



# Isotope paleoecology of episodic mid-to-late Holocene bison population expansions in the Southern Plains, U.S.A.



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## ABSTRACT

We used a XAD-purified AMS radiocarbon method to date 62 bison specimens from different contexts on the very southern extent of the Great Plains of North America to produce a precise chronology of bison population expansions spanning the last 6000 years. Sixty-one of these samples provide stable carbon and nitrogen isotope data indicating relative temperature and moisture conditions during intervals defined by the presence of bison within this time span. This chronology indicates climatic conditions favorable to bison were present in the greater central Texas area, including the uplifted Edwards Plateau and extending to the Coastal Plain during periods from ~5955 to 5815, ~3290 to 3130, 2700 to 2150, and 650 to 530 cal BP. However, isotope results suggest climatic conditions differed for each period. The earliest “Calf Creek” period was characterized by cool but dry conditions, the later “Late Archaic 1 & 2” periods were increasingly warmer and wetter, and the latest “Toyah” period was cooler and drier than the Late Archaic periods, but warmer and wetter than Calf Creek. Both the Calf Creek and Toyah periods had higher variability within these overall trends. Comparison with regional records suggests that these periods represent variation within generally cool–dry climates. Human adaptive response to increased bison availability resulted in significant cultural changes across all four periods.

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## 1. Introduction

Following the megafauna extinctions of the Terminal Pleistocene, the North American genus *Bison* remained the top-ranked resource available to Great Plains hunter-gatherers throughout the Holocene. A variety of bison hunting strategies on the Plains are documented for early Younger Dryas-age occupations onward (Guthrie, 1980; Bamforth, 1988, 2011; Frison, 1991, 1998, 2004; Bement and Buehler, 1994; Cooper, 2008; Bozell et al., 2011; Carlson and Bement, 2013). Even in Late Prehistoric times, agriculturalists in the American Southwest and in Mississippi River drainages to the east often hunted for or traded bison parts, including robes and dried meat, bringing them into frequent contact with Plains tribes (Vehik, 1990, 2002; Creel, 1991; Spielmann, 1991; Speth and Newlander, 2012). It is not an overstatement to say that bison exploitation played a significant role in shaping regional prehistoric and early historic economies across the Plains.

Yet the population dynamics and distribution of bison are incompletely known in much of south-central North America, especially in areas on the peripheries of the Great Plains. Bison are generally associated with habitats ranging from grasslands to boreal forests (McDonald, 1981), but in prehistoric times were sensitive to climatic and environmental changes that affected the quality and availability of forage (Koch et al., 2004; Widga et al., 2010). Modern bison are predominantly, though not exclusively, grazers, subsisting primarily on grasses but occasionally including browse into their diet (Bamforth, 1988; Owen-Smith, 2008). Similarly, prehistoric bison populations are closely linked with the availability of grassland habitats, the composition of which varies according to factors like soil type, temperature, and rainfall (von Fischer et al., 2008), but especially temperature (Teeri and Stowe, 1976; Paruelo and Laurenroth, 1996).

Presumably, *Bison bison* were present in predominantly C<sub>3</sub> or mixed C<sub>3</sub>/C<sub>4</sub> grassland plains nearly continually since they evolved from earlier forms (McDonald, 1981; Meagher, 1986; Wilson et al., 2008; see Bamforth, 2011). Only occasionally, at least in the middle to late Holocene, did they extend into areas not typically defined by Plains-like habitats, such as parts of the Great Basin

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(Grayson, 2006), northern Mexico (List et al., 2007), or Central and Coastal Texas (Dillehay, 1974; Lynott, 1979; Baugh, 1986; Huebner, 1991; Ricklis, 1992). Understanding when and under what climatic conditions bison moved into regions where they were not continuously present is important not only for our general knowledge regarding cultural and environmental records in North America, but also for providing insights into bison ecology and related human responses throughout the Holocene.

Here, we present stable carbon and nitrogen data on AMS radiocarbon dated bison specimens recovered from central and south Texas. The chronology of this record, presented in detail elsewhere (Lohse et al., 2014b), begins immediately after 6000 cal BP and extends to historic times. At certain times during the Holocene, this study area shared many environmental (von Fischer et al., 2008) and archaeological (Kay, 1998) traits in common with the Great Plains to the north. Our directly dated bison specimens cluster into four concise temporal periods. Using isotope data, we evaluate and compare regional environmental conditions for each period.

As we review below, a variety of climate proxy records in or near the central Texas and the extreme Southern Plains region suggest century- to millennial-scale climate cycles significantly altered local Holocene landscapes. Unfortunately, most of these data are chronologically poorly controlled and often contradictory. Moreover, many paleoenvironmental records come from adjacent areas that were differentially affected by local weather systems during the same climate cycles, make extrapolation to the central Texas area problematic. This study helps to resolve this record in a part of North America where directly dated, high-resolution paleoclimate and environmental data are lacking (Wanner et al., 2011). It also contextualizes the spread of important ungulate species as well as the human responses to these climatic changes.

## 2. Stable isotopes from bison and reconstructing environments

As grassland grazers, bison potentially provide high-resolution records of the environmental conditions that characterize their territorial range. During photosynthesis, stable carbon ( $^{12}\text{C}$  and  $^{13}\text{C}$ ) isotopes are integrated into plant tissues. Nitrogen ( $^{14}\text{N}$  and  $^{15}\text{N}$ ) is also integrated into plants, but as a function of soil chemistry and moisture (DeNiro and Epstein, 1981). Herbivores ingest these elements, which are incorporated into tissues like bone collagen, where they have residence periods of many years or longer (Ambrose and DeNiro, 1986b; Dalerum and Angerbjörn, 2005) and can be subject to measurement. Stable carbon and nitrogen isotope measurements on animal tissue, including collagen, have been shown to indicate relative temperature and precipitation (effective moisture) conditions that affect available forage (Stafford, 1984; Chisholm et al., 1986; McKinnon, 1986; Tieszen, 1994; Lovvorn et al., 2001; Hoppe et al., 2006).

Stable carbon isotopes have been proven to be sensitive indicators of changes in temperature, either synchronously by latitude or over time. Bender (1968) observed a systematic effect of photosynthetic pathways ( $\text{C}_3$  and  $\text{C}_4$  systems) on the ratios of  $^{13}\text{C}$ – $^{12}\text{C}$  in different kinds of grasses and other plants. While both  $\text{C}_3$  and  $\text{C}_4$  plants discriminate against  $^{13}\text{C}$ ,  $\text{C}_4$  plants take in greater amounts of  $^{13}\text{C}$ .  $\text{C}_3$  and  $\text{C}_4$  plants can therefore be differentiated based on their ratios of  $^{13}\text{C}$ – $^{12}\text{C}$ , reported in per mil (‰) notation with respect to the VPDB standard as  $\delta^{13}\text{C}$  (Tieszen, 1994). Eco-systems characterized by  $\text{C}_3$  pathways are defined by  $\delta^{13}\text{C}$  values that average  $-27 \pm 3\text{‰}$  while  $\delta^{13}\text{C}$  values of  $\text{C}_4$ -dominated environments average  $-13 \pm 2\text{‰}$  (Tieszen and Boutton, 1989). Many trees, herbs, and cool-season grasses use a  $\text{C}_3$  photosynthetic

pathway while  $\text{C}_4$  pathways are associated with warm-season grasses and sedges.

When plants are consumed by herbivores and carbon is integrated into collagen,  $\delta^{13}\text{C}$  is enriched by  $\sim 5$ – $6\text{‰}$  (van der Merwe and Vogel, 1978; Krueger and Sullivan, 1984; Ambrose and DeNiro, 1986b). Importantly, this value is an approximation, and several studies have indicated species-specific enrichment factors. Feranec (2007), for example, reports a fractionation of  $+6.3\text{‰}$  for modern bison in Yellowstone National Park. Considering the documented variation in species-specific fractionation (Dalerum and Angerbjörn, 2005), we use this figure rather than  $+5\text{‰}$  that, while more commonly reported, is not calculated specifically from *B. bison*. Accordingly, prehistoric bison subsisting on a 100%  $\text{C}_3$  diet can be expected to have  $\delta^{13}\text{C}$  values from approximately  $-23.7\text{‰}$  to  $-17.7\text{‰}$  while those consuming 100%  $\text{C}_4$  plants will have  $\delta^{13}\text{C}_{\text{COLLAGEN}}$  values between  $-8.7\text{‰}$  and  $-4.7\text{‰}$ . Relying on these principles, paleoecologists and archaeologists have used  $\delta^{13}\text{C}$  as an indication of the percentage of  $\text{C}_4$  plants as a way to understand prehistoric and modern environments that have been associated with bison (Stafford, 1984; Chisholm et al., 1986; McKinnon, 1986; Huebner, 1991; Tieszen, 1994; Jahren et al., 1998; Lovvorn et al., 2001; Koch et al., 2004; Hoppe et al., 2006:Table DR2; Meltzer, 2006).

Regarding the effect of different environmental conditions on  $\delta^{13}\text{C}$ , von Fischer et al. (2008) showed that July climate, including average daily high temperature and total rainfall, is a better predictor of the percentage of  $\text{C}_4$  plants than other values, and indicates that reconstructing  $\text{C}_4$ -diet using  $\delta^{13}\text{C}$  values can effectively track climate, especially temperature. Given that  $\geq 66\%$  of the variability in  $\text{C}_4$  composition in the Great Plains is explained by mean annual temperature (MAT), Hoppe et al. (2006) reconstruct MAT using bison tooth enamel carbonate. Caution is warranted, however, since many factors affect  $\delta^{13}\text{C}$  values from bison, and variability of  $\geq 3\text{‰}$  is common within a single herd (see Tieszen, 1994: Fig. 14; Meltzer, 2006: Fig. 6.15). In addition to intraherd variation of this scale, individual ungulates within herds can show extreme variation far in excess of a single standard deviation (e.g., Fenner, 2009 for pronghorn; Lovvorn et al., 2001 for Agate Basin bison; Meltzer, 2006 for Folsom bison). We argue that, although these statistical outliers can skew local or regional climate reconstructions, they can be important for understanding herd dynamics and mobility patterns during certain periods. In addition to grazing habits, soil texture, and precipitation, depositional conditions such as soil moisture as well as whether sampled material was subjected to heating in prehistoric times can all affect  $\delta^{13}\text{C}$  (Jahren et al., 1998). Given these factors, Hoppe et al. (2006:650) note the importance of using mean values of multiple animals ( $\geq 5$ ) for any paleoclimatic reconstruction, and warn that results should be considered as relative indicators of temperature rather than as precise estimates. Our discussion of stable carbon isotopic variation considers mean values for each time period without outliers and also considers the potential significance of these outliers in temporal reconstructions.

In addition to using stable carbon isotopes as a general indication of temperature, research using stable nitrogen isotopes has shown how this isotope can be used to understand relative prehistoric moisture. The ratio of  $^{14}\text{N}$  and  $^{15}\text{N}$ , reported as  $\delta^{15}\text{N}$ , is a useful indicator of environmental stress, particularly drought (Ambrose and DeNiro, 1986a,b; Cormie and Schwarcz, 1995). Schwarcz et al. (1999) examined this relationship and found that the loss of isotopically light ammonia from topsoil during xeric conditions results in  $^{15}\text{N}$  enrichment of plants, which in turn is reflected in animal tissues. This process is likely to outweigh the effects of concentrated ( $^{15}\text{N}$ -depleted) uric acid in grazers (Ambrose and DeNiro, 1986b), resulting in what Schwarcz et al.

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