

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

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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 C₃ plants, but bison regularly incorporated C₄ plants into their diets, while horses ate C₄ 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 C₄ plants into their diets during winter, which corresponds to previous studies suggesting that Rancho La Brea, primarily surrounded by C₃ 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.

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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 C₃ 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,

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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:

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

where $X = \delta^{13}\text{C}$ or $\delta^{18}\text{O}$ in parts per mil (‰) and $R = {}^{13}\text{C}/{}^{12}\text{C}$, ${}^{18}\text{O}/{}^{16}\text{O}$. 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). Herbivores 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 $\delta^{18}\text{O}$ 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 $\delta^{18}\text{O}_{\text{enamel}}$ 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 $\delta^{18}\text{O}$ 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 $\delta^{18}\text{O}_{\text{enamel}}$ cycle may be dampened because matrix formation and mineralization are processes that generally occur at different times. In this study, we scrutinize the $\delta^{18}\text{O}_{\text{enamel}}$ pattern archived within the tooth and not the absolute $\delta^{18}\text{O}$ values ingested in order to understand seasonal differences during individual growth and not for climatic reconstruction.

Body size and metabolism also can affect the $\delta^{18}\text{O}_{\text{enamel}}$ values, with smaller animals more likely to reflect a biotic imprint on environmental $\delta^{18}\text{O}_{\text{enamel}}$ values. Large mammals that are obligate drinkers and have low metabolisms are suggested as the most likely to accurately reflect ingested $\delta^{18}\text{O}$ 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 $\delta^{18}\text{O}_{\text{enamel}}$ 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 $\delta^{13}\text{C}$ values of $-27.0\% \pm 3.0\%$. In contrast, tropical, warm-season grasses and sedges using the C_4 -photosynthetic pathway have a mean isotopic value of $-13.0\% \pm 2.0\%$ (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 ${}^{12}\text{C}$ and ${}^{13}\text{C}$ (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 $+14.6\% \pm 0.3\%$ for large ruminants (Passey et al., 2005). Further, for ancient animals, carbon isotope values are expected to be $1.5\% \pm 1\%$ more positive than modern species due to $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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

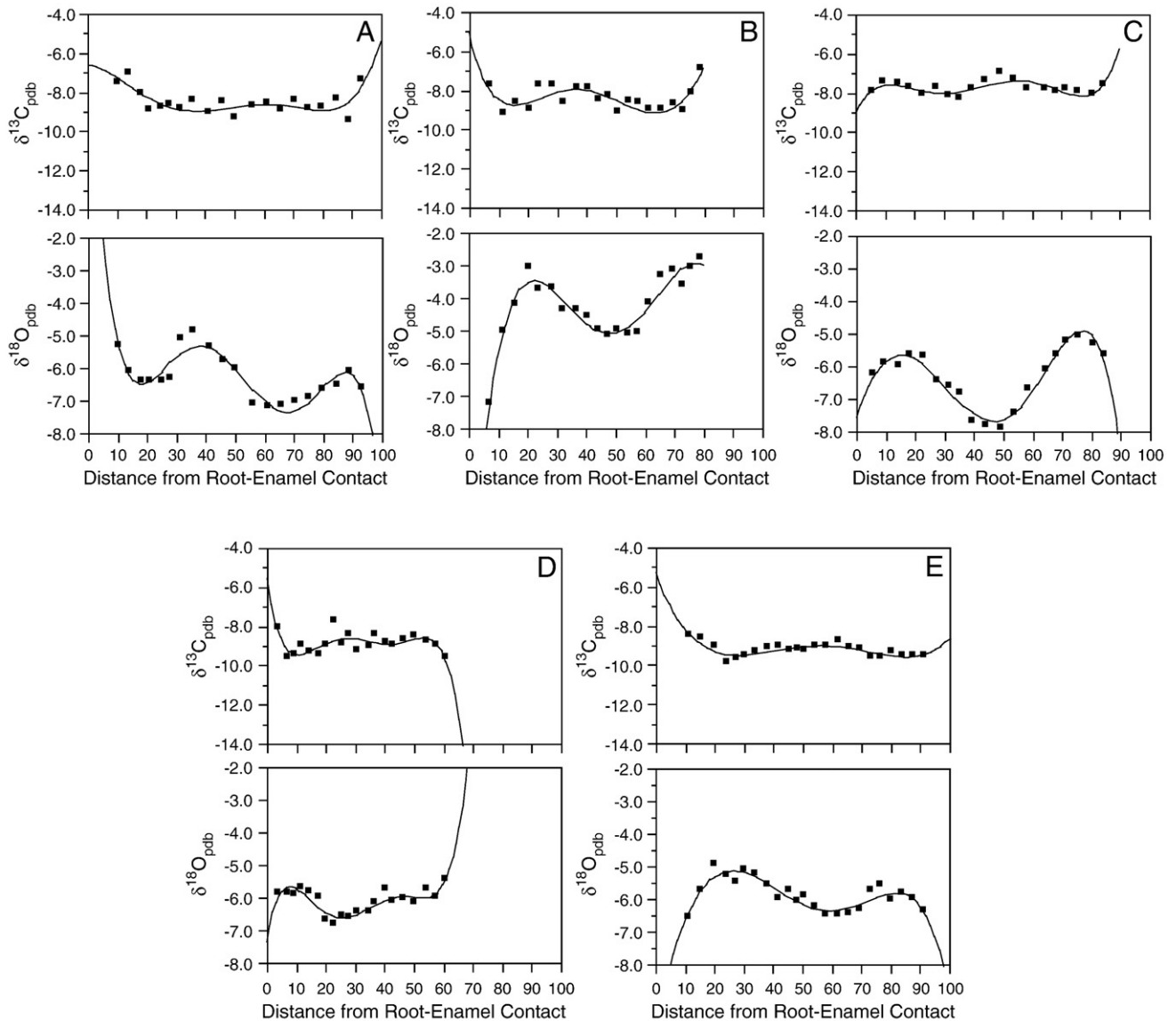


Fig. 1. Stable carbon and oxygen isotope values for the five Rancho La Brea horse specimens analyzed within this study. A, UCMP 18611; B, UCMP 18718; C, UCMP 18736; D, UCMP 41737; E, UCMP 158255.

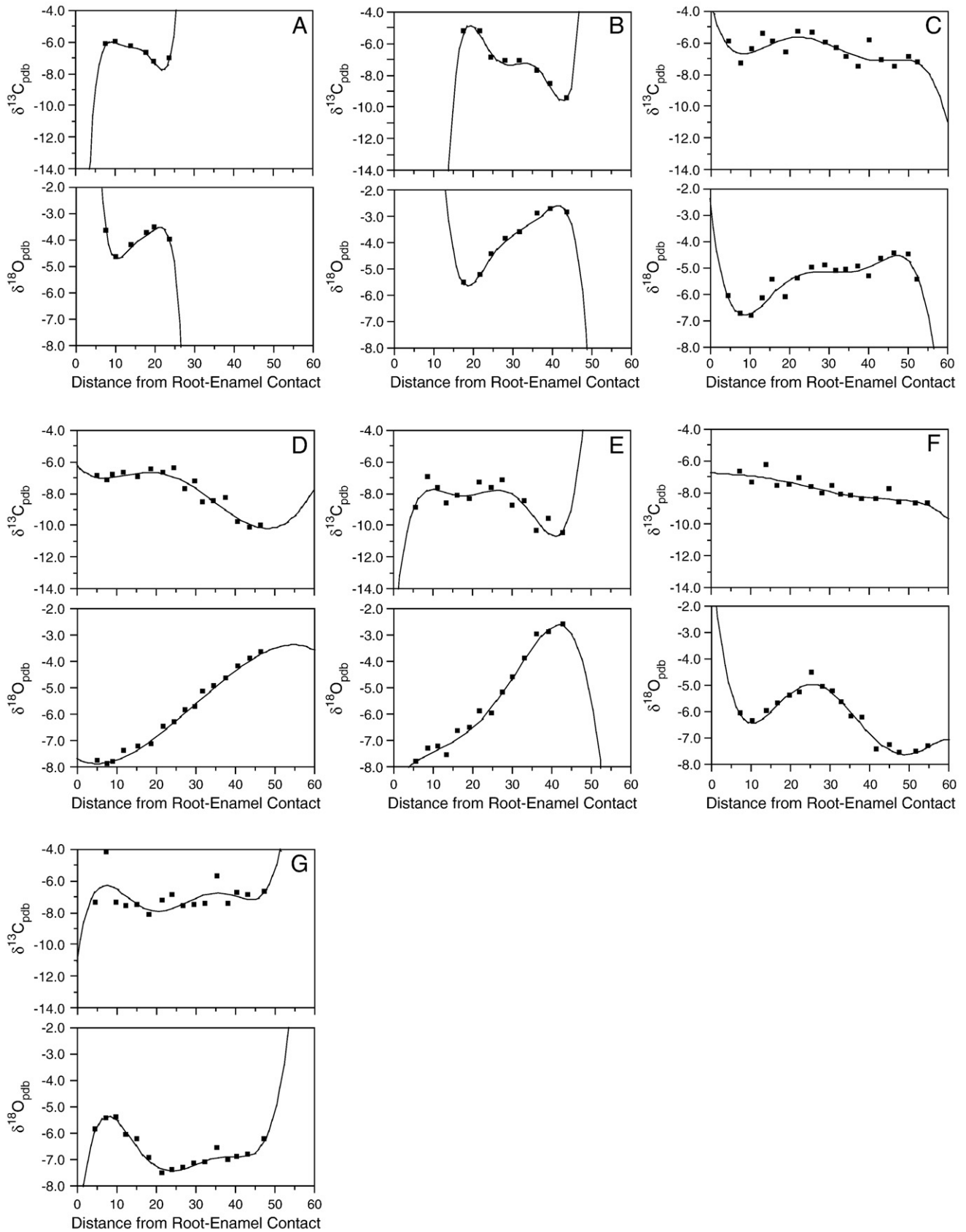


Fig. 2. Stable carbon and oxygen isotope values for the seven Rancho La Brea bison specimens analyzed within this study. A, UCMP 17528; B, UCMP 153132; C, UCMP 189665; D, UCMP 189666; E, UCMP 189667; F, UCMP 189668; G, UCMP 189669.

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 $\delta^{18}\text{O}$ (‰)	$\delta^{18}\text{O}$ SD (‰)	$\delta^{18}\text{O}$ Range (‰)	Mean $\delta^{13}\text{C}$ (‰)	$\delta^{13}\text{C}$ SD (‰)	$\delta^{13}\text{C}$ Range (‰)	Crown Height (mm)
<i>Bison</i>										
UCMP 17528	-2051	p or m	94	-5.7	1.4	-8.0 to -2.6	-7.4	1.2	-10.6 to -4.3	54.4
UCMP 153132	-3874	M ³	6	-4.0	0.4	-4.7 to -3.6	-6.6	0.5	-7.3 to -6.1	27.6
UCMP 189665	-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 189666	-3874	m	17	-5.5	0.7	-6.9 to -4.5	-6.5	0.8	-7.6 to -5.4	62.3
UCMP 189667	-3874	m	16	-6.0	1.5	-8.0 to -3.7	-7.8	1.3	-10.2 to -6.5	57.2
UCMP 189668	-3874	m	14	-5.6	1.8	-7.9 to -2.6	-8.5	1.1	-10.6 to -7.0	51.7
UCMP 189669	-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
<i>Equus</i>										
UCMP 18611	-2051	RM ^{1or2}	102	-5.8	1.0	-7.9 to -2.8	-8.6	0.7	-9.9 to -6.9	89.7
UCMP 18718	-2051	Frag.	20	-6.3	0.7	-7.2 to -4.8	-8.5	0.6	-9.5 to -7.1	101.2
UCMP 18736	-2051	Frag.	20	-4.3	1.1	-7.2 to -2.8	-8.4	0.6	-9.1 to -6.9	85.4
UCMP 41737	-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 compete 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 CO₂. 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 $\delta^{18}\text{O}_{\text{enamel}}$ patterns include about 1 year of growth data for bison and 1.5 years 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 $\delta^{18}\text{O}_{\text{enamel}}$ increases the $\delta^{13}\text{C}_{\text{enamel}}$ (%C₄) 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 C₄ plants in their diets (Table 1; Fig. 3). Assuming that all values more negative than -8.0‰ indicate 100% C₃ feeding and 0.0‰ indicates 100% C₄ feeding, the average sampled bison diet was 10% C₄ plants ($N = 94$ samples). Maximum percentage C₄ plants included in a bison diet was 47% (UCMP 189669) and minimum inclusion of C₄ plants in an individual diet was 3% (UCMP 189667). In contrast, the five horse individuals ($N = 102$ serial samples) only rarely foraged on C₄ plants, or had isotope values more positive than -8.0‰ (Table 1; Fig. 3). The average horse diet included only 1% C₄ plants and the maximum percentage C₄ plants included in the diets was only 14% (UCMP 18718) while the minimum was 0% (UCMP 158255).

The range of values for $\delta^{13}\text{C}_{\text{enamel}}$ 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 $\delta^{13}\text{C}_{\text{enamel}}$ 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 $\delta^{13}\text{C}$ values was

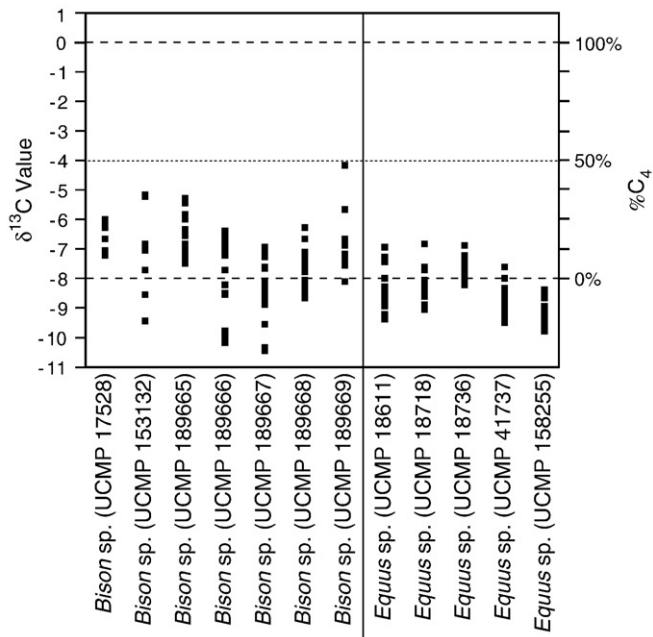


Fig. 3. Stable carbon isotope values and percent C₄ included in the diet for sampled individuals of horse and bison.

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

In contrast to the $\delta^{13}\text{C}$ results, comparison of all $\delta^{18}\text{O}_{\text{enamel}}$ 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 $\delta^{18}\text{O}_{\text{enamel}}$ values was greater in bison than in horse. The pooled range of $\delta^{18}\text{O}_{\text{enamel}}$ values for bison was 5.8‰ and 5.1‰ for horse. For individual bison the maximum range in $\delta^{18}\text{O}_{\text{enamel}}$ was 5.3‰ (UCMP 189667), and the minimum range 1.1‰ (UCMP 17528). Similar to the $\delta^{13}\text{C}_{\text{enamel}}$ 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 $\delta^{18}\text{O}_{\text{enamel}}$ was 4.4‰ (UCMP 18718), and the minimum range 1.4‰ (UCMP 41737). Correlation in the range of $\delta^{18}\text{O}_{\text{enamel}}$ and $\delta^{13}\text{C}_{\text{enamel}}$ 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 C₄ 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 C₃ plants along the California coast (Sage et al., 1999), the inclusion of higher percentages of C₄ plants in bison diets would suggest migration from the east. Seasonal migration into the C₃-dominated Los Angeles Basin is likely to have been during spring or summer because the $\delta^{13}\text{C}_{\text{enamel}}$ values in a few of the bison individuals showed the incorporation of a higher percentage of dietary C₄ plants during the winter (when $\delta^{18}\text{O}_{\text{enamel}}$ 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 $\delta^{13}\text{C}_{\text{enamel}}$ values over the course of the year, and little consumption of C₄ 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 C₄ plants in the diets of the herbivores preserved at Rancho La Brea. The tooth enamel data do show that C₄ 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 $\delta^{13}\text{C}_{\text{enamel}}$ value (-8.6‰) is indicative of a 100% C₃ diet, and the mean bison $\delta^{13}\text{C}_{\text{enamel}}$ value (-7.4‰) is indicative of a 93% C₃ 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 C₃ feeders, bison regularly integrated C₄ plants into their diet; horses only rarely ate C₄ 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.

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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.

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