Available online at www.sciencedirect.com
SCIENCE DIRECT
ELSEVIER
Palaeogeography, Palaeoclimatology, Palaeoecology 206 (2004) 337–353
PALAEO
www.elsevier.com/locate/palaeo

"Amount Effect" recorded in oxygen isotopes of Late Glacial horse (*Equus*) and bison (*Bison*) teeth from the Sonoran and Chihuahuan deserts, southwestern United States

Pennilyn Higgins*, Bruce J. MacFadden

Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA

Received 16 June 2003; accepted 17 December 2003

Abstract

Stable oxygen isotopes from fossils, both vertebrate and invertebrate, or inorganic sedimentary minerals frequently have been used to make interpretations about ancient global climates. Oxygen isotope values measured from terrestrial vertebrates or sedimentary carbonates provide information about paleotemperature and amounts of precipitation at a particular site. In general, these inferences are made on the centennial to millennial scale.

Serial, i.e. ontogenetic, sampling of *Equus* and *Bison* tooth enamel provides climatic data on the scale of months to a few years. We present models showing how annual environmental patterns of $\delta^{18}O$ would be replicated in the tooth enamel of *Equus* and *Bison*. Changes in $\delta^{18}O$ due to shifts in temperature (in terrestrial environments $\delta^{18}O$ increases with increased temperature) and amount and timing of precipitation (increased precipitation may result in a decrease in $\delta^{18}O$; a phenomenon called the "Amount Effect") are archived in both *Equus* and *Bison* teeth. The input signal is better resolved in *Bison* due to its more rapid enamel growth.

Modeled patterns are compared with actual data from modern sites in the Sonoran and Chihuahuan deserts of the southwestern United States. The isotopic patterns from modern teeth agree with that predicted from known variations in meteoric water. Known floral and faunal assemblages as well as computer models suggest summer rain for the Chihuahuan Desert of Late Glacial time (15,000–10,000 years ago), but little summer rain for the Sonoran Desert at that same time. Serial data from fossil teeth show a clear pattern interpreted to represent the Amount Effect that includes increased summer rains in the Chihuahuan Desert and only minor summer rains in the Sonoran Desert.

Keywords: Amount Effect; Oxygen isotopes; Paleoclimate; Sonoran and Chihuahuan deserts; *Equus*, *Bison*, *Bos*

1. Introduction

Inferences about ancient climates are often made based upon floral and faunal assemblages at a particular site. Also, computer models (CLIMAP, 1976; COHMAP, 1988; Kutzbach et al., 1993) have been used to propose general, continent-wide climatic variations. Stable isotopes of oxygen, measured from diatoms and sedimentary minerals, have been used to investigate centennial to millennial patterns of global climate (Abell and Hoelzmann, 2000; Jouzel et al., 2000; Poage et al., 2000; Bard et al., 2002). Through

* Corresponding author. Tel.: +1-352-392-1721x251; fax: +1-352-846-0287.
E-mail address: loligo@flmnh.ufl.edu (P. Higgins).

0031-0182/$ - see front matter © 2004 Elsevier B.V. All rights reserved.
doi:10.1016/j.palaeo.2004.01.011

the study of oxygen isotopes obtained by serial or ontogenetic sampling of fossil tooth enamel of horse (*Equus*) and bison (*Bison*), inferred climate patterns for a short period of time (months to years) in a specific geographic area may be examined (Bryant et al., 1996; Fricke and O'Neil, 1996; Gadbury et al., 2000). A single third molar records these changes over a period of 18 months (*Bison*) to 3 years (*Equus*) (Bryant et al., 1996; Fricke and O'Neil, 1996; Gadbury et al., 2000; Hoppe et al., 2004). Seasonal patterns in temperature change, and rainfall amounts can be interpreted from the pattern of serial values of the $^{18}O/^{16}O$ ratio collected from these teeth.

1.1. The Amount Effect

Traditionally, variation in oxygen isotope ratios studied from terrestrial environments has been ascribed to environmental temperature changes, where warmer weather results in an enrichment of ^{18}O and cooler weather results in depletion of ^{18}O in meteoric water (McCrea, 1950; Bryant et al., 1996). From this, a sinusoidal pattern for the $^{18}O/^{16}O$ ratio, with high values indicating summer and low values indicating winter, is predicted for data collected from tooth enamel (Fricke and O'Neil, 1996 Feranec and MacFadden, 2000). However, other factors clearly influence the oxygen isotopic archive in terrestrial settings. One of these factors, the "Amount Effect", is an important relationship between precipitation/humidity, temperature, and the $^{18}O/^{16}O$ ratio (Dansgaard, 1964). The main result of the Amount Effect is that when environmental temperatures rise above approximately 20 °C (the Amount Effect threshold) and there is significant precipitation and/or high humidity, ^{18}O abundance in meteoric water decreases (Rozanski et al., 1993; Bard et al., 2002; Straight et al., 2004) (Fig. 1).

The pattern discussed above is readily seen in data from sites all over the world (IAEA/WMO, 2001). Isotopic data are reported in the conventional delta (δ) notation, where $\delta^{18}O$ (parts per mil, ‰)=$(R_{sample}/R_{standard}) - 1) \times 1000$, and $R = {}^{18}O/^{16}O$.

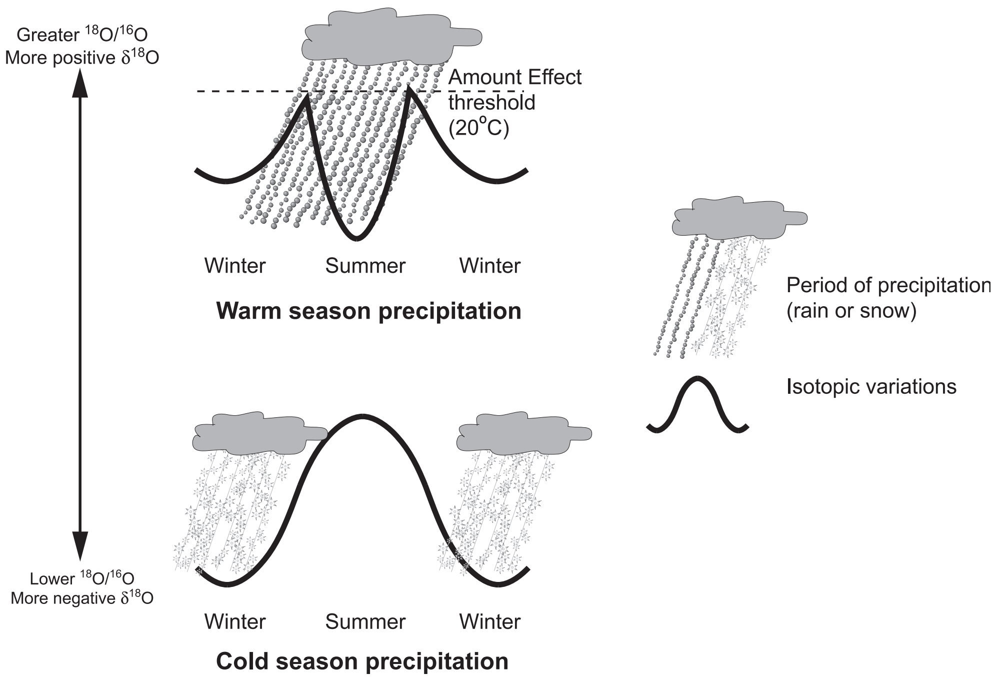

Fig. 1. Illustration of the isotopic effect of heaviest precipitation (rain or snow) during different parts of the year, and the relationship to ambient temperature. Summer rains, when ambient temperatures are greater than about 20 °C result in a marked decrease in the $^{18}O/^{16}O$ ratio in meteoric water (and thus $\delta^{18}O$ values).

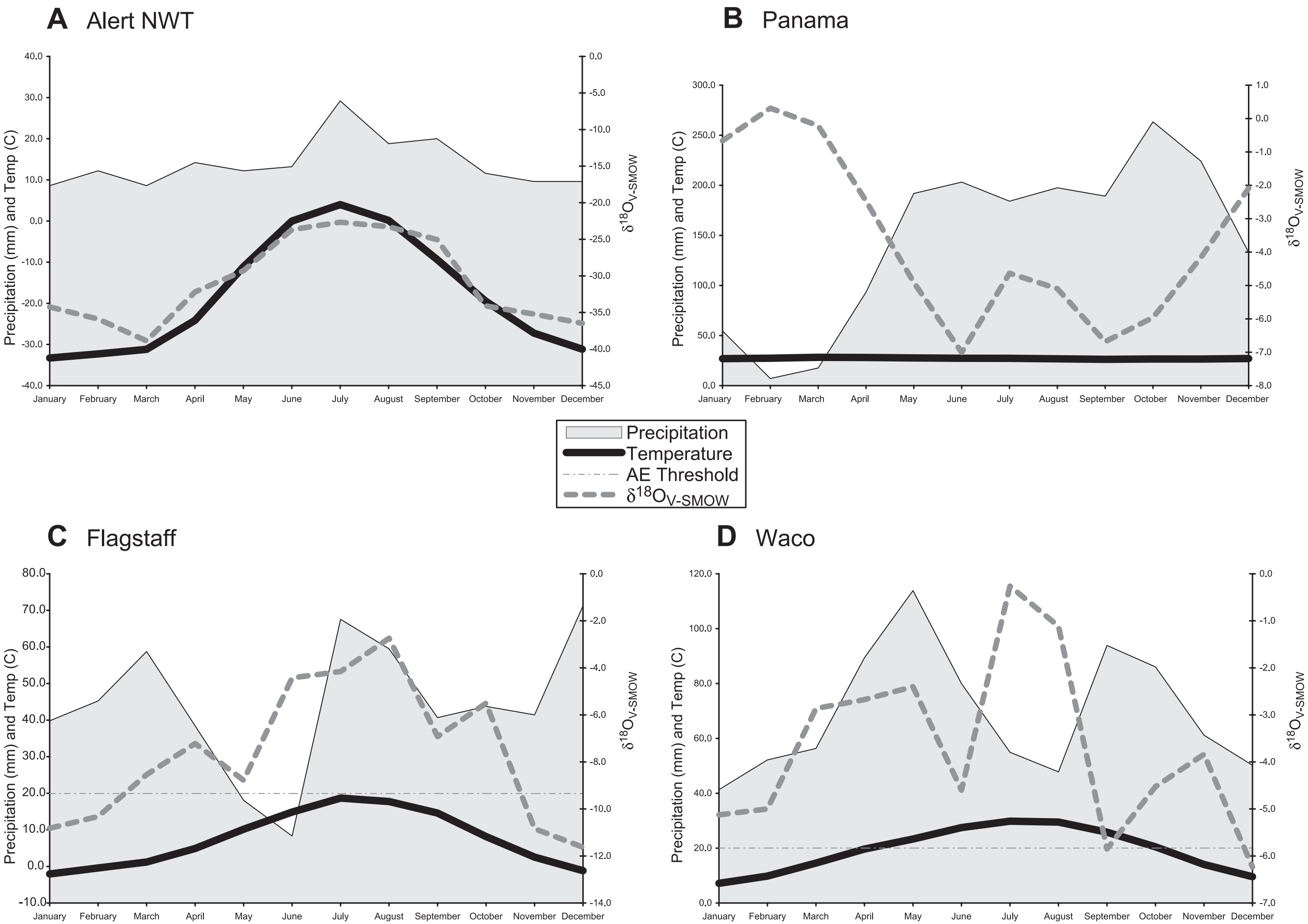

Fig. 2. Average monthly values of temperature, amount of precipitation, and $\delta^{18}O_{V\text{-}SMOW}$ for four sites on the Global Network of Isotopes in Precipitation (http://isohis.iaea.org; IAEA/WMO, 2001). (A) Alert, Northwest Territories, Canada; (B) Panama; (C) Flagstaff, AZ, USA; (D) Waco, TX, USA. The Amount Effect threshold (20 °C) is shown in C and D.

A site located at high latitudes, such as the Alert Station, in the Northwest Territories, has an isotopic signal controlled principally by temperature variations, as temperatures seldom if ever rise above the Amount Effect threshold (Dansgaard, 1964; Rozanski et al, 1993; Straight et al., 2004) (Fig. 2A). At low latitudes, such as in Panama, average temperatures are relatively constant and always remain above the Amount Effect threshold. Isotopic values of meteoric water do show a strong annual variation (around 7‰) that varies inversely with amount of precipitation (Rozanski et al., 1993; Straight et al., this volume) (Fig. 2B).

More complex isotopic patterns are seen when average temperatures get close to or exceed the Amount Effect threshold. In Flagstaff, AZ (Fig. 2C), average temperatures only occasionally reach the Amount Effect threshold, resulting in an average isotopic pattern with some irregularities. In Waco, TX (Fig. 2D), average temperatures exceed the Amount Effect threshold for about half the year (the summer). Waco also generally has periods of increased rain in the spring and the fall. The result of this is a triple-cusped annual pattern of isotopic variation, where troughs occur in the spring and fall, corresponding to seasonal rain.

1.2. Climate in the Southwest

1.2.1. Modern climate

The southwestern United States is noted for its expansive deserts, of which three are recognized: Mojave, Sonoran, and Chihuahuan (Fig. 3). This research focuses on fossil sites located in the Sonoran and Chihuahuan deserts (no corresponding specimens were available for the Mojave). Average values of monthly temperature and precipitation for a few desert cities are shown in Fig. 4. Sites in the Chihuahuan Desert (Roswell, NM, Carlsbad, NM, and El Paso, TX) (Fig. 4A) generally experience a single rainy season during the summer. Tucson, AZ, and the nearby Arizona Sonora Desert Museum (Fig. 4B) have a bimodal distribution of precipitation, with some in the winter, but the majority in the late summer.

1.2.2. Late Glacial climate

The modern Sonoran and Chihuahuan deserts are characterized by an extreme climate in which relatively few large land mammals are able to survive the hardships of the arid terrain. During the Last Glacial Maximum (LGM, ~20ka), however, the Southwest was not the parched landscape that it is today (Van Devender and Spaulding, 1979; Harris, 1987; Thompson et al., 1993). At that time, glaciers were at their maximum extent over the continent of North America, which resulted in a weather regime for the Southwest featuring cooler-than-present summer and winter rains.

Fig. 3. Map of the southwestern United States and northwestern Mexico showing the approximate extent of the Mojave, Sonoran, and Chihuahuan deserts. Fossils used in this study are from Murray Springs and Dry Cave.

Much of the shift from the ice-controlled climate of the Full Glacial to the modern hot and dry deserts of today occurred during the Late Glacial, about 15,000–10,000 years ago (Thompson et al., 1993). During this interval, summers typically were cooler than at present, and the winters warmer. The Sonoran Desert experienced greater effective moisture than at present (Van Devender and Spaulding, 1979; Thompson et al., 1993), but with lower amounts of summer precipitation than today. Precipitation occurred throughout the year with common winter frontal storms (Van Devender and Spaulding, 1979). The Chihuahuan Desert, in contrast to today, did not experience the hard freezes that typify the modern weather regime (Thompson et al., 1993). Precipitation occurred year-round, but in greater amounts during the summer months (Harris, 1987).

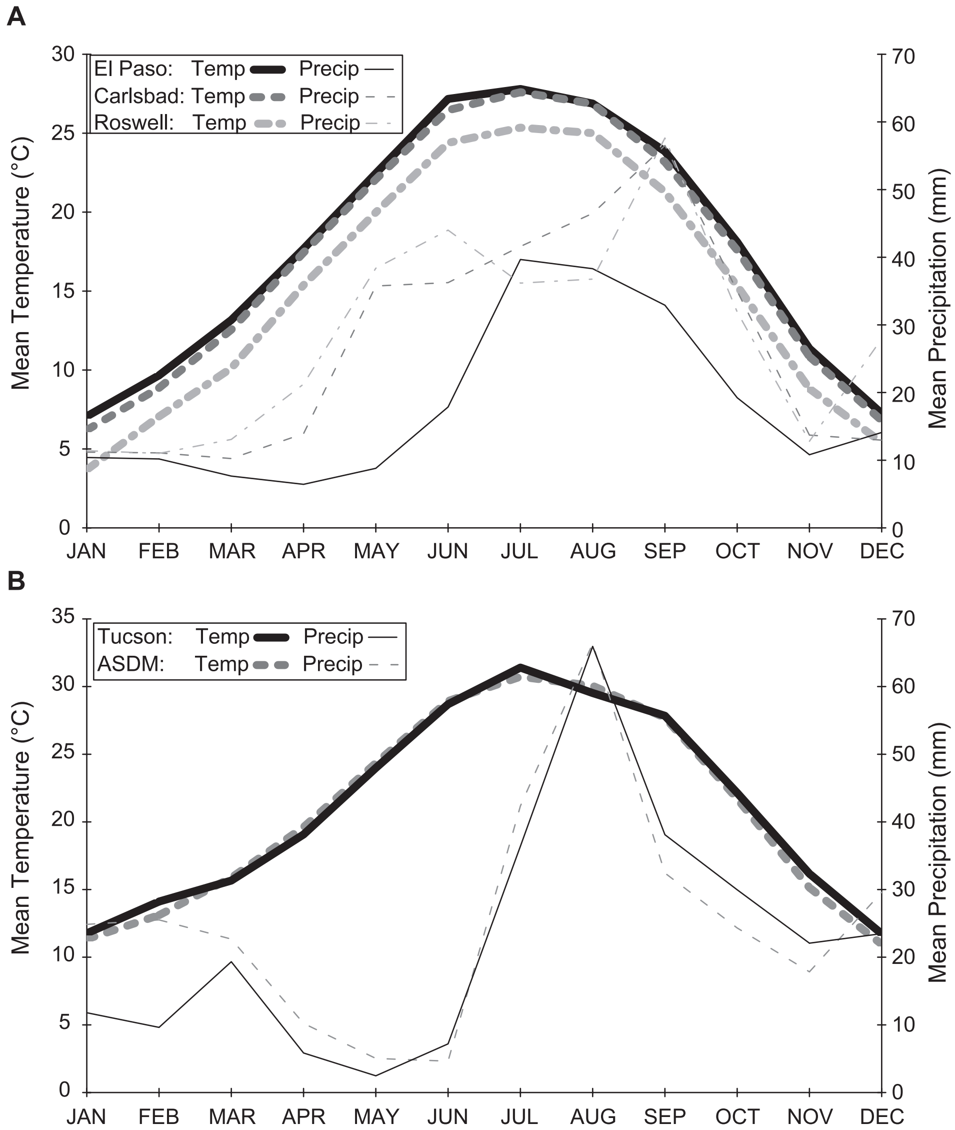

Fig. 4. Average monthly values of temperature and precipitation for cities in the modern (A) Chihuahuan Desert and (B) Sonoran Desert. Heavy lines denote temperature values (measured on the left scale). Light lines denote precipitation values (measured on the right scale). Data from the National Climatic Data Center (http://www.ncdc.noaa.gov).

1.3. Models and hypotheses

In this paper, $\delta^{18}O$ values of *Equus* or *Bison* tooth enamel at various points along the height of the tooth are modeled, taking into account biological factors such as rate of enamel mineralization and period of enamel maturation (Passey and Cerling, 2002). Variations in $\delta^{18}O$ values due to the Amount Effect are also modeled. Modern teeth of domesticated *Equus* and *Bos* (cattle) from areas of known climate patterns are serially sampled and analyzed. The isotopic data are then compared with data predicted from modeling in order to test the validity of the approach.

The overall pattern of $\delta^{18}O$ data from serially sampled fossil *Equus* and *Bison* are used to infer seasonal climate patterns for the deserts of the Late Glacial Southwest. It is expected that teeth from the Sonoran Desert preserve an isotopic pattern that is basically sinusoidal, tracking temperature changes. Minimal Amount Effect is expected, because the Late Glacial Sonoran Desert lacked a significant summer rainy season. The isotopic pattern from the Chihuahuan Desert, however, is expected to have an Amount Effect signal in the late summer months, due to increased precipitation in the late summer.

2. Methods

2.1. Taxa and teeth used

Equus and *Bison* are ideal for this study, because much of their water intake is through drinking surface water, which maximizes the isotopic effects of temperature and precipitation. Both taxa also have tall-crowned (i.e. hypsodont) teeth that mineralize over several months to years, providing a long record of isotopic change. *Equus* and *Bison* share similar food sources, mainly grass (Nowak, 1999), and were selected for this study to reduce any confusion that may result from multiple levels of fractionation from differences in food sources or trophic level.

Isotope fractionation due to various food and water sources or trophic level includes that which occurs between meteoric water sources and the milk that a mother provides for her foal or calf (Bryant et al., 1996). However, Zazzo et al. (2002) argue that the pre-weaning signal may be insignificant compared to the climate signal from ingested meteoric water, especially if only the pattern of isotopic variation is considered, and not absolute values. Notwithstanding Zazzo et al. (2002), in order to reduce the possibility of a maternally influenced isotopic pattern, and to maximize the total length of time preserved in a tooth, only third molars (M3) are analysed for this study. The M3 of *Equus* takes about 3 years to fully mineralize starting with the tip of the crown and continuing toward the root (Hoppe et al., 2004) (Fig. 5). In contrast, for *Bison*, this process takes 15–18 months (Brown et al., 1960; Erz, 1964; Hillson, 1986; Gadbury et al, 2000) (Fig. 5). As such, a single relatively unworn M3 from either *Equus* or *Bison* captures isotopic information for at least one entire year of the animal's life.

Stable isotope values are affected not only by climate and diet. Metabolic rate of the individual animal may have a pronounced effect (Kohn, 1996; Kohn et al., 1998; Zhow and Zheng, 2002; Owen et al., 2002). Metabolic rate may be affected by envi-

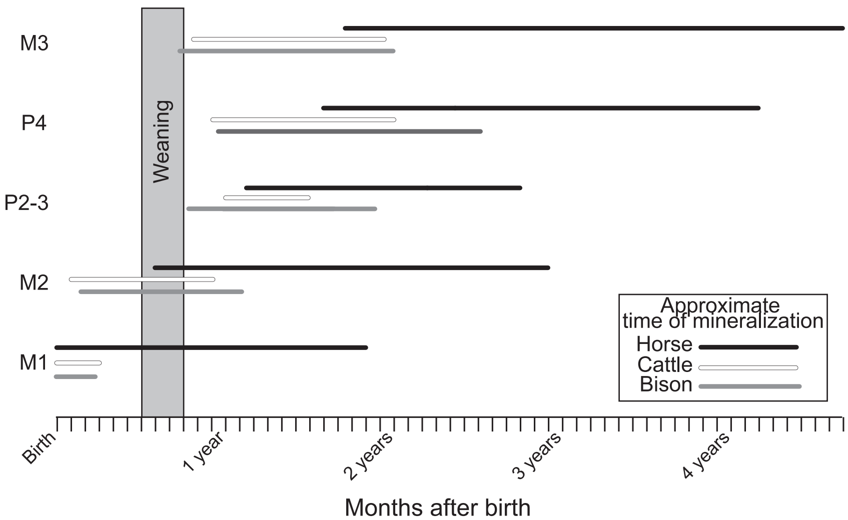

Fig. 5. Tooth mineralization duration in horses (*Equus*), cattle (*Bos*), and bison (*Bison*) plotted with respect to months following birth. Horse data from Hoppe et al. (2004); cattle from Fricke and O'Neil (1996); bison from Gadbury et al. (2000). P1–P3 and M1–M3 denote premolar and molar tooth positions regardless of whether the tooth comes from the upper jaw or the lower jaw.

ronmental stressors such as drought or by metabolic stresses like pregnancy or weaning. Annual or semi-annual changes in moisture sources may also affect $\delta^{18}O$ values. Winter precipitation that comes from the north will have a different isotopic signature from summer monsoon rains that come off the Gulf of Mexico. Finally, migration of herds may also affect the isotopic pattern as movements from one region to the next may include a change in food source and precipitation source. It is difficult to assess just how much of an effect each of these factors may have on the oxygen isotope composition of tooth enamel. For the sake of this study, such factors are considered negligible in most cases, and will be discussed in situations below where their effect is apparent.

Specimens from two fossil localities were selected for this study. Murray Springs (University of Arizona Laboratory of Paleontology, UALP locality 63) lies near the margin of the mapped Sonoran Desert. It has a radiocarbon date of 10800 ± 50 BP (Haynes, 1987). The Late Glacial Chihuahuan Desert is represented by Dry Cave, NM, from the Camel Room locality (University of Texas at El Paso, UTEP locality 25), with an approximate radiocarbon date of no older than 11880 ± 250 BP (Harris, 1980).

2.2. Sampling strategy

A total of 101 isotopic analyses were done from four fossil and two modern grazer teeth. One complete M3 of *Equus* and one of *Bison* were available and therefore sampled from each fossil locality (UTEP 25-537, *Equus*, and UTEP 25-543, *Bison*, from the Camel Room; and UALP 63-3433, *Equus*, and UALP uncatalogued, Bovidae, from Murray Springs). One modern *Bos* M3 (UTEP 6381) from near Roswell NM, and one modern *Equus* M3 (UTEP 5167) from the El Paso area were also sampled.

Serial sampling was employed to collect data from the teeth, whereby small samples of enamel were taken at even increments along the height of the tooth. The samples were analyzed and data plotted against the height of the tooth. This provides useful information about annual variation during the period of enamel mineralization, as each sample is essentially an average record of a few weeks to months of the animal's life.

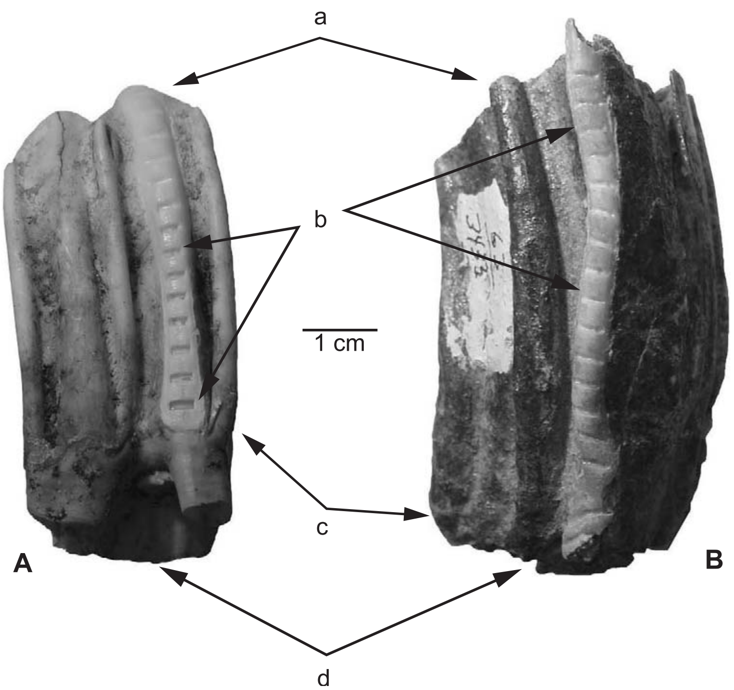

Fig. 6. Examples of teeth that have been serially sampled. (A) Modern *Bos* M3 from near Roswell, NM; (B) fossil *Equus* m3 from Murray Springs, AZ. Labeled features: (a) occlusal surface; (b) sample pits; (c) enamel dentine junction; (d) roots.

Isotopic analysis was done using between 5 and 10 mg of powdered enamel collected from the teeth using a low-speed Foredom™ dental drill and carbide dental burrs. Care was taken to avoid collecting any surficial cement on the tooth or dentine underlying the enamel. Serial samples were collected from grooves drilled perpendicular to the growth axis of the tooth, following growth lines if they are visible (Fig. 6). A sample was taken every 2–3 mm, resulting in about 12–20 samples per tooth. The position of each groove is recorded in millimeters starting with the groove closest to the root (assigned a value of 0).

2.3. Isotopic analysis

Powdered samples were chemically treated to ensure that only pure bioapatite was analyzed. Samples were first treated with H_2O_2, to remove any organic contaminants, and then with weak (0.1 N) acetic acid to remove any surficial carbonate, in preparation for analysis in the mass spectrometer. Samples were analyzed using the VG Prism mass spectrometer available in the Department of Geological Sciences at the University of Florida. About 1–2 mg of sample is needed for each analysis.

Data from samples were compared using the conventional delta (δ) notation for oxygen ($\delta^{18}O$), where $\delta^{18}O$ (parts per mil, ‰)=$(R_{sample}/R_{standard})-1)\times 1000$, and $R={}^{18}O/{}^{16}O$. Unknown sample analyses were calibrated to either an internal laboratory standard (MEme) or NBS-19, and ultimately back to the V-PDB (PeeDee Belemnite) or V-SMOW (Standard Mean Ocean Water), following Vienna convention, hence "V-" (e.g., Coplen 1994). Following Hoefs (1997), $\delta^{18}O$ data calibrated to V-PBD were corrected to V-SMOW as follows: $\delta^{18}O_{V\text{-}SMOW}=1.03091(\delta^{18}O_{V\text{-}PDB})+30.91$.

3. Enamel mineralization

3.1. Tooth enamel mineralization

Tooth enamel mineralizes incrementally, beginning at the crown of the tooth with a mineralization front moving toward the root of the tooth as enamel formation proceeds (Fricke and O'Neil, 1996; Gadbury et al., 2000; Hoppe et al., 2004). Total mineralization of any point along the growth axis of the tooth is not instantaneous. Instead, it may take several weeks to months for mineralization to be completed at a particular point on the tooth (Passey and Cerling, 2002; Hoppe et al., 2004). This period of tooth enamel formation from beginning to end is termed maturation. Because of maturation effects, the isotopic data from a single sample represents the average values over the interval of time during which maturation occurs. Hoppe et al. (2004) cite this period to be three to four months for horses. Presumably the maturation for *Bison* and cattle enamel takes about half the time (~ 2 months), because their teeth are about the same length, but completely develop in half the time compared to horses. This reduces the amount of time-averaging in the isotopic signal.

Furthermore, mineralization proceeds along a plane that is nearly parallel to the enamel–dentine junction of the tooth (an angle of 5–10°; Hoppe et al., 2004) (Fig. 7), rather than perpendicular to the external surface of the tooth. The combination of maturation and the angle of mineralization means that any sample collected through the entire depth of the enamel at any point along the tooth actually formed over a period of weeks to months. However, Passey and Cerling (2002) showed that although there is a averaging of the isotopic signal, the original signal is not lost.

Passey and Cerling (2002) provide a mathematical model for determining the isotopic ratio expected for any point along the growth axis of a tooth. Using their model, isotopic values for enamel were calculated for both *Equus* and *Bison* M3s assuming a sinusoidal annual variation. Fig. 7 illustrates and defines the model parameters la, lm, and ls (Passey and Cerling, 2002). Table 1 lists input variables used in this paper. Fig. 8A illustrates the relationships among real values of environmental isotopes and those recorded in tooth enamel of both *Equus* and *Bison*.

Examination of Fig. 8a illustrates several important features of the model isotope data with respect to input environmental values:

- The sinusoidal pattern is evident, though dampened somewhat.
- Dampening is greater in the *Equus* than in *Bison*, due to a longer period of maturation and therefore greater averaging of the input signal.

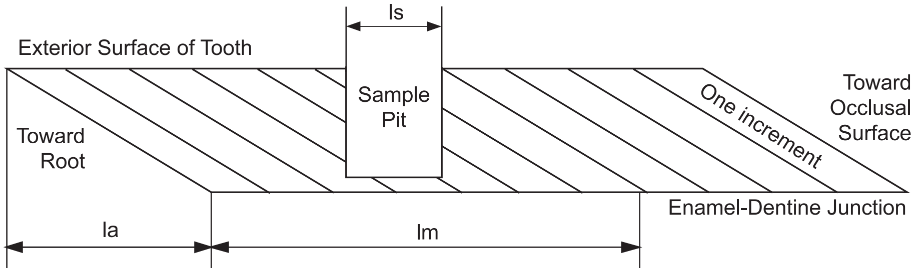

Fig. 7. The three input parameters used for understanding isotopic signals modeled for tooth enamel (Passey and Cerling, 2002): lm = length of maturation: the length of the tooth that is mineralizing at any one time; la = length of apposition: the distance along the tooth from where a new appositional layer contacts the enamel–dentine junction and where that layer contacts the external surface of the tooth; ls = length of the sample pit: measured perpendicular to the growth axis of the tooth, a measure of how wide the sampling intervals are.

- Peaks in the measured isotope curves are out of phase with peaks in the input signal, especially for *Equus*.

3.2. The Amount Effect predicted in tooth enamel

The Amount Effect, if present at the locality where the individual lived, is expected to be apparent within the isotopic signature of the tooth enamel. However, because of factors such as maturation time, and the obliqueness of the mineralization surface, the isotopic values might not trace the input values (from surface water) as clearly as they did in the case of the sinusoidal input (Fig. 8A). Therefore, the same model as in Fig. 8A was recalculated using an input signal that included a strong decrease in values during the summer as a result of Amount Effect (Fig. 8B). Decreased summer isotopic values are evident in the modeled values for both *Equus* and *Bison* M3s.

Table 1
Input parameters for Passey and Cerling (2002) model

Parameter from Passey and Cerling (2002)	*Equus*	Bison
lm	4 months = 27 increments	2 months = 14 increments
la	3 mm = 10 increments	5 mm = 10 increments
ls	1 mm = 4 increments	1 mm = 2 increments

One year is equivalent to 80 increments. Parameters are defined and illustrated in Fig. 7.

- Curves are much more dampened than they were for a purely sinusoidal seasonal variation.
- The summer-time double-cusped pattern in *Bison* is roughly symmetrical, as it is in the input signal. However, in *Equus*, the cusps are asymmetrical, with the second peak being greatly reduced in amplitude compared to the first, due to averaging in of the subsequent winter signal.

Only rarely does the rainy season fall exactly in the middle of the hottest point of the summer, as has been modeled in Fig. 8B. Fig. 8C models the isotopic signal preserved in teeth if there are discrete spring and fall rainy periods.

- As before, curves are much more dampened than they were for a purely sinusoidal seasonal variation.
- The triple-cusped pattern (with dips corresponding to spring and fall rains) in *Bison* is roughly symmetrical, as it is in the input signal. However, in *Equus*, the cusps are very asymmetrical, with the peak that follows the fall rainy period being almost indistinguishable.

Fig. 8D illustrates the expected $\delta^{18}O$ pattern if teeth with the signals shown in Fig. 8B were serially sampled using the techniques discussed above. It is assumed that a 1-mm-wide sample pit was drilled into the teeth at intervals of about 3 mm.

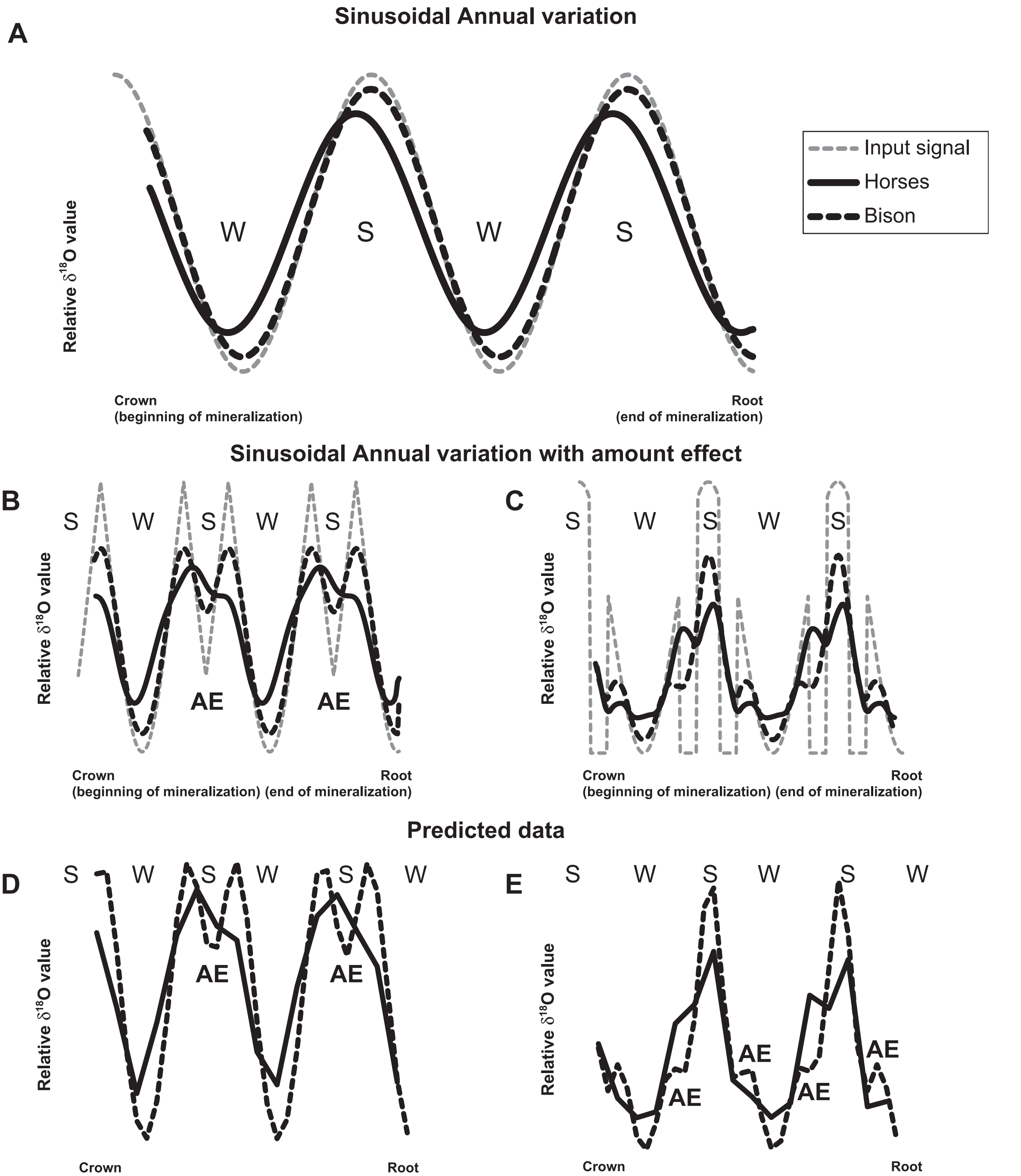

Fig. 8. (A) Modeled isotopic values for horse M3 (solid black line) and bovid M3 (dashed black line) using a sinusoidal input signal (dashed grey line). "S" and "W" denote periods of summer and winter, respectively. Note that models as shown are calculated according to mineralization rates and do not reflect the growth period within the animal. (B) Modeled isotopic values for horse M3 (solid black line) and bovid M3 (dashed black line) using a sinusoidal input signal (dashed grey line) that includes a strong summertime Amount Effect trough (AE). (C) Same data as B, but plotted as if samples were only collected every 3 mm, as might be expected from real data.

It is of value to note that the input signal is best preserved in the *Bison* M3. The double-cusped pattern is almost completely obliterated in the *Equus* M3. Fig. 8E shows the expected data from serial sampling of teeth with Fig. 8C isotopic signal incorporated. The triple-cusped pattern is still evident in the data from the *Bison* M3. However, it would be very hard to interpret the Amount Effect from the *Equus* data.

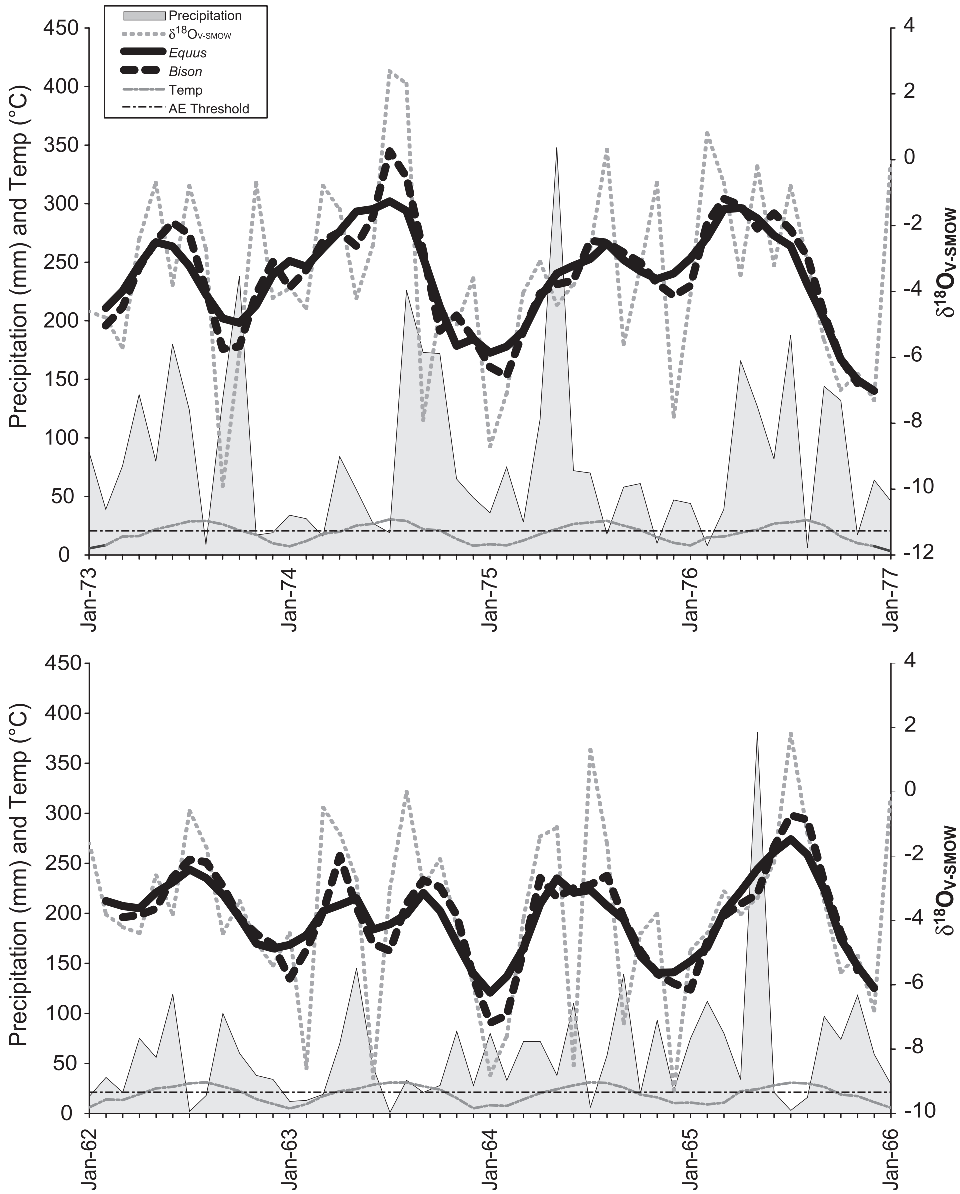

Fig. 9. Measured values of temperature, precipitation, and $\delta^{18}O_{V\text{-}SMOW}$ values in precipitation for two 4-year periods in Waco, TX (from IAEA/WMO, 2001). The Amount Effect threshold (20 °C) is also plotted. Isotopic values in tooth enamel for both *Equus* (heavy, solid line) and *Bison* (dashed, solid line) based upon measured isotope values in precipitation.

Table 2
Serial data from *Equus*, *Bos*, and *Bison* teeth discussed in text

Sample number	Position along tooth (mm from root/enamel boundary)	$\delta^{18}O_{V\text{-}PDB}$	$\delta^{18}O_{V\text{-}SMOW}$
UTEP 5167, Equus, M3, El Paso, TX			
PH 02-160	0.0	− 3.8	27.0
PH 02-161	4.0	− 5.4	25.3
PH 02-162	8.0	− 5.8	24.9
PH 02-163	12.0	− 5.4	25.4
PH 02-164	16.0	− 3.8	27.0
PH 02-165	20.5	− 8.8	21.8
PH 02-219	23.0	− 2.1	28.8
PH 02-166	25.5	− 2.9	28.0
PH 02-220	28.3	− 1.8	29.0
PH 02-167	31.0	− 4.1	26.7
PH 02-168	36.5	− 3.2	27.6
PH 02-169	41.0	− 2.5	28.4
PH 02-170	46.0	− 1.2	29.7
PH 02-171	50.0	− 1.1	29.8
PH 02-172	55.0	− 1.1	29.8
PH 02-173	59.0	− 0.1	30.8
PH 02-174	63.5	− 0.2	30.7
PH 02-175	68.0	− 0.6	30.3
PH 02-176	71.0	− 1.2	29.7
PH 02-177	75.0	− 0.9	30.0
	Mean	− 2.8	28.0
UTEP 6381, Bos, M3, near Roswell, NM			
PH 02-179	0.0	− 3.4	27.4
PH 02-180	3.5	− 3.0	27.8
PH 02-181	7.0	− 4.2	26.5
PH 02-182	11.0	− 4.5	26.3
PH 02-183	14.0	− 4.2	26.6
PH 02-184	17.0	− 4.8	26.0
PH 02-185	20.0	− 5.6	25.1
PH 02-221	21.5	− 3.5	27.3
PH 02-186	23.0	− 3.9	26.9
PH 02-187	26.5	− 3.8	27.0
PH 02-222	28.3	− 3.5	27.3
PH 02-188	30.0	− 4.9	25.8
PH 02-189	33.0	− 3.2	27.6
PH 02-190	37.0	− 3.4	27.4
PH 02-191	42.0	− 4.2	26.6
PH 02-192	45.5	− 4.4	26.4
	Mean	− 4.0	26.8
UTEP 25-543, Bison, LM3, Dry Cave, NM, Chihuahuan			
PH 02-35	0	− 9.4	21.2
PH 02-36	3	− 11.2	19.4
PH 02-37	6	− 11.5	19.0
PH 02-38	8	− 11.6	18.9
PH 02-39	11	− 11.4	19.1
PH 02-40	14.5	− 9.9	20.7
PH 02-41	18	− 10.7	19.9
PH 02-42	21	− 11.4	19.1

Table 2 (*continued*)

Sample number	Position along tooth (mm from root/enamel boundary)	$\delta^{18}O_{V\text{-}PDB}$	$\delta^{18}O_{V\text{-}SMOW}$
UTEP 25-543, Bison, LM3, Dry Cave, NM, Chihuahuan			
PH 02-43	24.5	− 10.2	20.4
PH 02-44	28	− 10.3	20.3
PH 02-45	31	− 10.6	20.0
PH 02-46	34	− 11.4	19.1
PH 02-47	37.5	− 12.5	18.1
	Mean	− 10.9	19.6
UTEP 25-537, Equus, RM3, Dry Cave, NM, Chihuahuan			
PH 02-20	15	− 8.7	21.9
PH 02-21	18.5	− 7.1	23.6
PH 02-22	22.5	− 6.7	24.0
PH 02-23	26.5	− 6.0	24.7
PH 02-24	30	− 5.4	25.4
PH 02-25	34	− 4.0	26.8
PH 02-26	38	− 3.7	27.1
PH 02-27	41.5	− 3.5	27.3
PH 02-28	45	− 5.0	25.8
PH 02-29	48.5	− 4.3	26.5
PH 02-30	51.5	− 4.8	26.0
PH 02-31	55	− 6.4	24.3
PH 02-32	58	− 5.7	25.0
PH 02-33	62	− 5.5	25.2
PH 02-34	65	− 6.2	24.6
	Mean	− 5.5	25.2
UALP uncatalogued, Bovidae, m3, Murray Springs, AZ, Sonoran			
PH 02-48	0	− 4.2	26.6
PH 02-49	3	− 2.9	28.0
PH 02-50	6.5	− 2.8	28.0
PH 02-51	10	− 1.9	29.0
PH 02-52	13	− 1.0	29.9
PH 02-53	16.5	− 2.9	27.9
PH 02-54	20	− 3.4	27.4
PH 02-55	23.5	− 4.7	26.0
PH 02-56	27	− 7.2	23.5
PH 02-57	31	− 6.9	23.8
PH 02-58	34	− 6.5	24.2
PH 02-59	38	− 5.9	24.8
PH 02-60	41	− 5.8	24.9
PH 02-61	45	− 5.8	25.0
PH 02-62	48	− 4.3	26.5
PH 02-63	51	− 3.5	27.3
PH 02-64	55	− 4.5	26.3
PH 02-65	59	− 2.0	28.9
PH 02-66	63	− 1.3	29.5
	Mean	− 4.1	26.7
UALP 3433, Equus, LM3, Murray Springs, AZ, Sonoran			
PH 02-67	0	−4.8	26.0
PH 02-68	3	− 4.7	26.0
PH 02-69	5	− 4.7	26.1

Table 2 (*continued*)

Sample number	Position along tooth (mm from root/enamel boundary)	$\delta^{18}O_{V\text{-}PDB}$	$\delta^{18}O_{V\text{-}SMOW}$
UALP 3433, Equus, LM3, Murray Springs, AZ, Sonoran			
PH 02-70	10	− 3.4	27.4
PH 02-71	13	− 4.5	26.2
PH 02-72	16	− 4.2	26.6
PH 02-73	20	− 2.6	28.2
PH 02-74	23	n/a	n/a
PH 02-75	26.5	n/a	n/a
PH 02-76	30	− 4.2	26.6
PH 02-77	33	− 5.0	25.7
PH 02-78	36.5	− 4.0	26.8
PH 02-79	40	− 3.1	27.7
PH 02-80	43	− 3.0	27.9
PH 02-81	46.5	− 3.8	27.0
PH 02-82	49.5	− 3.7	27.1
PH 02-83	53	− 3.5	27.3
PH 02-84	56.5	− 3.7	27.1
	Mean	− 3.9	26.8

Isotopic values are reported in V-PDB format. V-SMOW values calculated using the equation: $\delta^{18}O_{V\text{-}SMOW} = 1.03091(\delta^{18}O_{V\text{-}PDB}) + 30.91$ (Hoefs, 1997).

3.3. The Amount Effect in modern precipitation

Fig. 2 provides average annual patterns of precipitation, temperature, and $\delta^{18}O$ value of meteoric waters at four locations globally. The pattern of the Amount Effect is clear. However, temperatures and precipitation patterns may vary radically from year to year. Fig. 9 shows actual precipitation, temperature, and $\delta^{18}O$ values for two 4-year intervals in Waco, TX (IAEA/WMO, 2001). A drought year (e.g. 1974) will appear isotopically very different from a year marked by a short period of increased rain (e.g. 1963). The isotopic pattern for any single year may differ from a regular sinusoidal pattern or the average pattern shown in Fig. 2D. The expected isotopic pattern preserved in *Equus* (heavy, solid black line) and *Bison* (heavy, dashed black line) teeth is shown.

4. Results and discussion

Serial samples were collected from two teeth of modern grazers from the Southwest, an M3 of *Bos* (UTEP 6381) that was collected near Roswell, NM and an M3 of *Equus* (UTEP 5167) that was collected from the El Paso area, TX. Measured oxygen isotope values are presented in Table 2 and plotted in Fig. 10. As predicted from modeling (Figs. 8 and 9), annual variations in $\delta^{18}O$ in the *Equus* tooth (Fig. 10A) are dampened compared to those in *Bos*. Year-long intervals are shown in Fig. 10 as alternating grey boxes. In the first 2 years of mineralization, seasons are not easily distinguished, perhaps due to dry winters following wet falls (such as fall to winter 1973–1974, Fig. 9). The last year shows a pronounced summer peak, potentially due to a very warm, dry summer that year.

Bos was used as a proxy for *Bison*, because both are bovids and have similar rates and periods of enamel mineralization (Fig. 5). Data from the *Bos* M3 (Fig. 10B) show a clear Amount Effect pattern, quite similar to that of meteoric water from the Waco area (Fig. 2D). At least one extended period of late summer to early fall rain is apparent (noted by "AE"). A second period of spring rain might also exist. This is nearly identical to the known average precipitation pattern in Roswell, NM (Fig. 4B) and is similar to that in the Waco area, TX in the summer of 1964 (Fig. 9).

The data for the Late Glacial specimens of *Equus* and *Bison* are plotted in Fig. 11. Inspection of Fig. 11A shows considerable range in the $\delta^{18}O$ values for *Bison*, about 3‰ for the Chihuahuan Desert to about 6‰ for the Sonoran Desert. The smaller range in the Chihuahuan Desert specimen is interpreted as the signal of more significant summer rain (and therefore a significant Amount Effect) in the Chihuahuan Desert, rather than higher seasonality in the Sonoran Desert.

The gray box in Fig. 11A represents a period of about 1 year (also see Fig. 5). The single major peak of $\delta^{18}O$ for the Sonoran Desert *Bison* is interpreted as summer. Brief periods of summertime rain are notable as slight decreases in $\delta^{18}O$. Two major peaks, which both occur during a single year, appear in the Chihuahuan Desert specimen. Low $\delta^{18}O$ values for the Chihuahuan Desert specimens plot in coincidence with summer for the Sonoran Desert *Bison*. Because this pattern must represent about 1 year (gray box; Fig. 5), this is interpreted as the double-cusped pattern of the Amount Effect due to heavy summer rains (like Fig. 8B and D).

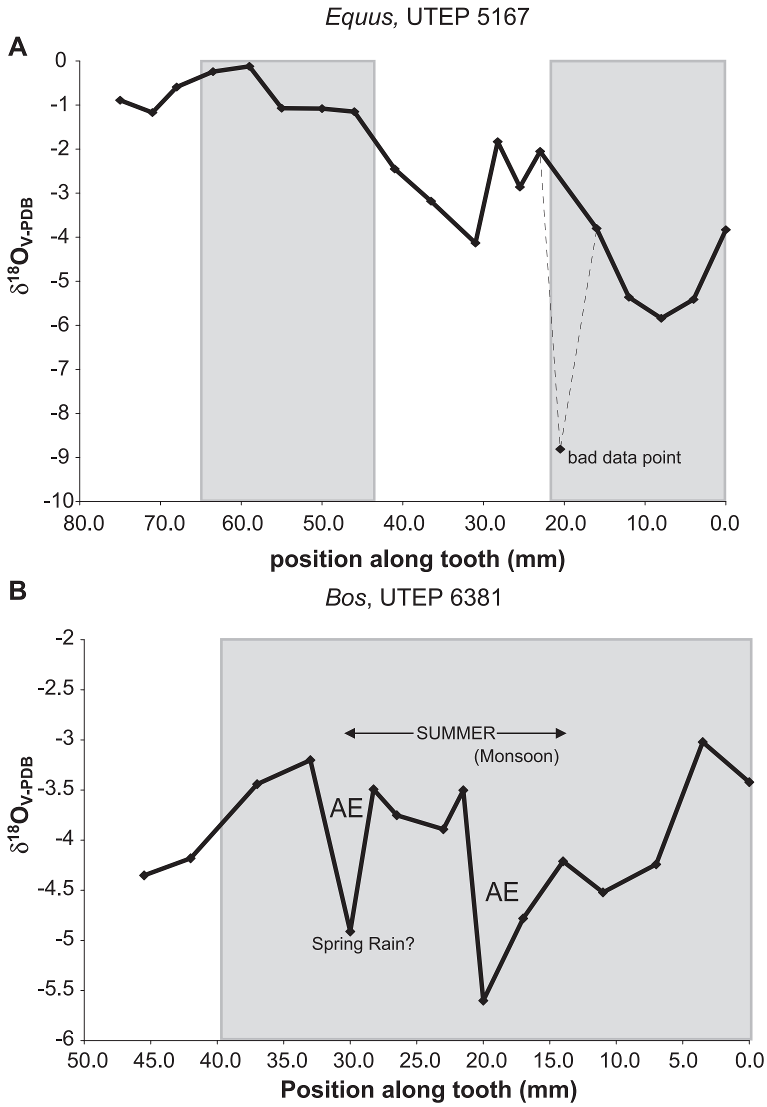

Fig. 10. (A) Data from a modern *Equus* M3 from El Paso, TX. Dashed lines indicate pattern if a questionable data point is also included. That data point is questioned due to a low volume of gas and poorly balanced reference and sample beams during analysis, and a low analytical precision. (B) Data from a modern *Bos* M3 collected near Roswell, NM. Units are $\delta^{18}O_{V\text{-}PDB}$.

These same patterns are present in the data analyzed from *Equus* teeth (Fig. 11B); however, there is apparent dampening of the curve and some predicted variations are averaged out and lost. Three summers are evident in the data from the Sonoran Desert *Equus*. Only one of these summers (the first) shows clear evidence of Amount Effect (noted as “AE”), and the general amplitude of the curve is much less than that of the bovid from the same locality. The data from the *Equus* specimen from the Chihuahuan Desert shows a profound Amount Effect in the first summer of development, but then the values diminish rapidly. The cause of this drop is uncertain, but may be due to a change in growth rate of the tooth, and concurrent dampening and averaging to the input isotopic signature may cause such a pattern (Zhow and Zheng, 2002; Owen et al, 2002). Another possible cause of this drop may be simply a

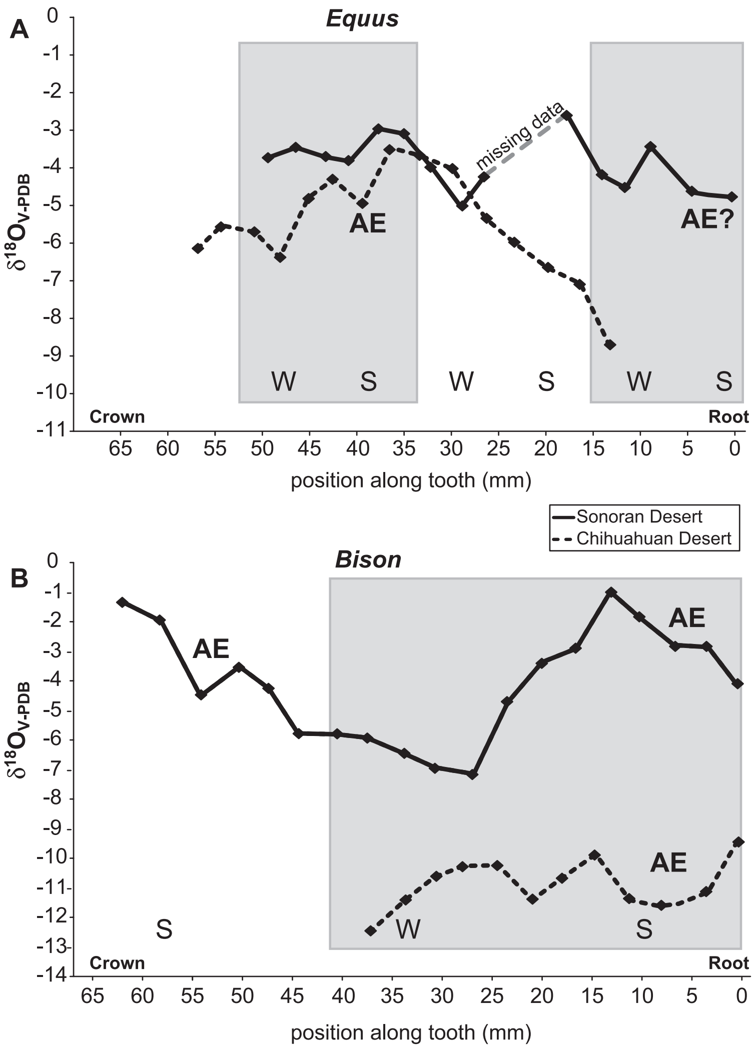

Fig. 11. (A) Data from Late Glacial equids in the Southwest. Solid line is data from the Sonoran Desert locality, dashed line from the Chihuahuan Desert locality. Gray boxes denote approximately a 1-year interval of mineralization. "AE" indicates depressions of the isotopic values due to the Amount Effect; "S" and "W" denote periods of summer and winter, respectively. (B) Data from Late Glacial bovids in the Southwest. Solid line is data from the Sonoran Desert locality, dashed line from the Chihuahuan Desert locality. The Sonoran Desert *Bison* is a fairly unworn tooth, showing clearly about 1.5 years of development. The specimen from the Chihuahuan Desert is worn specimen, and appears to record only about 1 year of development. See text for discussion. Units are $\delta^{18}O_{V\text{-}PDB}$.

period of extended summer and winter rains (as in Fig. 9).

In general, $\delta^{18}O$ values from the Sonoran Desert are greater for both *Equus* and *Bison* than those from the Chihuahuan Desert. This is interpreted to represent a wetter climate in the Chihuahuan Desert during the Late Glacial. Summer rains in the Chihuahuan Desert lowered isotope values to close to winter values. These isotopic data indicate that the Sonoran Desert of the Late Glacial did experience late summer rains, though not at the same magnitude as the Chihuahuan Desert.

It is possible that the data from Murray Springs reflects the onset of the Younger Dryas, rather than the general climate of the Late Glacial Sonoran Desert. The Younger Dryas was a thousand-year period when cooler, glacial-like conditions returned, which began about 11,000 years ago (Broecker, 2003). Cooler temperatures and greater effective moisture than during the Late Glacial characterized the Full Glacial Sonoran Desert (Thompson et al., 1993). Potentially, the summer rains that are interpreted from the *Bison* from Murray Springs represent a temporary return to glacial-like conditions during the Younger Dryas.

5. Conclusions

Rather than providing a centennial- or millennial-scale view of regional precipitation patterns, isotopic analysis of serially sampled teeth of large herbivores provides a detailed record of seasonal change for a short time interval, i.e. encompassing a few months to years during the life of a single animal. The pattern of summer warmth and rainfall is evident in the oxygen isotope values. Models show that although tooth enamel takes a period of weeks to months to fully mineralize, environmentally influenced isotopic patterns are still evident.

Data from the modern teeth show isotopic patterns that are predicted by modeling for an area influenced by the Amount Effect. The modern data illustrate the need to understand mineralization of tooth enamel and the potential influences of precipitation in a particular region. Data from *Equus* teeth can provide a general pattern of seasonality; however, averaging due to the period of maturation of the tooth enamel results in the loss of smaller excursions in isotopic values due to the Amount Effect. Therefore, *Equus* teeth are not the best choice for examination of short-term climate changes at any particular locality. The data from *Bos* and *Bison* teeth provide a much more complete picture of short-term changes in precipitation. Because *Bos* and *Bison* teeth develop on about the same time scale, *Bison* teeth are preferred for serial isotopic analysis of fossil specimens.

When combined with other interpretations of climate from paleontological and paleobotanical sources, or from computer modeling, serial isotope data from the Southwest agree with previous inferences about climate from sites in the Sonoran and Chihuahuan deserts. Isotopic values go further to show specific periods of rain in both the Chihuahuan Desert (heavy summer rains) and Sonoran Desert (possible late summer, early fall rains).

Acknowledgements

The authors thank Art Harris and Ev Lindsay for granting access to the University of Texas at El Paso and the University of Arizona Laboratory of Paleontology collections, respectively, Ben Passey at the University of Utah for sharing his enamel mineralization model spreadsheet and for helpful discussions on the subject, and Mark Clementz and Robert Feranec for their insightful reviews. This is University of Florida Contribution to Paleobiology number 561.

References

Abell, P.I., Hoelzmann, P., 2000. Holocene palaeoclimates in northwestern Sudan: stable isotope studies on mollusks. Global and Planetary Change 26, 1–12.

Bard, E., Delaygue, G., Rostek, F., Antonioli, F., Silenzi, S., Schrag, D.P., 2002. Hydrological conditions over the western Mediterranean basin during the deposition of the cold Sapropel 6 (ca. 175 kyr BP). Earth and Planetary Science Letters 202, 481–494.

Broecker, W.S., 2003. Does the trigger for abrupt climate change reside in the ocean or in the atmosphere? Science 300, 1519–1522.

Brown, W.A.B., Christofferson, P.V., Massler, M., Weiss, M.B., 1960. Postnatal tooth development in cattle. American Journal of Veterinary Research 21, 7–34.

Bryant, J.D., Froelich, P.N., Showers, W.J., Genna, B.J., 1996. Biologic and climatic signals in the oxygen isotopic composition of Eocene–Oligocene equid enamel phosphate. Palaeogeography, Palaeoclimatology, Palaeoecology 126, 75–89.

CLIMAP members, 1976. The surface of the Iceage Earth. Science 191, 1131–1137.

COHMAP members, 1988. Climatic changes of the last 18,000 years: observations and model simulations. Science 241, 1043–1052.

Coplen, T.B., 1994. Reporting of stable hydrogen, carbon, and oxygen isotopic abundances. Pure and Applied Chemistry 66, 273–276.

Dansgaard, W., 1964. Stable isotopes in precipitation. Tellus 16, 436–468.

Erz, W., 1964. Tooth eruption and replacement in Burchell's Zebra, *Equus burchelli* Gray 1825. Arnoldia Rhodesia 1, 1–8.

Feranec, R.S., MacFadden, B.J., 2000. Evolution of the grazing niche in Pleistocene mammals from Florida: evidence from stable isotopes. Paleogeography, Paleoclimatology, Palaeoecology 162, 155–169.

Fricke, H.C., O'Neil, J.R., 1996. Inter- and intra-tooth variation in the oxygen isotope composition of mammalian tooth enamel phosphate: implications for palaeoclimatological and palaeobiological research. Palaeogeography, Palaeoclimatology, Palaeoecology 126, 91–99.

Gadbury, C., Todd, L., Jahren, A.H., Amundson, R., 2000. Spatial and temporal variations in the isotopic composition of bison tooth enamel from the Early Holocene Hudson–Meng Bone bed, Nebraska. Paleogeography, Paleoclimatology, Palaeoecology 157, 79–93.

Harris, A.H., 1980. The paleoecology of Dry Cave, New Mexico. Research Reports-National Geographic Society, 331–338.

Harris, A.H., 1987. Reconstruction of mid-Wisconsin environments in southern New Mexico. National Geographic Research 3, 142–151.

Haynes, C.V., 1987. Curry Draw, Cochise County, Arizona: a late Quaternary stratigraphic record of Pleistocene extinction and paleo-Indian activities. Geological Society of America Centennial Field Guide—Cordilleran Section, 23–28.

Hillson, S., 1986. Teeth. Cambridge Univ. Press, Cambridge.

Hoefs, J., 1997. Stable Isotope Geochemistry. Springer-Verlag, Berlin.

Hoppe, K.A., Stover, S.M., Pascoe, J.R., Amundson, R., 2004. Tooth enamel biomineralization in extant horses: implications for isotopic microsampling. Palaeogeography, Palaeoclimatology, Palaeoecology (this volume).

IAEA/WMO, 2001. Global Network of Isotopes in Precipitation. The GNIP Database (available at: http://isohis.iaea.org.).

Jouzel, J., Hoffmann, F., Koster, R.D., Masson, V., 2000. Water isotopes in precipitation: data/model comparison for present-day and past climates. Quaternary Science Reviews 19, 363–379.

Kohn, M.J., 1996. Predicting animal δ^{18}O: accounting for diet and physiological adaptation. Geochimica et Cosmochimica Acta 60, 4811–4829.

Kohn, M.J., Schoeninger, M.J., Valley, J.W., 1998. Variability in oxygen isotope compositions of herbivore teeth: reflections of seasonality or developmental physiology? Chemical Geology 152, 97–112.

Kutzbach, J.E., Guetter, P.J., Behling, P.J., Selin, R., 1993. Simulated climatic changes: results of the COHMAP climate-model experiments. In: Wright Jr., H.E., Kutzbach, J.E., Webb III, T., Ruddiman, W.F., Street-Perrott, F.A., Bartlein, P.J. (Eds.), Global Climates Since the Last Glacial Maximum. University of Minnesota Press, Minneapolis, pp. 24–93.

McCrea, J.M., 1950. On the isotopic chemistry of carbonates and a paleotemperature scale. Journal of Chemical Physics 18, 849–857.

Nowak, R.M., 1999. Mammals of the World, 6th edition. Johns Hopkins Univ. Press, Baltimore, MD.

Owen, R., Kennedy, H., Richardson, C., 2002. Isotopic partitioning between scallop shell calcite and seawater: effect of shell growth rate. Geochimica et Cosmochimica Acta 66, 1727–1737.

Passey, B.H., Cerling, T.E., 2002. Tooth enamel mineralization in ungulates: implications for recovering a primary isotopic time-series. Geochimica et Cosmochimica Acta 66, 3225–3234.

Poage, M.A., Sjostrom, D.J., Goldberg, J., Chamberlain, C.P., Furniss, G., 2000. Isotopic evidence for Holocene climate change in the northern Rockies from a goethite-rich ferricrete chronosequence. Chemical Geology 166, 327–340.

Rozanski, K., Araguás-Araguás, L., Gonfiantini, R., 1993. Isotopic patterns in modern global precipitation. In: Swart, P.K., Lohmann, K.C., McKenzie, J., Savin, S. (Eds.), Climate Change in Continental Isotopic Records. American Geophysical Union Geophysical Monograph, vol. 78. American Geophysical Union, Washington, DC, pp. 1–36.

Straight, W.H., Barrick, R.E., Eberth, D.A., 2004. Reflections of surface water seasonality and climate in stable oxygen isotopes from tyrannosaurid tooth enamel. Palaeogeography, Palaeoclimatology, Palaeoecology (this volume).

Thompson, R.S, Whitlock, C., Bartlein, P.J., Harrison, S.P., Spaulding, W.G., 1993. Climatic changes in the western United States since 18,000 yr B.P. In: Wright Jr., H.E., Kutzbach, T., Webb III, T., Ruddiman, W.F., Street-Perrott, F.A., Bartlein, P.J. (Eds.), Global Climates Since the Last Glacial Maximum. University of Minnesota Press, Minneapolis, pp. 468–513.

Van Devender, T.R., Spaulding, W.G., 1979. Development of vegetation and climate in the southwestern United States. Science 24, 701–710.

Zazzo, A., Mariotti, A., Lecuyer, C., Heintz, E., 2002. Intra-tooth variations in late Miocene bovid enamel from Afghanistan: paleobiological, taphomic, and climatic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 186, 145–161.

Zhow, G.-T., Zheng, Y.-F., 2002. Kinetic mechanism of oxygen isotope disequilibrium in precipitiated witherite and aragonite at low temperatures: an experimental study. Geochimica et Cosmochimica Acta 66, 63–71.