Isotopic paleoecology of Clovis mammoths from Arizona

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The causes of megafaunal extinctions in North America have been widely debated but remain poorly understood. Mammoths (*Mammuthus* spp.) in the American Southwest were hunted by Clovis people during a period of rapid climate change, just before the regional onset of Younger Dryas cooling and mammoth extirpation. Thus, these mammoths may provide key insights into late Pleistocene extinction processes. Here we reconstruct the seasonal diet and climatic conditions experienced by mammoths in the San Pedro Valley of Arizona, using the carbon ($^{13}\text{C}/^{12}\text{C}$) and oxygen ($^{18}\text{O}/^{16}\text{O}$) isotope compositions of tooth enamel. These records suggest that Clovis mammoths experienced a warm, dry climate with sufficient summer rainfall to support seasonal C_4 plant growth. Monsoon intensity may have been reduced relative to the preceding time period, but there is no isotopic evidence for severe drought. However, it is possible that the “Clovis drought”, inferred from stratigraphic evidence, occurred suddenly at the end of the animals’ lives and thus was not recorded in the enamel isotopic compositions. Unlike mammoths that lived before the Last Glacial Maximum, Clovis mammoths regularly increased C_4 grass consumption during summer, probably seeking seasonally green grasslands farther from the river valley. This predictable seasonal behavior may have made mammoths easier to locate by Clovis hunters. Furthermore, Clovis mammoths probably had no previous experience of such sudden climatic change as is believed to have occurred at the time of their extinction.

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Despite decades of debate, there is no consensus about whether climate change, human impacts, or a combination of the two caused late Pleistocene megafaunal extinctions in North America (1–3). The sudden and widespread appearance of the Clovis archaeological culture (either between 11,500 and 10,900 ^{14}C yBP or between 11,050 and 10,800 ^{14}C yBP) (4, 5) coincided with significant climate changes and widespread megafaunal extinctions, including the extinction of mammoths, by 10,800 ^{14}C yBP (6). Grayson (7) argues that reconstructing the detailed histories of each affected species is necessary to understand the extinction processes. Here, we use stable isotope analyses of tooth enamel to reconstruct climate, diet, and seasonal behaviors of mammoths in the San Pedro Valley (SPV) of Arizona. The SPV contains the densest concentration of mammoth remains associated with Clovis artifacts in all of North America (8, 9). As such, the region is pivotal for understanding the relationship between hunting, climate change, and late Pleistocene extinctions.

From ~50,000–13,000 ^{14}C yBP (50,000–15,000 cal BP), southwestern Arizona was relatively wet (10). Large pluvial lakes were surrounded by hillsides covered with pinyon-juniper woodlands and rich understories of C_3 shrubs, C_4 annuals, and C_4 grasses (11, 12); springs and shallow ponds were supported by a high water table (10); and a C_4 grassland stretched from southern Arizona to central Texas (12–17). A warm and arid period began around 13,000 ^{14}C yBP (15,000 cal BP), culminating in a severe drought that coincided with mammoth extinction and Clovis occupation of the SPV (10,900 ^{14}C yBP or 12,800 cal BP) (18). Immediately thereafter, the Younger Dryas (YD) period brought a return to

cool, wet conditions (19) and deposition of an organic-rich “black mat” over the Clovis-age landscape (18).

Since the last glacial–interglacial transition, precipitation in the region has occurred primarily in winter and summer (13, 20). However, little else is known about seasonality in the Late Pleistocene SPV or how it affected mammoth ecology. Climate exerts a strong influence on modern elephant diet and migration patterns (21–24), and the same was likely true for mammoths.

We investigate seasonally averaged trends in the C- and O-isotope composition of mammoth diet and drinking water (respectively), using “bulk” sampling, and seasonal variations using “serial” sampling of the inner enamel surface (25). We obtained enamel samples from SPV mammoths that were Clovis associated (had direct Clovis artifact associations), Clovis age (buried directly under the black mat and/or in Clovis-age sediments, but lacking secure Clovis artifact associations), Clovis age or older (buried under the black mat in sediments that have clearly experienced erosion or in secondary contexts), and pre-Last Glacial Maximum (LGM) age (from sediments dating >29,000 ^{14}C yBP) (Table S1). Key specimens used in this study include the Naco site mammoth (which was certainly hunted, based on five Clovis fluted points in association with its ribs and vertebrae) and mammoths that were either hunted or scavenged at the Murray Springs and Lehner sites (26–28). Three of the only 14 sites in all of North America with secure Clovis–mammoth associations are represented in this study (8).

Results and Discussion

Diagenesis. Good preservation of enamel was indicated by macroscopic appearance (similar to modern enamel, yellowish to white and translucent to opaque), minimal differences in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values for pretreated and untreated aliquots (Methods), carbonate contents (mean $\pm 1\sigma = 4.9 \pm 1.1\%$) (Table S2) similar to those of modern enamel (2.7–5.0%) (29), and a lack of correlation between carbonate contents and $\delta^{13}\text{C}$ or $\delta^{18}\text{O}$ values, which might occur if significant quantities of diagenetic carbonate contributed to the gas produced during analysis. Also, the sinusoidal variation in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values obtained from serially sampled enamel (see below) is typical of seasonal variation and is unlikely to have been preserved if significant postmortem isotopic alteration had occurred.

Seasonally Averaged Diet and Drinking Water. There are no systematic differences in the isotopic compositions of Clovis-associated and Clovis-age mammoths (Fig. 1 and Table S2). Henceforth both are referred to as Clovis mammoths. Clovis mammoths consumed diets high in C_4 plants and drank water with

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Fig. 1. Carbon and oxygen isotope results obtained for “bulk” samples of SPV mammoth tooth enamel. The $\delta^{13}\text{C}_{\text{sc}}$ values expected for mammoths consuming C_3 - and C_4 -dominated diets ($<-8\text{‰}$ and $>0\text{‰}$, respectively) are depicted by dashed green lines, and the $\delta^{18}\text{O}_{\text{sc}}$ values expected for mammoths consuming water with the same isotopic composition as modern SPV summer and winter precipitation (26.2‰ and 21.5‰, respectively) are depicted by dashed red lines (*Methods*). *Clovis age or older SPV mammoth specimens analyzed by Connin et al. (15) are included for comparison and are depicted as smaller triangles.

similar $\delta^{18}\text{O}$ values to those of modern SPV summer precipitation (30), consistent with a relatively warm and dry climate and/or a greater proportion of summer precipitation. Pre-LGM mammoths and the Double Adobe mammoth (suspected to be pre-Clovis age) (31) consumed fewer C_4 plants and had lower $\delta^{18}\text{O}$ values, consistent with a cooler and/or wetter climate or a greater proportion of winter precipitation.

Seasonal Variations in Diet and Drinking Water. The serially sampled Clovis mammoth $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ results are approximately sinusoidal, and the locations of major peaks and troughs coincide for each individual (Fig. 2 and Table S3). The $\delta^{18}\text{O}$ values of meteoric water (and river, lake, or groundwater with meteoric water inputs) in most continental locations, including the modern SPV, are higher in summer and lower in winter (20, 30, 32, 33). Thus, the peaks in the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ curves in Clovis mammoths almost certainly represent summer, and the troughs, winter. There are no upward or downward trends in the multiseasonal data, which suggests that mammoths did not migrate to new areas each year, but likely remained within a “home range”. Although mammoths are known to have migrated long distances (>150 km) in some regions (34), a lack of very long-distance migrations (>600 km) was also inferred for Clovis-age mammoths from New Mexico, Colorado, Texas, and Florida (35, 36).

The magnitude of seasonal dietary changes in Clovis mammoth $\delta^{13}\text{C}$ values is very large and indicates mixed C_3 – C_4 plant consumption throughout the year, but a much greater proportion of C_4 plant consumption during summer. Because the same pattern of seasonal dietary change was observed in several individuals, whose enamel formed over a period of years to decades (37), we infer that Clovis mammoth seasonal dietary behavior was quite consistent over time.

Unlike the other Clovis mammoths, one individual from Horsethief Draw (AZ13) had large and sustained decreases in $\delta^{18}\text{O}$ values during the latter half of the inferred summers (Fig. 2D). This pattern is most easily explained as an “amount effect” (32, 33), consistent with sustained late-summer monsoon rains. A similar pattern occurs in modern precipitation at Waco, Texas during early fall, and was observed in Pleistocene horse and bison from the American southwest (38). Monsoon rainfall would also likely lead to more C_4 plant growth in summer, which could explain the slightly higher $\delta^{13}\text{C}$ values of this individual relative to

the other Clovis mammoths. Although this individual was buried directly under and in contact with the black mat, it was in pre-Clovis sediments and lacked artifact associations. Because a stratigraphic unconformity prevents precise age constraints, the possibility exists that it predates the Clovis mammoths with secure artifact associations. If so, the difference between this individual and the artifact-associated Clovis mammoths could reflect reduced monsoon intensity during the Clovis period.

The patterns for the two pre-LGM mammoths are very different from those of the Clovis mammoths (Fig. 2). One, from spring conduit sands at Murray Springs, Area 8 (AZ11), had lower $\delta^{18}\text{O}$ values than those of Clovis mammoths year-round, which suggests that it lived during a glacial/stadial period, when the $\delta^{18}\text{O}$ values of precipitation (and hence, proboscidean enamel) were lower because of lower temperatures. The other, from Moson Wash (AZ14), had a very small range of $\delta^{18}\text{O}$ values that overlaps that of the Clovis mammoths and no apparent seasonal signal. This mammoth likely lived during an interglacial period (when the $\delta^{18}\text{O}$ values in precipitation and enamel were higher because of higher temperatures) and relied on a primary water source with relatively invariant $\delta^{18}\text{O}$ values, such as a large lake. Both pre-LGM mammoths had seasonally inconsistent peaks in C_4 plant consumption, which indicate less predictable movements among environmental zones (e.g., grasslands, woodlands) throughout the year. Peak C_4 plant consumption for both was lower than that of Clovis mammoths, and the one from Moson Wash (AZ14) consumed no C_4 plants at all during parts of the year.

Clovis Drought? The Clovis drought (39) figures strongly in interpretations of mammoth extinction and Clovis hunting in the American Southwest, although some of the evidence for drought is equivocal (40). It has been suggested that mammoths weakened during the drought clustered around water sources in the SPV, making them easier targets for Clovis hunters and ultimately contributing to their extinction (24, 41). During droughts, modern African elephants constrict their feeding ranges to areas with permanent water and increase their reliance on woody vegetation, as a result of decreased grass availability (21, 42).

We define drought as a short-term (several years or less) decrease in rainfall amount, particularly during the growing season, in relation to the prevailing conditions at the time (43). In the SPV, there is stratigraphic evidence for a significant drop in the water table during the Clovis occupation (39). We expect that drought, as opposed to general aridity, would result in characteristic changes in the seasonal isotopic compositions of mammoth tooth enamel. First, drought would cause lower $\delta^{13}\text{C}$ values and smaller seasonal variations in enamel because of fewer C_4 grasses in the diet. The proportion of C_4 plants in North American grasslands decreases with decreasing mean annual and summer precipitation (44–46). Moreover, the growth of C_4 grasses and summer annuals would be severely inhibited during droughts because of their shallow root systems, whereas C_3 trees and shrubs would have been more likely to survive, especially in river valleys. However, all Clovis mammoths had diets high in C_4 plants, which suggests significant amounts of precipitation, especially during summer. Second, we expect that enamel formed during a drought would have low-amplitude seasonal changes in $\delta^{18}\text{O}$ values (if mammoths were tethered to a reliable water source like a groundwater spring) and/or highly irregular variations (if mammoths were migrating among different ephemeral water sources), neither of which were observed in Clovis mammoths. Thus, there is no isotopic evidence for seriously debilitating drought during the period recorded in the Clovis mammoth teeth. However, it is possible that the drought onset occurred so suddenly that it was not recorded in the enamel, which formed several years or decades before the animals’ deaths (*Methods*). This possibility is consistent with the sudden nature of the drought inferred from stratigraphic and archaeological evidence at Murray Springs (39).

Fig. 2. Carbon and oxygen isotope results for “serial” sampling of Clovis-associated (A–C), Clovis-age (D), and pre-LGM (E and F) mammoths from the SPV. The distance between successive subsamples has been transformed to time as described in *Methods*. The $\delta^{13}\text{C}_{\text{sc}}$ values expected for mammoths consuming C_3 - and C_4 -dominated diets ($<-8\text{‰}$ and $>0\text{‰}$, respectively) are depicted by dashed lines. Photographs depict the inner enamel surface of subsampled specimens. (Scale bar, 1 cm.) A, C, E, and F are midcrown or cervical portions of the tooth, whereas B and D are developing enamel cones, which formed closer to the time of death.

Clovis Mammoth Behavior and Extinction. During the Clovis period, evidence for C_4 grasses in the SPV riparian corridor is lacking, but C_4 grasses probably grew on the bajada and nearby hillsides

(9, 12, 13, 17). We propose that Clovis mammoths sought new C_4 plant growth farther from the river during the summer rainy season and remained closer to the river, foraging on mixed C_3 – C_4 plants, during the winter. A similar pattern of seasonal foraging occurs among modern elephants (21, 22, 47). Such predictable seasonal behaviors could have made SPV mammoths particularly easy for human hunters to track, even before the Clovis drought. Furthermore, a sudden drought would have been disruptive to these seasonal cycles. Modern elephants rely on knowledge of food and water sources gained through experience and passed on over generations (24). On the basis of the consistency in seasonal patterns among Clovis mammoths, they probably had little or no preceding experience with such a drastic change in climatic conditions within their lifetimes, making it potentially difficult for them to adapt.

Conclusions

Clovis mammoths in the SPV experienced a warm and relatively dry climate with sufficiently abundant summer rainfall to support seasonal C_4 grass growth. Clovis mammoths had consistent seasonal dietary patterns over a period of some years: Peak C_4 grass consumption occurred during summer, and fewer C_4 grasses were consumed during winter. This study provides direct evidence for the presence of C_4 grasslands that “greened up” during summer, as proposed by Holmgren et al. (13). We suggest that mammoths in the SPV sought the greenest portions of the landscape, as do modern elephants (47). These seasonal patterns may have played a role in mammoth extirpation from the SPV, whether by climate change or by human hunting. Knowledge of the seasonal behaviors of extinct proboscideans should be useful to researchers modeling Clovis foraging behavior and late Pleistocene extinction processes.

We present evidence for general aridity during the Clovis period, but not severe drought. There are limited data for greater monsoon rainfall during the period before Clovis occupation of the SPV (i.e., one individual, AZ13, with a record of two summers); additional specimens are needed to determine whether this pattern is representative. Additional work on developmental timing for proboscidean teeth (e.g., using histology) is necessary to determine how much time elapsed between formation of the enamel used for isotopic analysis and the death of the animal, which would constrain the timing of the purported Clovis drought. Histological analysis could also provide evidence for slow-growth periods that can result from dietary or water stress (48). Moreover, stress can produce characteristic changes in the isotopic compositions of skeletal remains, but these effects would likely be obscured by the much larger-magnitude changes in seasonal diet and drinking water.

Stable isotopes in mammalian enamel have great potential as “paleo-drought” proxies, because they allow the reconstruction of seasonal changes in precipitation and vegetation patterns at a much finer temporal resolution than is obtainable using “traditional” proxies such as lake sediment cores (43). The study of stable isotopes in tooth enamel also shows great promise for understanding animal life histories, which is a key step in understanding late Pleistocene extinctions (7). This approach can elucidate differences in megafaunal behavior around the time of extinction relative to that which occurred during earlier time periods.

Methods

Sampling. Sections of enamel from the lingual or buccal aspect of the tooth were removed using a Dremel diamond circular saw blade. The adhering dentin was soft and chalk-like and was removed easily with a dental pick and wire brush. For bulk sampling, pieces of enamel that spanned the entire enamel thickness and >1 cm of tooth height were removed and ground using a mortar and pestle. These samples should represent at least several seasons of growth. For serial sampling, subsamples from each specimen were

drilled on the inner enamel surface (IES), which records a “time series” of isotopic compositions with less damping of seasonal amplitudes than traditional approaches (49, 50). Specimens were mounted on drill plates with the IES facing up, and lines were drilled on the IES in the distal–mesial direction, perpendicular to the height of the tooth, using a Merchantek MicroMill (25). Drill lines were 100 μm wide (occlusal–basal direction), 1 mm apart (occlusal–basal direction), 125–250 μm deep (from IES), and ~8–15 mm long (anterior–posterior direction).

Enamel in most of the teeth studied here developed during late adolescence or early adulthood (M5) or during full adulthood (M6) (37). Two of the specimens chosen for serial sampling (AZ10 and AZ13) were enamel cones that were still developing at the time of death (Fig. 2), so their isotopic compositions reflect the conditions the animals experienced a few years or less before death. The other specimens were obtained from fully developed enamel plates from basal portions of the tooth (Fig. 2), which formed years or even decades before death, depending on the tooth and age at death for each individual. When possible, samples were obtained near the cervix, so they reflected conditions as close as possible to the time of death. However, because of the very long development time of mammoth adult molars (37), it is not currently possible to determine exactly when each specimen formed relative to the time of the animal's death.

Pretreatment and Analysis. The effects of pretreatment with 2–3% sodium hypochlorite (24 h) and 0.1 M acetic acid (4 h) on stable isotope measurements were investigated. The $\delta^{13}\text{C}$ values of pretreated and untreated aliquots of enamel ($n = 4$) were all within analytical error ($<0.1\text{‰}$). The $\delta^{18}\text{O}$ values of untreated samples were on average $0.5 \pm 0.2\text{‰}$ lower (range = 0.2–0.8‰ lower) than those of treated samples. Because these differences are relatively small, untreated enamel was used for the analysis of all serial samples and some bulk samples (as noted in Table S2). Eliminating the pretreatment step allowed shallower lines to be drilled, which should provide better temporal resolution, and also eliminated the potential for pretreatment-induced decreases in the amplitudes of isotopic variation (51).

Enamel samples were reacted with ortho-phosphoric acid at 90 °C using a MultiPrep automated sampling device coupled to an Optima isotope ratio mass spectrometer in dual-inlet mode. All bulk samples were analyzed twice or more with the MultiPrep in standard operating mode (in which evolved CO_2 is immediately frozen into a cold trap), and serial samples were analyzed with the MultiPrep configured for “sealed vessel” reaction conditions (in which CO_2 is transferred into a cold trap only after the reaction is complete) (52). The data are presented in Tables S2 and S3.

Stable isotope compositions are presented in the standard delta (δ) notation, in units of per mil (‰) relative to Vienna PeeDee Belemnite (VPDB, carbon) and Vienna Standard Mean Ocean Water (VSMOW, oxygen) (53, 54). The $\delta^{13}\text{C}$ values were calibrated using NBS-19 and Suprapur. The mean ($\pm 1\sigma$) $\delta^{13}\text{C}$ values of NBS-18 ($-4.97 \pm 0.15\text{‰}$) and internal laboratory standard WS-1 ($0.76 \pm 0.15\text{‰}$) were in good agreement with their accepted values (-5.0 and 0.76‰ , respectively). The $\delta^{18}\text{O}$ values were calibrated using NBS-19 and NBS-18. The mean ($\pm 1\sigma$) $\delta^{18}\text{O}$ values of Suprapur ($13.21 \pm 0.18\text{‰}$) and WS-1 ($26.33 \pm 0.15\text{‰}$) were in good agreement with their accepted values (13.32 and 26.23‰ , respectively). Reproducibility for enamel samples averaged 0.10‰ for $\delta^{13}\text{C}$ and 0.15‰ for $\delta^{18}\text{O}$ (1σ). Carbonate contents (weight percent) in enamel samples were determined using calibration curves derived from the intensity of the mass 44 beam and the carbonate contents of calcite standards (Tables S2 and S3).

Dietary Inferences. The $\delta^{13}\text{C}$ values of animal tissues are derived from the $\delta^{13}\text{C}$ values of foods, plus tissue-dependent isotopic fractionations. The $\delta^{13}\text{C}$ values of dietary plants can be estimated using an enamel-diet fractionation factor (α) of 1.0141 (55), where

$$\alpha = (\delta^{13}\text{C}_{\text{sc}} + 1,000) / (\delta^{13}\text{C}_{\text{diet}} + 1,000). \quad [1]$$

Calculation of dietary $\%C_4$ values from isotopic data are problematic because of the large range of values for both C_3 and C_4 plants. A solution to this problem is to calculate a range of $\delta^{13}\text{C}_{\text{sc}}$ values that corresponds to C_3 -dominated, mixed C_3 – C_4 , and C_4 -dominated diets (56). On the basis of the $\delta^{13}\text{C}$ values of modern plants, corrected for a 1.5‰ decrease resulting from fossil-fuel burning, we assume that the $\delta^{13}\text{C}$ values of C_3 - and C_4 -dominated diets are $<-21.5\text{‰}$ and $>-13.5\text{‰}$, respectively (56, 57). Using Eq. 1, these correspond to $\delta^{13}\text{C}_{\text{sc}}$ values of $<-8\text{‰}$ and $>0\text{‰}$ for animals consuming C_3 - and C_4 -dominated diets, respectively (Figs. 1 and 2). Any $\delta^{13}\text{C}_{\text{sc}}$ values between -8‰ and 0‰ represent mixed C_3/C_4 diets, but more positive values indicate a greater proportion of C_4 plant consumption.

Drinking Water Inferences. We estimate the $\delta^{18}\text{O}$ values of drinking water consumed by SPV mammoths (Tables S2 and S3), using a two-step calculation. First, the oxygen isotope composition of structural carbonate is converted to its equivalent as phosphate, using an equation that is robust for many different species (58, 59):

$$\delta^{18}\text{O}_p = 0.98 \delta^{18}\text{O}_{\text{sc}} - 8.32. \quad [2]$$

Second, the oxygen isotope composition of phosphate is converted to that of drinking water, using the relationship determined for modern elephants (60):

$$\delta^{18}\text{O}_w = (\delta^{18}\text{O}_p - 23.3) / 0.94. \quad [3]$$

This approach assumes that the physiology of mammoths did not differ substantially from that of modern elephants, which is reasonable given their similar body sizes and close evolutionary relationship (24, 61, 62).

For comparison, the $\delta^{18}\text{O}_{\text{sc}}$ values expected for mammoths consuming water with the same isotopic composition as modern SPV precipitation/runoff (mean $\pm 1\sigma = -6.3 \pm 1.0\text{‰}$ in summer and $-11.2 \pm 2.8\text{‰}$ in winter) (20) were calculated using the reverse of the above equations. These give $\delta^{18}\text{O}_{\text{sc}}$ values of 26.2‰ (summer) and 21.5‰ (winter) (Fig. 1).

Distance-to-Time Conversion of Serially Sampled Results. For Clovis mammoths, we assume that each half period in the $\delta^{13}\text{C}$ curve (i.e., distance between a successive maximum and minimum or vice versa) represents 1 y of growth. This assumption is reasonable because (i) sinusoidal variations in the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of tooth enamel are characteristic of seasonal changes in drinking water and diet, where one period typically represents 1 y, (ii) yearly growth rate estimates from histological study of one Clovis mammoth support the inference that the distance between isotopic maxima or minima represents 1 y (25), and (iii) periods for $\delta^{13}\text{C}$ curves among individuals were consistent with known differences in growth rate for different portions of the tooth (i.e., faster close to the occlusal surface, slower close to the cervix) (63). For each interval between successive maxima and minima, 0.5 y was divided by the number of increments to obtain the interval of time represented by each increment, and this value was used to transform the distance values to time. We note that the “zero” for time is arbitrary for each individual, but for illustrative purposes the curves for different individuals are displayed with $\delta^{13}\text{C}$ maxima beginning at 0 y (Fig. 2). This approach does not alter the relationship of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ curves within each individual specimen.

For one of the pre-LGM mammoths (AZ11), distance was transformed to time following the approach described above, but using the $\delta^{18}\text{O}$ curve rather than the $\delta^{13}\text{C}$ curve. (The former was more regular and had a period similar to that of the Clovis mammoths, whereas the latter had a much shorter period). The other pre-LGM mammoth's results lacked the regular periodicity present in the other specimens, so we assumed a constant growth rate (14 mm/y) equal to the mean of specimens AZ1 and AZ11, whose results were obtained from similar locations on the tooth (i.e., enamel near the cervix).

Our strategy of sampling only the innermost enamel surface should result in minimal damping of the “input” signal (50). However, some attenuation in the amplitudes of isotopic variation present in drinking water or diet likely occurs as a result of the geometry of sampling (i.e., it is impossible to sample discrete time increments) and the gradual maturation of enamel. Thus, our results represent a minimum degree of variation in seasonal diet and drinking water.

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