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**CARBON AND NITROGEN ISOTOPES IN
ARCHEOLOGICAL BISON REMAINS AS INDICATORS
OF PALEOENVIRONMENTAL CHANGE IN
SOUTHERN ALBERTA**

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ABSTRACT—Between 1995 and 1997, archeological excavations in northwest Calgary, Alberta, uncovered cultural materials from several occupations dating back 8,500 years. Samples of bison bone recovered at the sites were chemically prepared and analyzed for isotopic ratios. Using the resultant carbon and nitrogen isotope ratios, we reconstructed the diet of bison from four different cultural occupations spanning the last 8,500 years. Based on current and established models of bison subsistence behavior, this dietary information was used to infer large-scale environmental changes during this time interval in our study area. The inferred changes in vegetation and climate were compared with paleoenvironmental reconstructions for the study area specifically and with models of post-Pleistocene environmental change for the Northern Great Plains generally. Our results suggest that changes in the diet of bison in southern Alberta coincide with broader environmental changes reported for the Holocene and appear to reflect the adaptability of this species.

KEY WORDS: archeology, bison, carbon isotopes, collagen, nitrogen isotopes, Northern Plains, southern Alberta

Introduction

Isotopic analyses are commonplace in modern ecological investigations and are used to study animals and the environments in which they live (Boutton 1991b). Application of these techniques to archeological and paleontological materials provides a time dimension to ecological studies of modern species and ecosystems. In this paper we use carbon and nitrogen isotope ratios to reconstruct the diet of prehistoric bison from several time periods. These data are then used to infer changes in the environment exploited by these grazers. The inferred changes in the foraging environment and in bison ecology over time suggest that this species is adaptable to variation in forage quality. The results also enhance our understanding of the changes in bison behavior and subsistence (Tieszen 1994).

Our discussion begins with a brief outline of isotope studies and how these have been used to reconstruct the diet of animals that lived several thousands of years ago. We then examine the isotopic composition of grasses and note their distribution across the Great Plains before reviewing the literature on the diet and ecology of modern and prehistoric bison populations occupying this environment. Finally, we present the results of our study, focusing primarily on the correspondence between the grasses represented in the bison diets and the reconstructions of the local and regional plant communities.

Isotopes and Diet

Numerous researchers have studied the relationships between isotopes of nitrogen and carbon and the diets of mammals, including humans. In this study, we focused on the isotopic composition of plants on the Great Plains and how differences observed in forage could be reflected in the tissues of grazers. Having identified a link between modern forage composition and bison diets, we used the same procedures to investigate the impact of environmental change on bison diet. Before exploring these relationships, however, it is necessary to explain briefly the procedure used to calculate isotopic ratios.

A major problem affecting the recovery of isotopic data from archeological bone is its possible qualitative alteration during burial. The approach used to correct for possible contamination is the chemical extraction and purification of specific components of the sample bone (Ambrose 1993; Schoeninger et al. 1989). Collagen, a protein that may be isolated from the

organic portion of bone, is generally well preserved (Katzenberg 1992), and its isotopic composition reflects the diet of the animal (DeNiro and Epstein 1978, 1981). Collagen in adult mammal bone tissue also remodels at a slow rate and, as a result, isotopic values “reflect diet averaged over a period as long as ten to twenty years” (Stenhouse and Baxter 1979, as cited in McKinnon 1986:49).

Both carbon and nitrogen isotopic ratios may be determined reliably from the analysis of qualitatively intact bone collagen. However, the reported isotopic ratio is actually the relative difference between the isotope content of the sample and a known standard gas. Delta (δ) notation is used to express this difference. Thus, “ $\delta^{13}\text{C}$ is the parts per thousand, or per mil (‰), difference between the ^{13}C content of the sample and that of the standard” (Boutton 1991a:158). Let us now examine how the isotopes of nitrogen and carbon relate to the diet of an animal.

Nitrogen Isotopes

Heaton et al. (1986) demonstrated that climate influences nitrogen isotope ratios in mammals, such that $\delta^{15}\text{N}$ values were negatively correlated with annual rainfall. For example, plants occurring on saline soils tend to have higher $\delta^{15}\text{N}$ values than those found in forested environments. Not surprisingly then, forest-dwelling animal species have lower $\delta^{15}\text{N}$ values than do savanna species (Ambrose 1993). Assuming that the enrichment of ^{15}N compared to ^{14}N in herbivore tissues is as constant as has been previously reported, near 3 ‰ (Ambrose 1993), then these environmental differences should be reflected in $\delta^{15}\text{N}$ values of their bone collagen. In a comparison of East African herbivores from modern and prehistoric populations, Ambrose and DeNiro (1989) recorded differences in the $\delta^{15}\text{N}$ values of bone collagen and noted their relationship to reconstructions of environmental change. Their data suggested that shifts between 2 ‰ to 3 ‰ over time in an area appear to reflect significant environmental change.

Dietary and water stress may also affect $\delta^{15}\text{N}$ ratios within animal tissues. Many animals in arid environments, including bison, demonstrate physiological adaptations for water conservation (Fizet et al. 1995). This results in excretion of urine that is highly concentrated in urea, and it leads to an elevation in $\delta^{15}\text{N}$ values within the animal's tissues (Ambrose 1991). Urea excretion decreases when the quantity of protein in the food is reduced (Fizet et al. 1995). “Therefore, water stressed animals that concentrate their urine should have higher $\delta^{15}\text{N}$ values than un-stressed ones. Animals with

low nitrogen diets (usually grazers during the dry season) are expected to have lower $\delta^{15}\text{N}$ values than others (mainly browsers and mixed feeders) because they recycle their nitrogen" (Ambrose 1993). While these physiological adaptations may help to explain differences in $\delta^{15}\text{N}$ ratios between species, differences within a species using such a physiological mechanism must ultimately derive from differences in the degree of dietary or water stress affecting these animals. It is likely that these differences are environmentally dictated.

Carbon Isotopes

Dietary determinations from herbivore tissue using carbon isotopes are based on the occurrence of isotopically distinct plant groupings that form the bulk of an animal's diet. Tropical and subtropical grasslands consist almost exclusively of C_4 grasses (Boutton 1991b), whereas temperate grassland communities include primarily C_3 species (Keegan 1989). Fortunately, the isotope values for C_3 and C_4 plants exhibit a bimodal distribution in $\delta^{13}\text{C}$, with C_3 plants averaging -26.7‰ while C_4 plants average -12.5‰ (Chisholm et al. 1986; Tieszen et al. 1997).

Bison collagen is enriched by 5‰ relative to dietary forage. Thus, a bison diet consisting of 100% C_3 forage would be expected to produce $\delta^{13}\text{C}$ ratios in bone of -21.5‰ ($-26.5\text{‰} + 5\text{‰}$). Conversely, a diet of exclusively C_4 plants would produce mean $\delta^{13}\text{C}$ values of -7.5‰ ($-12.5\text{‰} + 5\text{‰}$) (Chisholm et al. 1986). Dietary $\delta^{13}\text{C}$ values for bison therefore should range between -21.5‰ and -7.5‰ , where a value of -7.5‰ would reflect a diet composed entirely of C_4 plant material while a value of -21.5‰ would represent a diet devoid of C_4 plants. Given a $\delta^{13}\text{C}$ value for an archeological bone sample, it is possible to calculate the relative amounts of C_3 and C_4 species in that particular animal's diet using a simple linear interpolation (Chisholm et al. 1986:197). In this study, we used the following linear regression equation to calculate approximate C_4 dietary contributions based on $\delta^{13}\text{C}$ ratios:

$$\% \text{C}_4 = 7.143(\delta^{13}\text{C measured}) + 153.571.$$

Plant Distributions

Although C_4 species occur primarily in tropical or subtropical grasslands, their northern limit in the Americas is defined as the Canadian grasslands (Chisholm *et al.* 1986). Coupland (1961) used the relative contribution

of major plant species to define the vegetative communities in southern Alberta. These communities are distributed in bands from the southeastern corner of the province toward the north and west. Morgan (1980) simplified this classification into three major vegetative zones, including the Xeric Mixed Prairie (short grass), Mesic Mixed Prairie (mid-grasses), and the Fescue Prairie (Fig. 1). The only dominant C₄ grass found in most vegetative communities in southern Alberta is *Bouteloua gracilis* (McKinnon 1986; Chisholm et al. 1986). According to Coupland (1961), *B. gracilis* contributes negligibly to the Fescue Prairie, comprising only about 1.0% of overall forage production. This representation increases to a mean value near 14.5% in the Mesic Mixed Prairie and ranges from 37.0% to 56.5% within the Xeric Mixed Prairie.

Looman (1983) verified this trend, suggesting that the major differences in the distribution of grasses were related to variations in moisture regimes. He suggested that high temperatures and increased aridity during the summer months serve to stimulate the growth of *B. gracilis*, a drought-tolerant species. Actually, Coupland (1961) had suggested that increasing moisture or temperature regimes could have a dramatic effect on the percentage of C₄ grasses. During the 1940s, annual rainfall was low in the Prairie Provinces, especially when compared to that of the early 1950s, and the mean cover of *B. gracilis* in the Mesic Mixed Prairie changed from 17.5% in the 1940s to roughly 11.6% in the 1950s (Coupland 1961).

In summary, distribution of C₃ and C₄ plants across the Plains is highly correlated with variations in temperature and precipitation (Teeri and Stowe 1976; Boutton et al. 1980; Looman 1983). Specifically, as temperature increases and precipitation decreases, the relative proportion of C₄ plants comprising the total vegetative cover should increase. Temperature and precipitation regimes vary across the Great Plains along both elevational and latitudinal gradients, as well as on a more regional basis. Generally, biomass of C₄ plants increases as latitude and elevation decrease. This trend is most apparent with changes in latitude. For example, Tieszen (1994:265) reported between “68 and 82 percent of ground cover as C₄ in southwestern and southern Texas, roughly 35 percent in South Dakota, and decreasing composition into Canada.” It is important to note, however, that although fixed factors such as latitude, elevation, soil composition, and topography are important, changes in C₃ and C₄ biomass are primarily functions of variable factors, such as temperature and precipitation (McKinnon 1986; Laurenroth et al. 1999).

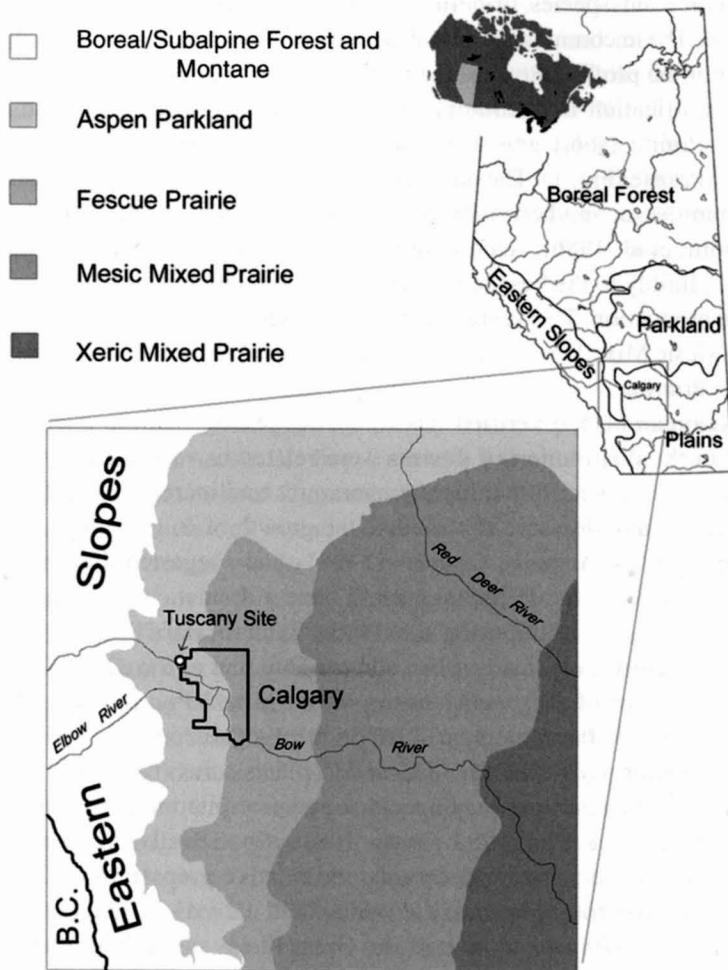


Figure 1. Map of the Calgary area showing the distributions of ecoregions.

Bison Ecology

The environmental sensitivity demonstrated by *B. gracilis* has important implications for diet reconstruction using bison bone tissue. Bison tend to be relatively unselective grass grazers (Tieszen 1991). Although they can tolerate a relatively low-quality diet, bison require fairly large absolute

volumes of forage due to their size (Peden 1976). Therefore, bison generally cannot be too selective when grazing. As a result, the isotopic values isolated from bison bone tissue should be representative of the relative proportion of C₃ and C₄ plants within their foraging range (Tieszen 1991). Bison do exhibit seasonal changes in the concentrations of C₃ versus C₄ forage consumed; however, due to the slow turnover of bone collagen in bison, such seasonal patterns become integrated and obscured and result in $\delta^{13}\text{C}$ values that are representative of longer term dietary averages (Tieszen 1994).

Differences in reconstructed diet through time also may be explained by changes in large-scale movements through ecozones with different forage production. Discerning the isotopic effects of a changing environment from those resulting from changing migration patterns relies on the predictability of migratory behavior in bison. Significant debate has been centered on this point. As Bamforth (1988) stated,

Bison migration and aggregation patterns have been the subject of most of the anthropological debate over bison ecology, and the essence of this debate is tied to the question of how predictable these patterns actually were. As plains anthropologists have used the term, *predictability* seems to mean the degree to which herds of the same size returned to the same point on the ground at the same time of the year in successive years.

Bamforth (1988) suggests that these aggregation and migration patterns may be quite predictable if one first recognizes the factors determining these patterns. Descriptions of historical and ecological observations suggest that bison on the Canadian plains may have exhibited a fairly regular pattern of seasonal migration (Roe 1951; Moodie and Ray 1976). As described by Morgan (1980), this likely entailed wintering within aspen parklands and moving out onto the prairie grasslands in the spring and summer months. In contrast, Hanson (1984) argued that bison did not undergo regular seasonal movements but instead demonstrated erratic patterns that were flexible and localized. Hanson (1984) based his reconstruction largely on an ecological analysis of bison in South Dakota, which suggested that adequate forage existed year round to sustain resident herds. Several historical accounts also dispute the nature of bison seasonal migration, suggesting that the movement either did not occur or involved short, sporadic seasonal dispersion (Garretson 1938; McHugh 1972; Arthur et al. 1975).

Using data on the migration patterns of several African ungulates and North American caribou, Epp (1988) proposed a model in which the bulk of the population migrated seasonally to and from the grasslands, while smaller resident populations remained throughout the foraging range (Varney et al. 1997). According to Bamforth (1988), the apparent differences between the Canadian herds and their southern counterparts were both understandable and predictable, given the different ecological contexts. Despite the apparent regularity of movement in Canadian herds, data compiled by Moodie and Ray (1976) suggest that during milder winters, when the forage would not have been deeply buried by snow, and the cold and wind would not have been severe, migratory behavior was reduced (Bamforth 1988). Therefore, erratic and dispersed patterns, observed by Hanson (1984) in South Dakota herds and depicted by some historical sources, are consistent with observations of Canadian bison behavior in less severe winters.

It seems reasonable to accept a model in which modern Canadian Plains bison move seasonally, east to west, between the parklands and plains, but less so in moderate winters. If this were the case, then bison bone isotope ratios from southern Alberta would not show significant variation as the result of short-term deviations associated with seasonal movement, since the isotopic composition of the bone averages the diet over a longer period of time. The variations in seasonal foraging behavior observed could also be interpreted as an attempt by bison to mediate the effects of climatic fluctuations on their subsistence base. Therefore, only significant environmental deviations over an extended period should have a major impact on the isotopic composition of bison bone tissue.

Despite evidence suggesting migratory behavior in Northern Plains bison during the later Holocene, it remains unclear whether this foraging strategy was used by earlier Holocene bison. It has been suggested that the only direct evidence for differences between bison populations throughout the Holocene comes from morphological change in bison remains through time (Guthrie 1966, 1970; Wilson 1978; McDonald 1981; Bamforth 1988). Changes in bison morphology have been assumed to be related to changes in bison behavior in the context of the larger environment. Bamforth (1988) suggested that the biological constraints of the bison digestive system likely acted in concert with large-scale environmental changes to produce a series of interrelated morphological and behavioral changes in Holocene bison. Specifically, he argued that bison at the outset of the Holocene were adapted to an essentially cooler, moister Pleistocene environment having relatively abundant forage. As the climate began a general warming trend throughout

the period known as the Altithermal, forage distributions changed and seasonal pressures, similar to those affecting modern bison, began to appear on a larger scale. In this scenario, the larger bison of the early Holocene required larger overall quantities of forage than did the later forms. As Bamforth (1988) described,

Smaller animals have lower total forage requirements because they have less mass to provide nutrients for. They thus need to spend less time eating, allowing them to spend more time searching for higher quality food.

The larger bison, thus, were constrained in terms of the time that they could devote to meeting their greater foraging requirements. This would result in selective pressure for a more mobile form as quality forage became more dispersed. The expected result was smaller bison that were less constrained and thus able to range farther for adequate sustenance (Bamforth 1988).

Bamforth's (1988) model provides a framework for examining the isotopic dietary values isolated from temporally distinct bison populations throughout the Holocene. If indeed the older forms were restricted in mobility relative to modern taxa, their diets should be more indicative of plant distributions on a more local scale. Since morphologically modern bison seem to appear consistently in the archeological record by 5,000 BP, it seems reasonable to hypothesize that the older bison were more sedentary in general, while the more recent forms likely exhibited migratory patterns similar to modern herds. To test some of these influences, we examined the isotopic composition of bison bone from four distinct cultural layers dating between 8,500 and 2,000 years ago. Significantly, the samples were derived from deeply stratified deposits that also yielded a great deal of information on the local environment.

Study Area

The samples of bison bones used in this study were derived from two archeological sites situated in northwest Calgary, Alberta. Specifically, the sites were located at 51° north latitude near the present boundary of the aspen parkland and fescue prairie. Site 1 (EgPn-375) is interpreted as a winter encampment occupied some 2,000 years ago (Oetelaar 2000). Site 2 (EgPn-377) was a deeply stratified, multicomponent site with at least three

well-defined cultural components dating from 5,000, 7,000, and 8,500 years ago (Oetelaar 1997; Oetelaar et al. 1996). Importantly, the sediments, buried soils, animal bones, gastropod shells, and botanical remains recovered from these sites have provided a wealth of information on changes in the local ecophysical environment.

Methods

For the present analysis, bison first and second phalanges were collected from each of the four cultural occupations. The number of specimens analyzed was determined and limited ultimately by the low number of individuals represented. Sample preparation involved mechanical cleaning of all skeletal specimens using double-distilled water followed by an ultrasonic bath. A small handsaw was then used to section the complete elements into small chunks. A few of these small chunks were selected from each specimen to achieve a sample mass of between 0.5 and 3.0 grams per sample.

Collagen was extracted and purified from each sample using the method of Sealy and van der Merwe (1986), as modified by Katzenberg (Erwin 1998). Bone chunks were demineralized at room temperature in a 0.25 M HCl solution that was changed every second day until demineralization was complete. Specimens were then rinsed to neutrality with double-distilled water. Humic materials were removed by further soaking each sample in a 0.125 M NaOH solution for about 20 hours. The samples were rinsed again to neutrality with double-distilled water and finally freeze-dried for 48 hours.

Following collagen extraction, samples were combusted and the stable carbon and nitrogen isotope values were determined using a mass spectrometer. All isotope values were reported using the delta (δ) notation in ‰ (parts per mil). All ^{13}C to ^{12}C ratios were reported relative to the PeeDee Belemnite (PDB) standard, whereas all ^{15}N to ^{14}N ratios were reported relative to the Ambient Inhalable Reservoir (AIR) standard.

Results

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios, and C_4 dietary inputs as calculated from the $\delta^{13}\text{C}$ values, are presented in Table 1. This table also includes the cultural associations and approximate ages of the samples. The only sample group that seemed to deviate significantly from the others was the 7,000-year old

TABLE 1

STABLE ISOTOPE VALUES AND CALCULATED C₄ PERCENTAGES OF DIET FOR BISON BONE FROM THE TUSCANY SITE, CALGARY

Sample	Cultural association	Approximate age (BP)	$\delta^{13}\text{C}$ of "collagen" (‰)	$\delta^{15}\text{N}$ of "collagen" (‰)	C ₄ of diet %
A	Pelican Lake	2000	- 19.2	5.7	16.4
B	Pelican Lake	2000	- 18.6	8.3	20.7
C	Oxbow	5000	- 18.6	6.6	20.7
D	Oxbow	5000	- 18.3	8.0	22.9
E	Oxbow	5000	- 18.8	9.2	19.3
F	Bitterroot	7000	- 16.5	11.2	35.7
G	Bitterroot	7000	- 17.6	8.5	27.9
H	Bitterroot	7000	- 17.1	8.6	31.4
I	Bitterroot	7000	- 17.8	8.5	26.4
J	Bitterroot	7000	- 17.5	8.5	28.6
K	Agate Basin	9000	- 17.7	7.7	27.1
L	Agate Basin	9000	- 18.8	7.7	19.3

set. For this group, the $\delta^{13}\text{C}$ of collagen tended to be lower, the $\delta^{15}\text{N}$ of collagen averaged higher, and the percentage of C₄ of the diet was high on average (Table 1). Most of the specimens analyzed in this study produced acceptable collagen yields and C/N ratios (Table 2). Acceptable ratios of carbon to nitrogen in collagen range between 2.9 and 3.6 (Katzenberg 1992). Since Sample E yielded an abnormally high C/N ratio (3.7), it was excluded from the remainder of the analysis.

We conducted a statistical analysis of the relationship of the $\delta^{15}\text{N}$ value to the $\delta^{13}\text{C}$ value for each sample, as represented by its calculated C₄ dietary composition (Fig. 2). The data set was first analyzed for normality of distribution using the Kolmogorov-Smirnov test. Given the small sample size, it is not surprising that the data did not indicate a normally distributed population. Thus, the nonparametric Spearman's rank order correlation was used to analyze the data. A strong positive correlation ($R_s = 0.871$) was observed between nitrogen and the percentage of C₄ in the diet.

TABLE 2
COLLAGEN YIELDS AND CARBON/NITROGEN RATIOS FOR
BISON BONE FROM THE TUSCANY SITE, CALGARY

Sample	Collagen yield (%)	C/N ratios
A	16.94	3.56
B	11.92	3.52
C	16.05	3.51
D	18.57	3.42
E	10.07	3.70
F	21.5	3.44
G	6.7	3.48
H	8.41	3.51
I	6.39	3.48
J	5.69	3.51
K	16.96	3.45
L	11.98	3.48

Discussion

Reconstructing the Regional Context

Reconstructions of the regional vegetation during the Holocene are generally based on detailed analyses of pollen sequences derived from lake cores, preferably from a lake located near the study area (Beaudoin 1993). For our study area, the record from cores of Toboggan Lake provides the best framework for interpreting early Holocene paleoenvironments in southern Alberta. Toboggan Lake is a small lake about 10 km south of Bragg Creek, or approximately 30 km south of the study area.

MacDonald (1989) divided the cores into five pollen zones, each corresponding to an observable change in the regional vegetation. Zone 1, which dates from 10,400 to 9,400 BP, was dominated by pollen from herbs and shrubs, suggesting the presence of grassland or parkland vegetation. Zone 2, which dates from 9,400 to 8,400 years BP, was dominated by spruce

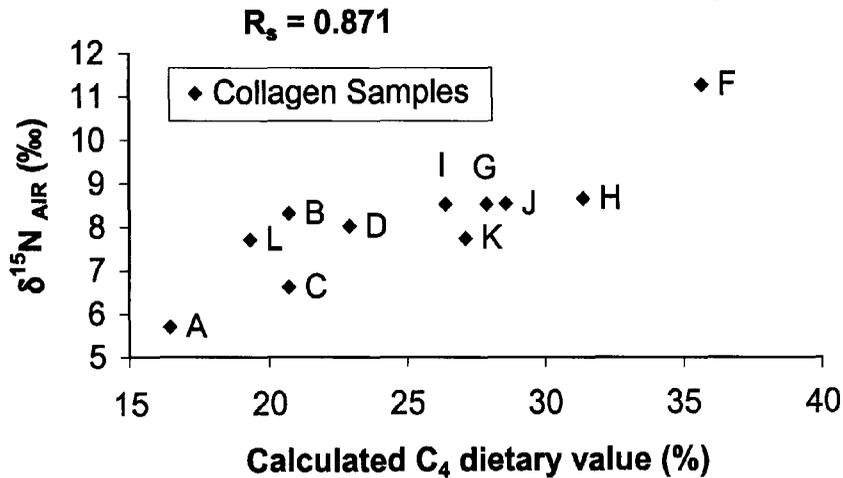


Figure 2. $\delta^{15}\text{N}$ ratios of bone collagen vs. calculated C₄ dietary percentages. Correlation analysis between $\delta^{15}\text{N}$ values of bison bone and their calculated percentages of C₄ dietary input (1-tailed test, 11 d.f., $P < 0.05$).

and pine pollen but also included a substantial amount of grass pollen. According to MacDonald (1989), this pollen assemblage is indicative of an open spruce forest. Zone 3, which dates from 8,400 to 7,600 years BP, was interpreted as a transition to the arid conditions of the Altithermal, which lasted from 8,000 to 5,000 BP. Zone 4, dating from 7,600 to 5,500 BP, was represented by increases in grass pollen, suggesting a replacement of forest by prairie. Zone 5, which dates from 5,500 BP to the present, indicated a gradual expansion of spruce and pine populations to their current limits in the area. This sequence of ecological changes is generally consistent with Vance's (1986) reconstruction of the vegetation history for the province.

Reconstructing the Local Environment

At the local level, reconstructions of the changing natural and biological environments are based on detailed analyses of the sediments, buried soils, plant remains, animal bones, and gastropod shells recovered from the deeply stratified site. Not surprisingly, the changes inferred in the local plant and animal communities mirror those identified in the pollen cores. During the first episode of human occupation, the site was situated near a

small marsh within an open woodland or parkland setting. By 7,000 years ago, the time of the second occupation, the forest had been replaced by a grassland community. Shortly after the deposition of the Mazama ash layer, the increasingly warm, dry weather reduced the grassland community and promoted the displacement of sediments by wind. Around 5,000 years ago, an increase in precipitation as well as a slight decrease in temperature enabled the grassland community to become re-established. This vegetation community remained essentially unchanged until the advent of Euro-Canadian settlers (Oetelaar et al. 1996; Oetelaar 2000).

Isotopic Data

The isotopic data from this study are consistent with the scenario of environmental change proposed above. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each time period represented suggest that changes in the pattern of C_4 consumption are discernible (Table 3). Nonisotopic lines of paleoenvironmental evidence suggest that both the 2,000- and 5,000-year old cultural components at the Tuscan site are roughly representative of the modern environment in the study area (Oetelaar et al. 1996). The estimated C_4 dietary percentages calculated from the mean carbon isotope ratios isolated from these cultural components ranged between 18.6% and 21.4%. This is reasonably close to the grassland values presented by Chisholm et al. (1986), and it suggests that modern bison in southern Alberta should exhibit C_4 dietary consumption of around 20% of their total diet.

The significance of the differences between the mean values for the 2,000- and 5,000-year old components at Tuscan is unclear. Modern populations of bison with largely restricted diets have been observed to vary at least as much. The 2,000-year old material does include, however, the most negative $\delta^{13}\text{C}$ ratios of the cultural components analyzed in this study. The mean value of -18.9‰ translates to approximately 18.6% C_4 plants in the diet. This value is not entirely unexpected, as the general paleoecological sequence for southern Alberta suggested that these times may have been characterized by decreased temperature and increased moisture (Vickers 1986).

The reconstructions of the local and regional environments both identify the 7,000- to 6,000-year interval as one of increased temperature and aridity. The mean values for the 7,000- to 6,000-year old bone samples suggest a diet composed of a higher proportion, roughly 30%, of C_4 grasses, as would be expected. However, although an approximation, this value is

TABLE 3

MEAN STABLE ISOTOPE VALUES AND CALCULATED C₄ PERCENTAGES OF DIET FOR BISON BONE FROM THE TUSCANY SITE, CALGARY

Cultural association	N	Approximate age (BP)	Mean $\delta^{13}\text{C}$ of "collagen" (‰)	Mean $\delta^{15}\text{N}$ of "collagen" (‰)	Mean C ₄ of in diet %
Pelican Lake	2	2000	- 18.9	7.0	18.6
Oxbow	2	5000	- 18.5	7.3	21.4
Bitterroot	5	7000	- 17.3	9.1	30.0
Agate Basin	2	9000	- 18.3	7.7	22.9

higher than most published $\delta^{13}\text{C}$ values from within southern Alberta (Chisholm et al. 1986; McKinnon 1986, 1990; Varney et al. 1997). Further, this average value suggests a higher percentage of C₄ in the diet than appears in bison from any other isotopically sampled cultural occupation in southern Alberta (Chisholm et al. 1986; McKinnon 1986, 1990; Varney et al. 1997). To find an analog in modern herds, one must look as far south as Wyoming and South Dakota (Tieszen 1994).

Unfortunately, it is difficult to put these prehistoric isotopic data into a modern context since there are currently no modern free-ranging bison herds from southern Alberta. However, Tieszen (1994) reported a linear increase in both C₄ ground cover and bison dietary compositions with decreasing latitude. Data collected by Chisholm et al. (1986) also indicate a similar latitudinal gradient in the dietary composition of late prehistoric bison from Alberta. That study depicted a 16% increase in C₄ consumption proceeding south from Peace River, in northern Alberta, toward the grasslands. This equals an average 2.5% change for every degree of latitude (McKinnon 1986). The $\delta^{13}\text{C}$ values for samples from southern Alberta indicated between 20% and 22% C₄ grasses in the diet (Chisholm et al. 1986), values which agree well with the trend identified by Tieszen (1994). The calculated values for the bone samples from the 7,000- to 6,000-year old component thus represent significant deviations from previous data.

The reconstructions of the local and regional environment for the interval between 9,000 and 8,000 years ago suggest a cooler, moister climate that supported an open spruce forest with isolated patches of grassland. Analysis of the $\delta^{13}\text{C}$ values produced by samples from this time period is also complex. The carbon values suggest an average dietary composition of 22.9% C_4 grasses (-18.3‰). Without an estimate from a modern bison diet in the area, it is difficult to say whether this value is consistent with a cooler moister environment than the present. A slightly higher proportion of C_4 grasses was indicated than during either the 2,000- or 5,000-year old time periods. The significance of this difference can be questioned; however, it should be noted that the nonisotopic paleoenvironmental data for the area at this time is contradictory. Some of the recovered skeletal and botanical remains suggest the occurrence of grassland in the immediate vicinity (Oetelaar et al. 1996). It is possible therefore that all of these data combine to indicate the presence of a compositionally distinct ecosystem, one without a modern analog.

Consideration of the nitrogen values in this study lend some support to the implications of the carbon data for environmental reconstruction. Again, the importance of the small deviations that occur in the nitrogen values obtained from the 9,000-, 5,000-, and 2,000-year old assemblages is not clear. However, the nearly 2‰ increase in the mean $\delta^{15}\text{N}$ ratios of the 7,000- to 6,000-year old sample set suggests an important difference for this time period. This value may indicate a period of either dietary or water stress in which mechanisms for water conservation led to a ^{15}N enrichment in the tissues of these bison (Ambrose 1993, Fizet et al. 1995). Conversely, this value may result from aridity and salinity factors leading to increases in the $\delta^{15}\text{N}$ values of the available forage (Ambrose 1993; Fizet et al. 1995). Both situations, however, occur in response to environmental conditions. Therefore, it is likely that this highly positive value ultimately reflects the same environmental change toward a hotter, drier climate that is suggested by all of the other lines of evidence from the site, including the carbon data.

Statistical analysis suggested a positive correlation between the nitrogen values and calculated C_4 dietary percentages. This correlation would seem to verify an environmental sensitivity of nitrogen within this system. Since no relationship between photosynthetic pathway and ^{15}N concentration has been reported, the correlation must result from a shared variable affecting both the distribution of C_4 plants and the ratio of nitrogen in plant tissues. The most likely candidate driving such a correlation is precipitation, which has been previously linked to both. Furthermore, the strong correla-

tion suggests that even minor fluctuations in nitrogen values, such as those evidenced during the 9,000-, 5,000-, and 2,000-year old time periods, may be related to environmental influences.

Conclusions

Paleoenvironmental reconstruction for the Calgary region based upon several independent lines of nonisotopic evidence has provided a model against which the carbon and nitrogen isotope ratios produced in this study could be interpreted. Generally, the trends indicated by the isotopic data seem to agree with the other ecological inferences made for each of the sampled cultural occupations at the Tuscan site. It would therefore seem that the isotopic analysis of bison bone collagen demonstrates some potential as a technique of paleoenvironmental reconstruction in relatively simple ecological contexts having significant, prolonged environmental changes through time. In addition, the isotopic data have suggested that at approximately 7,000 years BP, southern Alberta bison were either foraging in an environment that was warmer and drier than modern times or exhibiting a foraging strategy different from that expected in extant herds.

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