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CARBON STABLE ISOTOPIC ANALYSIS OF BISON DENTITION

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ABSTRACT—Understanding how bison behaved in the past can provide key insights for today's managers, ecologists, and anthropologists. However, the direct application of both historic documentation and modern field observations may not provide the necessary insights for understanding bison behaviors in archeological and paleontological contexts. In order to develop a better understanding of possible behavior within these contexts, we have developed individual foraging histories for 22 *Bison bison* from the Glenrock Buffalo Jump assemblage of the Plains Late Prehistoric period in Wyoming and four Pleistocene *B. priscus* from the Ukraine. Incremental stable carbon isotopic values of dental enamel were used to determine foraging histories. The progressive development of enamel allows for samples to be selected that represent distinct periods of an individual's life. Comparison of these dietary patterns among members of a herd can demonstrate foraging behaviors of

cohorts and, in turn, the entire assemblage. Application of this high-resolution paleodietary technique provides new information on bison behaviors in a paleontological and archaeological context.

KEY WORDS: archeology, bison, dentition, grasslands, paleoecology

Introduction

Bison research can be divided into three temporal perspectives. The first perspective covers the present, with modern observations being made by biologists, ecologists, and managers (Peden et al. 1974; Green and Rothstein 1993a, 1993b; Komers et al. 1993; Berger and Cunningham 1994; Delgiudice et al. 1994). The second perspective exists through historic documentation (Hornaday 1887; Schultz 1974; Bamforth 1987; Turpin 1987). These records recount some of the earliest Euro-American encounters with *Bison bison*, providing the popular image of great herds swarming across the Great Plains. Historic records also document the bison's near decimation during the late 19th century (Garretson 1938). The third perspective encompasses the many millennia prior to Euro-American expansion in North America. This "precontact" period extends from the early 19th century, with *B. bison* and earlier forms such as *B. antiquus* and *B. occidentalis,* into the early Pleistocene, when *B. sivalensis* ranged the Eurasian woodlands, or even back to the bison primogenitor, *Leptobos,* of the late Pliocene (MacDonald 1981).

Knowledge of precontact North American bison is primarily limited to fossil and subfossil remains of individuals and assemblages. In archaeological and paleontological contexts, bonebeds consist of the remains of individuals from discrete mortality events. All of the individuals from a mortality event comprise an assemblage. Physical data such as an assemblage's composition, the season of its mortality, and the biometrics of its members can be directly assessed from bonebeds (Bedord 1974; Reher 1974; Zeimens and Zeimens 1974; Todd 1987a; 1987b; Todd et al. 1996), but subtler information regarding bison behavior is not so easy to discern. Developing ideas about behavior from paleontological and archeological contexts can be difficult. While analogies for precontact bison behaviors can be developed from the historic and modern periods, these data may not reflect well what occurred in the past.

During the historic period, bison were responding to changes in Native American predation brought about by the horse and gun, the loss of secondary

range due to Euro-American expansion and settlement, and also the wholesale slaughter for coarse fur (Hornaday 1887; Garretson 1938; Schultz 1974).

Modern observations of bison behavior do serve as a general basis for models, but bison are no longer a free-ranging and freely interbreeding species. Modern herds have been revived after passing through a tremendously narrow genetic bottleneck from the few bison left at the turn of the 20th century (Garretson 1938; Berger and Cunningham 1994). Thus, direct observations of modern bison and models developed from the historic record should be applied with caution to precontact bison.

Refining our understanding of bison paleoecology can aid in understanding the ecological processes of both the Pleistocene and Holocene. Until recently, bison played a major role in shaping their environments. By the late Pleistocene, bison had become one of the three dominant, above-ground mammalian herbivores of North America (Guthrie 1990). With the dramatic ecological restructuring of the Pleistocene-Holocene transition, bison became the principal large-bodied herbivore on the continent. But as much as these creatures shaped the expanding continental grasslands, their environment also shaped them (Wilson 1974, Walker 1986; Guthrie 1990). Although there is no consistent agreement on the taxonomy, the phenotypic changes in bison (Geist 1991) and the remarkable persistence and success of this genus make it a prime candidate for paleoecological studies. Large numbers of fossil and subfossil specimens, as well as many distinct assemblages, range across North America, covering the middle Pleistocene through the historic period, providing good representation in both space and time (Fawcett 1987).

The archeological record from the late Pleistocene, approximately 12,000 years before the present, to the mid-19th century indicates that for some human groups, bison were an extremely important resource. Subfossil bison assemblages resulting from human predation also demonstrate good spatial and temporal representation (Fawcett 1987). Thus, a more robust understanding of bison paleoecology can provide interpretative insights into cultural processes of the bison's chief Holocene predator, *Homo sapiens sapiens*. Additionally, developing a better understanding of bison paleoecology may provide further insights into the evolution of continental grasslands from the perspective of its dominant, above-ground consumer. Unfortunately, bonebeds do not provide straightforward information concerning behaviors. But concrete insights into behaviors, such as seasonal landscape use, foraging patterns, herd fidelity or home range overlap, can be developed from these contexts.

This study builds upon several lines of evidence to advance our understanding of bison behavior in the undocumented past. We begin by defining a bison's diet at specific points in its life through stable carbon isotopic analysis of dental enamel. Progressively developing tissues such as hair, horn sheaths, and teeth provide a chain of temporally specific isotopic values (White 1993; Tieszen 1994; Larson 1995; Cerling and Sharp 1996; Gadbury et al. 2000). Stable carbon isotopic, or $\delta^{13}C$, values of these tissues provide insights into forage selection of C_3 or C_4 plants (Chisholm et al. 1986; Huebner 1991; MacFadden and Cerling 1996; Connin et al. 1998). The relative distributions of these plants are generally predictable in major biomes (Terri and Stowe 1976; Sims et al. 1978; Tieszen et al. 1979; Boutton et al. 1980; Rundel 1980; Tieszen 1994) (Fig. 1). Changes in ^{13}C values of progressively formed tissues can document changes in an animal's forage and possibly its habitat. If an isotopic value can be tied to a specific period of an individual's life, it then becomes possible to reconstruct a temporally specific foraging history.

After establishing a temporally specific foraging history for an individual, we then take advantage of bison herd structure. Bison herds are comprised of successive, like-aged groups known as cohorts. Comparisons within cohorts of individual members' foraging histories can provide ideas of cohort dietary patterns, fidelity, and possible landscape use. Comparisons of foraging patterns and behaviors between cohorts of an assemblage help to build insights into long-term landscape use and herd behavior.

Bison have been chosen for our exploratory study based upon a number of factors. Bison have been the dominant mammalian herbivore for North American grassland ecosystems during the Holocene. Earlier, during the Pleistocene, bison were a significant member of steppe, savanna, and woodland ecosystems as well (MacDonald 1981; Gutherie 1990). A significant body of literature on bison has been built on modern, historical, archaeological, and paleontological data and observations. Our study can be replicated to both verify and potentially enhance the original results of numerous archaeological and paleontological collections containing large numbers of bison bones. Exploration of bison paleoecology can significantly advance our understanding of the evolution North American grassland-savanna ecosystems.

Bison are not limited only to the Pleistocene and Holocene of North America. They have been a component in human cultural systems of the Northern Hemisphere for at least 100,000 years, as evidenced by the Upper Paleolithic cultural associations with the large bison bonebeds of

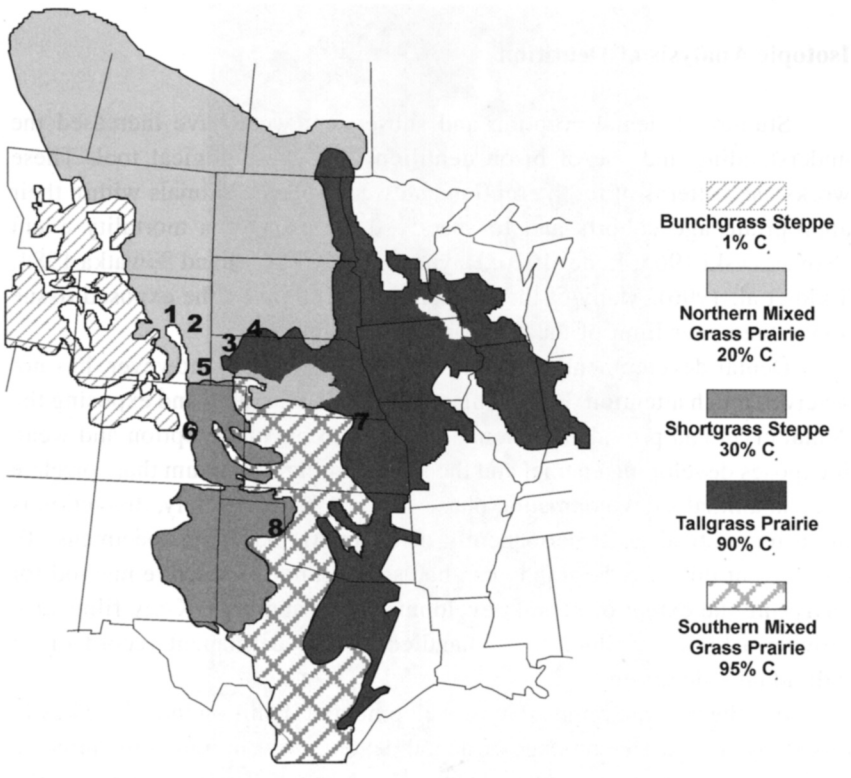

Figure. 1. Distribution of major grasslands illustrating percentage composition of C_4 grasses, and the sampling sites used in this study: 1 = Casper, WY; 2 = Glenrock, WY; 3 = Ft. Robinson, NE; 4 = Hudson-Meng Site, NE; 5 = Wheatland, WY; 6 = Hartsel, CO; 7 = Lake Theo, TX.

Amvrosievka and Anetovka II in the Ukraine and of Coudlous and Maural in France, and by renditions of bison in Upper Paleolithic art of central Europe. This paper represents an important beginning for future studies encompassing a larger variety of temporally and spatially dispersed assemblages. In turn, we may gain potentially significant insights into possible changes in bison foraging habits, adaptive behaviors, ecological changes, and adaptive responses in cultural systems that included bison as a prey species not necessarily constrained to late Pleistocene to Holocene North American systems.

Isotopic Analysis of Dentition

Studies of dental eruption and subsequent wear have increased the understanding and use of bison dentition as a chronological tool. These works use patterns of tooth eruption and wear to place animals within their appropriate age cohorts and to specify the season of a mortality event (Novakowski 1965; Reher 1970; Haynes 1984; Wegrzyn and Sewatka 1984; Todd et al. 1996). Many of these studies concentrate on the exposed tissue above the upper limit of the alveolus, or gum line.

Dental development occurring below the gum line, however, has not received much attention. Removing portions of a mandible and exposing the dental crypt can provide additional information beyond eruption and wear. It exposes developing enamel and the root-forming cementum that correlate with an animal's developmental phase (Fig. 2). Unfortunately, dissection is often impractical, as it permanently damages irreplaceable specimens. To circumvent this, x-radiography can be used as a nondestructive method for analyzing the extent of dental development in mandibles. X-ray films also provide a highly visible, easily handled, nearly permanent record of an individual's dentition.

It is the orderly, progressive development of dentition that is the key to this study. The degree or stage of dental development in immature animals, and the dental wear patterns of mature animals, provide age estimates. In the context of an assemblage, these data are used to define the cohorts and to develop the age structure of an assemblage. By linking the progressive stages of dental development to an individual's age, it becomes possible to target specific zones within the dentition for isotopic sampling that can be tied to certain periods of an individual's life.

To link $\delta^{13}C$ values of incrementally formed tissues with distinct periods of an individual's life, a zero-point needs to be established. When analyzing teeth, as in this study, a baseline can be developed for both the individual and for an entire bison assemblage. This is because bison are a pulsed-birth species, forming a hierarchical herd structure of cohorts that are separated in age by approximately one year. Calves in a particular herd, and possibly across a region, are born during a very limited period, normally in early spring (Rutberg 1984; Green and Rothstein 1993b). Each pulse of calves (p) forms a cohort. Successive cohorts form the herd (p, p+1, p+2, p+3, etc.). Timing the birth pulse to early spring sets the zero-point for the individual. The distinctive, immature dentition from the young-of-the-year

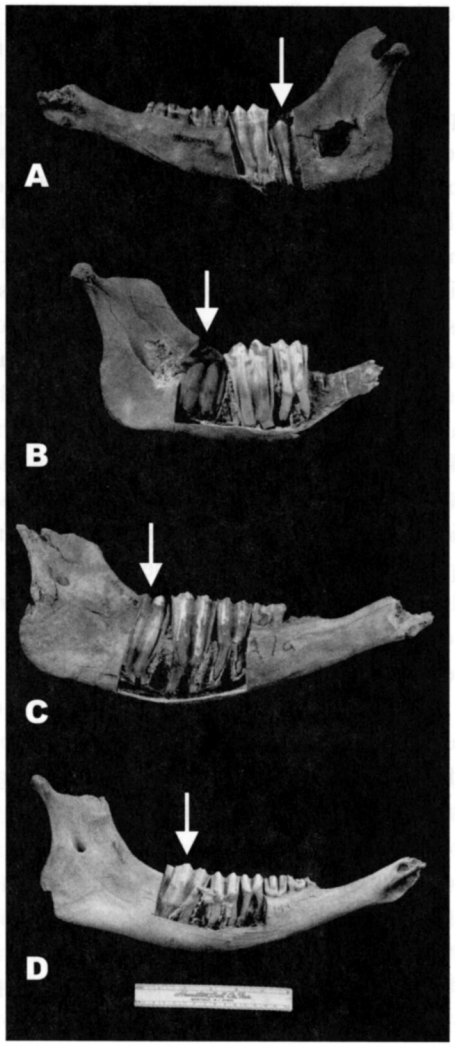

Figure 2. Sequential dental development in bison illustrated by mandibles from cohorts 1 through 4 of the Glenrock assemblage. Example A from cohort 1, the young-of-the-year, shows the first molar partially calcified, while the second molar (arrow) is not yet fully formed nor erupted. Example B from cohort 2 shows all of molar 1 and half of molar 2 calcified, while molar 3 (arrow) is partially developed within the dental crypt. Example C from cohort 3 shows the third molar (arrow) in eruption but not yet fully calcified. Example D from cohort 4 is fully developed, and the arrow indicates the third molar.

provides the needed baseline for an assemblage, while the characteristic stages in dental development are used to identify the next three senior cohorts (Fig. 2).

The development of the first molar and the majority of the second molar occur while a calf is *in utero*, suckling, and weaning (Gadbury et al. 2000). Except for the lowest portion of the second molar, $\delta^{13}C$ values derived from either the first or second molar will therefore reflect the mother's diet. While the first and second molars can provide important data, the isotopic fractionation effects between mother and offspring have yet to be defined for bison. An isotopic value from the third molar, which forms after an individual is weaned, reflects only the individual and its forage selections. Enamel of a bison's mandibular third molar begins to form at eight months of age, and develops over the next 16 months (Gadbury et al. 2000). Stable carbon isotopic values of enamel sequentially extracted from this tooth will indicate forage selection during this period of the animal's development. This study focuses specifically upon data from third molars.

Due to the progressive formation of dental tissues, multiple isotopic samples from individual bison teeth can be linked to estimated ages, illustrating forage selection for specific periods and possible changes between them. We estimate that the three sampling zones from the third molars used in this study were formed while the bison were approximately 14, 19, and 22 months old. Based upon observations of modern bison, a birth pulse of May has been assumed (Green and Rothstein 1993b). Sampling zones 1 through 3 are therefore thought to represent mid-summer, early winter, and early spring of the bison's second year.

The ultimate success of tying sampled dental zones, and their $\delta^{13}C$ values, to specific periods of time is largely dependent upon two factors. The first factor is the timing and extent of cohort birth pulses, which in archeological and paelontological contexts are all but impossible to determine. As such, we are dependent upon empirically-derived contemporary data.

The second factor influencing the assessment of seasonality for enamel development is possible variations in enamel formation rates among individuals. Our ability to temporally distinguish specific tooth zones would suffer if extreme developmental variations existed. To gain a better understanding of potential variability of enamel formation, x-rays of 40 bison mandibles from the Bison Pete herd in Wheatland, WY, were assessed. These bison were all slaughtered at 19.5 months of age. Measurements from the cementum-enamel junction to the uppermost extent of mature enamel of

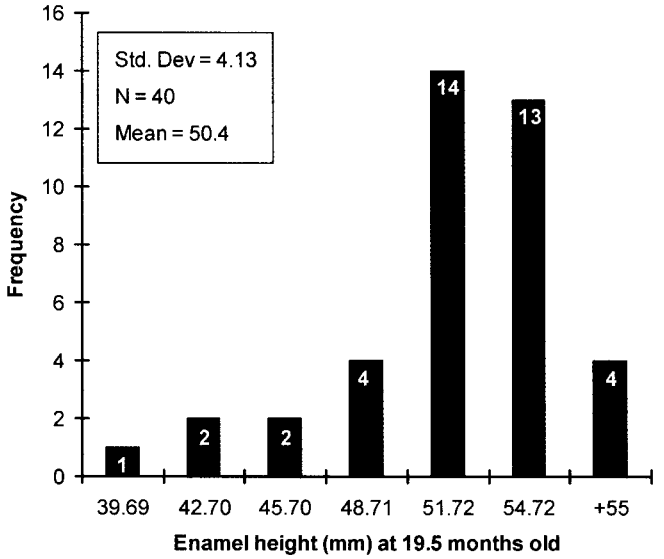

Figure 3. Histogram indicating the frequencies of various enamel heights from the third molar of 40 19.5-month-old bison from the Bison Pete Herd in Wheatland, WY.

third molars produced a standard deviation of 4.1 mm around an average height of 50.4 mm (Fig. 3). Possible variations in the timing and width of birth-pulses, along with slight variations in the rate of enamel development among individuals, will affect the temporal distinctions of sampling zones within teeth. Limited data indicate that slight variations in rates of enamel formation accompany fairly discrete birth pulses in modern bison (Green and Rothstein 1993b); however, the temporal assignment of sampled tooth zones should not be considered as absolute in archeological and paleontological contexts at this time. Thus, by understanding and weaving together various elements from biogeochemistry, dental embryology and histology, bison physiology, and ecology, it may be possible to develop a better understanding of bison paleoecology.

Stable Carbon Isotopes

The carbon atom has two stable isotopes, ^{12}C and ^{13}C. When stable isotopic values are used in ecological applications, analyses are presented as

a δ value expressed in parts per mil. The δ value is derived from the ratio of the rare, or heavy, isotope, ^{13}C, to the common isotope, ^{12}C, relative to the same ratio of an international standard. The common, or light, isotope, ^{12}C, has a natural abundance of 99.89%. The disparity between the light and heavy isotope provides the high level of precision in stable isotopic analyses. The $\delta^{13}C$ value is defined as (Craig 1957):

$$\delta^{13}C = [(R_{sample} / R_{PDB}) - 1] \times 1000.$$

The stable isotopic ratio ($^{13}C/^{12}C$) for the sample, R_{sample}, is obtained from stable isotope mass spectroscopy, and R_{PBD} is the established isotopic ratio of the international reference PeeDee belemnite (PDB). The PDB standard remains the universally accepted one used in reporting stable carbon isotope compositions of carbonates (Craig 1957; Friedman and O'Neil 1977; Boutton 1991). The result of the equation is expressed in parts per mil (‰) depleted or enriched relative to this reference standard.

Unless one is familiar with isotopic nomenclature, it is often difficult to see the ecological significance of a $\delta^{13}C$ value. Another way of looking at a $\delta^{13}C$ value is to convert it into a percentage from C_4 plant material relative to C_3 material by using the equation:

$$X = 1 - (\delta_m + \delta_{C_4}) / (\delta_{C_3} - \delta_{C_4}).$$

Here, δ_m equals the measured isotopic value for a sample; δ_{C4} and δ_{C3} are the extreme values for the substrate in question. In our case, the end values for apatite are used (-0.5‰ ± 1‰ for C_4 and -14.5‰ ± 2‰ for C_3). Thus X represents percentage of C_4 forage. Our discussion of animal tissues will place an emphasis upon the $\%C_4$ format.

The atmosphere is a good point of initiation to describe the biogeochemical pathway of carbon that can be followed through to bison. Current $\delta^{13}C$ values for carbon dioxide in nonindustrial areas are approximately -7.8‰ to -8‰ (Trolier et al. 1996). When plants use atmospheric carbon dioxide in photosynthesis, the carbon isotopic value fractionates or shifts as it is incorporated into developing tissue. Plants utilize one of three type of pathways in photosynthesis: C_3, C_4, or CAM (crassulacian acid metabolism). Plants that use the CAM pathway are generally succulents, such as cactus. Plants that use the C_3 pathway include trees, shrubs, and cool-season grasses that are generally associated with cool, moist conditions. Many grasses use the C_4 pathway. The C_4 grasses are better suited to

TABLE 1
MAJOR NORTH AMERICAN GRASSLAND TYPES
AND PERCENTAGE OF LIFE FORMS (BY BIOMASS)

Grassland type	Grass (%)	Forbes (%)	Shrubs (%)	Succulents (%)	C_4 (%)
Bunchgrass steppe	65	10	25	A	1
Northern mixed-grass prairie	90	5	5	P	20
Shortgrass steppe	40	10	30	20	30
Southern mixed-grass prairie	80	10	10	P	95
Tallgrass prairie	95	5	P	A	90

Note: P = present; A = absent.

conditions of decreased levels of carbon dioxide and are normally found under higher light, warmer, and drier growing conditions (Bender 1968; Boutton et al. 1980; Ehleringer 1991).

The distributions of plants with C_3 and C_4 photosynthetic pathways are controlled by the relative amounts of temperature and precipitation (Terri and Stowe 1976; Tieszen et al. 1979; Boutton et al. 1980; Rundel 1980; Tieszen 1994). In environments where both plant types coexist, a temporal difference occurs. The C_3 plants green up earlier in the spring and postpone senescence until later in the fall, while C_4 plants reach a peak in biomass and production in late spring to early summer. Thus, general landscape patterns emerge for the distribution of C_3 and C_4 plants (Table 1). Higher latitudes and elevations tend to be cooler and moister, creating optimal conditions for C_3 plants. Boutton et al. (1980) examined the contribution of both C_3 and C_4 plant types to communities along an elevational transect in Wyoming. They

found that at lower elevations (1400 m) in the shortgrass prairie, community composition was exclusively C_4. With an increase in elevation to 2600 m, alpine plant communities were composed entirely of C_3 plants. Similar investigations in Kenya and in the Hawaiian Islands confirm these observations, with 100% community shift with elevation increases of 1200-1400 m (Tieszen et al. 1979; Rundel 1980). Also, a shift in dominance from C_3 to C_4 occurs with decreasing latitude (Sims et al. 1978). The bunchgrass steppe of the northern Great Basin is noted as being 1% C_4, while the northern mixed prairie generally exhibits 20% C_4 biomass. At the southern extreme, the southern mixed prairie demonstrates the influence of warmer, drier conditions and increased solar radiation, with a community composition that is 95% C_4 plants.

The extent of plant carbon isotopic fractionation from atmospheric carbon dioxide is dependent upon the photosynthetic pathway. CAM plants have a very wide breadth of $\delta^{13}C$ values, ranging from -37‰ to -7‰. On the other hand, both C_3 and C_4 plants have fairly narrow ranges of isotopically distinct values. The C_3 plants have $\delta^{13}C$ values from -33‰ to -22‰, while the C_4 plants have $\delta^{13}C$ values of -16‰ to -9‰. Stable carbon isotopic analysis of non-CAM plant tissues can therefore be used to discern the relative contribution of C_3 and C_4 plant photosynthetic pathways (Bender 1968; Smith and Epstein 1971) (Fig. 4).

Stable Carbon Isotopes in Faunal Tissues

Stable carbon isotopic analysis is an effective tool in discerning C_3 and C_4 plant tissues, providing information concerning primary production. But stable carbon isotopic analysis can also be applied to tissues of primary consumers (DeNiro and Epstein 1981; van der Merwe 1982; Tieszen 1994). In both modern and paleoecological studies, $\delta^{13}C$ values of various tissues are used in determining diets of herbivores. Bone collagen and biogenic hydroxyapatite (or apatite) are the two of the main substrates in animal tissues that have been used for isotopic investigations of paleontological, archeological, and modern faunal assemblages (Kingston 1992; Gu et al. 1996; Bocherens et al. 1997; Connin et al. 1998).

Developing tissue incorporates ingested carbon. Thus, the isotopic value of these tissues reflects the relative amounts of the ingested isotopes. During metabolism, dietary carbon in collagen is enriched, or becomes a more positive value by some 5‰ to 6‰ relative to the $\delta^{13}C$ of ingested forage (Fig. 5A). Apatite is enriched, or becomes more positive, by some

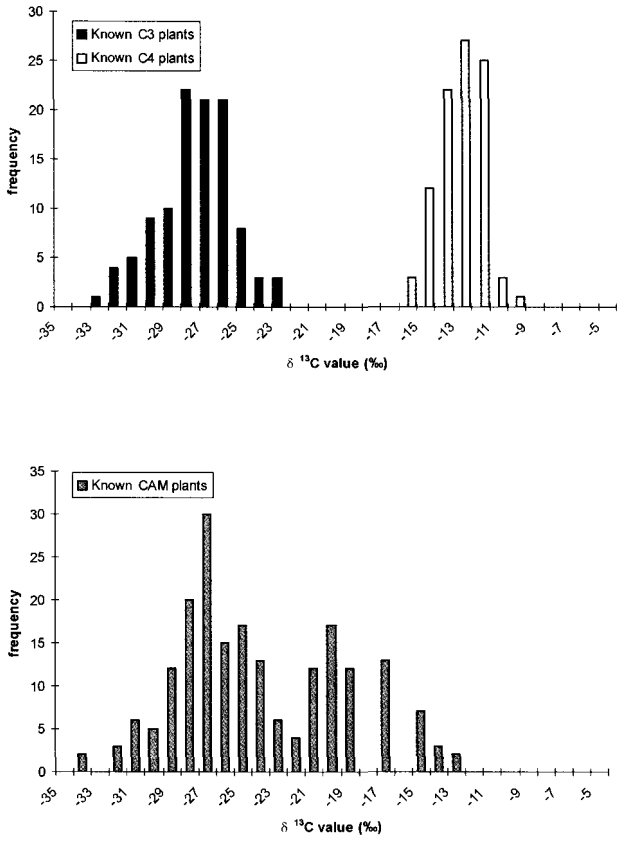

Figure 4. Stable carbon isotopic values can be used to delineate two of the three photosythetic pathways. Note the separation in isotopic values between C_3 and C_4 pathways (A) as compared to the overlap of both by CAM plants (B). Adapted from Dienes (1980).

12‰ of ingested forage (Fig. 5B). The skeletal system serves as a "warehouse" for the body's mineral needs, so bone is in a constant state of growth and modification. Stable carbon isotopic values for bone collagen and bone apatite reflect this, and can go from one end of the isotopic spectrum to the other within 10 years (Chisholm 1989; Tieszen 1994). Stable carbon isotopic values derived from bone therefore provide an aggregate or averaged record of diet over an extended period.

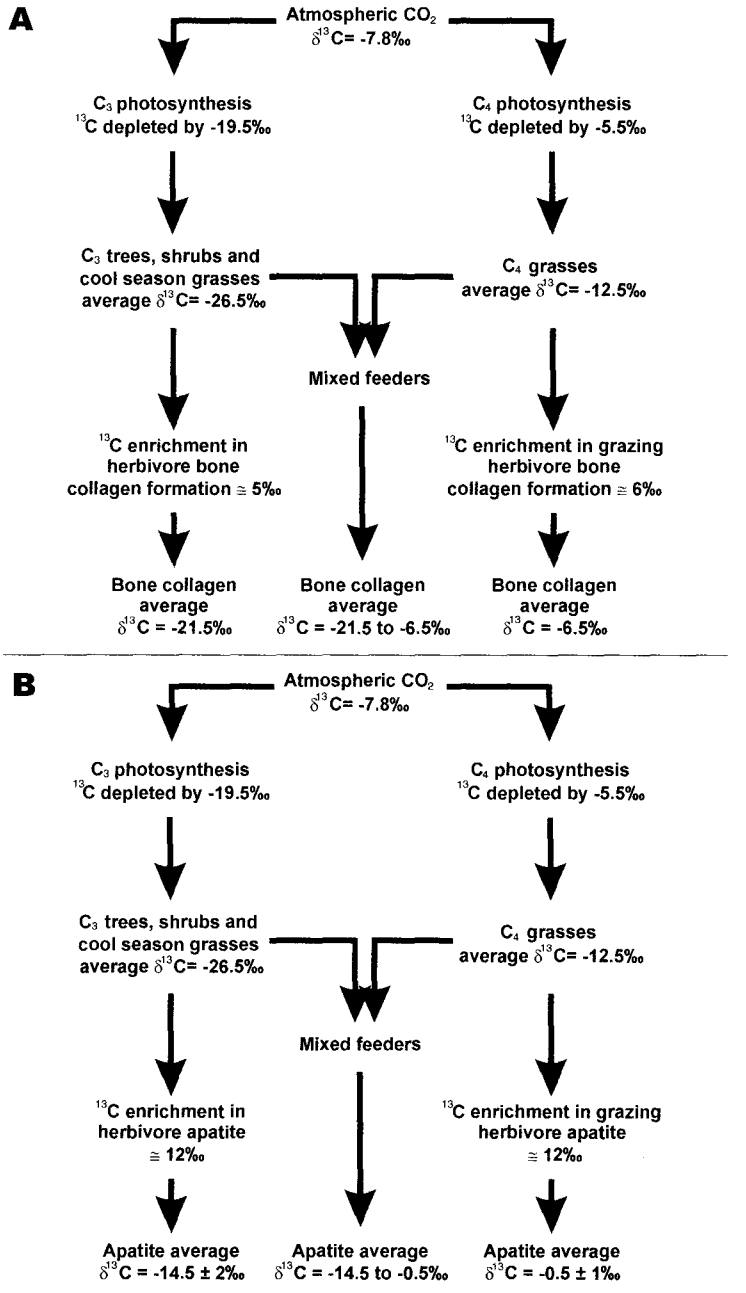

Figure 5. Two models demonstating the progressive steps in stable carbon isotopic fractionation for bone collagen (A) and apatite (B). Adapted from van der Merwe (1989).

Biogenic hydroxyapatite is a mineral component of both bone and dental enamel. As opposed to bone that is in a constant state of growth and resorption, mature enamel is a "hard tissue." This means that little or no structural and chemical modifications occur in the calcified, mature phase of this tissue (Schmidt and Keil 1971; Bryant et al. 1994). As the dental enamel forms and is calcified, its $\delta^{13}C$ value is locked in. Enamel forms and matures in an orderly progression, both within an individual tooth and through the mandibular and maxillary tooth rows. As such, a sample taken from a specific location on a tooth is related to a specific period of the life cycle. Progressive series of isotopic values within a tooth and through tooth rows record discrete changes in forage selection throughout seasons and years.

In addition to providing a temporally-specific isotopic value, dental enamel exhibits other analytical advantages. Using Mohs' scale of hardness, where 1 is talc and 10 is diamond, enamel is 5 to 8 moh, with a density of 2.84 to 3.00 g/ml (Kraus et al. 1969). The permeability for enamel is also low. These factors help ensure that dental enamel is often well preserved in archeological and paleontological contexts. In archeological contexts, mandibles are considered a low-utility item, which means they are not associated with high-quality, transportable pieces of meat, are not particularly meat bearing, nor are they useful in making bone tools or other items. In bone-bearing deposits, low cultural utility and excellent physical preservation ensures good representation of mandibles in general and teeth in particular. The physical properties of enamel also make it far less subject than bone to postmortem chemical alterations (Wang and Cerling 1994). Additionally, Tieszen and Fagre (1993) have shown that $\delta^{13}C$ values of apatite provide a more precise reflection of overall dietary carbon whereas bone collagen values reflect the dietary carbon specific to synthesized proteins.

Mature, calcified enamel consists of 96%-98% inorganic, highly mineralized material, 4% water, and 1% organic material that in-fills the interstices of the enamel-forming prisms. The two main inorganic components of the mineralized material are calcium and phosphate. Along with hydroxyl ions, the phosphate and calcium form a crystalline lattice of hydroxyapatite [$Ca_{10}(OH)_2(PO_4)_6$]. Hydroxyapatite makes up 90% of the inorganic component of enamel. Substitution of phosphate can occur with strontium, radium, vandium, and carbonate. Structural or primary carbonates replace hydroxyl and phosphate groups in small amounts (Kraus et al. 1969; Hillson 1986; Kingston 1992; Wang et al. 1993; Wang and Cerling 1994). Carbonate substitution is important to this study, as it is the molecule extracted from the enamel for carbon stable isotopic analysis.

Methods

Our investigation builds on a previous study that encompassed a small number of temporally and geographically dispersed specimens of *B. antiquus* and *B. bison*. The initial study tested the assumption that temporal sequences of $\delta^{13}C$ values could be derived from bison dentition (Larson 1995). Teeth selected for both phases of the study consisted of the mandibular molars numbered, M_1 through M_3. These teeth were either loose singles or still part of a mandible. The specimens used in the initial study were chosen to represent temporal and geographic variation (N = 15, representing 10 individuals). Five individuals originate from four contemporary herds, providing a correlation with modern conditions.

In this study, we evaluated a portion of the Glenrock Buffalo Jump Site assemblage, a *B. bison* bonebed of the Plains Late Prehistoric period, from Converse County, WY (Frison 1970). Two radiocarbon dates from this site yielded dates of 210 ± 100 and 280 ± 100 years before present (Frison 1970). Additionally, four *B. priscus* molars from Upper Paleolithic bison kills were sampled. These specimens were from the Ukrainian sites of Amvrosievka (Krotova and Belan 1993) and Anetovka II (Praslov et al. 1989), dating to approximately 20,000 years before present. A single second molar came from the site of Anetovka II (Praslov et al. 1989). This tooth exhibited early stages of wear, indicating mortality at perhaps 1.5 to 2.5 years of age. Three other third molars were from the site of Amvrosievka (Praslov et al. 1989; Krotova and Belan 1993). These teeth each exhibited different degrees of wear, ranging from very slight (individual 27) to heavy (individual 29) (see Appendix). These bison are believed to have died in youth, midlife, and old age.

Modern analogies are important in any paleoecological study (Ambrose and DeNiro 1989; Thackeray and Lee-Thorp 1992). Our selection of individuals representing modern herds encompassed several ecological settings. One individual originated from the Downare commercial herd near Hartsel, Colorado. This herd is located in a large, high-elevation intermountain park dominated by C_3 vegetation. Two other modern specimens came from the Bison Pete commercial herd in Wheatland, WY, located near the interfaces of shortgrass steppe, tallgrass prairie, and northern mixed-grass prairie. The final modern specimen came from Fort Robinson State Park, NE. This location, near the Pine Ridge Escarpment, is within the northern mixed-grass prairie, but is also very close to both the tallgrass prairie to the east and shortgrass steppe to the south.

The five other individuals also used in the initial study came from four separate archeological assemblages. Three of these assemblages represent the late Pleistocene-to early Holocene, while the fourth came from the late Holocene. Cultural affiliations of the early sites are Folsom from Lake Theo, TX (Harrison and Smith 1974); Hell Gap Complex from the Casper Site, WY (Frison 1974); and Alberta-Cody Complex from Hudson-Meng, NE (Agenbroad 1978; Todd et al. unpublished data 1994). The late specimen is from the Plains Late Prehistoric period site of Glenrock, WY (Frison 1970).

Through the use of a small number of specimens during the first phase, we were able to test, refine, and develop various laboratory techniques, based upon the work of Kingston (1992). This phase sampled enamel from various mandibles as well as within isolated molars. We avoided bias by intra-individual sampling in the study specimens, but this presented a potential problem in sampling the Glenrock assemblage. To minimize this potential bias, only left mandibles and teeth were used except in the case of the two Glenrock calves (p + 0.5), in which right mandibles were used.

In the first phase, the sample zones for enamel extractions were chosen to emphasize quantity of tissue and ease of extraction. The majority of sampling zones were located near the crowns of the teeth. Two long, parallel extraction cuts were made, beginning at and perpendicular to the occlusal, or chewing, surface. Three study samples were drawn from the protoconid, two from the entaconid, while all other pilot samples were drawn from the hypoconid regions of the sampled molar (Fig. 6). In this study, a better understanding of enamel formation and structure led us to abandon this vertically orientated extraction procedure. In teeth, which develop from the crown downward, a long, vertical extraction represents a prolonged period of dental development and can blur temporal distinctions. Thus, we used a new extraction strategy, horizontal in orientation and parallel to the occlusal surface, on samples from the Wyoming site. A horizontal extraction encompassed a much shorter period of dental development, and so provided a more temporally discrete sample.

Since results from the first study demonstrated that $\delta^{13}C$ values varied within bison dentition, we focus here upon the Glenrock assemblage. Selected mandibles and loose molars were grouped into cohorts based upon dental attributes. Cohorts 1-4 represent young-of-the-year through three year olds and were determined specifically by the degree of dental development. Cohorts A-E represent mature animals, and these were grouped by the more tentative observations of dental wear patterns. All of the Ukrainian

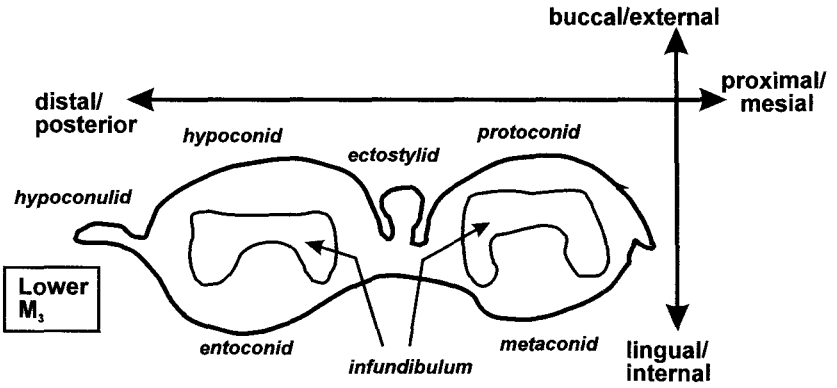

Figure 6. Illustration of terms used in the text to describe features of molars. Adapted from Frison (1970).

samples of *B. priscus* are designated as cohort U, though they varied in site of origin and in dental wear.

Once the mandibles and loose teeth were grouped into their respective cohorts, specific molar zones were selected for enamel extraction. These extraction zones were located at 5, 20, and 40 mm above the cementum-enamel junction of the three mandibular molars and correlate with specific periods of the animals' lives. These sampling zones were numbered 1, 2, or 3, with zone 1 being the earliest enamel to form, placing it nearest to the crown. Zone 2 is intermediate (20 mm), while zone 3 is nearest the cementum-enamel junction (5 mm).

The enamel surface of a selected molar was cleaned with distilled water and then lightly ground to a uniform white using a Dremel® moto-tool with a small, abrasive attachment. This procedure stripped away potential contamination from secondary carbonates associated with a weathered surface. Two incisions parallel to the occlusal, or chewing surface, of the tooth were then made with a Dremel® moto-tool cutting wheel about 1 mm above and 1 mm below the sampling zone. The depth of the incisions barely exposed the underlying dentine. Incisions crossed the outwelling of either the meta- or protoconid region (see Fig 6). The sample was then removed with a minimum of physical impact by gentle prying with a fine screwdriver.

It is important that only enamel was removed. Dentine is prone to a postmortem process that can contaminate stable isotopic values (Wang et al. 1993). As an organic tissue, it possesses its own characteristic $\delta^{13}C$ values. Any dentine that remained on the underside of the enamel sample was ground off using the Dremel® moto-tool with a fine grinding attachment. Subsequent use of a precision pneumatic dental tool, provided by the Veterinarian College, Colorado State University, proved to be highly superior to the Dremel® tool, and its use is strongly recommended.

As noted, enamel structure significantly precludes diagenetic contamination, the postmortem chemical alteration caused by soil and groundwater processes. The greatest potential for postmortem alteration occurs at the surface of the enamel. So, possible contamination may occur along fissures, dislocations of enamel prism faces, organic interstices between prisms, or at the surface hydration level (Kraus et al. 1969; Kingston 1992). Fissure and dissociation contamination are rare, and organic interstices make up only 0.4%-1% of mature enamel (Kraus *et al.* 1969; Hillson 1986). To eliminate contamination by postmortem deposits, we used both mechanical and chemical pretreatments (Kingston 1992).

Chemical pretreatment consisted of two steps. The sample was first soaked in 2% sodium hypochlorite (NaOHCl) for 2 hours to digest any organic material associated with the surface of the sample. In the second step, we applied 1M hydrochloric acid to remove secondary carbonates, possibly associated with surface weathering or translocated along fractures and fissures. Kingston (1992), who tested three different acid treatments to remove potential carbonate contamination, found the hydrochloric acid procedure was most successful. This procedure required the enamel to be ground to a powder, followed by a 16 hour acid treatment. Unfortunately this procedure dissolved our enamel samples. In a second attempt, the enamel was not powdered but broken into small pieces. Near total dissolution of the samples still occurred, making apparent one of the differences between Kingston's fossilized assemblage and our subfossil assemblage. Consequently, we agitated each sample in 3 ml of 1M hydrochloric acid for 5 minutes. This resulted in an average loss of 40% of the sample by weight (high = 67%, low = 20%, mode = 33%, standard deviation 11%, n = 77). Enamel samples became noticeably smaller, all edges became round, and the color changed to an opaque whitish-blue. The average loss of these samples exceeded Kingston's (1992) losses, but the mode was similar to his results from another method, the application of 1M acetic acid (CH_3COOH).

Although postmortem contamination of biogenic hydroxyapatite in enamel is considered to be minimal (Wang and Cerling 1994), we do not know the extent to which hydrochloric acid infiltrated the enamel and removed possible "deep," secondary carbonates in the unpowdered samples. Given the amount of dissolution, as discussed above, surface contaminants and secondary carbonates were likely removed. Other studies have suggested that acetic acid is a more effective, less destructive alternative to hydrochloric acid (Lee-Thorp and van der Merwe 1991).

After pretreatment, we ground our samples to a fine powder in preparation for gas extraction. A major concern of this study was to keep sample size to a minimum, in order to preserve the integrity of irreplaceable paleontological/archeological specimens. Results indicated that samples at or below 0.02 g did not produce sufficient carbon dioxide for successful mass spectroscopy. Pretreated and ground enamel samples were placed in glass vials, oven dried at 90°C for 10 hours, sealed, and placed in a desiccator for storage.

For conversion to carbon dioxide, samples weighing 0.3 to 0.7 g were placed in glass boats and loaded into a reaction chamber containing 100% phosphoric acid (H_3PO_4) held at 90°C. The chamber was then evacuated to pressures less than 1×10^{-4} torr or 1.3×10^{-7} atm. Individual samples were reacted with the acid, producing carbon dioxide and water. Once the reaction had ceased, the products were introduced into a high-vacuum glass line. The gas was cryogenically distilled by drawing it through a trap immersed in an acetone-dry-ice slush of approximately -80°C. The purified carbon dioxide was then frozen in a helical carbon dioxide trap cooled with liquid nitrogen (-190°C) while noncondensable gases, such as argon and nitrogen, were pumped away. The liquid nitrogen was removed from the carbon dioxide trap and placed on an evacuated 5 mm pyrex tube. The carbon dioxide trap was warmed, and the gas was then cryo-pumped into the pyrex tube. A torch was used to seal the tube of frozen gas. The vacuum line was purged to a minimum of 1×10^{-4} torr before processing the next sample. Stable isotopic ratios of the carbon dioxide were measured on a Finnigan Delta S mass spectrometer at the University of Utah, Department of Biology.

Results

Carbon stable isotopic values from dental enamel have been assessed for a number of individual bison from archaeological ($n = 31$) and modern

contexts ($n = 4$). The values from four analytical subsets, initial modern, and archaeological, as well as the Glenrock and the Priscus sets, are presented in the Appendix 1. Unfortunately, the initial study was conducted before a detailed understanding of enamel development had been reached. Nearly all of these samples were taken inadvertently from first and second molars. As previously explained, these teeth form while a bison is still dependent upon its mother, introducing the possibility of an undefined contribution by the mother, to the calf. Additionally, the use of replicate sampling zones of uniform size was not implemented. Thus, the seasonality of the initial samples did not correspond with that of the Glenrock data. These factors make direct comparisons between data sets tentative.

The $\delta^{13}C$ values of Glenrock samples ranged from -15.75‰ to 2.42‰, which encompasses the entire range of $\delta^{13}C$ values for apatite. This suggests that at certain periods, individual Glenrock bison had diets that were exclusively C_3 or C_4 plants. The *B. priscus* $\delta^{13}C$ values fell within a more limited span of -10.8‰ to -8.8‰, indicating a diet of 19.3% to 33.6% C_4.

Similarly, at Wind Cave National Park, South Dakota, Tieszen (1994), used the composition of feces and of hornsheath rings to define temporally specific foraging histories. The feces data had excellent temporal control and showed a heavy winter emphasis upon C_3 plants, with only about 30% C_4 input. An increase in C_4 grazing, up to approximately 56%, began in mid-spring and lasted until late summer or into early fall. This corresponds well to the new growth and subsequent early senescence of C_4 grasses during the warmer months. The pattern of $\delta^{13}C$ values within and across the hornsheath rings also revealed regular but limited seasonal shifts of approximately 4‰ between C_4 grazing and C_3 foraging (Tieszen 1994).

The Glenrock assemblage is only several hundred years old. Thus, we might expect a pattern similar to the increasing summer C_4 grazing demonstrated by Tieszen's (1994) isotopic data from Wind Cave. If so, our sampling zone 1, formed when the Glenrock bison were 14 months old at mid-summer, should have the greatest emphasis on C_4 grazing. Both sampling zones 2 and 3, representing early winter at 19 months old and early spring at 22 months old, would be expected to be more isotopically depleted, or more negative, due to a decreased availability of C_4 forage. However, only a weak consensus can be reached regarding summer to winter shifts of C_4 to C_3 forage in the Glenrock assemblage (Fig. 7). Since the third molar is not completely formed in the young-of-the-year or yearlings (cohorts 1 and 2) from the Glenrock assemblage, and because sampling zone 1 has been worn away in the older animals (cohorts C-E), the

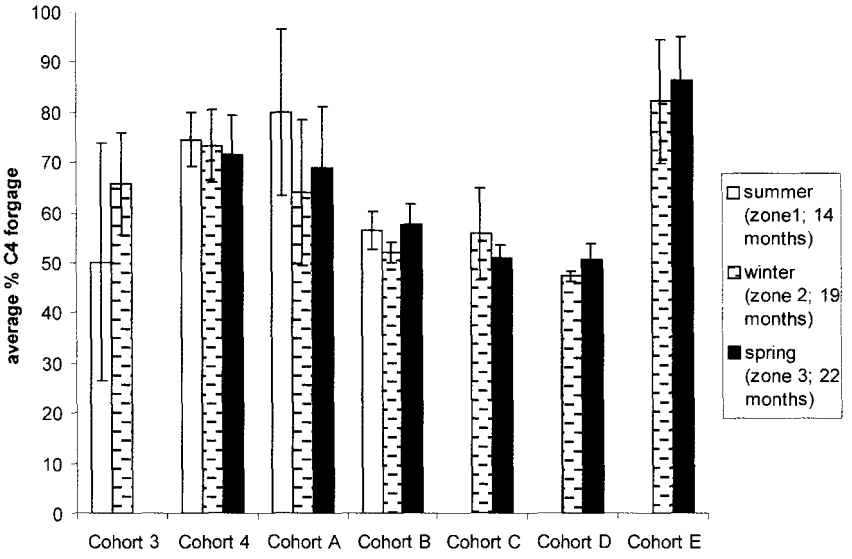

Figure 7. Year-to-year changes in forage selection by the Glenrock assemblage can be determined by comparing the average seasonal C_4 consumption of a cohort with the next oldest cohort. The chain of successively senior cohorts provides data that can possibly be related to long-term landscape use by bison herds in archeological and paleontological contexts.

summer to winter comparison can be made only in cohorts 3, 4, A, and B. Of the 13 individuals having sampling zones 1 and 2, five show the expected decrease in C_4 forage, five animals show changes in diet of less than ±5%, while three individuals demonstrate an increase in C_4 grazing.

Changes between winter and spring foraging can be assessed for the Glenrock assemblage in cohorts 4, and A through E, by comparing sampling zones 2 and 3. Based upon the Wind Cave results (Tieszen 1994), we expected a slight shift from C_3 forage to C_4 grass with the spring green-up. Of 18 winter and spring foraging comparisons that can be made for the Glenrock assemblage, 11 are within ±5% of each other, essentially indicating little to no seasonal change. Of the remaining seven, two demonstrate a decreased C_4 emphasis, while five individuals show an increased use of C_4 grasses. An increase in C_4 grazing in late spring or early summer is not

unexpected. However, sampling zone 3 is thought to represent early spring, possibly too early for the green-up of C_4 grasses in central Wyoming. The increase of C_4 grazing in these five individuals could represent an early green-up or the use of more southern, springtime feeding patches.

The standard deviation of isotopic values for each sampling zone within a cohort represents a cohort's foraging variability for a specific period. A cohort with a low standard deviation may have foraged closely together, experienced little or no immigration, fed on a homogeneous range, or had a small foraging radius. Samples from cohorts B and D show very low standard deviations for all sampled zones. However, zone 1, representing month 14 in cohort 3 had an extreme variance for a single period. Here, isotopic values indicated that the three sampled individuals had diets of 96%, 52.6%, and 1.5% C_4 vegetation. This produces a standard deviation of 47% around an average of 50% C_4 forage (Table 2). This variation could be due to immigration, the use of extremely different foraging patches, or the chance sampling of late- or early-born members of this cohort. It is necessary to sample a larger number of individuals within a cohort in order to better determine general patterns.

Year-to-year changes in foraging by the Glenrock assemblage also can be tentatively identified. These long-term changes may represent how a herd cycled through the landscape, since each successive cohort represents a one-year step in time. In the case of this analysis, the Glenrock assemblage provided data for four successive years of summer foraging, seven years of winter and six years of spring (Fig. 7). For example, when the animals of cohort 3 were 19 months old, their diet averaged 66% C_4 grasses. Averaged values for cohort 4 at 19 months old, illustrating forage selection approximately one year earlier, indicates a diet of 74% C_4 grasses.

Although the data are limited from the *B. priscus* dentition and they do not represent an assemblage, they serve as an initial comparison of a separate group of bison. The overall average of Glenrock third-molar samples demonstrated that 65% (SD = 22%; n = 52) of the diet was provided by C_4 grazing. Fifty-nine percent of sampled Glenrock individuals demonstrated seasonal shifts in C_3-C_4 foraging greater than 10%. In contrast, data from the *B. priscus* third molar samples showed that only 37% (SD = 3.4%; n = 8) of their diet consisted of C_4 plants. Even though the third-molar data of this set is limited to only three individuals of differing ages, the variability within individuals as well as among individuals was remarkably low compared to that of the *B. bison* data. For example, the greatest shift among the Ukrainian samples was a 9.25% increase in C_4 intake, while the other two individuals

TABLE 2
AVERAGE VALUE OF C_4 FORAGE, WITH STANDARD DEVIATIONS AND NUMBER OF INDIVIDUALS SAMPLED, ARRAYED BY THIRD-MOLAR SAMPLING ZONES FOR COHORTS 3 TO E OF THE GLENROCK ASSEMBLAGE AND UKRANIAN *B. PRISCUS* SPECIMENS

Pulse:	p+1.2	p+1.6	p+1.8
Sample position:	M3-1	M3-2	M3-1
Month:	July	December	March
Months old:	14	19	22
Cohort 3	50.08	65.65	
SD	(47.30)	(20.50)	
N	3	3	
Cohort 4	74.54	73.29	71.5
SD	(10.69)	(14.67)	(15.60)
N	3	3	3
Cohort A	79.83	63.92	68.85
SD	(33.21)	(29.25)	(24.60)
N	3	3	3
Cohort B	56.42	52.02	57.63
SD	(7.78)	(3.89)	(8.21)
N	4	4	4
Cohort C		55.69	51.00
SD		(18.56)	(5.04)
N		2	2
Cohort D		47.34	50.63
SD		(1.99)	(6.54)
N		2	2
Cohort E		82.19	86.30
SD		(24.72)	(17.56)
N		4	4
Ukrainian	34.53	37.00	40.27
SD	(2.70)	(2.27)	(4.07)
N	2	2	3

demonstrated only shifts of 1% and 2%. The seemingly stable diet expressed by stable carbon isotopic values for the 20,000-year-old Ukrainian *B. priscus,* within and between individuals, may demonstrate a bison habitat with little or no seasonal differentiation in forage selection.

Discussion

This study is one of the first to test the effectiveness of isotopic analysis of an assemblage. With a total of 65 isotopic samples representing 22 individuals, the Glenrock data provide one of the most in-depth isotopic studies of a single assemblage. Yet these data do not provide enough information to make definitive statements about this assemblage's foraging behavior in other than the most general sense. Ideally, more zones sampled within the third molar would provide a more precise foraging history. Furthermore a larger sample, of more individuals per cohort, would provide a more accurate assessment of cohort variability. However, the results provide some insights and encourage future, more exhaustive studies.

We found that stable carbon isotopic analysis conducted at the assemblage level allowed us to make multiple comparisons at several organizational levels. These comparisons contribute unique insights into the interpretation of bison foraging behavior in paleontological and archeological contexts. For example, we have found that foraging variability can be demonstrated by multiple stable carbon isotopic samples from an individual, allowing the elucidation of an individual's foraging history by distinct life-period. The individual foraging histories showed a wide range in forage selection through time for *B. bison*, but varied only a little in the *B. priscus* data.

The $\delta^{13}C$ values taken redundantly from similar sampling zones from numerous individuals of an assemblage allowed us to compare foraging behaviors between individuals, both across the entire assemblage and constrained within a particular cohort. Comparison of individual foraging histories within a cohort can reveal how that cohort might have interacted. For example, a cohort might show small differences among the 14-, 19-, and 22-month sampling zones. Such a scenario could represent a cohort with little immigration, one that foraged as a unit, utilized a very homogeneous landscape, and/or stayed within a very confined foraging radius. At the other extreme, a high degree of isotopic variability among sampling zones within a cohort may indicate its dispersion across the landscape, the heterogeneity of its range, or mixing with other herds.

It must be noted, however, that the success of intra-cohort comparisons depends largely upon the duration of that particular cohort's birth pulse. Unfortunately, defining the absolute timing and length of bison birth pulses in archeological and paleontological contexts is difficult. While we assume fairly tight birth pulses for the Glenrock assemblage, variation among similar sampling zones across a cohort may be the result of an extended birthing season, and the chance sampling of early- or late-born calves. The seasonality or timing of samples from the Glenrock assemblage is based upon modern bison birth pulses (Green and Rothstein 1993). This is not an unacceptable application, as the Glenrock assemblage is only 300 years old and comprised entirely of *B. bison*. However, this may not be the case for our *B. priscus* samples. As a different subspecies that existed in an entirely different ecological regime 20,000 years before *B. bison*, the direct application of seasonality to sampling zones for *B. priscus* is perhaps quite tenuous.

Results organized by cohort allow for comparisons across an entire assemblage. If birth pulses occur approximately at the same time of year for each cohort, foraging patterns can be examined through the hierarchy of cohorts, revealing year-to-year shifts in forage availability and/or selection of the entire assemblage. Our data provide comparisons for four springs, seven winters, and six springs that can be consecutively linked together (Table 2). If a herd returned to the same foraging patch year after year, these values should remain relatively stable. If a herd cycled across the landscape, these annual values would be expected to be more variable.

Additional insights into bison paleoecology could be gained by expanding the methodology of this study to include additional assemblages, and by holding geographic space constant, rather than time. First, adding assemblages would make possible similar comparisons among bison across both time and space. For example, by sampling assemblages from distinct periods based on radiocarbon dates, or cultural horizons such as Clovis, Folsom or Hell Gap, time would serve as a constant. This form of analysis could potentially illustrate how foraging behaviors of bison might have varied between regions during a particular period. Additional analyses comparable to this study could utilize stratified sites or regionally aggregated sites. A few examples of stratified bonebeds are Agate Basin (Frison and Stanford 1982), Head Smashed In (Reeves 1978), or Vore (Reher and Frison 1980). In these cases, bison foraging behaviors could be assessed for a limited region through time. Another regional approach might focus on a larger area. The Black Hills could serve as a regional focus, using the Agate

Basin (Frison and Stanford 1982), Hawken (Frison et al. 1976), and Vore (Reher and Frison 1980) sites, representing the Paleoindian, Archaic, and Late Prehistoric periods. In combination with local paleoenvironmental records, a localized investigation could measure the effects of environmental change on aspects of bison foraging behavior. Combined with changes in bison morphology, such data should help define bison response to alterations in ecosystem structure, composition, and function.

When developed in an assemblage context, the high-resolution paleodietary technique of this study can be used to assess the dispersion or aggregation of herds, to provide an initial perspective into foraging behavior within a herd structure. Temporally discrete $\delta^{13}C$ values can be thought of as representing foraging patches. These, in turn, are a reflection of actual plant communities. But how well do collections of foraging patches reflect actual plant community composition and, by extension, landscape position? The overall Glenrock bison diet showed that C_4 grasses constituted roughly 65% of their forage. This average does not mirror the photosynthetic composition of any major, modern grassland (Sims et al. 1978) (Table 1, Fig. 1). An important consideration of dietary $\delta^{13}C$ analyses is their applicability to actual landscape settings. How well and to what degree does bison foraging, or that of any other herbivore, reflect actual plant community composition? Can such values be used in "tethering" an individual, a cohort, or an assemblage to actual physical settings, such as those illustrated in Table 1 and Fig. 1?

Modern grassland biomes can be identified by their C_3 and C_4 composition (Table 1, Fig. 1), thus tempting one to use $\delta^{13}C$ values to infer landscape use by the Glenrock assemblage. However, $\delta^{13}C$ values of primary consumers need to be evaluated as direct proxies for landscape positioning. Several studies of foraging patterns of modern bison show that bison are relative generalists compared to highly selective herbivores such as antelope (Peden et al. 1974; Schwartz and Ellis 1981; Chisholm et al. 1986). Landscape use by bison might be inferred from temporally limited $\delta^{13}C$ values, but only insofar as a generalized "bison as lawn mowers" scenario might apply. This lawn-mower scenario views bison as a head-down, forward-moving, nondiscriminating eating machine, consuming whatever plant happens to lie in the line of travel. If bison foraging behavior can be so generally characterized, then $\delta^{13}C$ dietary values would be directly applicable as landscape proxies. And, the lawn-mower scenario might be accurate under certain circumstances. For example, increased foraging competition is likely to occur in large, highly aggregated herds of females and

their young, rather than in the more solitary bull groups (Guthrie 1990; Komers et al. 1993; Berger and Cunningham 1994; Larter and Gates 1994). Intense competition would likely force these bison into consuming whatever forage is at hoof. Thus, a very generalized "lawn-mower" model may be relevant to a large cow-calf assemblage.

When the patch size of a resource exerts certain controls over potential herd size, the smaller groups of bison in woodland and montane settings are expected to be somewhat less competitive but more restricted, for example, by more limited foraging options (Ford 1983; Van Vuren 1983). Limitations of "choice" in forage would decrease the "lawn-mower" effect, and bison in such settings would be more selective and less reflective of the landscape. However, woodland and montane environments have a much higher percentage of C_3 plants. As in the case of the modern specimen in the initial study from the high elevation setting of Hartsel, CO, which exhibited only 22% of C_4 forage in its diet, animals in woodland and montane environments can be identified by their depleted, or more negative, isotopic composition.

The generalist "lawn-mower" foraging model for bison has been applied to animals in shortgrass prairie settings (Peden et al. 1974; Schwartz and Ellis 1981). Therefore, the applicability of such a model could be limited to such a biome. Patterns of herbivory in modern *B. bison* often reflect selection for the highest level of available crude protein as well as the resources that are available (Larter and Gates 1991). The amounts of C_3 and C_4 forage represented by $\delta^{13}C$ values from third-molar samples in the Glenrock assemblage do not accurately reflect the biomass of modern grassland biomes. This observation challenges the validity of a general bison foraging pattern, at least for the Glenrock assemblage, or it suggests that current plant composition does not mirror former ecosystem composition.

One way to explore the relation of past foraging to past vegetation is the use of stable carbon isotopic values of soil carbonates and soil organic matter to ascertain the degree of C_3 or C_4 plants that were present during soil formation (Cerling et al. 1989; Kelly et al. 1991; Kingston 1992; Nordt et al. 1994). Research on soil carbonates and organic matter in modern and dated soil horizons provides both potential analogies for former ecosystems and indications of the distribution of vegetative communities through space and time. This leads to valuable insights into primary production, or what vegetation was potentially available for forage in a specific area. With the additional information gained through soil isotope measurements, some foraging areas possibly could be determined, and others eliminated, based

upon the degree of similarities among the isotopic compositions of primary production and primary consumers. For example, in the Glenrock analysis, a number of individuals had high C_4 values during specific times of the year. Areas determined by soil investigations to have a high concentration of C_3 vegetation could be ruled out as primary foraging patches used by these bison.

Beyond $\delta^{13}C$ values, additional independent lines of evidence are readily available from dentition. The analysis of macro- and micro-botanical remains, such as phytoliths in dental residues for example, of the impacta and calculus, can provide more detailed insights into forage selection (Armitage 1975; Akersten et al. 1988; Middleton and Rovner 1994; Larson 1995). Stable oxygen isotopic ($\delta^{18}O$) analysis of enamel can be used as seasonal temperature proxies (Quade et al. 1992; Cerling and Sharp 1996). Isotopic analysis of dentine, the underlying organic dental tissue, allows the assessment of dietary stresses through incremental changes in ^{15}N (Wright and Schwarcz 1999). Morphological studies of dentition can also provide a wide array of important data (Reher 1970, 1974; Goodman and Rose 1990; Todd et al. 1996).

The emphasis placed upon bison by indigenous inhabitants of the Great Plains beginning as early as the late Pleistocene makes understanding bison an extremely important archaeological and ethnohistorical pursuit. But human subsistence and the faunal assemblages in the Great Plains have not been strictly limited to bison. This study offers insights into possible behaviors of one assemblage, consisting of one species. The application of these insights to understanding cultural systems may become increasingly viable only through the examination of *prey* paleoecology, not specifically bison paleoecology. To this end, this study's techniques could be applied to a suite of large-bodied mammalian herbivores. For example, in North America, bighorn sheep (*Orvis canadensis*), elk (*Cervus canadensis*), mule and white-tailed deer (*Odocoileus hemionus, O. virginianus*), and pronghorn (*Antilocapra americana*), form a modern catena of species that spans from high elevation, montane settings to lowland, prairie environments. The application of high-resolution paleodietary techniques to these species would aid in defining foraging ranges, and potential changes therein, for these species. Examination of an extended temporal scale could elucidate stability, continuity, disturbance, or change in these foraging patterns. The definition of these states, or the coexistence of locally defined stable and altering foraging patterns and social structures, for a variety of prey species would have direct relevance to understanding predation strategies of human hunters and to the ecological development of a variety of habitats.

Reconstruction of various components in Pleistocene and Holocene ecosystems can be accomplished through overlapping analyses of a number of species. With a sufficiently robust database, intra- and inter-species interactions, environmental settings, and various social aspects of herd dynamics may be defined. If pursued in a mid- to late-Pleistocene time frame, these analyses would "set the stage" for the human entrance into North America. Scientists could establish a "baseline" against which an assessment of human impact and subsequent prey reaction then may be measured (Kelly and Todd 1988). Also, the effects of environmental perturbation could be monitored in animal populations using the paleodietary techniques explored in this study. Changes in diet, whether gradual or extreme, could potentially indicate significantly stressful periods.

Comparing such paleoecological databases with archeological information, such as site structure and location, seasonal land use and technological changes in response to potential alterations in prey structure, would allow for the integration of theoretical models of human cultural systems with empirical data that is directly coupled to food and materials resources. The techniques developed in this study have a unique temporal quality that allows for an extremely detailed, sequential look at paleoecological variations. Identifying variation at this level in prey ecology, as well as for paleoecology in general, has the potential to significantly enhance our understanding and interpretations of previously generalized behavioral and ecological patterns.

Conclusion

This study provides more detailed exploration of $\delta^{13}C$ variations in bison enamel then presently available. Incremental $\delta^{13}C$ values from dental enamel generally vary in response to seasonal inputs from dietary carbon during dental formation. The technique in this study provides discrete, intra-annual insights into foraging behavior. Isotopic values can be linked among successive and concurrently developed teeth, providing extended temporal insights. We focused specifically upon three sampling zones of the mandibular third molar. Enamel formation of these zones corresponds to mid-summer, early winter, and early spring of a bison's second year. Foraging patterns generally can be reconstructed based upon these periods. Comparisons of foraging patterns by individual, by cohort, and among cohorts can provide insights into social structure, potential landscape use, and assemblage foraging patterns.

Exploration of paleodietary techniques, as applied to a sizable sample of geographically and temporally restricted bison, has yielded a data set that allows for tentative interpretations concerning social aspects of bison from the archeological record. Such behaviors, not only of the Glenrock assemblage but also of other bison and mammalian herbivores, had real consequences for human predation strategies (Frison 1991). The initial success encountered in developing techniques to better define bison paleoecology has the potential to contribute significantly to various models of human predation and adaptation. Thus, continued research to further our understanding of bison and other prey species behavior is strongly supported.

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APPENDIX

Sample	Cohort	Individual	Position	$\delta^{13}C$ (‰)	C_4(%)
1	1	1	1,3	-4.89	69.44
3	1	1	2,1	-7.05	55.94
11	3	6	2,2	-9.13	42.94
12	3	6	2,1	-8.33	47.94
13	3	6	3,2	-7.44	53.50
14	3	6	3,1	-0.63	96.06
15	3	7	3,2	-1.71	89.31
16	3	7	3,1	-15.75	1.56
17	3	8	3,2	-7.34	54.13
18	3	8	3,1	-7.58	52.63
19	4	10	3,1	-4.69	70.69
20	4	11	3,3	-6.95	53.94
21	4	11	3,2	-7.37	56.56
22	4	11	3,1	-5.39	66.31
23	A	12	3,3	-8.1	49.38
24	A	12	3,2	-8.77	45.19
25	A	12	3,1	-0.32	98.00
26	A	13	3,3	-0.56	96.50
27	A	13	3,2	-0.38	97.63
28	A	13	3,1	2.42	100.00
29	A	14	3,3	-6.29	60.69
30	A	14	3,2	-8.17	48.94
31	A	14	3,1	-9.36	41.50
32	B	15	1,3	-7.51	53.06
33	B	15	2,3	-5.51	65.56
34	B	15	2,2	-6.37	60.19
35	B	15	3,3	-5.02	68.63
36	B	15	3,2	-7.17	55.19
37	B	15	3,1	-5.51	65.56
38	B	16	3,3	-6.83	57.31
39	B	16	3,2	-7.13	55.44
40	B	16	3,1	-6.67	58.31
41	B	17	3,3	-7.08	55.75
42	B	17	3,2	-8.05	49.69
43	B	17	3,1	-8.51	46.81
44	B	18	3,3	-8.19	48.81
45	B	18	3,2	-8.36	47.75
46	B	18	3,1	-7.2	55.00
47	C	19	3,3	-7.27	54.56
48	C	19	3,2	-4.99	68.81
49	C	20	3,3	-8.41	47.44
50	C	20	3,2	-9.19	42.56
51	D	21	3,3	-8.64	46.00
52	D	21	3,2	-8.2	48.75
53	D	22	3,3	-7.16	55.25
54	D	22	3,2	-8.65	45.94
55	E	23	2,3	-0.32	98.00

APPENDIX continued

Sample	Cohort	Individual	Position	$\delta^{13}C$ (‰)	C_4(%)
56	E	23	3,3	1.59	100.00
57	E	23	3,2	0.61	100.00
58	E	24	3,3	-6.01	62.44
59	E	24	3,2	-8.63	46.06
60	E	25	3,3	-2.6	83.75
61	E	25	3,2	-2.13	86.69
62	E	26	3,3	-0.16	99.00
63	E	26	3,2	-0.64	96.00
64	4	10	3,3	-2.6	83.75
65	4	10	3,2	-3.3	79.38
66	4	9	1,3	-6.1	61.88
67	4	9	1,2	-6.19	61.31
68	4	9	2,3	-1.94	87.88
69	4	9	2,2	-4.56	71.50
70	4	9	2,1	-5.92	63.00
71	4	9	3,3	-3.71	76.81
72	4	9	3,2	-2.57	83.94
73	4	9	3,1	-2.14	86.63
75	U(amv)	27	3,3	-10.01	37.44
76	U(amv)	27	3,2	-9.66	39.63
77	U(amv)	27	3,1	-10.17	36.44
78	U(amv)	28	3,3	-9.85	38.44
79	U(amv)	28	3,2	-10.29	35.69
80	U(amv)	28	3,1	-10.78	32.63
81	U(amv)	29	3,3	-8.81	44.94
82	U(amv)	29	3,2	-10.29	35.69
83	U(anet)	30	2,3	-8.88	44.50
84	U(anet)	30	2,2	-10.06	37.13
85	U(anet)	30	2,1	-9.83	38.56
PM-19	Hartsel	8503b	2,1	-12.41	22.44
PM-20	Wheatland39	39	2,1	-5.17	67.69
PM-21	Wheatland39	39	1,1	-5.02	68.63
PM-22	Wheatland41	41	2,1	-4.12	74.25
PA-23	Hudson-MengM3	398	3,1	-4.8	70.00
PA-24	Hudson-MengM2	397	2,1	-5.55	65.31
PA-26	Lake Theo	210	2,1	-0.78	95.13
PA-27	Casper A hyp	8488	2,2	-8.24	48.50
PA-28	Casper A post	8488	2,3	-7.4	53.75
PA-30	Casper B M1	8500	1,2	-8.37	47.69
PA-31	Casper B pre	8500	2,1	-7.94	50.38
PA-32	Casper B hyp	8500	2,2	-6.68	58.25
PA-33	Casper B post	8500	2,3	-6.58	58.88
PA-34	Ft. Rob 0		2,1	-8.27	48.31
PA-35	Glenrock		2,1	-7.93	50.44

Notes: Initial study samples (Larson 1995) are designated as modern (PM) and archeological (PA). *Bison priscus* samples were called cohort U.