"They Went as High as They Choose:" What an Isolated Skull Can Tell Us about the Biogeography of High-altitude Bison

Author: Cannon, Kenneth P.

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Kenneth P. Cannon

Midwest Archaeological Center, Federal Building Room 474, 100 Centennial Mall North, Lincoln, Nebraska 68508-3873, U.S.A., *and* Department of Anthropology and Geography, 810 Oldfather Hall, University of Nebraska, Lincoln, Nebraska 68588-0368, U.S.A. ken_cannon@nps.gov

Abstract

In 2003 a partial bison skull was recovered by Ashley National Forest archaeologists from an elevation of 3840 m (12,600 ft) above mean sea level on Gilbert Peak in the Uinta Mountains of Utah. The skull consists of a portion of the frontal, occipital region, and horn cores including horn sheaths. Through the analysis of the individual cones of the horn sheath, a record of the animal's dietary and migration patterns were obtained. While high-altitude bison remains have been discussed in the scientific literature periodically, they have not gone beyond the descriptive. In addition to descriptive and metric analysis of the skull, radiometric assay and stable isotope analyses were applied. The radiocarbon age of the specimen is 150 ± 40 yr BP (cal. A.D. 1725–1778). Metric analysis of the skull indicates it was an older adult male, which compares well with *Bison bison athabascae* (wood bison) in size and is larger than either *Bison bison bison* (plains 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.

Introduction

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

Documenting the range of mammalian species was an important focus for biologists working in the late 19th and early 20th centuries, especially with respect to shrinking habitat from expanding settlement in the Intermountain West of the United States. This was particularly true of the North American bison (*Bison bison* Linnaeus 1758); it had been reduced to a few hundred individuals at the beginning of the 20th century, and its long-term preservation was uncertain (Shell, 2002: p. viii).

Altitudinal range, as well as latitudinal and longitudinal, were often reported in scientific journals. Fryxell (1926) reported on bison specimens in the Medicine Bow Mountains of Wyoming at altitudes ranging from 2895 to 3658 m (9500 to 12,000 ft), followed by a report on high-altitude bison records from Colorado, Wyoming, and Montana (Fryxell, 1928). High-altitude bison sightings in southern and northern Colorado are also reported by Cook (1930), Warren (1927), and Beidleman (1955). More recently, Wilson (1974a) reported on bison remains from above timberline in the Bighorn Mountains of northern Wyoming. With climate-driven ice/snowfield melting in high-altitude and high-latitude regions, a new source of bison remains has been uncovered (Lee et al., 2006).

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 (2981 m [9780 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. While the Gilbert Peak bison represents a single individual, it does contribute significantly to our knowledge of high-elevation fauna.

This study takes its cue from Fryxell (1928: p. 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; Cannon, 2001). 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. As Walker (1992) explained, there are still temporal and spatial gaps in the Holocene record of bison, and isolated skulls can help fill them. 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: p. 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).
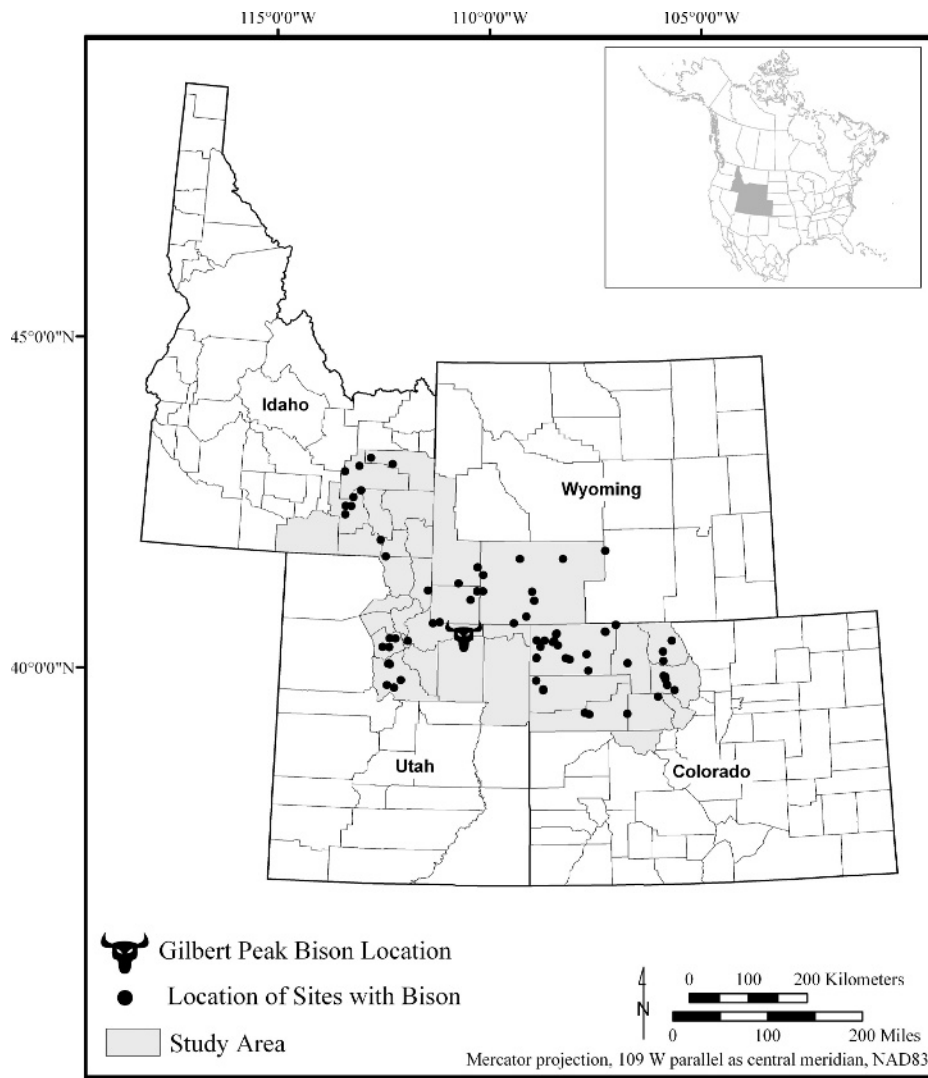
FIGURE 1. Regional map illustrating location of precontact sites with bison remains in relation to Gilbert Peak bison find location.

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 research goal to understand the biogeography of bison in the Intermountain West within the context of long-term climate change (Cannon, 2001; Lyman, 2004).

Environmental Context

U.S. Forest Service archaeologists recovered the Gilbert Peak bison skull from a steep gravel- and boulder-covered ridge southwest of Gilbert Peak at an elevation of 3840 m (12,600 ft) above mean sea level (AMSL) in Summit County along the boundary between the Ashley and Wasatch National Forests (Fig. 1). The area consists of alpine vegetation with surface cobbles common. Soils are shallow and well-drained. Tundra vegetation is present in the immediate area. As defined by Edwards et al. (1995), common species include perennial herbs (*Geum rossi, Silen acaulis, Paronychia pulvinata, Arenaria obtusi-loba, Trifolium nanum, Kobresia myouroides, Polygonum bistor-oides, Eriophorum chamissonis*), perennial grasses (*Deschampsia caespotosa, Festuca ovina, Koeleria cristata, Trisetum spicatum*), sedges (*Carex* sp.), and willow (*Salix* sp.).

To the east, the landscape slopes dramatically into a boggy area with an unnamed lake that is drained by Gilbert Creek, near 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.

Regional Evidence of Bison

The record of bison remains from late Quaternary sites in the region is extensive, and almost exclusively the result of human predation (Cannon, 2004; Fig. 2). The distribution in northern Utah (Lupo and Schmitt, 1997), southeastern Idaho (Butler, 1978; Cannon, 1997; Plew and Sundell, 2000), and southwestern Wyoming (Lubinski, 2000) indicates bison were present throughout the Holocene with population density possibly fluctuating in relation to climate patterns. However, several authors have argued that the sagebrush-steppe never supported large herds of bison (Mack and Thompson, 1982; Daubenmire, 1985), therefore making for an inconsistent resource (Henrikson, 2003, 2004).

Lubinski's (2000) research in southwestern Wyoming focused on the dietary selection of antelope and bison within the context of shifting climatic regimes (Eckerle and Hobey, 1995). His results indicate that archeological bison were more prevalent during
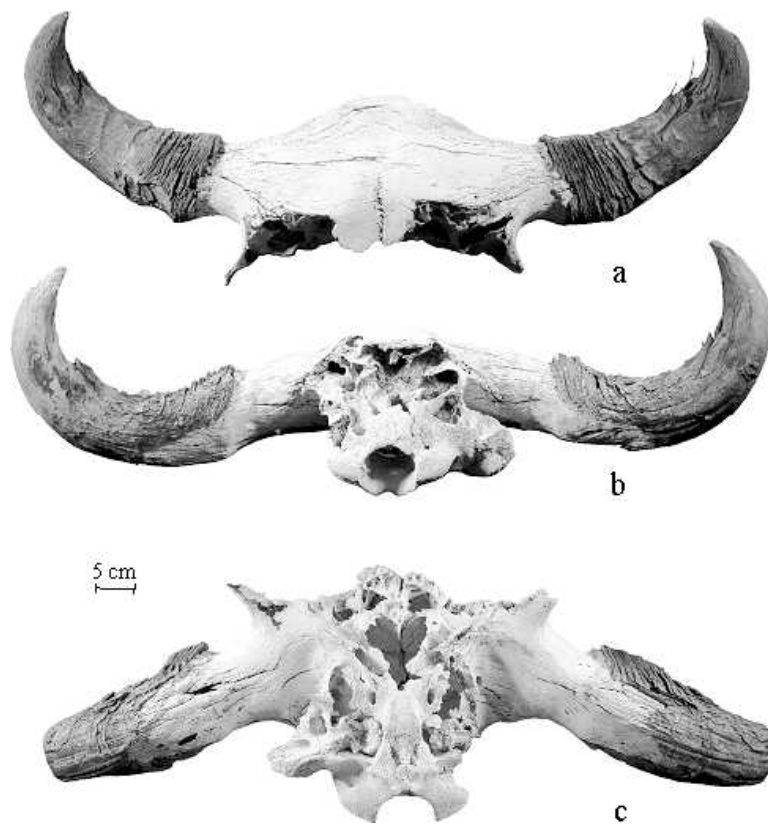
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FIGURE 2. Gilbert Peak bison skull: (a) dorsal view, (b) nuchal view, and (c) basal view.

moist periods of the Holocene (10,000–9000 yr BP; 3500–1800 yr BP; 500–150 yr BP).

In the southern Rocky Mountains, preservation of faunal remains 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 (Kornfeld and Frison, 2000; Stiger, 2001; Pitblado, 2003).

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 (*Mammuthus* sp.), mastodon (*Mammut* sp.), horse (*Equus* sp.), camel (*Camelops* sp.), and bison (*Bison* sp.). 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) and Yellowstone National Park (Meagher, 1973).

Regional evidence indicates bison 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.

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 foramen magnum present (Fig. 2). Colonies of the lichen *Xanthoria elegens* are present on the horn sheaths and in the interior of the skull. 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: p. 344).

Sexing of the Gilbert Peak bison was initially 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: p. 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. All available skull measurements follow those defined by McDonald (1981a: pp. 43–47) as modified from Skinner and Kaisen (1947) and are presented in Table 1. 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 (Fig. 3; Table 2).

Assessing age at death of archaeological 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. McHugh (1958) and Fuller (1959) suggested 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 for individuals. Counting the number of growth rings on the horn sheath was also suggested by McHugh (1958) as a means of estimating age. However, Reynolds et al. (1982) disregarded the counting of rings as a reliable estimate of age.

Suture closure is another means of assessing relative age (McDonald, 1981a). For the Gilbert Peak skull, the sagittal frontal suture is almost completely fused (Fig. 2a), suggesting an adult.

TABLE 1

Skull measurements following McDonald (1981a). All measurements are presented in millimeters except for those marked in degrees. Data on *Bison antiquus occidentalis* are from McDonald (1981a:Table 25), *Bison bison athabascae* from McDonald (1981a: Table 34), *Bison bison bison* from McDonald (1981a: Table 29), and high altitude bison from McDonald (1981b: 550–553) and Wilson (1974: Table III). All specimens used in analysis are males.

Measurement	Gilbert Peak	Bison antiquus occidentalis				Bison bison athabascae				Bison bison bison				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
Dorsoventral 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
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 premaxillae (OP)	—	25	564.3	511–606	24.8	7	578.6	562–604	15.2	56	535.2	500–583	17.0	—	—	—	—
Distance, nuchal lint to 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°	—	—	—	—

Wilson (1975: Figs. 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 an 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: Fig. 7 lower), an estimated age at death for the Gilbert Peak bison is 12 years (Fig. 4).
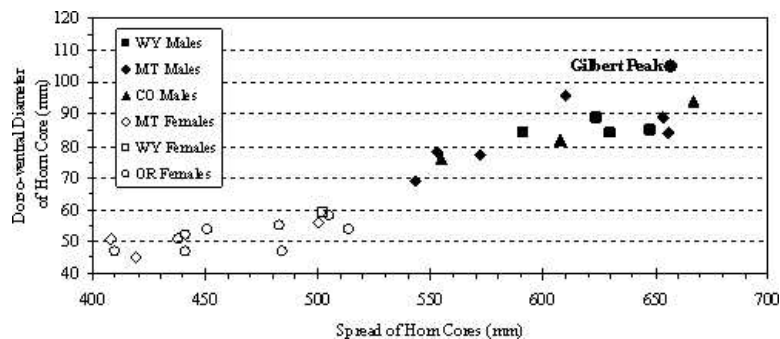

FIGURE 3. Plot of Gilbert Peak bison skull in relation to male bison skulls from western United States specimens. Data presented in Table 2. WY = Wyoming, MT = Montana, CO = Colorado, and OR = Oregon.

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TABLE 2

Craniometric data for high altitude and western bison used in comparative study. Measurement abbreviations are presented in Table 1. All measurements are presented in millimeters except for those marked in degrees. AMNH = American Museum of Natural History, CoMNH = Colorado Museum of Natural History, UCy = University of Calgary, UCM = University of Colorado Museum, UM = University of Montana, USGS = U.S. Geological Survey, USNM = University of Nebraska State Museum, UWy = University of Wyoming, BH = Bighorn Mountains, Wyoming, specimen, FC = Fawn Creek, Idaho, specimen.

| 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
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
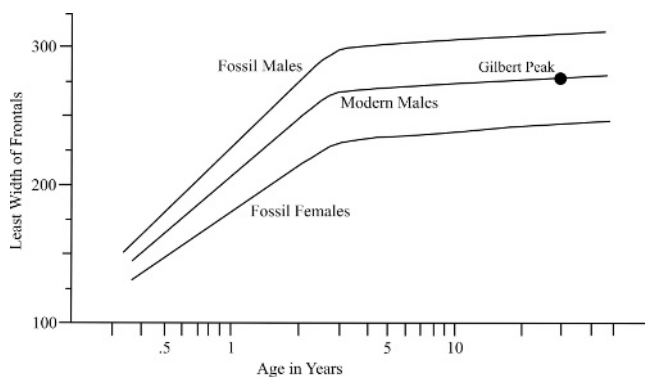
FIGURE 4.   Semi-log plot of least width of frontals to individual age in late Pleistocene and modern bison skulls (adapted from Walker, 1992: Fig. 7).

PREPARATION

The bison skull was recovered from the surface on the southwest slope of Gilbert Peak. The skull had been known for several years in the Ashely National Forest prior to it being recovered. A cursory survey of the immediate area did not produce any post-cranial elements. While the context of the substrate would normally not preserve bone, and transport by humans is possible and has been noted ethnohistorically (Reeves and Peacock, 2001), I am assuming the bison died close to its find spot. No formal stabilization of the specimen was conducted, except for the removal of adhering sediments with a soft brush.

RADIOCARBON DATING RESULTS

An 11.79 g sample from the occipital bone of the skull was removed and submitted to Beta Analytic (Miami, Florida) for

TABLE 3

Results of stable isotope analysis of modern North American bison specimens. Alaska data from Bocherens et al. (1994: Table 4); Konza, Kansas; Niobrara, Nebraska; Wood Buffalo, Northwest Territories; and Yellowstone, Wyoming, data from Tieszen et al. (1996); Wind Cave, South Dakota, data from Tieszen (1994: Table 5); and Fawn Creek, Idaho, data from Cannon (1997: Table 6). $\delta^{13}C$ values presented for the pre-1800 specimens, Gilbert Peak and Fawn Creek are those measured and uncorrected. The values in parentheses are adjusted by 1.5‰ as suggested by Tieszen et al. (1996) when comparing Holocene samples prior to A.D. 1800 with modern samples.

Specimen	Collagen rank	Yield (%)	Nitrogen (%)	Carbon (%)	C/N	$\delta^{13}C$	$\delta^{15}N$	Apatite $\delta^{13}C$
Gilbert Peak	—	—	—	—	—	−18.8 (−20.3)	+7.3	—
Fawn Creek, ID	3	25.9	14.8	41.5	3.3	−19.6 (−21.1)	+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±0.2	+6.4±0.23	—
Wood Buffalo, NWT	—	—	—	—	—	−23.9	+6.6	—
Yellowstone, WY	—	—	—	—	—	−23.4	+6.9	—

radiocarbon assay using the accelerator mass spectrometry (AMS) technique. The radiocarbon dating procedure proceeded normally, and the sample contained adequate carbon for dating. The $^{13}C/^{12}C$ 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 $^{15}N/^{14}N$ ratio was also measured for this specimen, which produced a value of 7.3‰ (Hood, 2004a). Published $\delta^{15}N$ values for bison range from 2.9‰ to 6.9‰ (Cannon, 1997; Table 3; Fig. 5).

The radiocarbon age obtained is 150 ± 40 yr BP (Beta-192144). At the 2σ level (95%), the calibrated results range from cal. A.D. 1660 to 1950 with intercepts at cal A.D. 1680, 1740, 1810, 1930, and 1950 (Talma and Vogel, 1993; Stuiver et al., 1998; Table 4). Statistically, this bison likely died during the early to mid-18th century.

Bison Taxonomy

Since the 19th century, there has been controversy surrounding the species of bison occupying the Rocky Mountains. The earliest accounts are rife with descriptions of the exploits of the "Woodland or Mountain Bison" (e.g., Christman, 1971). Various historical accounts (e.g., Norris, 1880) of the "mountain" bison indicate they "were more hardy, fleet, and wary, and had darker finer, curlier hair" than the plains bison (Meagher, 1973: pp. 14–15).

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: p. 1). In the latter part of the 19th century, biologists recognized a distinct form of bison in northern Canada, formally described as the subspecies *B. b. athabascae* by Rhoads (1897), based on a single specimen he did not directly observe (van Zyll de Jong, 1986: p. 1). While most biologists agreed with Rhoads's designation of *B. b. athabascae* being at least subspecifically distinct (e.g., Skinner and Kaisen, 1947; McDonald, 1981a), some felt that the differences in the two subspecies, *B. b. athabascae* and *B. b. bison*, were of little consequence (van Zyll de Jong, 1986: p. 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 (van Zyll de Jong, 1986). 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.

In response to Skinner and Kaisen, 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. He suggested 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) suggested 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. athabascae* is more probably "a direct and little differentiated descendant of
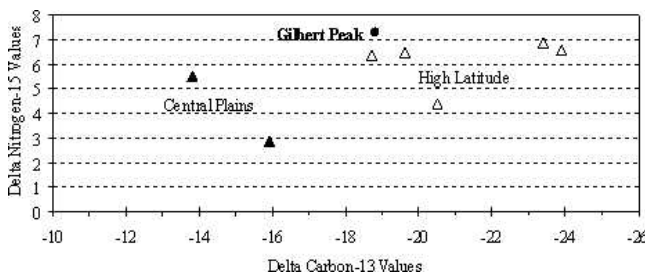

FIGURE 5. Plot of $\delta^{15}N$ against $\delta^{13}C$ values for modern North American bison specimens from high altitude, high latitude, and central Great Plains. Data from Bocherens et al. (1994), Tieszen (1994), Tieszen et al. (1996), and Cannon (1997).

TABLE 4
Results of calibration using CALIB 4.4.

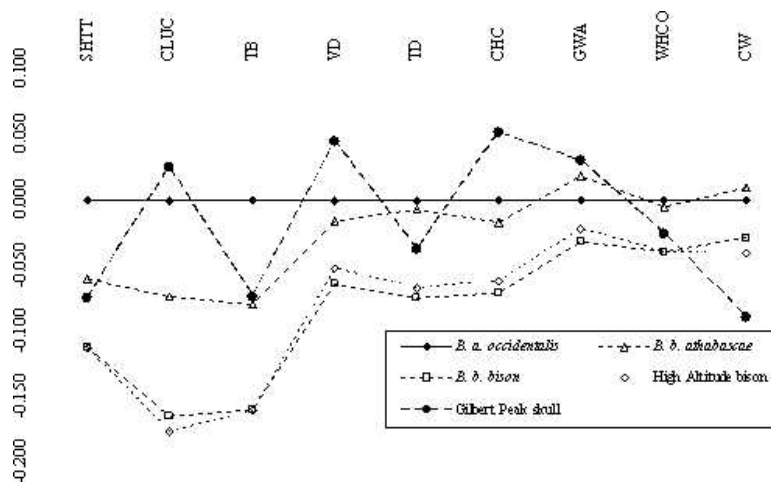| Percent area enclosed	cal. A.D. age ranges	Relative area under probability distribution
68.3 (1σ)	1672–1695	0.150
	1725–1778	**0.362**
	1799–1813	0.097
	1839–1876	0.199
	1917–1949	0.192
95.4 (2σ)	**1665–1784**	**0.480**
	1790–1890	0.346
	1909–1950	0.174

FIGURE 6. Ratio diagram comparing 10 skull dimensions of the Gilbert Peak specimen in comparison with *Bison bison bison*, *Bison bison athabascae*, 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. athabascae* and *B. b. bison* from McDonald, 1981a: Tables 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. See Table 1 for measurement abbreviations.

[Beringian] *B. b. occidentalis*" (van Zyll de Jong, 1986: p. 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: p. 18; Fig. 6).

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 according to van Zyll de Jong (1986: pp. 54–55). Specifically, the boreal forest ecotone acted as a natural barrier to contact with *B. b. bison* in the grasslands to the south minimizing interbreeding and potentially promoting "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 genetic study, Wilson and Stroebeck (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. Stroebeck's (1992) results from an earlier study led him to conclude that the genetic isolation of bison populations produced the morphological variability apparent in these populations.

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 was probably a result of the founder effect and genetic drift which resulted "from the small number of transfers between herds that have occurred, [which] are probably responsible for the uniqueness of these populations" (Wilson and Stroebeck, 1999: p. 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 indicated indigenous Yellowstone bison were "driven to the area by hunters" (Wilson and Stroebeck, 1999: p. 493) and, therefore, represent *mountain-dwelling plains bison* (emphasis mine).

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. athabascae* 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: Fig. 16), as well as that of Walker (1992: Fig. 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 (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 characteristic is smaller with a positive value indicating a larger attribute (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 (Fig. 6). Specifically, a comparison of select horn core measurements indicates that the Gilbert Peak bison skull is within the range of each of these groups (Fig. 7).

The Gilbert Peak skull horn core morphology is more similar to *B. bison athabascae*, 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 is that genetic isolation of populations may be expressed in the phenotype (see Wilson and Stroebeck, 1999). Wilson (1974b) illustrated a similar situation from the 10,000-year-old Casper site in which phenotypic characteristics of two populations may have contributed to the single herd. However, he suggested 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). More interestingly, the Gilbert Peak bison is larger than all of the sample populations, including the standard (*B. antiquus occidentalis*) in several horn core dimensions (Fig. 6). A more definitive understanding of the genetic relatedness of intermountain populations will have to wait for genetic analysis, such as mtDNA (e.g., Shapiro et al., 2004).

Results of Stable Isotope Analyses

One aspect of this research is addressing the ecology and seasonal movement of mammals that no longer occupy their
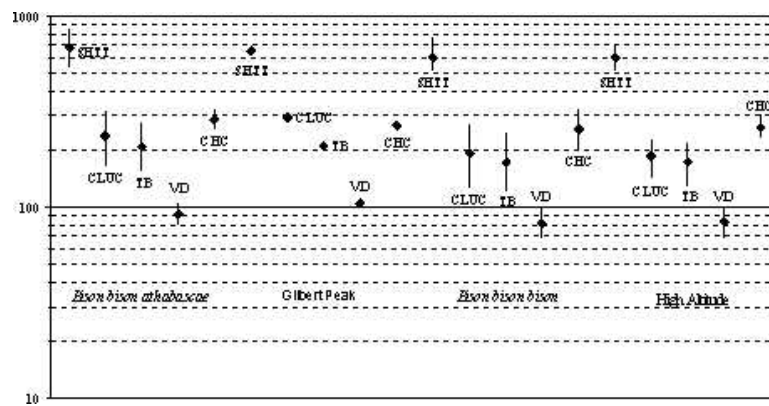
FIGURE 7. Comparison of select horn core measurements of Gilbert Peak bison skull with other taxonomic and regional groups to illustrate amount of overlap in range of measurements. See Table 1 for measurement abbreviations.

original range. This can provide us with information that may be useful in reestablishment of habitats and other conservation biology issues (e.g., Lyman and Cannon, 2004), 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 predicament 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 had different food resources, we should expect this to be evident in the bison's diet (Chisholm et al., 1986: p. 193; Table 3). Stable isotope analysis has been applied to modern ungulates (e.g., Tieszen et al., 1979; Vogel et al., 1978) as well as to 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). 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). In terrestrial environments, two main categories of plants are recognized based on their carbon-fixation pathways, which are clearly distinguished by their stable carbon isotope ratios. The C_3 plants 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‰.

Warm weather and tropical herbaceous plants, such as blue grama (*Bouteloua gracilis*), big bluestem (*Andropogon gerardi*), and buffalo grass (*Buchloe dactylides*), are classified as C_4 and have a $\delta^{13}C$ value between −9 and −16‰ with an average around −13‰ (Smith and Brown, 1973; Bocherens et al., 1994). 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 (crassulacian 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.

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 altitude, a corresponding increase in C_3 species is expected (Boutton et al., 1980; Tieszen, 1994).

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%, respectively, decreasing to 35% 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).

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. 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 (e.g., Thompson et al., 1993). This temporal variable is another complicating factor involved in the interpretation of isotopic signals from paleosamples (Tieszen, 1994). A number of recent studies have demonstrated the value of herbivore isotopic signatures for discerning changes in vegetation communities (e.g., Connin et al., 1998) within herd variability (e.g., Gadbury et al., 2000) and behavior (e.g., Larson et al., 2001).

STABLE NITROGEN ISOTOPE ANALYSIS

Another stable isotope that is linked to trophic level and potentially important for investigating diet and herbivore migration is $\delta^{15}N$. Nitrogen (N_2) 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 $\delta^{15}N$ values. In examining horn sheath annuli of bison from the Central Plains, Tieszen (1994) identified a change in $\delta^{13}C$ values accompanied by changes in $\delta^{15}N$ that he interpreted as a large degree of stress undergone by these individuals with shifts in diet. The researcher did not identify the specific cause of the

TABLE 5

Results of stable isotopic analyses of horn sheath samples (Hood, 2004b). Adj $\delta^{13}C$ values illustrate enrichment of 3.1‰ between keratin and diet (Cerling and Harris, 1999). Percent C_4 vegetation is following Brooks (1995).

Sample no.	Weight (g)	Beta no.	$\delta^{13}C$	Adj $\delta^{13}C$	$\%C_4$	$\delta^{15}N$
HS-1	0.43	195622	−21.9	−18.8	15.20	+6.9
HS-2	3.28	195623	−21.7	−18.6	16.50	+7.4
HS-3	5.54	195624	−20.7	−17.6	23.40	+7.4
HS-4	0.33	195625	−20.3	−17.2	26.21	+8.1
HS-5	1.44	195626	−22.0	−18.9	14.48	+6.5
HS-6	0.71	195627	−20.7	−17.6	23.45	+8.6
HS-7	1.57	195628	−22.1	−19.0	13.79	+9.4
HS-8	2.39	195629	−22.1	−19.0	13.79	+6.4
HS-9	3.25	195630	−21.6	−18.5	17.24	+8.3
HS-10	2.29	195631	−22.0	−18.9	14.48	+5.2

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 $\delta^{15}N$ ratios. They suggested 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 yr^{-1} 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 Holocene bighorn sheep (*Ovis canadensis*) from Mummy Cave in northwestern Wyoming, argued that changes in $\delta^{15}N$ 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 climate change. Bison from the high altitudes moving into lower elevation grasslands of the surrounding basins should illustrate similar patterns: low $\delta^{15}N$ values for high-elevation grasslands and high $\delta^{15}N$ values for low-elevation grasslands.

RESULTS

The horn is a solid, bony core which is part of the animal's skull and is covered by a sheath of hard fibrous horn. The shape that the horn sheath takes is formed by the inner bony core, both of which continue to grow and are correlated with age (Miura, 1985).

Horn sheath samples were removed from the dorsal portion of the right horn using a Dremel variable-speed rotary tool. A 10- × 4-cm section was removed from the sheath and placed in distilled water for approximately 8 h 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), they do provide a periodic record of the individual bison that can provide us with information on its ecology, diet, health, and possible migration.

Ten samples of the horn sheath, each representing a single horn cone, were submitted to Beta Analytic for stable carbon and nitrogen isotopic analysis. The samples were numbered consecutively from the oldest (HS-1) to most recent (HS-10). The pretreatment protocol used by Beta Analytic involves collagen extraction with alkali. Each sample supplied sufficient carbon and nitrogen for accurate measurements, and the analyses proceeded normally (Table 5).

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 (1994). The values, adjusted by 3.1‰ for enrichment between keratin and diet (Cerling and Harris, 1999), indicate variability in $\delta^{13}C$ values that range between −17.2‰ and −19.0‰, with a mean of −22.51‰, which indicates a diet that is oriented toward C_3 vegetation (Fig. 8). This is not unexpected and represents a diet that is similar to modern bison in the Henry Mountains (Van Vuren, 1984). However, the large percentage of C_4 vegetation in the diet is unusual for a bison living in high-altitude environments. The C_4 vegetation may result from seasonal migrations to low elevations, but may also represent a climatic signal of drought conditions during the 18th century.

The pattern of changes in $\delta^{15}N$ values of the Gilbert Peak bison tend to follow that of $\delta^{13}C$ values (Fig. 9). In general, as $\delta^{15}N$ values increase, the $\delta^{13}C$ values become less negative. The Gilbert Peak values may reflect a similar migratory pattern of this 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 consume. With the elimination of urea collagen, $\delta^{15}N$ values are elevated. As Fizet et al. (1995) related, protein quality also has an effect of lower $\delta^{15}N$ 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 $\delta^{15}N$ 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) argued that higher $\delta^{15}N$ 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 yr BP. Other paleoclimatic proxy data support this interpretation. The elevated levels of $\delta^{15}N$ 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 A.D. 1450 to 1800 has been labeled the Little Ice Age (Fagan, 2000) and was characterized by reduced temperatures and increased effective moisture, as indicated by a final high stand of the Great Salt Lake (Currey, 1990). An increase in sagebrush pollen and higher water levels at Ruby Marsh during the last 500 years indicates "the coolest and/or moistest conditions since the early Holocene," presumably a Little Ice Age signal (Thompson, 1992). Glacial advances have also been suggested for this period in the Wind River Range
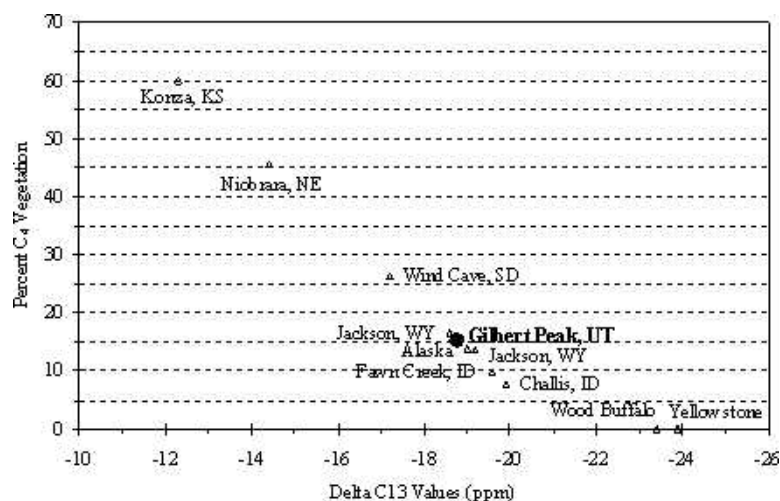
FIGURE 8. Percent C$_4$ vegetation is individual bison diet based upon δ^{13}C values as computed by Brooks (1995: p. 77). Samples are arranged from south (left) to north (right). KS = Kansas, NE = Nebraska, SD = South Dakota, WY = Wyoming, ID = Idaho, and UT = Utah.

(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) provided evidence of growing season depression prior to A.D. 1870. While uniform cooler temperatures and increased effective moisture have traditionally been suggested for the Little Ice Age, recent research is suggesting more variability (e.g., Jacoby and D'Arrigo, 1989; Kaplan et al., 2002).

Local tree-ring records from the Uinta Basin Watershed indicate "the most intense dry regime in the proxy record [A.D. 1226–2000] occurred during the late 18th century from 1772 through 1786." 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 (Gray et al., 2004: p. 953). Earlier in the 18th century, decade-long droughts are also present. These periods of drought overlap with the radiocarbon date obtained from the Gilbert Peak bison and may provide an explanation for elevated δ^{15}N values and the small C$_4$ vegetation component derived from the δ^{13}C value obtained from the skull (−18.8‰ or 15.17%). Another possibility is that the bison lived a majority of its life at lower alpine elevations, and the skull was transported to the high country by humans.

Conclusions

In 2003 a partial bison skull was recovered by Ashley National Forest archaeologists from an elevation of 3840 m (12,600 ft) AMSL in the Uinta Mountains. The skull consists of a portion of the frontal, occipital region, and horn cores including horn sheaths. While high-altitude bison remains have been discussed in the scientific literature periodically, they have not

gone beyond the descriptive. The radiocarbon age of the specimen is 150 ± 40 yr BP (cal A.D. 1725–1778). Metric analysis of the skull indicates it was an older adult male, which compares well with *Bison bison athabascae* (wood bison) in size and is larger than either *Bison bison bison* (plains 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. Stable carbon and nitrogen isotopic signatures were obtained from 10 individual cones from the preserved horn sheath. The results suggest a diet oriented toward cool season C$_3$ vegetation but with a significant contribution from warm season C$_4$ vegetation. The more positive δ^{13}C values and higher δ^{15}N values may be a climate signal of warmer or more arid conditions, a record preserved in the local Uinta Basin tree-ring record. 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 paleoecology.
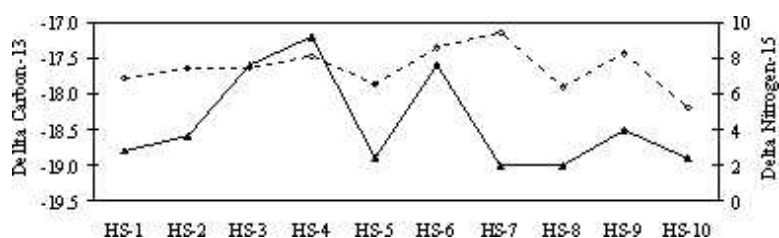
Acknowledgments

FIGURE 9. Results of stable carbon and nitrogen analyses preformed on horn sheath cones of the Gilbert Peak bison. Results are oriented from oldest (HS-1) on the left to youngest (HS-10) on the right. Upper dotted line is δ^{15}N values. δ^{13}C values (solid line) have been adjusted for keratin enrichment of 3.1‰.

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Hughes, Alan Osborn, and Larry Tieszen. I also thank Mary Anne Davis, Kristen Jensen, Joel Janetski, and Mary Sullivan for providing information on bison site locales. Danny Walker, Jerry McDonald, Michael Wilson, and C. R. van Zyll de Jong also graciously provided me with information on bison and access to their databases.

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