Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

PALAEO 3
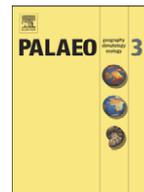
Stable isotopes reveal seasonal competition for resources between late Pleistocene bison (*Bison*) and horse (*Equus*) from Rancho La Brea, southern California

Robert S. Feranec [a,*], Elizabeth A. Hadly [b], Adina Paytan [c]

[a] New York State Museum, 3140 Cultural Education Center, Albany, New York, 12230, United States
[b] Department of Biology, 371 Serra Mall, Stanford University, Stanford, CA 94305-5020, United States
[c] Institute of Marine Science, University of California Santa Cruz, Santa Cruz, CA 95064, United States

ARTICLE INFO

ABSTRACT

Determining how organisms partition or compete for resources within ecosystems can reveal how communities are assembled. The Late Pleistocene deposits at Rancho La Brea are exceptionally diverse in large mammalian carnivores and herbivores, and afford a unique opportunity to study resource use and partitioning among these megafauna. Resource use was examined in bison and horses by serially sampling the stable carbon and oxygen isotope values found within tooth enamel of individual teeth of seven bison and five horses. Oxygen isotope results for both species reveal a pattern of seasonal enamel growth, while carbon isotope values reveal a more subtle seasonal pattern of dietary preferences. Both species ate a diet dominated by C_3 plants, but bison regularly incorporated C_4 plants into their diets, while horses ate C_4 plants only occasionally. Bison had greater total variation in carbon isotope values than did horses implying migration away from Rancho La Brea. Bison appear to incorporate more C_4 plants into their diets during winter, which corresponds to previous studies suggesting that Rancho La Brea, primarily surrounded by C_3 plants, was used by bison only during late spring. The examination of intra-tooth isotopic variation which reveals intra-seasonal resource use among bison and horse at Rancho La Brea highlights the utility of isotopic techniques for understanding the intricacies of ecology within and between ancient mammals.

© 2008 Elsevier B.V. All rights reserved.

1. Introduction

Examining how biotic and abiotic factors affect the ecology of animals can lead to a better understanding of why particular species are assembled in ecosystems and what drives diversity (Walther et al., 2002; Holt, 2003; Martinez-Meyer et al., 2004; Millien et al., 2006). Within ecosystems, species that share a similar ecology can coexist through resource partitioning, which acts to increase diversity (Pianka, 1967; Schoener, 1974a; McKane et al., 2002). Herbivores can partition resources by selecting different parts of plants, using different food or habitats, or being active at different times (Schoener, 1974a,b). Theoretical models suggest that species coexistence of competitors is possible only when competitors diverge in resources, known as the competitive exclusion principle (Hardin, 1960), although empirical data demonstrating this process are difficult to obtain. Study of coexistence by similar animal species has generally taken the form of competitive exclusion experiments, diet studies using gut contents or isotopic analyses, or population inventories (Connell, 1961; Dayton, 1971; Jaeger, 1971; Menge and Sutherland, 1976; Genner et al., 1999). In contrast, pursuit of evidence of competition between extinct species is largely confined to studies based on fossilized remains, and convincing evidence of discrimination of resource use by species from the fossil record is possible only where potential competitors are co-occurring in a fossil assemblage and isotopic or other data are obtained (MacFadden et al., 1994; Bocherens et al., 1996; MacFadden and Cerling, 1996; Koch et al., 1998; MacFadden, 1998).

One unique and highly diverse ancient locality is found in the late-Pleistocene deposits of Rancho La Brea (RLB) in the Los Angeles Basin of southern California. Rancho La Brea is a large deposit with several distinct pits containing specimens of similar age (Stock, 1972; Marcus and Berger, 1984; Binder et al., 2002). Large carnivores dominate the assemblage, but large herbivores are also abundant, including those of bison (*Bison* sp.) and horse (*Equus* sp.) (Stock, 1972). While the diets of modern bison and horse in North America are dominated by grass (Meagher, 1973; Kingdon, 1979; Meagher, 1986; Penzhorn, 1988; Churcher, 1993; Nowak, 1999; Hoppe et al., 2006), examination of ancient diets in these two species at RLB reveals that non-grass C_3 plants were regularly ingested (Akersten et al., 1988; Coltrain et al., 2004). Further, assessment of the eruption sequence and wear patterns in the teeth of *B. antiquus* shows a frequency distribution of yearly groups suggesting that this species was a seasonal late spring migrant to the Los Angeles Basin (Jefferson and Goldin, 1989), which would have influenced the food to which it had access. In contrast,

* Corresponding author.
E-mail addresses: rferanec@mail.nysed.gov (R.S. Feranec), hadly@stanford.edu (E.A. Hadly), apaytan@ucsc.edu (A. Paytan).

horse tooth-wear patterns were more typical of a non-migratory population (Coltrain et al., 2004).

Understanding the coexistence of bison and horse at RLB hinges on whether these taxa were competing for the same food resources at the same time at this locality. The migration of bison away from RLB for much of the year would significantly reduce competition between the two species at least during part of the year. Although the tooth-wear study shows that bison do not show a continuous age distribution at Rancho La Brea, it is not clear whether taphonomic bias has effectively created the distribution or whether it is indeed due to bison migration out of the area. Our study focused on understanding competition and species coexistence between horse and bison at Rancho La Brea. We addressed the following questions: (1) Did bison and horse from Rancho La Brea use the same food resources? (2) Were there seasonal differences in the diet of each species, and were there certain times of the year when competition is more significant? (3) Are the bison diets typical of a migrating species?

To address these questions, we examined resource use in bison and horse at RLB by determining the stable isotope values incorporated into tooth enamel. Analysis of stable isotope values from tooth enamel has proven a valuable method to examine several topics in the paleoecology of fossil taxa, including whether taxa partitioned resources within an ancient community (Quade et al., 1992; Koch et al., 1998; Feranec and MacFadden, 2000, 2006; Bocherens, 2003; Kohn et al., 2005). The isotopic signatures reflecting food sources are incorporated into the enamel while the tooth is growing during the life of the individual animal. Primary techniques used to obtain these isotopic values and to address paleoecological questions include taking a single bulk sample from a single tooth and taking multiple intra-tooth samples. Bulk sampling provides an average value of resource use during the time spanned by the life of that individual tooth, while serially sampling within a tooth provides much finer temporal detail into resource use, generally on the order of weeks, months or seasons (Fricke and O'Neil, 1996; Balasse et al., 2001; Passey and Cerling, 2002; Balasse et al., 2003; Kohn, 2004). Here we concentrate on investigating intra-tooth isotope variation for a series of individuals of both species, thus revealing intricacies of resource use over the course of many seasons during the late Pleistocene.

2. Background

2.1. Isotopes in mammalian enamel

Isotope values recovered from fossil tooth enamel have proven useful for understanding ecology in ancient mammals (Quade et al., 1992; Koch et al., 1998; Feranec and MacFadden, 2000, 2006; Bocherens, 2003; Kohn et al., 2005). Tooth enamel is used to obtain isotope values from ancient animals because it reliably reflects values derived from feeding (Wang and Cerling, 1994; Koch et al., 1997). Additionally, because tooth enamel is created incrementally, intra-seasonal variation in ecology, based on isotope values, is possible to identify, particularly in high-crowned species, using serially sampled enamel from individual teeth (Fricke and O'Neil, 1996; Balasse et al., 2001, 2003; Passey and Cerling, 2002; Kohn, 2004). Isotopic data are reported in delta notation using the following equation:

$$X = \left[\left(R_{sample} / R_{standard} \right) - 1 \right] \times 1000$$

where $X = \delta^{13}C$ or $\delta^{18}O$ in parts per mil (‰) and $R = {}^{13}C/{}^{12}C$, ${}^{18}O/{}^{16}O$. All isotope values reported here are relative to the V-PDB standard.

Oxygen isotopes in mammalian enamel depend on the isotopic composition of ingested water, fractionation of isotopes between enamel and body water, and the metabolism of the individual (Land et al., 1980; Longinelli, 1984; Luz et al., 1984; Luz and Kolodny, 1985; Koch et al., 1989; Bryant and Froelich, 1995; Kohn, 1996; Kohn et al., 1996, 1998). Herbi-vores ingest water either through drinking or from the plants they

consume. Water isotopic composition is affected by climatic factors (e.g. temperature and humidity), such that $\delta^{18}O$ values generally are more positive where and when it is warmer (e.g. summer) and more negative where and when it is colder (e.g. winter) (Dansgaard et al., 1982; Rozanski et al., 1992; Fricke and O'Neil, 1996; Kohn and Welker, 2005). Mammal teeth grow from tip to base (Hillson, 2005) thus sequential sampling in a tooth may reflect isotopic changes in water source through the tooth growth time. Accordingly, an animal drinking meteoric water in the same general area and whose teeth grow over the course of a year will display a sinusoidal curve in $\delta^{18}O_{enamel}$ values where a complete cycle represents one year (Cerling and Sharp, 1996; Fricke and O'Neil, 1996; Passey and Cerling, 2002; Balasse et al., 2003; Zazzo et al., 2005). However, the cycle does not necessarily reflect the total variation of $\delta^{18}O$ values ingested because oxygen isotopes get incorporated into the tooth during a two-part process: matrix formation and mineralization (Passey and Cerling, 2002; Kohn, 2004). The $\delta^{18}O_{enamel}$ cycle may be dampened because matrix formation and mineralization are processes that generally occur at different times. In this study, we scrutinize the $\delta^{18}O_{enamel}$ pattern archived within the tooth and not the absolute $\delta^{18}O$ values ingested in order to understand seasonal differences during individual growth and not for climatic reconstruction.

Body size and metabolism also can affect the $\delta^{18}O_{enamel}$ values, with smaller animals more likely to reflect a biotic imprint on environmental $\delta^{18}O_{enamel}$ values. Large mammals that are obligate drinkers and have low metabolisms are suggested as the most likely to accurately reflect ingested $\delta^{18}O$ values, closer to environmental values (Longinelli, 1984; Luz et al., 1984; Bryant and Froelich, 1995). Both species in our study are large (>44 kg), with lower metabolisms, and based on modern analogs are predicted to be obligate drinkers. Thus, the $\delta^{18}O_{enamel}$ pattern we observed is likely due predominantly to environmental rather than biotic factors.

For carbon, mammalian herbivore tooth enamel reflects the isotope ratio of the plants ingested (DeNiro and Epstein, 1978; Vogel, 1978). There are three different photosynthetic pathways used by plants, C_3, C_4, and Crassulacean Acid Metabolism (CAM), and each of these impart different isotope values. Most trees, shrubs and cool-growing-season grasses use the C_3-photosynthetic pathway and have a mean $\delta^{13}C$ values of −27.0‰±3.0‰. In contrast, tropical, warm-season grasses and sedges using the C_4-photosynthetic path-way have a mean isotopic value of −13.0‰±2.0‰ (O'Leary, 1988; Koch, 1998; Kohn and Cerling, 2002). The third pathway is the CAM pathway, characteristic of succulents (e.g. cacti), and incorporates intermediate ratios of ${}^{12}C$ and ${}^{13}C$ (O'Leary, 1988; Ehleringer et al., 1991; Ehleringer and Monson, 1993).

In individual mammals, there is a consistent fractionation in carbon isotope value from the diet to tooth enamel, measured as +14.6‰±0.3‰ for large ruminants (Passey et al., 2005). Further, for ancient animals, carbon isotope values are expected to be 1.5‰±1‰ more positive than modern species due to $\delta^{13}C$ differences that are the result of fossil fuel burning since the Industrial Revolution (Friedli et al., 1986; Marino and McElroy, 1991; Marino et al., 1992; Passey and Cerling, 2002). Previous studies demonstrate that individuals consuming a diet of 100% C_3 plants would have enamel isotope values more negative than −8.0‰, while individuals eating a diet of 100% C_4 plants have values more positive than 0.0‰ (Cerling et al., 1997; Koch, 1998). Therefore, based on a continuum of 100% C_3 to 100% C_4 feeding, an individual consuming a 50% C_3:50% C_4 diet would have an enamel isotope value of −4.0‰.

Relevant to investigating diet in migrating species are temporal and spatial variations in the carbon isotope values of plants (O'Leary, 1988; Garten Jr. and Taylor Jr., 1992; Mole et al., 1994; Heaton, 1999; Codron et al., 2005). Across communities within ecosystems, carbon isotopes values can vary tremendously. However, at a particular locality, the carbon isotope values of plants using a particular photosynthetic pathway do not appear to have a large total variation (O'Leary, 1988; Garten Jr. and Taylor Jr., 1992; Mole et al., 1994; Heaton,

1999; Codron et al., 2005). Within a population the total variation in carbon isotope values is generally less than 3‰ (O'Leary, 1988; Garten Jr. and Taylor Jr., 1992; Mole et al., 1994; Heaton, 1999; Codron et al., 2005). Similarly, intra-population δ^{13}C variation due to seasonal changes is usually less than 1‰ (O'Leary, 1988; Garten Jr. and Taylor Jr., 1992; Mole et al., 1994; Heaton, 1999; Codron et al., 2005). Because of the limited intra-population variation in δ^{13}C value at a particular locality even over different seasons, individuals that do not migrate are expected to have less total isotopic variation relative to migrating individuals. Migrants are likely to encounter different species of plants that use alternate photosynthetic pathways (i.e., C_3 or C_4 plants), which would result in higher variation in δ^{13}C values than year-round resident animals.

2.2. Dietary studies of modern bison and horse

Confined to a fraction of their historic range, modern North American bison (*Bison bison*) are predominantly grazers, with grasses making up almost their entire diet (Meagher, 1986; Nowak, 1999). In general, the diet of extant bison is similar to that of feral horses

(*Equus caballus*) in North America, whose diets are usually about 90% grass. While both species are usually grazers, browse can comprise up to half of North American wild horse diet (Hansen, 1976; McInnis and Vavra, 1987; Smith et al., 1998; Bennett and Hoffman, 2004). Browsing in bison is generally rare, although both North American bison (*B. bison*) and European bison (*B. bonasus*) make twigs, bark, and leaves a measurable part (over 30% for *B. bonasus*) of their diet (Nowak, 1999; Pucek et al., 2004). *Equus* species outside of North America (e.g., *E. burchelli*) show a pattern of grazing with some, although limited, browsing (Grubb, 1981; Kingdon, 1982; Penzhorn, 1988; Churcher, 1993). Thus, data from modern bison and horse analogs suggest that the fossil *Bison* and *Equus* in this study will yield isotopic data characteristic of foraging predominantly by grazing but including some browse in their diets.

3. Materials and methods

Tooth enamel samples were taken from seven individuals of *Bison* (*Bison antiquus* samples: UCMP 189666, UCMP 189667, UCMP 189668, UCMP 189669; *Bison* sp. samples: UCMP 17528, UCMP 153132, UCMP
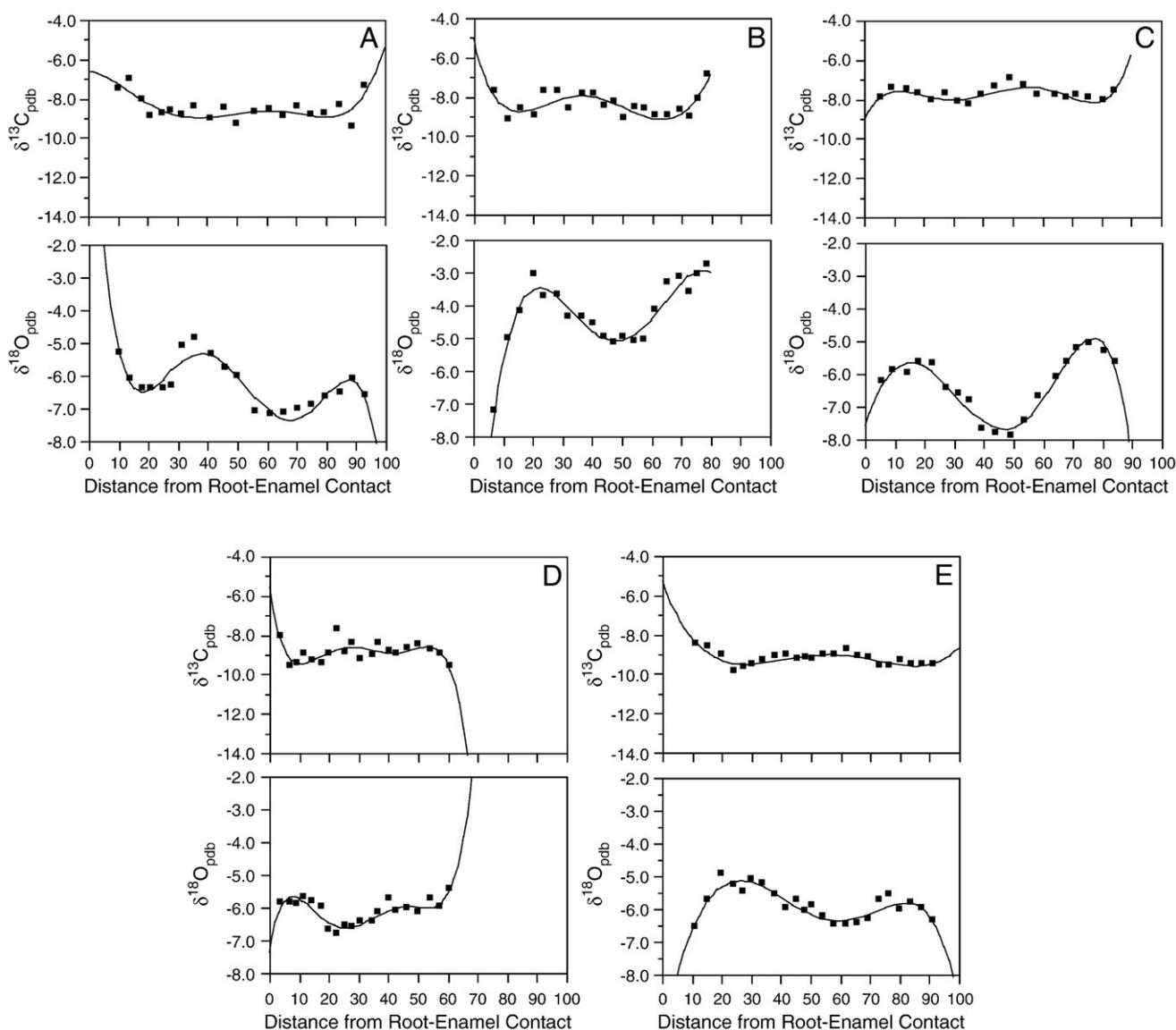
Fig. 1. Stable carbon and oxygen isotope values for the five Rancho La Brea horse specimens analyzed within this study. A, UCMP 18611; B, UCMP 18718; C, UCMP 18736; D, UCMP 41737; E, UCMP 158255.
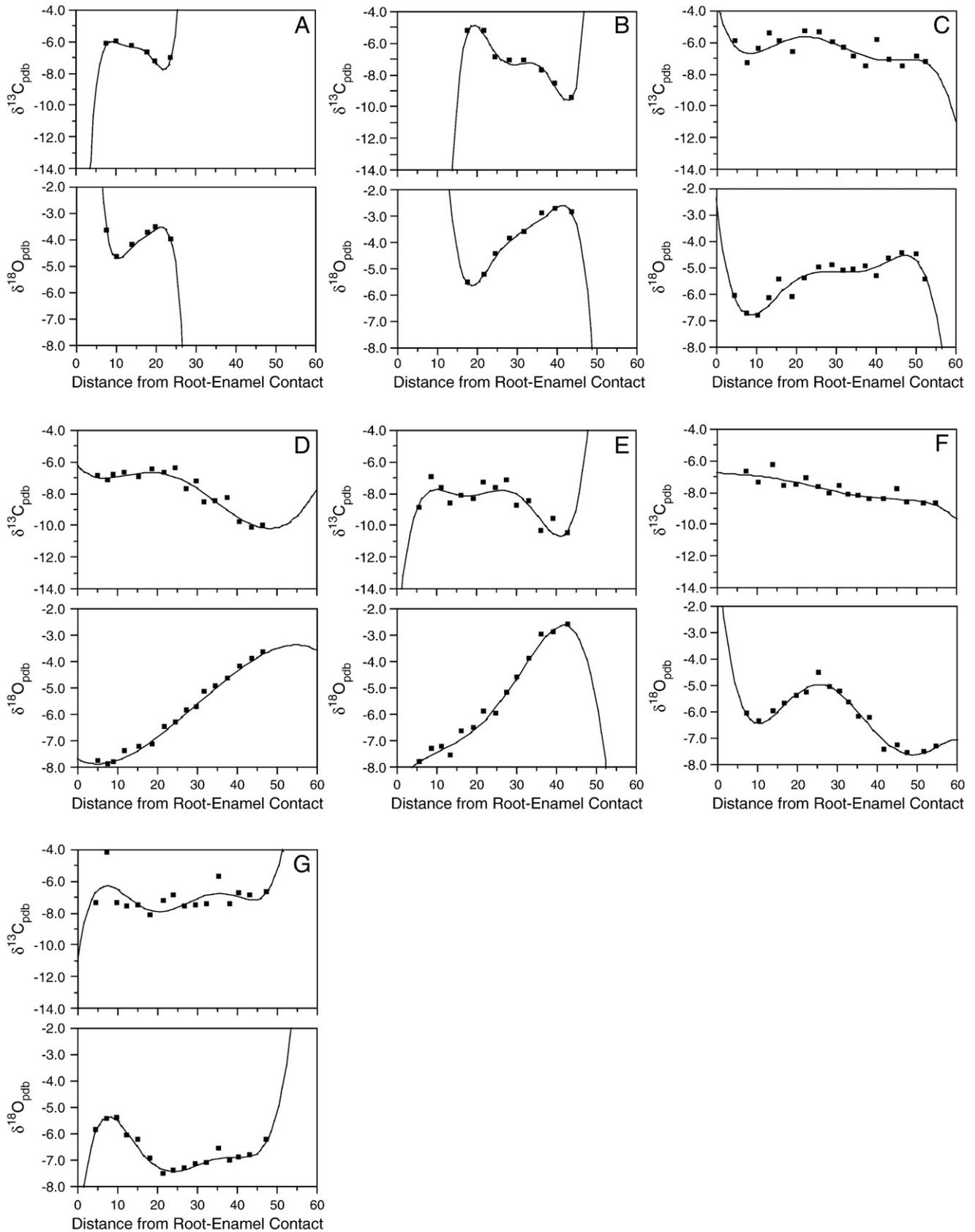
Fig. 2. Stable carbon and oxygen isotope values for the seven Rancho La Brea bison specimens analyzed within this study. A, UCMP 17528; B, UCMP 153132; C, UCMP 189665; D, UCMP 189666; E, UCMP 189667; F, UCMP 189668; G, UCMP 189669.

Table 1
Mean, standard deviation, range of carbon and oxygen isotope values, and measured crown height from the sampled bison and horse individuals from Rancho La Brea, southern California. Tooth abbreviations: uppercase, upper tooth; lowercase, lower tooth; L, left; R, right; M, molar; P, premolar; Frag., fragment of tooth

Taxon	Locality	Tooth	N	Mean $\delta^{18}O$ (‰)	$\delta^{18}O$ SD (‰)	$\delta^{18}O$ Range (‰)	Mean $\delta^{13}C$ (‰)	$\delta^{13}C$ SD (‰)	$\delta^{13}C$ Range (‰)	Crown Height (mm)
Bison			94	−5.7	1.4	−8.0 to −2.6	−7.4	1.2	−10.6 to −4.3	54.4
UCMP 17528	−2051	p or m	6	−4.0	0.4	−4.7 to −3.6	−6.6	0.5	−7.3 to −6.1	27.6
UCMP 153132	−3874	M^3	8	−3.9	1.1	−5.6 to −2.8	−7.2	1.5	−9.5 to −5.3	54.5
UCMP 189665	−3874	m_3	17	−5.5	0.7	−6.9 to −4.5	−6.5	0.8	−7.6 to −5.4	62.3
UCMP 189666	−3874	m	16	−6.0	1.5	−8.0 to −3.7	−7.8	1.3	−10.2 to −6.5	57.2
UCMP 189667	−3874	m	14	−5.6	1.8	−7.9 to −2.6	−8.5	1.1	−10.6 to −7.0	51.7
UCMP 189668	−3874	m	17	−6.2	1.0	−7.6 to −4.6	−7.9	0.7	−8.8 to −6.4	69.3
UCMP 189669	−3874	Frag.	16	−6.7	0.7	−7.6 to −5.3	−7.1	0.9	−8.2 to −4.3	58.0
Equus			102	−5.8	1.0	−7.9 to −2.8	−8.6	0.7	−9.9 to −6.9	89.7
UCMP 18611	−2051	RM^{1or2}	20	−6.3	0.7	−7.2 to −4.8	−8.5	0.6	−9.5 to −7.1	101.2
UCMP 18718	−2051	Frag.	20	−4.3	1.1	−7.2 to −2.8	−8.4	0.6	−9.1 to −6.9	85.4
UCMP 18736	−2051	Frag.	19	−6.3	0.9	−7.9 to −5.1	−7.7	0.3	−8.3 to −7.0	96.2
UCMP 41737	−3874	RP^2	20	−6.1	0.4	−6.8 to −5.4	−8.9	0.5	−9.6 to −7.7	67.7
UCMP 158255	−2051	LM^{1or2}	23	−5.9	0.5	−6.6 to −5.0	−9.2	0.3	−9.9 to −8.5	97.8

189665) and five individuals of *Equus* (*Equus occidentalis* samples: UCMP 18611, UCMP 18718; *Equus* sp. samples: UCMP 18736, UCMP 41737, UCMP 158255) all housed at the University of California Museum of Paleontology (UCMP). Even though species-level identification was not possible for some of the sampled material (Appendix A), all bison samples are likely to be *B. antiquus* because *B. latifrons* is rare at RLB (Stock, 1972; Jefferson, 2001). Similarly, all horse specimens are likely to be *E. occidentalis*, because of the rarity of *E. conversidens* at RLB (Stock, 1972; Scott, 2001). Because the goal of our study was to recognize the variation in diet in adult animals, we sampled premolars and third molars when available because these teeth are among the last ones to develop, mineralize, and erupt (Hillson, 2005). Alternate teeth were sampled if premolars or third molars were not available. Our approach attempted to ensure that we did not sample the same individual multiple times.

All specimens within this study derive from two localities at Rancho La Brea. The first, UCMP locality-2051, has been radiocarbon dated with a range from 14 ka to about 30 ka (Marcus and Berger, 1984). The second, UCMP locality-3874, is the UCMP's Rancho La Brea General locality and does not have absolute dating associated with it. With regards to competition and sympatry of specimens, based on the dates of the different localities at RLB, we do not assume that the sampled individuals lived concurrently, and therefore, did not directly competed with one another in the past. This is an improbable expectation for nearly all fossil deposits. What we do suggest is that these individuals are representative of the bison and horse populations present at RLB in the past and that their niches (e.g. resource use) were conserved over time (Peterson et al., 1999; Martínez-Meyer et al., 2004), permitting the examination of competition for resources among these two species.

The method for stable isotope sampling of tooth enamel followed MacFadden and Cerling (1996) and Koch et al. (1997). Sampling involved drilling 20–30 mg of enamel powder off the tooth along a non-occlusal surface parallel to the growth axis using a 0.5 mm inverted cone carbide drill bit and a variable speed dental drill. The powder was first collected and treated with 30% hydrogen peroxide overnight to remove organics. It then was decanted and washed with distilled water, and soaked in 0.1 N acetic acid overnight to remove any adsorbed diagenetic carbonate. The following day it was again decanted and washed with distilled water, and let dry.

After treatment, the samples were analyzed using an ISOCARB automated carbonate preparation system attached to a Micromass Optima gas source mass spectrometer within the Geology Department at the University of California, Davis. The ~1 mg samples were dissolved in 100% phosphoric acid at 90 °C to create CO_2. A total of 94 *Bison* and 102 *Equus* serial samples were collected, prepared, and

analyzed from a total of five horse and seven bison individual teeth. All samples were corrected to NBS-19 and UCD-SM92 an in-house marble standard. Precision for the enamel samples was 0.1‰.

Isotopic values were compared among taxa using both parametric (Anova, Tukey's HSD) as well as non-parametric (Kruskal–Wallis, Kolmogorov–Smirnov) tests where appropriate. Statistical analyses were run on JMP IN 5.1 for Students, with significance set at $p < 0.05$.

4. Results

We sampled between 6 and 23 serial samples for each specimen of each species, amounting to a total of 196 serial samples. Analysis of the serially-sampled oxygen isotope values reveals a sinusoidal pattern indicative of tooth enamel growth during different seasons for both species (Figs. 1 and 2). In general, the $\delta^{18}O_{enamel}$ patterns include about 1 year of growth data for bison and 1.5 year s for horse. In contrast, the carbon isotope values show either a much dampened seasonal pattern or no pattern at all (Figs. 1 and 2). For the few individuals with a carbon isotope pattern (UCMP: 17528, 18736, 153132, 189666), the data show that as $\delta^{18}O_{enamel}$ increases the $\delta^{13}C_{enamel}$ (%C_4) decreases.

Pooled specimen data demonstrate significantly different ($p < 0.0001$) carbon isotope values between bison (mean = −7.4‰) and horse (mean = −8.6‰; Table 1). Our data show that all seven bison individuals sampled included some percentage of C_4 plants in their diets (Table 1; Fig. 3). Assuming that all values more negative than −8.0‰ indicate 100% C_3 feeding and 0.0‰ indicates 100% C_4 feeding, the average sampled bison diet was 10% C_4 plants (N = 94 samples). Maximum percentage C_4 plants included in a bison diet was 47% (UCMP 189669) and minimum inclusion of C_4 plants in an individual diet was 3% (UCMP 189667). In contrast, the five horse individuals (N = 102 serial samples) only rarely foraged on C_4 plants, or had isotope values more positive than −8.0 (Table 1; Fig. 3). The average horse diet included only 1% C_4 plants and the maximum percentage C_4 plants included in the diets was only 14% (UCMP 18718) while the minimum was 0% (UCMP 158255).

The range of values for $\delta^{13}C_{enamel}$ was greater for bison than for horse (Table 1). The overall range for pooled specimens for bison spanned 6.3‰ (−10.6‰ to −4.3‰), while for horse the pooled range spanned only 3.0‰ (−9.9‰ to −6.9‰). For bison individuals, the maximum range in $\delta^{13}C_{enamel}$ was 4.2‰ (UCMP 153132), and the minimum 1.2‰ (UCMP 17528). The low range on UCMP 17528 may be due to its being well worn (crown height = 27.6 mm) thus only a small number of samples were taken (N = 6). For horse individuals, the maximum range spanned only 2.4‰ (UCMP 18611), and the minimum 1.3‰ (UCMP 18736). For the horses, the small range of $\delta^{13}C$ values was
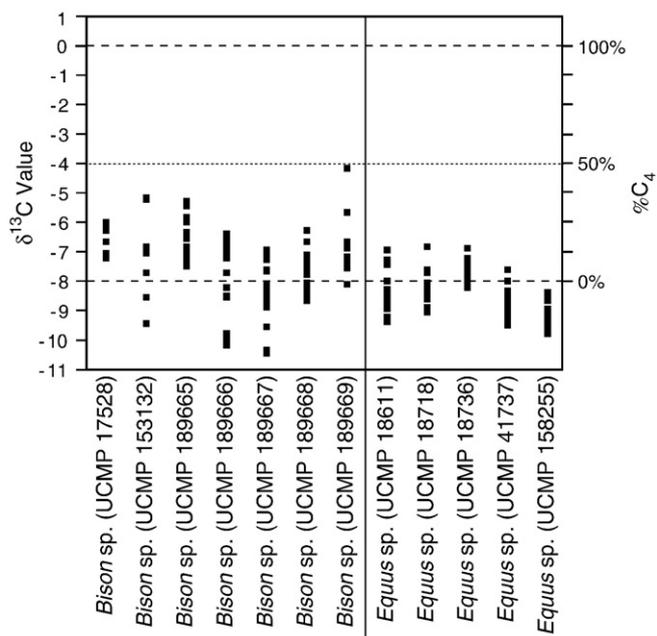
Fig. 3. Stable carbon isotope values and percent C_4 included in the diet for sampled individuals of horse and bison.

not due to sample size and tooth wear. All horse teeth were relatively unworn (Table 1).

In contrast to the $\delta^{13}C$ results, comparison of all $\delta^{18}O_{enamel}$ values sampled from bison (mean=−5.7‰) and horse (mean=−5.8‰) show no significant difference ($p<0.68$) between these two genera (Table 1), although the overall range of $\delta^{18}O_{enamel}$ values was greater in bison than in horse. The pooled range of $\delta^{18}O_{enamel}$ values for bison was 5.8‰ and 5.1‰ for horse. For individual bison the maximum range in $\delta^{18}O_{enamel}$ was 5.3‰ (UCMP 189667), and the minimum range 1.1‰ (UCMP 17528). Similar to the $\delta^{13}C_{enamel}$ values, the minimum range observed in UCMP 17528 for oxygen is likely the result of the small number of samples taken on this particular well-worn tooth. For horse individuals, the maximum range in $\delta^{18}O_{enamel}$ was 4.4‰ (UCMP 18718), and the minimum range 1.4‰ (UCMP 41737). Correlation in the range of $\delta^{18}O_{enamel}$ and $\delta^{13}C_{enamel}$ values is not significant ($p<0.11$).

5. Discussion

Differences in carbon isotope values between two large mammal species emerge either because the herbivores are specializing on different resources within a plant community or because they use different plant communities. Previous studies of bison and horses in North American grasslands tend to indicate the former: while both share high-crowned dentition typical of grazers, bison tend to specialize on grasses, while horses incorporate more browse in their diet (Connin et al., 1998; Koch et al., 1998; MacFadden et al., 1999; Feranec and MacFadden, 2000; Feranec, 2004, 2007; Higgins and MacFadden, 2004; Koch et al., 2004). Our study of horse and bison at Rancho La Brea supports resource competition theory: horse and bison demonstrate statistically significant differences in carbon isotope values. However, counter to previous studies, the bison of Rancho La Brea had a much higher range of carbon isotope values indicative of regularly eating more C_4 plants than did horses. Our serially sampled data show that annual variation in bison diet is the explanation. Based solely on carbon isotope values, bison show greater seasonal variability in their diets than do horses from the same deposits.

Because horses do not demonstrate the seasonal variation, we conclude that it is not turnover in the plants that animals might choose in the local community. Instead, we propose that seasonal

movement into other plant communities, or migration, would expose the bison to plants with alternate isotopic signatures. We contend that the carbon isotope data support bison as seasonal migrants, likely in the immediate vicinity of the Rancho La Brea fossil locality, allowing them to sample a different plant community. Because of the low diversity of C_3 plants along the California coast (Sage et al., 1999), the inclusion of higher percentages of C_4 plants in bison diets would suggest migration from the east. Seasonal migration into the C_3-dominated Los Angeles Basin is likely to have been during spring or summer because the $\delta^{13}C_{enamel}$ values in a few of the bison individuals showed the incorporation of a higher percentage of dietary C_4 plants during the winter (when $\delta^{18}O_{enamel}$ values were low). Based on an age-class distribution derived from dentition, bison are suspected to have come to the Los Angeles Basin in late spring or early summer (Jefferson and Goldin, 1989). In comparison to bison, our isotopic data for horses imply that they maintained a more restricted range in habitat and/or plant choice, showing low variability in $\delta^{13}C_{enamel}$ values over the course of the year, and little consumption of C_4 plants at all. While extant feral horses are known to migrate (Grubb, 1981; Berger, 1986; Hoppe and Koch, 2007), our study shows that the Rancho La Brea individuals did not migrate outside the Los Angeles Basin or encounter another plant community locally.

The data presented here differ in some respects from a previous study conducted by Coltrain et al. (2004), which found no evidence of the use of C_4 plants in the diets of the herbivores preserved at Rancho La Brea. The tooth enamel data do show that C_4 plants were included in the diet of all sampled bison individuals. The difference in results is likely due to the fact that the Coltrain et al. (2004) study analyzed collagen, a tissue that averages diet over many years (Stenhouse and Baxter, 1979; Hedges et al., 2007), while the tooth enamel samples likely represent the diet over one month or less. Examining the results of the two studies more closely does show agreement between the enamel and collagen isotope values. The mean horse $\delta^{13}C_{enamel}$ value (−8.6‰) is indicative of a 100% C_3 diet, and the mean bison $\delta^{13}C_{enamel}$ value (−7.4‰) is indicative of a 93% C_3 diet. Additionally, the difference in mean values between bison and horse collagen (1.1‰) is similar to the difference found in the tooth enamel (1.2‰) results. The differences between the two studies highlight the utility of examining intra-tooth isotopic variability. These data permit for a better understanding of the complexity of resource use among ancient species, and further provide insights into the variation of individual use of plant communities over several seasons.

Documenting resource partitioning or competition among taxa within an ecosystem can be important for understanding how ecosystems function and how diversity is generated and maintained. For example, knowing which animals are competing in an ecosystem can permit a better understanding of trophic relationships and connectedness (Connor and Simberloff, 1979; Connell, 1983; Kelt et al., 1995; Suominen and Danell, 2006). We show through serially sampling the dentition of both species that partitioning did not occur by selection of different diets in the same habitat, but by having different diets in different habitats. Our data demonstrate that horses were likely year-round residents of the Los Angeles Basin while bison were only spring-summer migrants. Thus, these two grazing species were not in direct competition for resources in the Los Angeles Basin during the winter.

Our results have implications for other isotopic studies, especially those conducted by analyzing bulk enamel samples, or tissues like collagen, that average isotope values over long periods of time. Resource partitioning can be obscured by bulk isotope values because the diet signatures are time-averaged. Thus, in order to detect temporal and/or spatial separation of resources, serially-sampling individuals of multiple species are essential. Our isotopic comparison of two potential competitors, when combined with an analysis of intra-tooth isotopic variability, highlights some of the complexities of paleoecological reconstructions and provides a clearer picture of the ecology of ancient organisms.

6. Conclusions

The analysis of individual intra-tooth oxygen isotope variability in the tooth enamel of bison and horse from Rancho La Brea, California, shows seasonal patterns. Carbon isotope values revealed significant differences between bison and horse. While both taxa were predominantly C_3 feeders, bison regularly integrated C_4 plants into their diet; horses only rarely ate C_4 plants. Bison also showed greater variability in carbon isotope values compared to the horses over the year. The higher variability is different from previous studies, which show horses as having a more generalized diet, but is consistent with diet in migratory animals. The analysis of intra-seasonal isotopic variability provides a powerful tool for reconstruction of the ecology of ancient mammals.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2008.10.005.

References

Akersten, W.A., Foppe, T.M., Jefferson, G.T., 1988. New source of dietary data for extinct herbivores. Quaternary Research 30, 92–97.

Balasse, M., Bocherens, H., Mariotti, A., Ambrose, S.H., 2001. Detection of dietary changes by intra-tooth carbon and nitrogen isotopic analysis: an experimental study of dentine collagen of cattle (*Bos taurus*). Journal of Archaeological Science 28, 235–245.

Balasse, M., Smith, A.B., Ambrose, S.H., Leigh, S.R., 2003. Determining sheep birth seasonality by analysis of tooth enamel oxygen isotope ratios: the Late Stone Age site of Kasteelberg (South Africa). Journal of Archaeological Science 30, 205–215.

Bennett, D., Hoffman, R.S., 2004. *Equus caballus*. Mammalian Species 628, 1–14.

Berger, J., 1986. Wild Horses of the Great Basin. The University of Chicago Press, Chicago.

Binder, W.J., Thompson, E.N., van Valkenburgh, B., 2002. Temporal variation in tooth fracture among Rancho La Brea dire wolves. Journal of Vertebrate Paleontology 22, 423–428.

Bocherens, H., 2003. Isotopic biogeochemistry and the paleoecology of the mammoth steppe fauna. Deinsea 9, 57–76.

Bocherens, H., Koch, P.L., Mariotti, A., Geraads, D., Jaeger, J.-J., 1996. Isotopic biogeochemistry (13C, 18O) of mammalian enamel from African Pleistocene hominid sites. Palaios 11, 306–318.

Bryant, J.D., Froelich, P.N., 1995. A model of oxygen isotope fractionation in body water of large mammals. Geochimica et Cosmochimica Acta 59, 4523–4537.

Cerling, T.E., Sharp, Z.D., 1996. Stable carbon and oxygen isotope analysis of fossil tooth enamel using laser ablation. Palaeogeography, Palaeoclimatology, Palaeoecology 126, 173–186.

Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., Ehleringer, J.R., 1997. Global vegetation change through the Miocene/Pliocene boundary. Nature 389, 153–158.

Churcher, C.S., 1993. *Equus grevyi*. Mammalian Species 453, 1–9.

Codron, J., Codron, D., Lee-Thorp, J.A., Sponheimer, M., Bond, W.J., de Ruiter, D., Grant, R., 2005. Taxonomic, anatomical, and spatio-temporal variations in the stable carbon and nitrogen isotopic compositions of plants from an African savanna. Journal of Archaeological Science 21, 1757–1772.

Coltrain, J.B., Harris, J.M., Cerling, T.E., Ehleringer, J.R., Dearing, M.-D., Ward, J., Allen, J., 2004. Rancho La Brea stable isotope biogeochemistry and its implications for the palaeoecology of late Pleistocene, coastal southern California. Palaeogeography, Palaeoclimatology, Palaeoecology 205, 199–219.

Connell, J.H., 1961. Effects of competition, predation by Thais lapillus, and other factors on natural populations of the barnacle *Balanus balanoides*. Ecological Monographs 61–104.

Connell, J.H., 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. The American Naturalist 122, 661–696.

Connin, S.L., Betancourt, J.L., Quade, J., 1998. Late Pleistocene C4 plant dominance and summer rainfall in the southwestern United States from isotopic study of herbivore teeth. Quaternary Research 50, 179–193.

Connor, E.F., Simberloff, D., 1979. The assembly of species communities: chance or competition. Ecology 60, 1132–1140.

Dansgaard, W., Clausen, H.B., Gundestrup, N., Hammer, C.U., Johnson, S.F., Kristinsdottir, P.M., Reeh, N., 1982. A new Greenland deep ice core. Science 218, 1273–1277.

Dayton, P.K., 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 351–389.

DeNiro, M.J., Epstein, S., 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42, 495–506.

Ehleringer, J.R., Monson, R.K., 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. Annual Review of Ecology and Systematics 24, 411–439.

Ehleringer, J.R., Sage, R.F., Flanagan, L.B., Pearcy, R.W., 1991. Climate change and the evolution of C4 photosynthesis. Trends in Ecology and Evolution 6, 95–99.

Feranec, R.S., 2004. Geographic variation in the diet of hypsodont ungulates from the Rancholabrean of Florida reveals more than discrete feeding categories. Palaeogeography, Palaeoclimatology, Palaeoecology 207, 361–371.

Feranec, R.S., 2007. Ecological generalization during adaptive radiation: evidence from Neogene mammals. Evolutionary Ecology Research 9, 555–577.

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

Feranec, R.S., MacFadden, B.J., 2006. Isotopic discrimination of resource partitioning among ungulates in C3-dominated communities from the Miocene of Florida and California. Paleobiology 32, 191–205.

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.

Friedli, H., Lotscher, H., Oeschger, H., Siegenthaler, U., Stauffer, B., 1986. Ice core record of the 13C/12C ratio of atmospheric CO_2 in the past two centuries. Nature 324, 237–238.

Garten Jr., C.T., Taylor Jr., G.E., 1992. Foliar d13C within a temperate deciduous forest: spatial, temporal, and species sources of variation. Oecologia 90, 1–7.

Genner, M.J., Turner, G.F., Barker, S., Hawkins, S.J., 1999. Niche segregation among Lake Malawi cichlid fishes? Evidence from stable isotopes. Ecology Letters 2, 185–190.

Grubb, P., 1981. *Equus burchelli*. Mammalian Species 157, 1–9.

Hansen, R.M., 1976. Foods of free-roaming horses in southern New Mexico. Journal of Range Management 29, 347.

Hardin, G., 1960. The competitive exclusion principle. Science 131, 1292–1297.

Heaton, T.H.E., 1999. Spatial, species, and temporal variations in the 13C/12C ratios of C3 plants: implications for paleodiet studies. Journal of Archaeological Science 26, 637–649.

Hedges, R.E.M., Clement, J.G., Thomas, C.D.L., O'Connell, T.C., 2007. Collagen turnover in the adult femoral mid-shaft: modeled from anthropogenic radiocarbon tracer measurements. American Journal of Physical Anthropology 133, 808–816.

Higgins, P., MacFadden, B.J., 2004. "Amount Effect" recorded in oxygen isotopes of Late Glacial horse (*Equus*) and bison (*Bison*) teeth from the Sonoran and Chihuahuan deserts, southwestern United States. Palaeogeography, Palaeoclimatology, Palaeoecology 206, 337–353.

Hillson, S., 2005. Teeth, 2nd Ed. Cambridge University Press, Cambridge.

Holt, R.D., 2003. On the evolutionary ecology of species' ranges. Evolutionary Ecology Research 5, 159–178.

Hoppe, K.A., Koch, P.L., 2007. Reconstructing the migration patterns of late Pleistocene mammals from northern Florida, USA. Quaternary Research 68, 347–352.

Hoppe, K.A., Paytan, A., Chamberlain, P., 2006. Reconstructing grassland vegetation and paleotemperatures using carbon isotope ratios of bison tooth enamel. Geology 34, 649–652.

Jaeger, R.G., 1971. Competitive exclusion as a factor influencing the distributions of two species of terrestrial salamanders. Ecology 52, 632–637.

Jefferson, G.T., 2001. Rancho La Brea bison. Terra 38, 33.

Jefferson, G.T., Goldin, J.L., 1989. Seasonal migration of Bison antiquus from Rancho La Brea, California. Quaternary Research 31, 107–112.

Kelt, D.A., Taper, M.L., Meserve, P.L., 1995. Assessing the impact of competition and community assembly: a case study using small mammals. Ecology 76, 1283–1296.

Kingdon, J., 1979. East African Mammals: an atlas of evolution in Africa. Universiy of Chicago Press, Chicago.

Kingdon, J., 1982. East African Mammals: an atlas of evolution in Africa. Academic Press, London.

Koch, P.L., 1998. Isotopic reconstruction of past continental environments. Annual Review of Earth and Planetary Science 26, 573–613.

Koch, P.L., Diffenbaugh, N.S., Hoppe, K.A., 2004. The effects of late Quaternary Climate and pCO2 change on C4 plant abundance in the south-central United States. Palaeogeography, Palaeoclimatology, Palaeoecology 207, 331–357.

Koch, P.L., Fisher, D.C., Dettman, D., 1989. Oxygen isotope variation in the tusks of extinct proboscideans: a measure of season of death and seasonality. Geology 17, 515–519.

Koch, P.L., Hoppe, K.A., Webb, S.D., 1998. The isotopic ecology of late Pleistocene mammals in North America Part 1. Florida. Chemical Geology 152, 119–138.

Koch, P.L., Tuross, N., Fogel, M.L., 1997. The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. Journal of Archaeological Science 24, 417–429.

Kohn, M.J., 1996. Predicting animal d18O: accounting for diet and physiological adaptation. Geochimica et Cosmochimica Acta 60, 4811–4829.

Kohn, M.J., 2004. Comment: tooth enamel mineralization in ungulates: implications for recovering a primary isotopic time-series, by B. H. Passey and T. E. Cerling (2002). Geochimica et Cosmochimica Acta 68, 403–405.

Kohn, M.J., Cerling, T.E., 2002. Stable isotope compositions of biological apatite. Reviews in Mineralogy and Geochemistry 48, 455–488.

Kohn, M.J., Welker, J.M., 2005. On the temperature correlation of d18O in modern precipitation. Earth and Planetary Science Letters 231, 87–96.

Kohn, M.J., McKay, M.P., Knight, J.L., 2005. Dining in the Pleistocene—who's on the menu? Geology 33, 649–652.

Kohn, M.J., Schoeninger, M.J., Valley, J.W., 1996. Herbivore tooth oxygen isotope compositions: effect of diet and physiology. Geochimica et Cosmochimica Acta 60, 3889–3896.

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

Land, L.S., Lundelius, E.L., Valastro, S., 1980. Isotopic ecology of deer bones. Palaeogeography, Palaeoclimatology, Palaeoecology 32, 143–151.

Longinelli, A., 1984. Oxygen isotopes in mammal bone phosphate: a new tool for paleohydrological and paleoclimatological research? Geochimica et Cosmochimica Acta 48, 385–390.

Luz, B., Kolodny, Y., 1985. Oxygen isotope variations in phosphate of biogenic apatites, IV. Mammal teeth and bones. Earth and Planetary Science Letters 75, 29–36.

Luz, B., Kolodny, Y., Horowitz, M., 1984. Fractionation of oxygen isotopes between mammalian bone-phosphate and environmental drinking water. Geochimica et Cosmochimica Acta 48, 1689–1693.

MacFadden, B.J., 1998. Tale of two rhinos: isotopic ecology, paleodiet, and niche differentiation of Aphelops and Teloceras from the Florida Neogene. Paleobiology 24, 274–286.

MacFadden, B.J., Cerling, T.E., 1996. Mammalian herbivore communities, ancient feeding ecology, and carbon isotopes; a 10 million -year sequence from the Neogene of Florida. Journal of Vertebrate Paleontology 16, 103–115.

MacFadden, B.J., Solounias, N., Cerling, T.E., 1999. Ancient diets, ecology, and extinction of 5-million-year-old horses from Florida. Science 283, 824–827.

MacFadden, B.J., Wang, Y., Cerling, T.E., Anaya, F., 1994. South American fossil mammals and carbon isotopes: a 25 million -year sequence from the Bolivian Andes. Palaeogeography, Palaeoclimatology, Palaeoecology 107, 257–268.

Marcus, L.F., Berger, R., 1984. The significance of radiocarbon dates for Rancho La Brea. In: Martin, P.S., Klein, R.G. (Eds.), Quaternary Extinctions: A Prehistoric Revolution. University of Chicago Press, Chicago, pp. 159–188.

Marino, B.D., McElroy, M.B., 1991. Isotopic composition of atmospheric CO_2 inferred from carbon in C4 plant cellulose. Nature 349, 127–131.

Marino, B.D., McElroy, M.B., Salawitch, R.J., Spaulding, W.G., 1992. Glacial-to-interglacial variations in the carbon isotopic composition of atmospheric CO_2. Nature 357, 461–466.

Martinez-Meyer, E., Townsend, P.A., Hargrove, W.W., 2004. Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. Global Ecology and Biogeography 13, 305–314.

McInnis, M.L., Vavra, M., 1987. Dietary relationships among feral horses, cattle, and pronghorn in southeastern Oregon. Journal of Range Management 40, 60–66.

McKane, R.B., Johnson, L.C., Shaver, G.R., Nadelhoffer, K.J., Rastetter, E.B., Fry, B., Giblin, A. E., Kielland, K., Kwiatkowski, B.L., Laundre, J.A., Murray, G., 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. Nature 415, 68–71.

Meagher, M., 1986. *Bison bison*. Mammalian Species 266, 1–8.

Meagher, M.M., 1973. The bison of Yellowstone National Park. National Park Service Scientific Monograph Series 1, 1–161.

Menge, B.A., Sutherland, J.P., 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. The American Naturalist 110, 351–369.

Millien, V., Lyons, S.K., Olson, L., Smith, F.A., Wilson, A., Yom-Tov, Y., 2006. Ecotypic variation in the context of global climate change: revisiting the rules. Ecology Letters 9, 853–869.

Mole, S., Joern, A., O'Leary, M.H., Madhaven, S., 1994. Spatial and temporal variation in carbon isotope discrimination in prairie graminoids. Oecologia 97, 316–321.

Nowak, R.M., 1999. Walker's mammals of the world. Johns Hopkins University Press, Baltimore.

O'Leary, M.H., 1988. Carbon isotopes in photosynthesis. BioScience 38, 328–336.

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.

Passey, B.H., Robinson, T.F., Ayliffe, L.K., Cerling, T.E., Sponheimer, M., Dearing, M.-D., Roeder, B.L., Ehleringer, J.R., 2005. Carbon isotope fractionation between diet, breath CO_2, and bioapatite in different mammals. Journal of Archaeological Science 32, 1459–1470.

Penzhorn, B.L., 1988. *Equus zebra*. Mammalian Species 314, 1–7.

Peterson, A.T., Soberón, J., Sánchez-Cordero, V., 1999. Conservatism of ecological niches in evolutionary time. Science 285, 1265–1267.

Pianka, E.R., 1967. On lizard species diversity: North American Flatland Deserts. Ecology 48, 333–351.

Pucek, Z., Belousova, I.P., Krasinska, M., Olech, W., 2004. European Bison. Status Survey and Conservation Action Plan. IUCN, Gland, Switzerland, Cambridge, UK.

Quade, J., Cerling, T.E., Barry, J.C., Morgan, M.E., Pilbeam, D.R., Chivas, A.R., Lee-Thorp, J. A., van der Merwe, N.J., 1992. A 16-Ma record of paleodiet using carbon and oxygen isotopes in fossil teeth from Pakistan. Chemical Geology (Isotope Geosciences Section) 94, 183–192.

Rozanski, K., Araguas-Araguas, L., Gonfiantini, R., 1992. Relation between long-term trends of Oxygen-18 isotope composition of precipitation and climate. Science 258, 981–985.

Sage, R.F., Wedin, D.A., Li, M., 1999. The biogeography of C4 photosynthesis: patterns and controlling factors. In: Sage, R.F., Monson, R.K. (Eds.), C4 Plant Biology. Academic Press, New York, pp. 313–373.

Schoener, T.W., 1974a. Resource partitioning in ecological communities. Science 185, 27–39.

Schoener, T.W., 1974b. The compression hypothesis and temporal resource partitioning. Proceedings of the National Academy of Sciences 71, 4169–4172.

Scott, E., 2001. The horses of Rancho La Brea. Terra 38, 31.

Smith, C., Valdez, R., Holecheck, J.L., Zwank, P.J., Cardenas, M., 1998. Diets of native and non-native ungulates in south central New Mexico. The Southwestern Naturalist 43, 163–169.

Stenhouse, M.J., Baxter, M.S., 1979. The uptake of bomb 14C in humans. In: Berger, R., Seuss, H.E. (Eds.), Radiocarbon Dating. University of California Press, Berkeley, pp. 324–341.

Stock, C., 1972. Rancho La Brea: a record of Pleistocene life in California. LACM Science Series No. 20, 1–81.

Suominen, O., Danell, K., 2006. Effects of large herbivores on other fauna. Cambridge University Press, Cambridge.

Vogel, J.C., 1978. Isotopic assessment of the dietary habits of ungulates. South African Journal of Science 74, 298–301.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389–395.

Wang, Y., Cerling, T.E., 1994. A model of fossil tooth and bone diagenesis: implications from paleodiet reconstruction from stable isotopes. Palaeogeography Palaeoclimatology Palaeoecology 107, 281–289.

Zazzo, A., Balasse, M., Patterson, W.P., 2005. High-resolution d13C intratooth profiles in bovine enamel: implications for mineralization pattern and isotopic attenuation. Geochimica et Cosmochimica Acta 69, 3631–3642.