wind Cave data from Tieszen (1994:Table 5), and Fawn Creek data from Cannon (1997:Table 6).

Specimen	Collagen Rank	Percent Yield	Percent Nitrogen	Percent Carbon	C/N	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Appatite $\delta^{13}\text{C}$
Gilbert Peak	-	-	-	-	-	-18.8	+7.3	-
Fawn Creek	3	25.9	14.8	41.5	3.3	-19.6	+6.5	-10.8
Alaska	-	-	-	-	-	-20.5	+4.4	
Konza, KS	-	-	-	-	-	-13.8	+5.5	
Niobrara, NE	-	-	-	-	-	-15.9	+2.9	
Wind Cave, SD	-	6.5	-	-	3.22	-18.7 \pm 0.2	+6.4 \pm 0.23	
Wood Buffalo, NWT	-	-	-	-	-	-23.9	+6.6	
Yellowstone, WY	-	-	-	-	-	-23.4	+6.9	

Table 5. Results of calibration using CALIB 4.4.

Percent Area Enclosed	cal AD Age Ranges	Relative Area Under Probability Distribution
68.3 (1 sigma)	1672-1695	0.150
	1725-1778	0.362
	1799-1813	0.097
	1839-1876	0.199
	1917-1949	0.192
95.4 (2 sigma)	1665-1784	0.480
	1790-1890	0.346
	1909-1950	0.174

Figure 13. Plot of $\delta^{15}\text{N}$ against $\delta^{13}\text{C}$ values for modern North American bison specimens from high altitude, high latitude, and central Great Plains. Data from Bocherens et al. (1994), Tieszen (1994), Tieszen et al. (1996), and Cannon (1997).

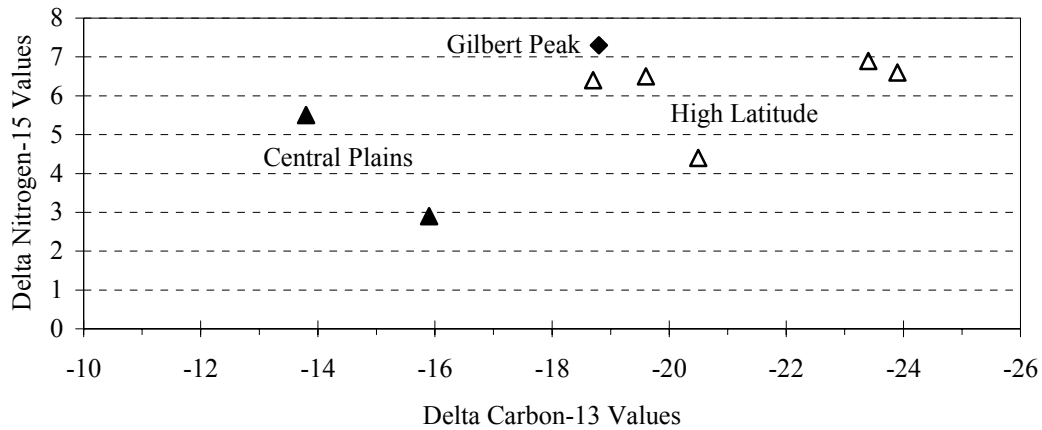
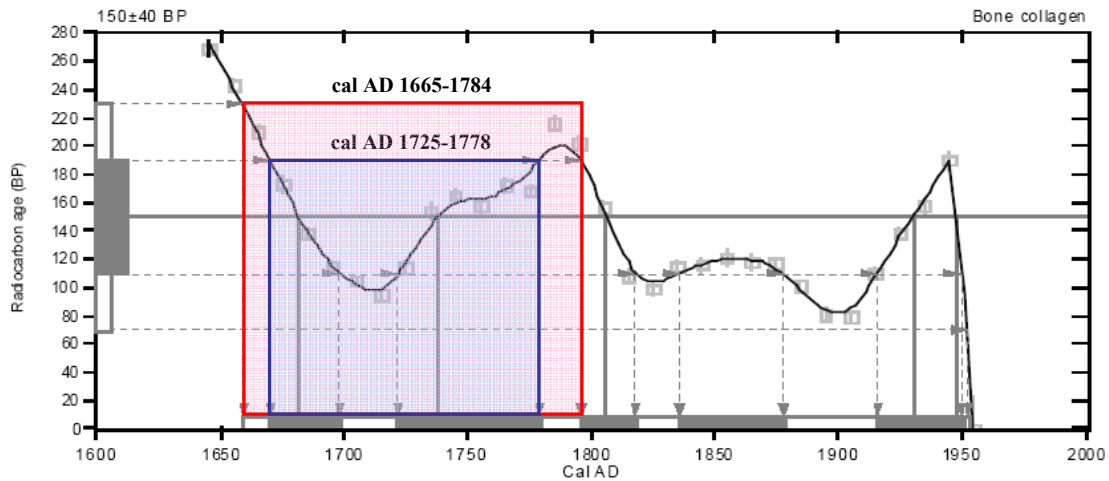


Figure 14. Results of calibration of radiocarbon age to calendar years. The calibration range presented in red represents the 2-sigma range and the area in blue represents the 1-sigma range.



Bison Taxonomy

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 ripe 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) describes 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 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. 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 1986:1). 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 1986:1). While most biologists agreed with Rhoads designation of *B. b. athabasca* being at least subspecifically distinct (e.g., Skinner and Kaisen 1947; McDonald 1981a), some felt that the differences in the two subspecies, *B. b. athabas-*

cae and *B. b. bison*, were of little consequence (van Zyll de Jong 1986:1).

According to van Zyll de Jong (1986:1), the decimation of the bison herds prior to firsthand 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. athabasca* 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. athabasca* range was limited to the northern Rocky Mountains and the boreal forests of Canada (Figure 15). 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. athabasca* 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. athabasca*. However, van Zyll de Jong (1986), studying presumed pure *B. b. athabasca* 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 differentiates the two modern species. According to his analyses, *B. b. athabasca* 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. athabasca* there is only a reduction in horn core length (van Zyll de Jong 1986:18 [Figure 16]).

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 a molecular study of DNA 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 from 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 being 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.

Understanding the taxonomy of the Gilbert peak bison may not be adequately addressed without genetic analysis, but morphological differences in adult skulls has been commonly used to determine how individual animals, or populations, compare. In differentiating between *B. b. athabasca* and *B. b. bison*, McDonald (1981a) used horn core morphology as key characteristics both in size and shape.

Using a ratio diagram (Simpson 1941) we can explore how the Gilbert Peak bison compares 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 occi-*

dentalis 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 (e.g., high altitude bison) and the log of the measurement of a conspecific specimen. The comparative specimen 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 results of this comparison are interesting and suggest the Gilbert Peak bison is larger in some dimensions and smaller in others than the standard (Figure 16). Specifically, a comparison of select horn core measurements indicates that the Gilbert Peak bison skull is within the range of each of these groups (Figure 17).

The Gilbert Peak skull horn core morphology is more similar to *B. bison athabasca* being larger than either the high altitude or the *B. bison bison* populations. The large size of the Gilbert Peak skull and its incompleteness may influence the results of the comparison. 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 gene flow between the two populations. Genetic isolation of intermountain populations in the west may be expressed phenotypically, as discussed by van Zyll de Jong (1986:54-55). More interestingly, the Gilbert Peak bison is larger than all populations, including the standard (*B. antiquus occidentalis*) in several horn core dimensions (Figure 16). A more definitive understanding of the genetic relatedness of intermountain populations will have to wait for genetic analysis, such as mtDNA.

Figure 14. Range of modern bison species based upon distribution map of Reynolds et al. (1982: Figure 49.1).

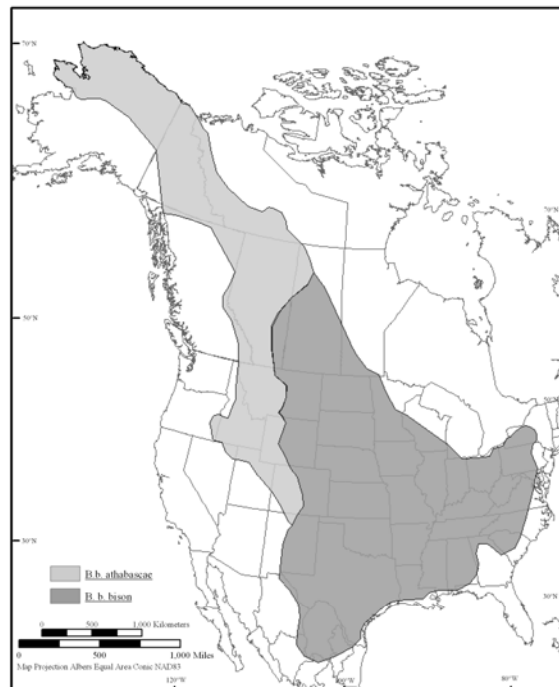


Figure 16. Ratio diagram comparing 10 skull dimensions of the Gilbert Peak specimen in comparison with *Bison bison bison*, *Bison bison athabasca*, and *Bison antiquus occidentalis*, with the latter serving as a standard. All measurements included in analysis are from male skulls. (*B. antiquus occidentalis* (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). McDonald's data used in analysis is only from males. Only those measurements that were available from the Gilbert Peak bison skull were used in this analysis.

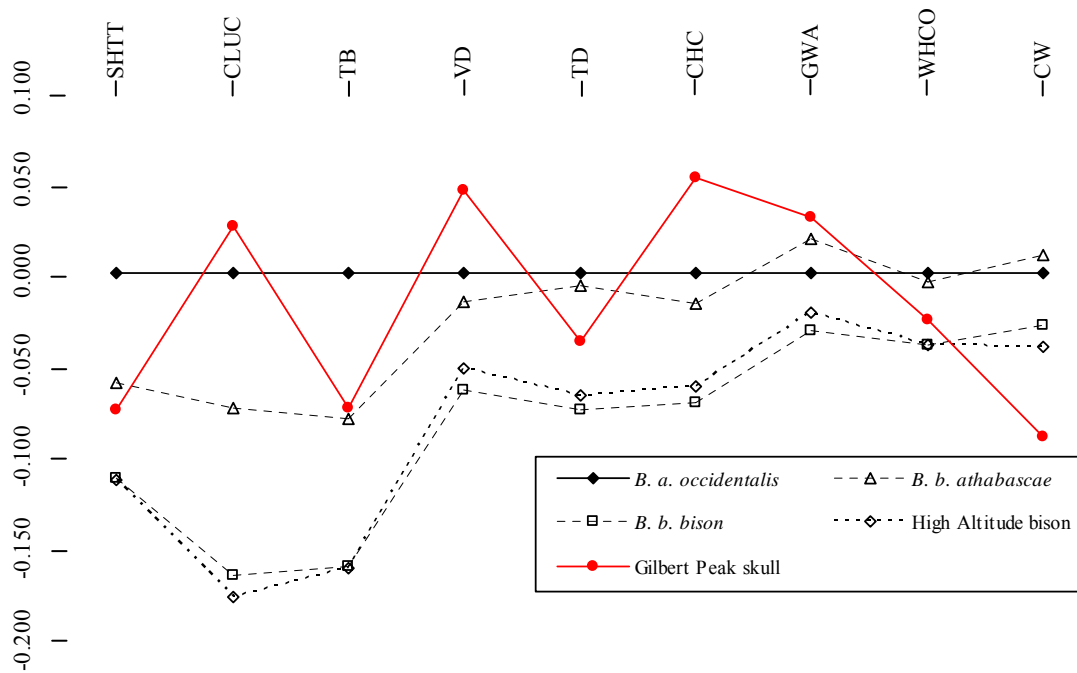
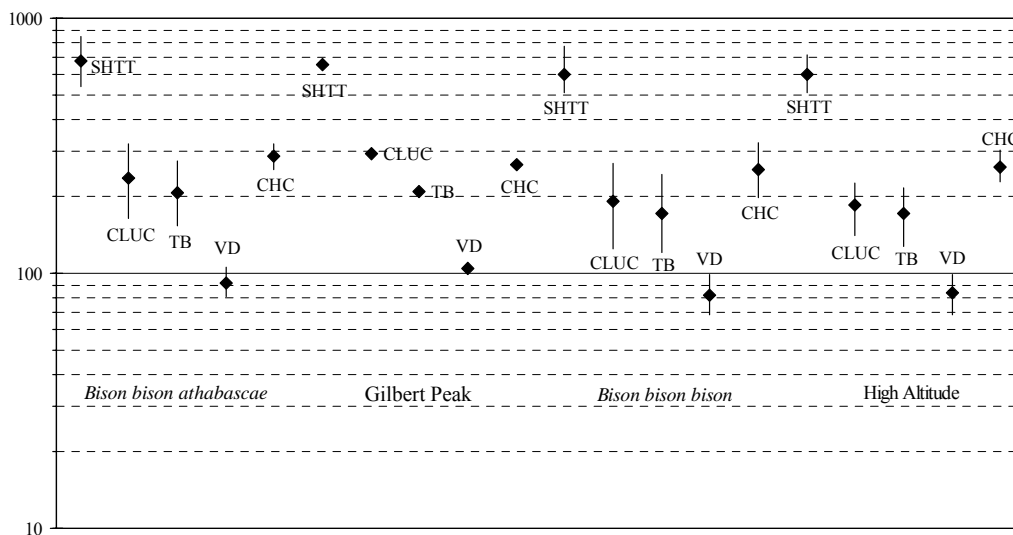


Figure 17. Comparison of select horn core measurements of Gilbert Peak bison skull with other taxonomic and regional groups to illustrate amount of overlap in range of measurements. See Table 3 for measurement abbreviations.



Results of Stable-Isotope Analyses

Introduction

As was mentioned in the introduction, there are several reasons for the investigation of isolated skulls. One aspect of this research is addressing the ecology and seasonal movement of mammals that no longer occupy their original range. This can provide us with information that may be useful in reestablishment of habitats, but may also contribute to understanding past behavior of bison as a prey species for past human groups (e.g., Widga 2004).

One way of approaching this problem is by applying analyses of diet to the study of foraging patterns. If bison were moving through various ecosystems during seasonal migrations, and if these environments have different food resources, we should expect this to be evident in the bison's diet (Chisholm et al. 1986:193; Table 5). Stable isotope analysis has been applied to populations of modern ungulates in South Africa (e.g., Tieszen et al. 1979; Vogel et al. 1978), as well as to other fossil vertebrates (e.g., Bocherens et al. 1994; Heaton 1995) in order to understand their dietary selection.

Stable Carbon Isotope Analysis

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 $^{13}C/^{12}C$ isotopic abundance in bone collagen, which is linked through the food web to the primary producers—photosynthetic plants (Bocherens et al. 1994:214). In terrestrial environments, two main categories of plants are recognized based on their carbon-fixation pathways, which are clearly distinguished by their stable carbon isotope ratios (Figure 18). The C_3 plants represent about

90% of all plants and include all trees and herbaceous plants from cold and temperate climates. Their $\delta^{13}C$ values range between -23‰ and -32‰ with an average of about -26‰. These plants probably evolved earlier than the C_4 plants during periods of lower atmospheric CO_2 concentrations.

Warm weather and tropical herbaceous plants, such as maize, sugar cane and millet, are classified as C_4 and have a $\delta^{13}C$ value between -9 and -16‰, averaging around -13‰ (Smith and Brown 1973:505; Bocherens et al. 1994:214). C_4 plants probably evolved during the Tertiary and are more competitive than C_3 plants during periods of stress, specifically under conditions of high light intensity and moisture stress. These plants are more efficient in capturing CO_2 at high leaf temperatures and low stomatal conductance. Patterns of C_4 diversity in North America indicate a strong positive relationship with growing season temperature. On the Great Plains, both relative and absolute C_4 grass abundances correlate with mean annual temperature (MAT) and mean annual precipitation (MAP). In contrast, C_3 grass abundance decreases with MAT and summer precipitation. Since C_3 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 C_4 grasses. With this understanding of the $\delta^{13}C$ values, the amount of C_3 and C_4 plants consumed by herbivores can be quantified and applied to various biogeographic questions.

A third group of plants, uses the CAM (crassulacean acid metabolism) photosynthetic pathway 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 varia-

tions in 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 being 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. 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). The presence and distribution of C_3 and C_4 plants in the environment is not random but related to environmental factors, specifically temperature. C_3 and C_4 plant abundance can be predicted from surface energy and moisture balance characteristics of the soil. With increasing latitude and longitude a corresponding increase in C_3 species is expected (Figure 19). An example from Kenya illustrates this point—within low altitude, open savannas all grasses are C_4 and nearly all trees and shrubs are C_3 ; above 1800 m, C_4 grasses begin to be replaced by C_3 grasses and at 3000 m nearly all grasses are C_3 (Tieszen 1994:265).

In a study from southeast Wyoming, Boutton et al. (1980) demonstrated that the percentage of C_3 biomass increased with elevation (Figure 20). 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 also a factor the authors felt strongly influenced the ratios.

On the Great Plains, increases 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, decreasing to 35 percent in South Dakota. Browse species, such as the 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). Grass composition for Idaho estimates about 18 percent C_4 species (Teeri and Stowe 1976:Table 2).

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 (Table 6). However, since climatic changes have been demonstrated for various periods during the course of the Holocene, vegetation values should be expected to reflect these climatic shifts (Whitlock 1993). This temporal variable is another complicating factor involved in the interpretation of isotopic signals from paleosamples (Tieszen 1994:166).

In a paper by Connin and colleagues (1998), they 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 this data implies a pattern of significant availability of C_4 plants, and a pattern of significant summer rainfall in parts of southern Arizona and New Mexico throughout the last glaciation.

Figure 18. $\delta^{13}C$ values in parts per million for common graminoid plants and forb species of the Niobrara Valley Preserve, Nebraska (from data in Steuter et al. 1995).

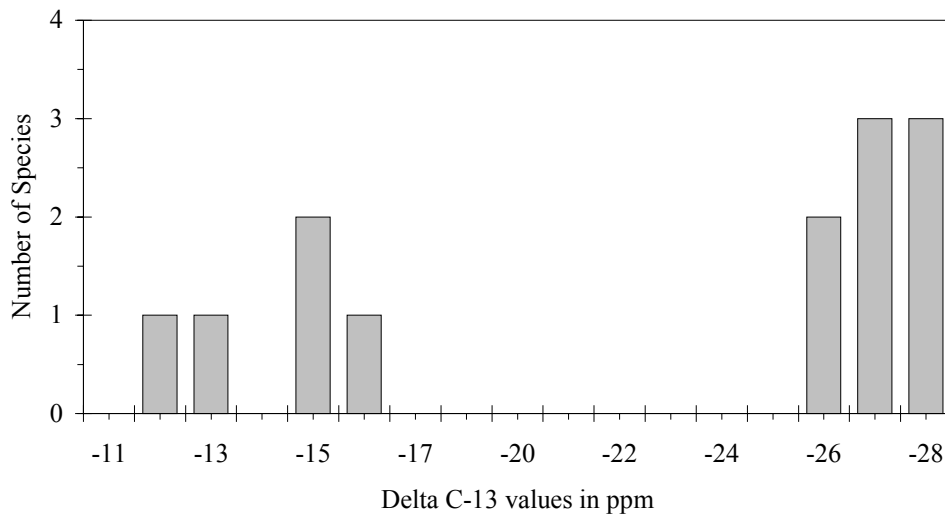


Table 6. List of plants identified in diet of bison from Yellowstone National Park (Meagher 1973:Table 17), Henry Mountains, Utah (Van Vuren 1984:Table 1), shortgrass plains of northeastern Colorado (Peden 1976:Table 1), and northern mixed prairie of Badlands National Park, South Dakota (Plumb and Dodd 1993:Table 2) and their photosynthetic pathway. Pathway data provided by 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 caespitosum</i>	Dwarf huckleberry	C ₃
<i>Amelanchier</i> sp.	Serviceberry	C ₃
<i>Artemisia frigida</i>	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
<i>Festuca octoflora</i>	Sheep fescue	C ₃

Species	Common Name	Pathway
<i>Sphaeralcea corymbosa</i>	Sand Dropseed	
<i>Stipa comata</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 lanuginosa</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 cuspidata</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 crassicaulis</i>	Milkvetch	C ₄
<i>Mellilotus officinalis</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>Glycyrrhiza lepidota</i>	American licorice	C ₄

Figure 19. Map of the United States illustrating approximate percentage of C_4 plants (after Teeri and Stowe 1976).

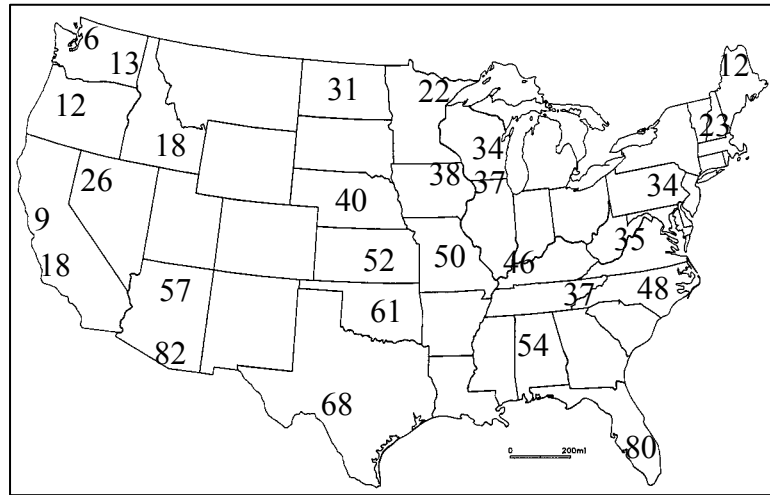
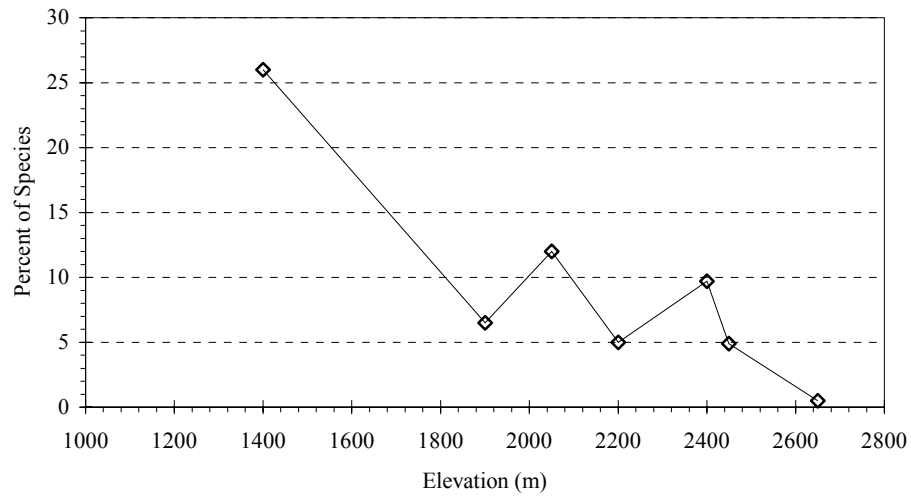


Figure 20. Percent of species with C_4 pathway along an altitudinal transect in southeast Wyoming (after Boutton et al. 1980).



Stable Nitrogen Isotope Analysis

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 (N_2). 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).

Hughes (2003) in her analysis of bighorn sheep (*Ovis canadensis*) from Mummy Cave in northwestern Wyoming argued that changes in $\delta^{15}\text{N}$ values were related to migration of sheep between summer and winter range. She argued that changes in these values reflect shifts in migratory behavior resulting from climatic change. Bison from the high altitudes of the Greater Yellowstone Ecosystem to 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.

The Western North American Isotopic Record

A review of the stable carbon isotopic record of bison in western North America (data base compiled by author) indicates a pattern of studies that is not unexpected. The majority of the samples come from the Central Plains states (Figure 21) where bison research has been a focus (e.g., Bozell 1995). The record is also indicative of a pattern that probably is reflective of preservation and research questions, with a significant increase in the Late Holocene (Figure 22). This pattern mirrors the radiocarbon date curve which Frison (1991: Figure 2.5) has indicated is not a reflection of prehistoric human occupation, but a reflection of the intensity of cultural resource management investigations. The long-term collaboration between Dr. Larry Tieszen and the Nebraska State Historical Society accounts for the large number of Nebraska and South Dakota samples (J.R. Bozell, personal communication 1997; see also Bozell et al. 1997). More focused case studies, such as Gadbury et al. (2000), are also included in the data set and reflect specific research topics.

Figure 21. Stable carbon isotope samples (n=412) by state and Canadian Province.

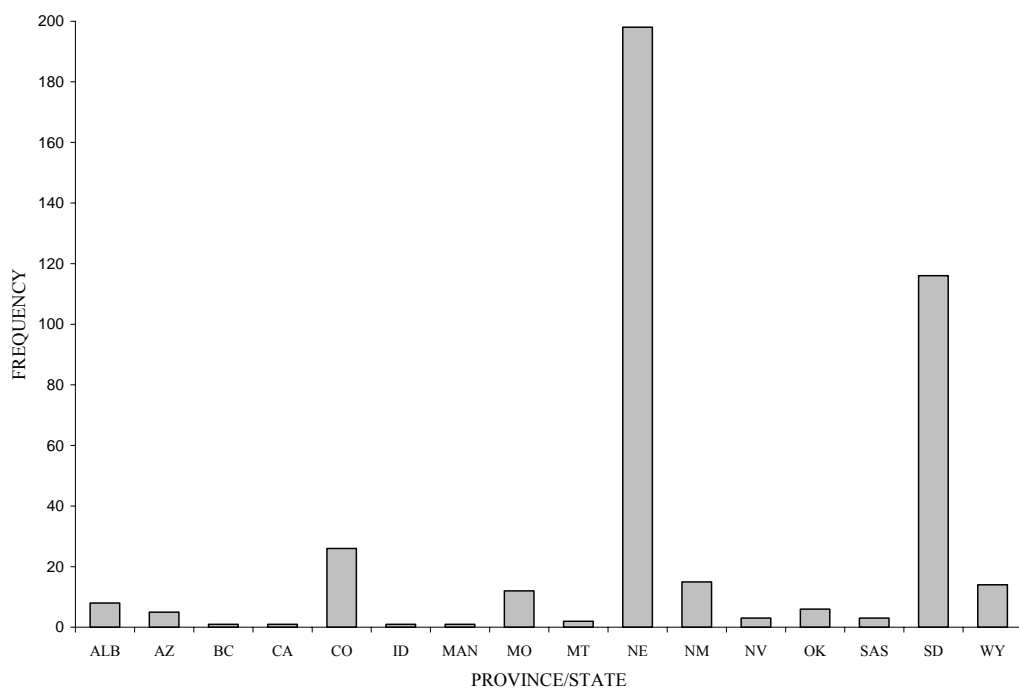
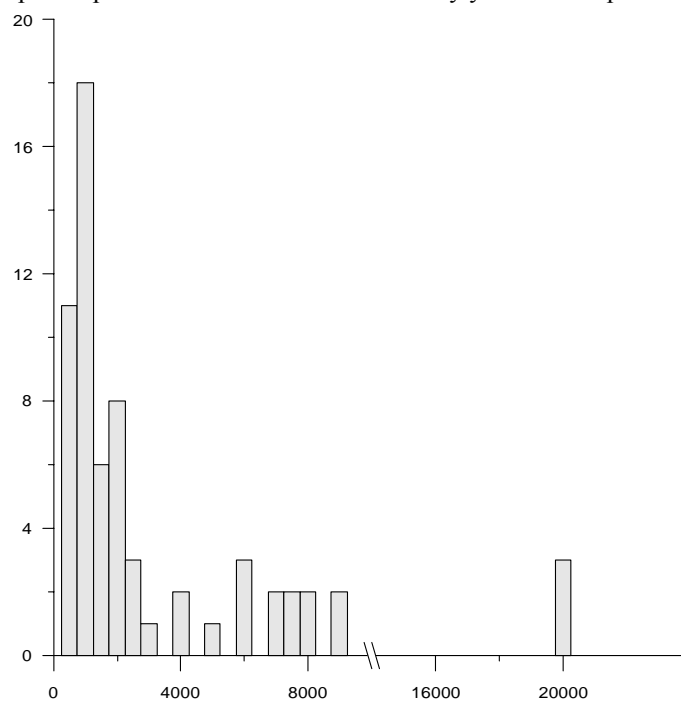


Figure 22. Stable isotope samples for western North America by years before present.



Results

The horn is a solid, bony core which is part of the animal's skull covered by a sheath of hard fibrous horn. The horn sheath grows from the base or skin at the skull. As new growth is formed the old growth is forced away from the skull. The shape that the horn sheath takes is formed by the inner bony core, which also continues to grow and is correlated with age (Miura 1985). Horns are never shed but continue to grow throughout the animal's life. In bison both males and females have horns but vary in size.

The horn sheath samples were removed from the dorsal portion of the right horn using a Dremel variable-speed rotary tool (Figure 23). A 10-x-4-cm section was removed from the sheath and placed in distilled water for approximately 8 hours in order to rehydrate the sheath to allow for the separation of the individual cones. Although the growth rings or cones do not necessarily represent an annual record (Reynolds et al. 1982:997), they do provide a periodic record of the individual bison that can provide us with information on its ecology, diet, health, and possible migration.

Table 7. Samples removed from Gilbert Peak bison skull horn sheath.

Sample No.	Weight (g)
HS-1	0.43
HS-2	3.28
HS-3	5.54
HS-4	0.33
HS-5	1.44
HS-6	0.71
HS-7	1.57
HS-8	2.39
HS-9	3.25
HS-10	2.29

Ten samples of the horn sheath, each representing a single horn cone, were submitted to Beta Analytic for stable carbon and nitrogen isotopic analysis (Table 7). The samples were numbered consecutively from the oldest (HS-1) to most recent (HS-10). In a

similar study, Tieszen et al. (1996) used the horn sheath in determining annual and seasonal diet patterns by further sectioning the annuli. For this study, we did not further section the annuli.

Figure 23. Close-up of horn sheath following removal of sample.



The samples were submitted to Beta Analytic for stable carbon and nitrogen isotope analyses. The pretreatment protocol used by Beta Analytic involves collagen extraction with alkali, which is discussed in detail in the radiocarbon dating section. Each sample supplied sufficient carbon for accurate measurements and the analyses proceeded normally (Hood 2004b). The results are listed in Table 8.

Table 8. Results of stable isotopic analyses of horn sheath samples.

Sample No.	Beta No.	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
HS-1	195622	-21.9	+6.9
HS-2	195623	-21.7	+7.4
HS-3	195624	-20.7	+7.4
HS-4	195625	-20.3	+8.1
HS-5	195626	-22.0	+6.5
HS-6	195627	-20.7	+8.6
HS-7	195628	-22.1	+9.4
HS-8	195629	-22.1	+6.4
HS-9	195630	-21.6	+8.3
HS-10	195631	-22.0	+5.2

The analyses indicate that the horn sheaths provide a record of stable carbon and nitrogen isotope signatures of assimilated foods as was demonstrated in an earlier study by Tieszen et al. (1996). The values indicate

variability in $\delta^{13}\text{C}$ values that range between -20.3‰ and -22.1‰ with a mean of -22.51‰ that indicates a diet that is highly oriented towards C_3 vegetation (Figure 24). This is not unexpected and represents a diet that is similar to modern bison in the Henry Mountains (Van Vuren 1984; Table 6).

The results of the $\delta^{13}\text{C}$ values show little variation which may suggest that C_4 vegetation was not available to this bison (Figure 25). Tieszen et al. (1996) saw similar patterns in high elevation (i.e., Yellowstone) and high latitude (i.e., Wood Buffalo) bison. In areas, such as at Konza and Niobrara, bison have access to a more variable plant community and this is indicated by their $\delta^{13}\text{C}$ values.

In comparing the $\delta^{15}\text{N}$ values with respect to $\delta^{13}\text{C}$ values, Tieszen et al. (1996) found that shifts in values were correlated in the Konza and Niobrara specimens and suggest a shift in diet may have been accompanied by a large degree of stress. However, the circumstances surrounding the diet changes is unknown and may have involved the individuals being moved to its respective preserve which may also account for the stress.

The pattern of changes in $\delta^{15}\text{N}$ values of the Gilbert Peak bison tend to follow that of $\delta^{13}\text{C}$ values (Figure 24). 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 $\delta^{15}\text{N}$ values were an indication of use of lower elevation range. The Gilbert Peak values may reflect a similar migratory pattern of bison using various habitats over the course of its life.

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.

The period from approximately AD 1450 to 1800 has been labeled the Little Ice Age (Fagan 2000) and characterized by reduced temperatures and increased effective moisture, as indicated by a final high stand of the Great Salt Lake (Currey 1990). Glacial advances have also been suggested for this period in the Wind River Range (Richmond 1986), the Colorado Front Range (Benedict 1973), and the Teton Range (Richmond 1986). Mesic indicator small mammal species reappear in deposits from Lamar Cave in Yellowstone National Park (Hadly 1996) and bison are reported as being at their highest Holocene levels (Butler 1978; Frison and Reher 1980). Using historic and modern photographic evidence from the northern Uinta Mountains, Munroe (2003) provides evidence of growing season depression prior to AD 1870. While uniform cooler temperatures and increased effective moisture have traditionally been suggested for the Little Ice Age, more recent research is suggesting more variability (e.g., Jacoby D'Arrigo 1989; Kaplan et al. 2002)

While the Gilbert Peak bison skull alone does not provide definitive evidence for un-

derstanding past climatic conditions, it does provide us with a beginning towards this end. Because herbivores were so abundant in the past they provide important climate proxy. Comparison with modern bison of

known ecology and migration patterns, suggest as those from the Henry Mountains, would provide a more meaningful comparison.

Figure 24. 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).

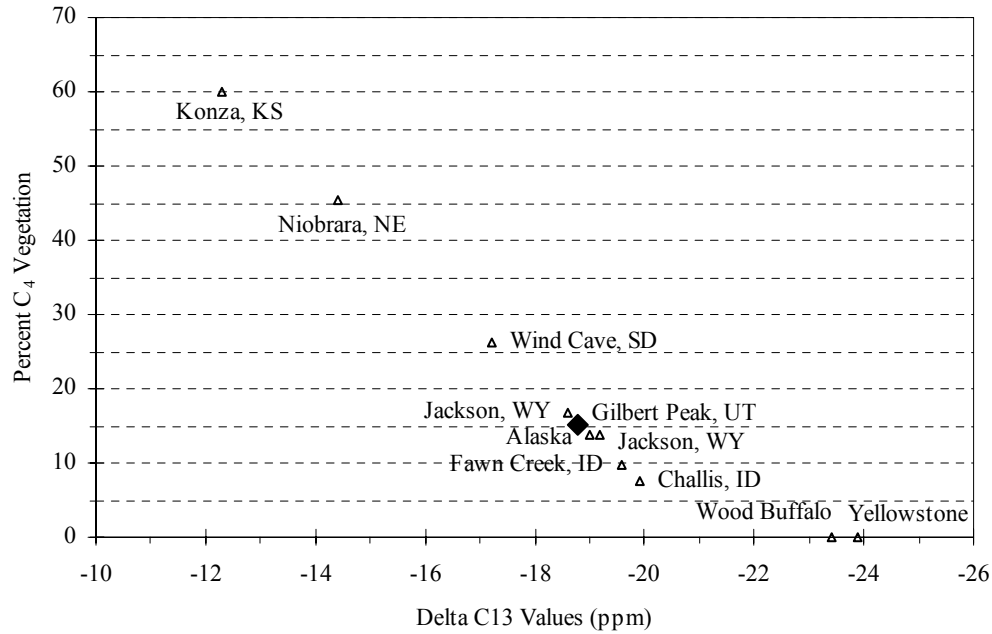
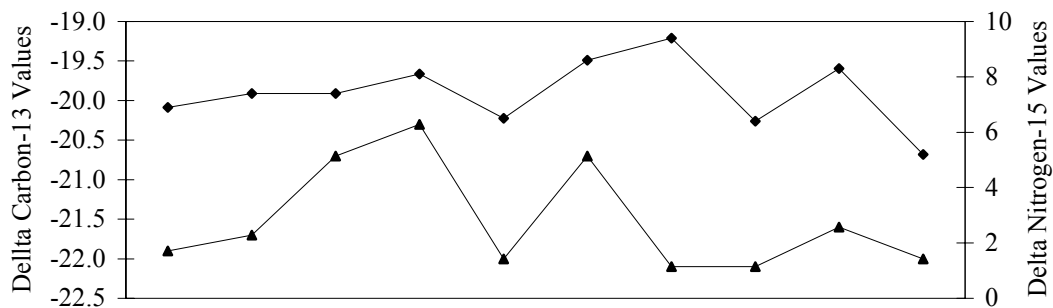


Figure 25. Results of stable carbon and nitrogen analyses performed on horn sheath cones. Results are oriented from oldest (HS-1) on the left to youngest (HS-10) on the right. Upper line is $\delta^{15}N$ values.



Conclusions

By the time Mormon pioneers began settling in Utah bison were probably largely extinct from its western range, all but eliminating the opportunity for biologists to study the animal. Bison today are limited to two small reintroduced herds in the state—the Antelope Island herd in the Great Salt Lake and the Henry Mountains herd in southeastern Utah (Durrant 1952).

A partial bison skull was recovered from the vicinity of Gilbert Peak in the high Uinta Mountains of northeastern Utah at an elevation of 3840 m. Vegetation in the immediate area is generally alpine, but to the east of the find location is the headwaters of Gilbert Creek, a boggy area surrounded by Engelmann spruce. Although bison remains have been discussed in the zoological and archaeological literature these reports tend to be descriptive. This study is unique because it combines traditional craniometric analyses to understand the sex, species, and age at death of the individual, but also uses contemporary chemical analyses to date the age of the specimen and to understand its ecology and potential migration patterns.

Metric analysis of the skull suggests the animal was a mature male, possibly over 10 years of age. The individual was very large and in several measurements of the horn cores is larger than either *B. b. bison* or *B. b. athabasca*, considered to be the largest of the modern bison (McDonald 1981a:108). However, the taxonomic classification of the individual is probably not possible without DNA analysis (e.g., Richards et al. 1993).

Radiometric assay of the skull produced an age of 150 ± 40 yrs BP which calibrates to between cal AD 1665 to 1784. The age of this bison is significant because it falls within a climatic episode known as the Little Ice Age. This climatic period is characterized as a time when temperatures were colder than previous centuries and alpine glaciers around the world were advancing.

The results of the stable carbon and nitrogen isotope analyses suggest this individual was subsisting almost exclusively on C_3 vegetation. The isotopic values from the ten horn sheath samples indicates variability in the $\delta^{15}N$ values that may either reflect annual use of high and lower elevation areas, or possibly periods in the bison's life when water conservation was important. Higher $\delta^{15}N$ values have been linked to higher concentrations of urea in urine either due to water stress or lower quality food protein. This signal may have a climatic component and provide clues to more variability in climate patterns during the Little Ice Age. Larger samples of bison and comparison with modern bison with known ecologies will help to sort out these issues.

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

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 the Great Plains post-glacial ecosystem and a major prey species of native groups prior to European 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 unselective grazers due to their requirement of large volumes of forage. This requirement limits their ability to be selective (Peden 1976). In contrast, an-*

telope are highly selective herbivores, subsisting almost exclusively on sagebrush (Schwartz and Ellis 1981).

4. *Stable carbon 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.*
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 Chisholm (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 the incremental growth of the tooth enamel. By sampling a tooth, particularly the third molar, a geochemical record reflecting the individuals foraging history*

can be extracted at the resolution of subannual (Gadbury et al. 2000; Larson et al. 2001).

Understanding bison ecology and migration patterns through the study of sub-fossil bison is one of the few methods we can reconstruct past conditions. Bison today are confined to small, isolated herds that are typically not allowed to range freely within their historic ranges. If we are to truly manage the few surviving intact public areas in a meaningful way, we must be willing to expend the effort to study how ecosystems have developed through time (e.g., Lyman and Cannon 2004; Cannon and Cannon 2004). 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 (CUMYNP 2002). Studies, such as stable-isotope analysis, provide a means to decipher paleoenvironmental conditions to model future changes and the restoration of habitats. As this study has demonstrated, and previously articulated by Walker (1992), isolated bison skulls can provide significant information that can be used to fill gaps in our understanding of bison.

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**Appendix A:
Sites with Bison Remains**

State	Site Number	State	Site Number
CO	5EA799	ID	10BK26
CO	5GA639	ID	10BM56
CO	5GA1119	ID	10BV30
CO	5GA1155	ID	10BV93
CO	5GA1513	ID	10OA2
CO	5GA1847	ID	ISUM52002
CO	5GA2414	ID	ISUM72003
CO	5JA239	ID	American Falls
CO	5JA344	ID	Rainbow Beach
CO	5JA712	ID	Weston Rockshelter
CO	5MF3	ID	Moonshiner
CO	5MF9	ID	Middle Butte
CO	5MF309	UT	42RI1
CO	5MF398	UT	42UT104
CO	5MF605	UT	42UT150
CO	5MF625	UT	42UT591
CO	5MF630	UT	42UT592
CO	5MF638	UT	42UT636
CO	5MF969	WY	48LN74
CO	5MF1215	WY	48LN317
CO	5MF2631	WY	48LN1468
CO	5MF2747	WY	48SW5
CO	5MF2775	WY	48SW101
CO	5MF2877	WY	48SW998
CO	5MF2912	WY	48SW2302
CO	5MF2913	WY	48SW2385
CO	5MF3450	WY	48SW2590
CO	5RB716	WY	48SW2981
CO	5RB729	WY	48SW5057
CO	5RB2435	WY	48SW5222
CO	5RB2727	WY	48UT199
CO	5RT487	WY	48UT390
CO	5RT971	WY	48UT1186
CO	5RT973		

Appendix B:
Provenience Information of Comparative Bison Specimens
Used In Analyses from Western North America

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 1974: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
Female Specimens			
AMNH M16322	Montana	-	McDonald 1981b:562-565
USNM M122672	Big Dry Creek, Montana	-	McDonald 1981b:562-565
USNM M122685	Big Dry Creek, Montana	-	McDonald 1981b:562-565
UWy C3071	Buffalo Creek, Wyoming	-	McDonald 1981b:562-565
UWy C30	Glenrock, Wyoming	-	McDonald 1981:550-553b
USNM M248950	Malheur Lake, Oregon	-	McDonald 1981b:566-569
USNM M249844	Malheur Lake, Oregon	-	McDonald 1981b: 566-569
USNM M249847	Malheur Lake, Oregon	-	McDonald 1981b: 566-569
USNM M249848	Malheur Lake, Oregon	-	McDonald 1981b: 566-569
USNM M249849	Malheur Lake, Oregon	-	McDonald 1981b: 566-569
USNM M250089	Malheur Lake, Oregon	-	McDonald 1981b: 566-569
USNM M250090	Malheur Lake, Oregon	-	McDonald 1981b: 566-569
USNM M250091	Malheur Lake, Oregon	-	McDonald 1981b: 566-569
USNM M250095	Malheur Lake, Oregon	-	McDonald 1981b: 566-569
<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>			

Appendix C:
Craniometric Data For High Altitude And Western Bison
Used In Comparative Study

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	-	-
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

Specimen	Sex	SHTT	CLUC	TB	VD	CHC	TD	WHCO	GPW	ON	OP	GWA	CW	DEP	AHC	BF	OF
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 M250095	F	410	120	111	47	144	45	199	256	211	478	192	111	85	65	111	137

