Palaeogeography, Palaeoclimatology, Palaeoecology 437 (2015) 132–140

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Inland California during the Pleistocene—Megafaunal stable isotope records reveal new paleoecological and paleoenvironmental insights

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ARTICLE INFO

Article history:
Received 3 October 2014
Received in revised form 16 July 2015
Accepted 21 July 2015
Available online 30 July 2015

Keywords:
Stable isotopes
California
Pleistocene
Irvingtonian
McKittrick
Fairmead Landfill
Rancholabrean

ABSTRACT

We measured oxygen and carbon isotope compositions from teeth from three fossil localities in California, The McKittrick Tar seeps (Rancholabrean), Fairmead Landfill, and Irvington (both Irvingtonian). These sites have produced a variety of megafauna fossils, and to date are relatively understudied. Previous ecological studies of Pleistocene California megafauna have focused on the coastal Rancho La Brea tar seeps (RLB), neglecting inland faunas. Both Fairmead Landfill and McKittrick are located in California's San Joaquin Valley, and provide the first isotopic data from the region. We sampled a wide range of taxa; *Equus, Camelops, Mammuthus, Mammut, Hemiauchenia, Odocoileus, Tetrameryx, Capromeryx, Platygonus, Canis dirus, Canis latrans, Arctodus simus, Smilodon, Homotherium, Miracinonyx, Panthera onca* and *Panthera atrox.* Stable carbon values from both middle Pleistocene localities are consistent with a C_3 dominated environment. Mean annual precipitation (MAP) estimates for the middle Pleistocene localities are ~340 mm/year for Fairmead Landfill and ~900 mm/year for Irvington. While the inland MAP estimate is similar to modern levels, Irvington MAP estimates are significantly higher than the modern average. In contrast, the McKittrick tar seeps show clear evidence of C_4 consumption among *Equus*, *Bison* and *Camelops*, suggesting a mixture C_4 grasses and halophytes. Similarly, comparing between McKittrick and published data for RLB indicate a higher level of C_4 resources inland. Serially sampled teeth from both inland localities reveal diet and resource partitioning between browsers and grazers.

1. Introduction

Previous ecological studies of fossil megafauna from California have focused primarily on the coastal, late Pleistocene Rancho La Brea tar seeps (Coltrain et al., 2004; Feranec, 2004; Feranec et al., 2009). Currently no detailed studies exist for either inland or non-Rancholabrean aged faunas, leaving a substantial gap, both temporally and geographically in our understanding of Pleistocene ecology and climate. In this study we present new carbon and oxygen isotope values from tooth enamel from three fossil localities in California—Fairmead Landfill, Irvington, and the McKittrick tar seeps (Fig. 1). Each locality has produced abundant fossils of large herbivores and carnivores (Schultz, 1938; Savage, 1951; Dundas et al., 1996; Dundas and Chatters, 2013), allowing us to address several questions. 1) How did large herbivore taxa partition resources among taxa within localities and did the diet of these animals shift temporally and geographically? 2) How did dietary and climate seasonality among inland California sites compare with coastal California? 3) How did carnivores, including co-occurring large canids, felids and ursids, at all three sites, partition their diets? 4) How did precipitation amounts and meteoric water $\delta^{18}O$ values vary during the Pleistocene?

2. Localities

Hosting the type fauna of the Irvingtonian North American Land Mammal Age (NALMA), Irvington strata represent fluvial deposits at gravel quarries in the San Francisco Bay Area at Fremont, California. Fifty-four taxa are recognized from the site: 5 mollusks, 4 fish, 4 amphibians, 3 reptiles, 8 birds and 30 mammals (Stirton, 1939; Savage, 1951; Firby, 1968). Age of the fauna and associated "Irvington Gravels" is not well constrained. Sediment samples from the fossil bearing strata are magnetically reversed (Lindsay et al., 1975). Coupled with biostratigraphy, Irvington's age is inferred to be within the upper Matuyama magnetic polarity chron (i.e. greater than 780 ka), but the maximum age is unresolved. Consideration must be given to the possibility that the fauna may be older than 1.21 Ma (Bell and Bever, 2006).

Fairmead Landfill, in Madera County, sits on the distal portion of the Chowchilla River alluvial fan. Fossils have been recovered from the upper unit of the Turlock Lake Formation in alluvial fan channel, overbank flood, and marsh/lacustrine deposits. The sediments are magnetically normal (Dundas et al., 1996) and the unit regionally contains the Friant pumice near the base (750.1 ± 1.5 ka) (Sarna-Wojcicki

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http://dx.doi.org/10.1016/j.palaeo.2015.07.034
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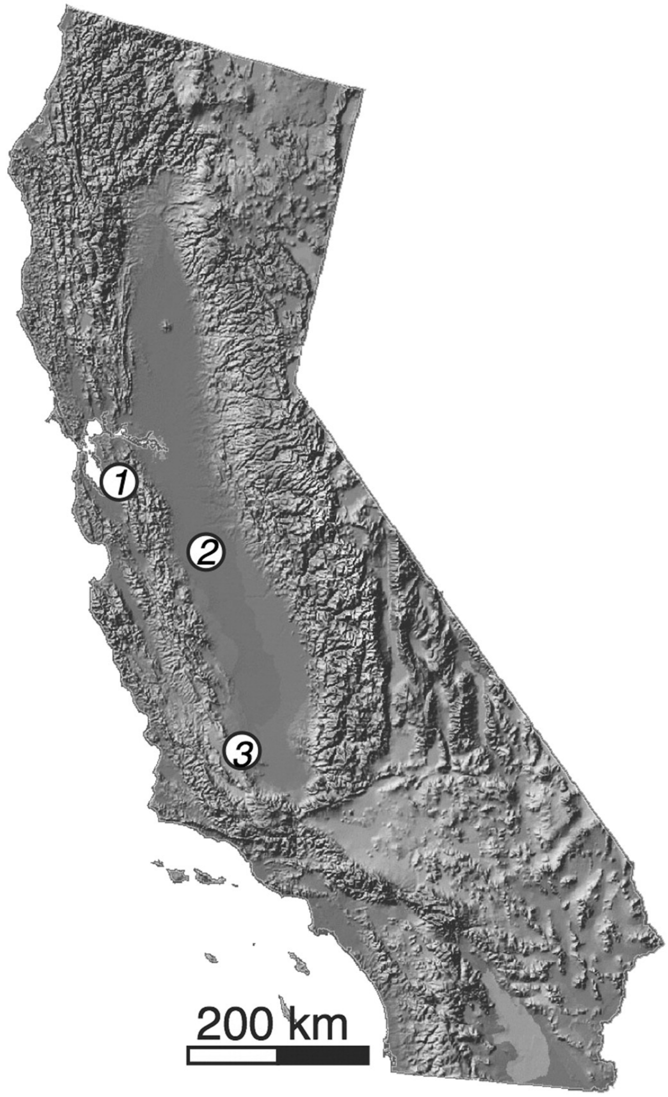

Fig. 1. Map of localities: 1) Irvington, 2) Fairmead Landfill and 3) McKittrick.

et al., 2000). Uranium trend dates of overlying paleosols constrain the age to older than 550 ka (Marchand and Allwardt, 1981). Coupled with the presence of *Tetrameryx irvingtonensis* these dates indicate that the site is mid-Irvingtonian in age (550–750 ka).

Macrofossil evidence of Fairmead's floral community is limited to molds of the cocklebur, genus *Xanthium*. Preliminary pollen analysis indicates a flora dominated by grass and pine (*Pinus*) although pine pollen transports great distances and may not have a local origin. Pollen of chenopods (Chenopodiaceae and Amaranthaceae), cattails (Typhaceae), sedges (Cyperaceae), willow (*Salix*), oak (*Quercus*), spruce (*Picea*), juniper (*Juniperus*) and sagebrush (*Artemisa*) were also recovered (Chatters and Van De Water, 2013). The mammalian fauna is dominated by large grazing and mixed feeding taxa with *Equus*, *Camelops*, *Mammuthus columbi* and *Paramylodon* being most common. Overall, 72 taxa have been identified at the site (2 fish, 2 amphibians, 3 reptiles, 6 birds, 29 mammals, 1 bivalve, 1 gastropod, 12 plants/paynomorphs and 16 diatoms) (Dundas and Chatters, 2013). Together the geological and biological data suggest a fluvial-marsh/lacustrine depositional environment surrounded by a grassy prairie with sparse oak and pine woodlands.

The McKittrick tar seeps, Kern County, yield a faunal assemblage similar to Rancho La Brea (Schultz, 1938). During the late Pleistocene, tar seeps were active at the site, permeating surficial sediments and entrapping animals. Recent ^{14}C ages from the site range from 15,290 to 11,040 indicating a late Rancholabrean age (Fox-Dobbs et al., 2014).

Six plant taxa; pine (*Pinus*), Juniper (*Juniperus*), saltbush (*Atriplex*), manzanita (*Arctostaphylos*) and wild cucumber (*Echinocystis*) are represented as macrofossils (Mason, 1944). Conifers, sagebrush (*Artemisia*) and greasewood (*Sacrobatus*) dominate pollen profiles from Late Pleistocene Tulare Lake, located 80 km north of McKittrick, with oak and giant sequoia (*Sequoiadendron*) less common (Davis, 1999).

3. Materials and methods

3.1. Stable isotope theory

Tooth enamel is resistant to diagenesis (Kohn and Cerling, 2002) therefore its isotopic composition is widely used as a proxy for paleodiet and paleoenvironment (see reviews of Koch, 1998; Kohn et al., 2002). All stable isotope analyses in this study are from the CO_3 component of enamel and are reported in the standard delta notation (Eq. (1)).

$$\delta = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000 \quad (1)$$

The carbon isotope composition of tooth enamel is controlled by diet (Koch, 1998; Cerling and Harris, 1999). Herbivore enamel $\delta^{13}C$ values reflect the plants they eat with an enrichment of $+14.6‰$ and $+13.3–14‰$ for ruminants and non-ruminants (Cerling and Harris, 1999; Passey et al., 2005). Three photosynthetic pathways control the $\delta^{13}C$ values of plants. Globally, C_3 plants are predominantly trees, shrubs and cool season grasses, with a mean $\delta^{13}C$ value of $-28.5‰$, although they range between $-23‰$ and $-32‰$ (Kohn, 2010). C_4 plants are predominately warm season grasses, sedges, and a small number of dicots (e.g. some species *Atriplex*). C_4 plants have a mean $\delta^{13}C$ value of $-12.5 \pm 1.1‰$. The third pathway (CAM) produces $\delta^{13}C$ values intermediate to C_3 and C_4 plants. CAM plants rarely contribute significantly to the diet of mammalian herbivores, however, so they were not considered for this study. Carnivore $\delta^{13}C$ values reflect those of their prey with an offset of $-1.3‰$ (Clementz et al., 2009). Pleistocene $\delta^{13}C$ values are expected to be ~1.5‰ more positive than modern values because fossil fuel burning has reduced atmospheric CO_2 $\delta^{13}C$ values (Friedli et al., 1986; Tipple et al., 2010). Thus, herbivores feeding entirely on C_3 plants should have an enamel $\delta^{13}C$ values less than $-8‰$ ($-23‰ + {\sim}14‰ + 1.5‰$) while a pure C_4 feeder would be more positive than 0‰ ($-12.5‰ + {\sim}14‰ + 1.5‰$). Intermediate values indicate a mixed diet of C_3 and C_4 resources.

The oxygen isotopic composition of tooth enamel in large mammals is primarily controlled by the composition of ingested water (Longinelli, 1984; Luz and Kolodny, 1985). In herbivores this water comes from two sources, drinking water and water contained within forage. The $\delta^{18}O$ of tooth enamel correlates well to mean meteoric water values (see summaries of Kohn, 1996; Kohn and Cerling, 2002). Plant $\delta^{18}O$ values are generally enriched relative to meteoric water and are also affected by relative humidity (Ayliffe and Chivas, 1990; Kohn, 1996). Large herbivores are predicted to be more sensitive to changes in plant $\delta^{18}O$ since they derive more of their water from forage than carnivores. Carnivore $\delta^{18}O$ values predicted to be less affected by humidity and to have similar $\delta^{18}O$ values to their prey (Kohn, 1996).

The seasonal range of $\delta^{18}O$ values in precipitation for the western United States is ~10‰ seasonally with higher vs. lower $\delta^{18}O$ values during the summer vs. winter (Henderson and Shuman, 2009). Because enamel forms in a multi-stage process (Passey and Cerling, 2002) enamel $\delta^{18}O$ values are inherently time-averaged and do not reflect the total variation in meteoric waters. Despite this, the expected pattern, if not the magnitude, of seasonal variation is preserved (Koch et al., 1989; Fricke and O'Neil, 1996; Kohn et al., 1998; Feranec, 2004; Feranec et al., 2009).

3.2. Sample selection and collection

All teeth sampled are housed in either the Madera County Paleontology Collection (MCPC) or the University of California Museum of Paleontology (UCMP). To ensure that each analysis represents an individual animal, teeth of a taxon were chosen from the same position (e.g. P_2 for *Equus*), when available. At Fairmead Landfill, where excavation records are known, teeth were selected from different stratigraphic levels when duplicates at the same tooth position were not available. Late erupting teeth were selected to insure that measured isotopic compositions reflected the animals' adult diet.

We sampled all teeth according to established protocols (Koch et al., 1997). All teeth were cleaned with a carbide burr and rinsed with ethanol to remove surficial material before sampling. Sampling then involved drilling ~10 mg of enamel powder from each tooth using a Dremel® rotary tool and either a 0.5 mm or 0.3 mm inverted cone carbide dental drill bit. For bulk samples, a single continuous groove was drilled parallel to the growth axis, for the length of the available enamel. Serial samples were drilled perpendicular to the growth axis of the tooth for the full width of the tooth. After drilling, enamel powder was collected and treated with 30% hydrogen peroxide overnight to remove residual organics. The hydrogen peroxide was decanted; the powder was washed twice with distilled water, and soaked with either buffered 1.0 M acetic acid (Irvington samples) or 0.1 M acetic acid (McKittrick and Fairmead Landfill samples) overnight to remove any labile carbonates. The acetic acid was decanted, the powder rinsed twice with distilled, water then dried in a vacuum oven at 40 °C for 48 h. Both pretreatment methods are appropriate for fossil material and should not bias resulting data (Koch et al., 1997).

Fairmead and McKittrick enamel was analyzed using a ThermoScientific Kiel IV carbonate device coupled to a ThermoScientific MAT-253 isotope ratio mass spectrometer at the University of California, Santa Cruz Stable Isotope Facility. Irvington enamel was analyzed using a Thermo Delta V Plus continuous flow isotope ratio mass spectrometer coupled with a GasBench II, in the Department of Geosciences, Boise State University. All values are reported in standard delta notation relative to the international VPDB ($\delta^{13}C$) and VSMOW ($\delta^{18}O$).

4. Results

4.1. Irvington fauna

We sampled 24 individuals representing 10 taxa from the Irvington fauna (Fig. 2). All stable isotope data are reported in Appendix A. Descriptive statistics for all localities are reported in Table 1. Carbon isotope values range from −16.1‰ to −9.9‰ with a mean of −12.5‰. Mean $\delta^{13}C$ values for carnivores and herbivores are −14.4‰ and −12.0‰. The Irvington fauna shows no statistically significant differences in $\delta^{13}C$ values for taxa where n > 1. (ANOVA, $p > 0.1$, Table 2). *Mammut americanum*, *Hemiauchenia*, *Homotherium*, *Arctodus simus* and *Panthera onca* are all represented by single individuals and were not included in statistical analysis. These taxa were considered significantly different only if their $\delta^{13}C^{13}C$ value fell beyond one standard deviation (2σ) of the mean of another taxon (Fox-Dobbs et al., 2008). $\delta^{18}O$ values for the Irvington fauna range from 18.1‰ to 27.4‰ with a mean of 25.1‰.

4.2. Fairmead Landfill fauna

We sampled 59 individuals from Fairmead Landfill, representing 14 taxa (Fig. 3). $\delta^{13}C$ and $\delta^{18}O$ values for the Fairmead Landfill fauna are reported in Appendix A.

Fairmead herbivore $\delta^{13}C$ values show statistically significant differences among taxa (ANOVA, $p < 0.01$). Pairwise comparisons (Bonferroni test; Table 3) reveal that *Camelops* differs significantly from all other herbivores, while excluding *Camelops* reveals no significant differences among the remaining herbivore taxa (ANOVA, $p > 0.05$). Similarly, no significant differences were detected among carnivores (ANOVA, $p > 0.05$). Adjusting for trophic level differences, pairwise comparisons of $\delta^{13}C$ values reveal that all carnivore and herbivore taxa are statistically indistinguishable, except for *Camelops,* which differs significantly from all other taxa. Fairmead Landfill $\delta^{18}O$ values are higher than those from the Irvington fauna, ranging from 22.4‰ to 34.4‰ with a mean of 27.5‰.

Three herbivore taxa were selected for serial sampling (Fig. 4). Ninety samples were collected serially from the teeth of three *Equus* (MCPC A1355a, A579, A1902a), one *Camelops* (MCPC A282) and one *Tetrameryx irvingtonensis* (UCMP 197567; Fig. 4; Appendix B). Pooled $\delta^{13}C$ values for each taxon demonstrate significant differences among taxa (ANOVA, $p < 0.05$). *Camelops* differs significantly from both *Equus* (ANOVA, $p < 0.05$) and *Tetrameryx irvingtonensis* (ANOVA, $p < 0.001$)

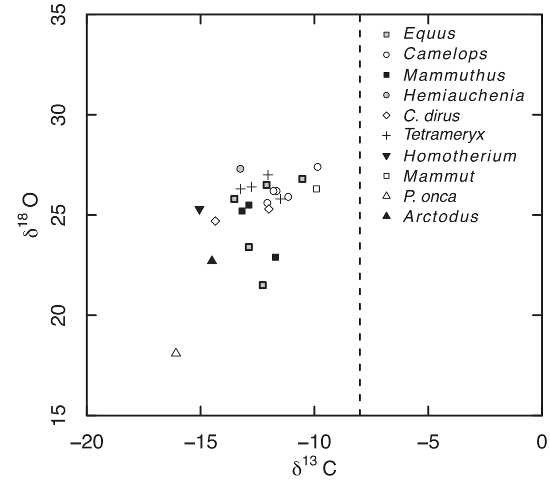

Fig. 2. $\delta^{13}C$ and $\delta^{18}O$ values for Irvington. Similar to Fairmead Landfill, the faunal $\delta^{13}C$ values show no evidence of C_3 vegetation. The mean values for all shared taxa are lower at Irvington than Fairmead, suggesting a more mixed grassland-woodland habitat. The dashed line indicates the −8‰ threshold for pure C_3 consumption.

Table 1
Descriptive statistics for for all taxa sampled. For taxa where n = 1 the associated $\delta^{13}C$ value is reported instead of a mean. Clementz and Koch (2001) recommend sampling at least five indivuduals to accurately estimate population statistics. However the limited fossil record means that several taxa in this study do not conform to this criteria. While these data may not reflect the intra-polulation varability, they do provide information about the overall community structure at each locality.

	Irvington			Fairmead Landfill			McKittrick tar seeps		
Taxa	*n*	Mean $\delta^{13}C$	S.D. $\delta^{13}C$	*n*	Mean $\delta^{13}C$	S.D. $\delta^{13}C$	*n*	Mean $\delta^{13}C$	S.D. $\delta^{13}C$
Arctodus simus	1	−14.5	–	1	−11.9	–	1	−10.9	–
Canis dirus	2	−13.2	1.7	8	−12.1	0.9	7	−5.3	3.5
Canis latrans	–	–	–	5	−12.3	0.9	7	−4.6	1.8
Homotherium sp.	1	−15.0	–	1	−13.5	–	–	–	–
Miracinonyx inexpectatus	–	–	–	1	−11.6	–	–	–	–
Panthera atrox	–	–	–	–	–	–	3	−9.9	2.0
Panthera onca	1	−16.1	–	–	–	–	–	–	–
Smilodon sp.	–	–	–	3	−12.2	1.1	–	–	–
Bison sp.	–	–	–	–	–	–	1	−4.9	–
Camelops sp.	5	−11.3	0.9	16	−9.4	1.0	5	−2.6	1.5
Capromeryx sp.	–	–	–	1	−11.1	–	–	–	–
Cervus elaphus	–	–	–	–	–	–	1	−11.3	–
Equus sp.	5	−12.3	1.1	7	−11.0	1.7	6	−6.4	2.1
Hemauchenia	1	−13.3	–	3	−11.4	2.0	1	−4.3	–
Mammut americanum	1	−9.9	–	–	–	–	1	−8.4	–
Mammuthus columbi	3	−12.6	0.8	7	−10.7	1.0	–	–	–
Odocoileus virginianus	–	–	–	1	−12.5	–	–	–	–
Platygonus vetus	–	–	–	1	−13.5	–	–	–	–
Tetrameryx irvintonensis	4	−12.4	0.8	4	−11.0	0.4	–	–	–

Table 2
Comparisons of taxa from Irvington where n = 1 to the means of taxa where n > 1. For taxa where n = 1, plus signs (+) indicates the $\delta^{13}C$ value fell within of the 2σ of the mean.

	Tetrameryx irvingtonensis	*Camelops*	*Equus*	*Mammuthus columbi*	*C. dirus*
Mammut americanum	−	+	−	−	+
Hemiauchenia	+	−	+	+	+
Arctodus simus	+	−	+	+	+
Panthera onca	−	−	−	−	+
Homotherium	+	−	+	+	+

while *Equus* and *Tetrameryx irvingtonensis* are indistinguishable (ANOVA, $p > 0.05$). $\delta^{13}C$ values for three *Equus* teeth range from −8.0‰ to −14.0‰, although individuals displayed considerably less variation with inter-tooth variation of 0.8‰ (MCPC A1902a), 1.2‰ (MCPC A579), and 1.8‰ (A1355a). *Tetrameryx irvingtonensis* $\delta^{13}C$ values ranged from −9.5‰ to −11.2‰ and *Camelops* (MCPC A282) −8.3‰ to −9.9‰.

Tetrameryx irvingtonensis has the widest range of $\delta^{18}O$ values of 6.4‰. Total variation in *Equus* teeth is lower; 3.1‰, 3.3‰ and 2.0‰ for MCPC A1355a, MCPC A579 and MCPC A1902a. MCPC A282 (*Camelops*) exhibits a $\delta^{18}O$ variation of 2.2‰.

4.3. The McKittrick tar seep fauna

We sampled 32 individuals representing 10 taxa from the McKittrick fauna (Appendix A). The $\delta^{13}C$ values range from −11.8‰ to −0.7‰ with a mean of −5.8‰. Carnivores exhibit a mean value of −6.1‰ while the herbivore mean is 5.4‰ (Fig. 5). $\delta^{13}C$ values for the McKittrick fauna reveal statistically significant differences (Table 3) between *Camelops hesternus* and *Equus*, and between *Canis latrans* and *Panthera atrox* ($p < 0.01$) $\delta^{13}C$ values are significantly different ($p < 0.01$) although neither differ significantly from *Canis dirus*. Pairwise comparisons between taxa are reported in Table 4. McKittrick $\delta^{18}O$ values range from 23.7‰ to 33.7‰, with a mean of 27.9‰.

Serial samples (Appendix B, Fig. 6) from one *Camelops hesternus* and two *Equus* teeth exhibit significant differences in both $\delta^{13}C$ and $\delta^{18}O$ values between taxa (ANOVA, $p < 0.001$). *Camelops hesternus* (UCMP 212893) has the highest variation in both isotopes with $\delta^{13}C$ ranging from −6.1‰ to −2.8‰ and $\delta^{18}O$ varying by 3.1‰. *Equus* displays slightly less variation in both isotopes; with UCMP 212874 $\delta^{13}C$ ranges from −7.9‰ to −6.1‰ and UCMP 212872 ranges from −8.7‰ to −7.1‰. Both individuals show similar changes in $\delta^{18}O$ with values varying by 2.6‰ and 2.4‰, respectively.

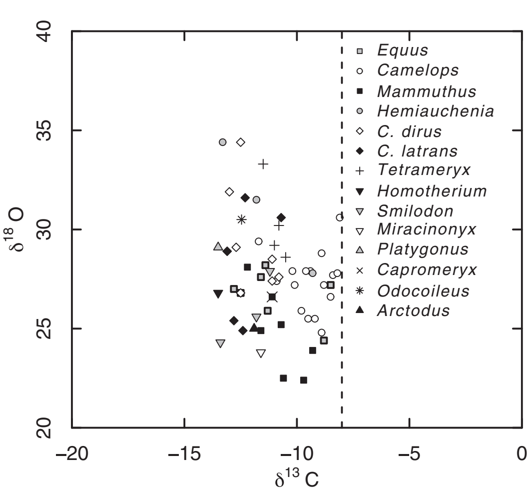

Fig. 3. $\delta^{13}C$ and $\delta^{18}O$ values for Fairmead Landfill. All individuals have $\delta^{13}C$ values indicative of pure C_3 vegetation (lower than −8‰, dashed line).

5. Discussion

5.1. Herbivore habitats and diet

Differentiating habitats within a C_3 plant dominated environment based solely on $\delta^{13}C$ values is challenging because since there is considerable overlap between habitat types. However, general trends do provide some constraints. Habitats can be referred to as either open (grassland, savanna, scrub) or closed (mosaic woodland, forest) based on the general relationship between environmental factors, particularly water availability (Kohn, 2010) and $\delta^{13}C$ values in C_3 plants. Habitat type can be associated with feeding strategy, with open and closed environments favoring grazers and browsers, respectively. Within a C_3 plant dominated environment, variations in plant $\delta^{13}C$ values are largely controlled by physiological differences among plants and the degree of water stress (aridity). More positive $\delta^{13}C$ values are expected for plants with higher water use efficiency, or which grow in more open or arid environments (Ehleringer et al., 1992; Ehleringer and Monson, 1993; Kohn, 2010). Plants of the same species may vary by ~2‰ depending on microhabitat and water availability (Ehleringer and Cooper, 1988). Closed environments are associated with more negative $\delta^{13}C$ values due to the "canopy effect", resulting from CO_2 recycling and lower light levels (Van Der Merwe and Medina, 1991; Cerling et al., 2004).

Although $\delta^{13}C$ values from both localities are indicative of a pure C_3 environment, Fairmead Landfill $\delta^{13}C$ and $\delta^{18}O$ values are systematically higher for all taxa shared with Irvington. Equus and other grazing taxa dominate the Fairmead Landfill (Asami et al., 2011). This abundance coupled with palynological (Chatters and Van De Water, 2013) evidence strongly suggests that Fairmead Landfill was an open prairie. Consequently we interpret *Equus* $\delta^{13}C$ values as indicative of C_3 grasses. A predominately C_3 grassland ecosystem is compatible with the remaining herbivore $\delta^{13}C$ values, although the presence of the mixed feeders *Hemiauchenia, Camelops* and *Paramylodon*, and browsers *Odocoileus* and *Platygonus* require at least some browsing forage, likely in riparian zones. The more positive $\delta^{13}C$ values of *Camelops* also suggest more arid regional habitats and the presence of halophytes on the landscape (Guy et al., 1980; Köhler-Rollefson, 1991; Vetter, 2007). Of the remaining herbivores, only *Mammuthus* is known to have grazed heavily (Gillette and Madsen, 1993; Koch et al., 1998, 2004) while both *Hemiauchenia* and the antilocaprids had more flexible diets (Feranec, 2003; Kohn et al., 2005; Semprebon and Rivals, 2010).

The Irvington Faunas $\delta^{13}C$ values are more negative than the inland Fairmead Landfill fauna. We interpret these ^{13}C-depleted carbon isotope values as evidence of more heavily wooded environment. The lack of significant differences between herbivore taxa limits our ability to separate herbivores based on habitat type. Grazing taxa (*Equus* and *Mammuthus*) necessitate at least some grass availability. *Mammut americanum* is usually associated with the presence and consumption of conifers (Dreimanis, 1968; Lepper et al., 1991; Minckley et al., 1997). Conifers have $\delta^{13}C$ values ~2‰ higher than other woody plants (Brooks et al., 1997; Heaton, 1999; Diefendorf et al., 2010) which may explain high $\delta^{13}C$ value of *Mammut americanum*.

Carbon isotope values from the McKittrick tar seep fauna show clear evidence of a mixed C_3–C_4 environment. *Cervus elaphus*, the most ^{13}C-depleted McKittrick herbivore, has a $\delta^{13}C$ value consistent with C_3 browsing. Similar to Irvington, McKittrick *Mammut* has a higher $\delta^{13}C$ value than other browsing taxa, which again supports the conclusion of conifer consumption, fossilized remains of which have been recovered from the McKittrick deposits (Mason, 1944).

The remaining McKittrick herbivore taxa have $\delta^{13}C$ values indicative of mixed C_3–C_4 feeding, although some individuals consumed almost entirely C_4 plants. *Bison, Hemiauchenia macrocephala* and *Equus* all have intermediate $\delta^{13}C$ values. *Camelops hesternus* is the most positive herbivore in the McKittrick fauna. Extant *Camelus* consume large amounts of *Atriplex* (Köhler-Rollefson, 1991; Towhidi et al., 2011),

Table 3
Statistical comparisons of Fairmead Landfill $\delta^{13}C$ values. Bold *p*-values indicate significant differences. Carnivore values were adjusted by 1.3‰ to correct for trophic level fractionation (Clementz et al., 2009). For taxa where n = 1, plus signs (+) indicates the $\delta^{13}C$ value fell within of the 2σ of the mean.

	Canis dirus	*Canis latrans*	*Smilodon* sp.	*Camelops* sp.	*Equus* sp.	*Hemiauchenia* sp.	*Mammuthus columbi*	*Tetrameryx irvingtonensis*
Canis dirus		0.77	0.07	**0.01**	0.80	0.47	0.89	0.73
Canis latrans			0.90	**0.01**	0.98	0.65	0.70	0.98
Smilodon sp.				**0.03**	0.92	0.69	0.86	0.86
Camelops sp.					**0.01**	**0.01**	**0.01**	**0.01**
Equus sp.						0.72	0.74	0.99
Hemiauchenia sp.							0.46	0.66
Mammuthus columbi								0.66
Capromeryx	+	+	+	+	+	+	+	+
Odocoileus	+	+	+	−	+	+	+	−
Platygonus	−	−	−	−	+	+	−	−
Homotherium	+	+	+	−	+	+	+	−
Arctodus	+	+	+	+	+	+	+	+
Miracinonyx	+	+	+	+	+	+	+	+

which include C_4 halophyte species, and the presence of (C_4) *Atriplex lentiformis* in the McKittrick deposits (Mason, 1944) demonstrates a potential food source for *Camelops hesternus* (Vetter, 2007).

5.2. Carnivore diets

Several genera of large carnivores co-occur at each locality. As predicted by Clementz et al. (2009), mean carnivore $\delta^{13}C$ values are lower than herbivore means at all three localities. Carbon isotope values for both Fairmead Landfill and Irvington carnivores indicate a diet of exclusively C_3 feeding herbivores. At Fairmead landfill, *Smilodon*, *Canis dirus*, and *Miracinonyx* $\delta^{13}C$ values are indistinguishable suggesting direct competition among these taxa. Fairmead *Homotherium* has a lower $\delta^{13}C$ value than that of the other carnivores suggesting less direct competition. In contrast, *Homotherium* at Irvington is indistinguishable from *Canis dirus* suggesting more direct competition for prey. The Irvington *Panthera onca* had the lowest $\delta^{13}C$ value of any carnivore sampled, consistent with its predicted niche as a forest dwelling felid (Seymour, 1989).

Similar to the pattern observed for Fairmead Landfill and Irvington, McKittrick felids have mean $\delta^{13}C$ values lower than the canids, with the *Canis dirus* and *Panthera atrox* means differing by 4.6‰. Because of this, we separate the McKittrick carnivores into two groups, browser specialists (*Panthera atrox*) and generalists (*Canis dirus*). McKittrick *Canis dirus* has the highest total range in $\delta^{13}C$ values of any carnivore in this study. *Canis dirus* $\delta^{13}C$ values differed significantly from only *Cervus elaphus* and *Mammut americanum*, both C_3 browsers. *Panthera atrox* is thought to have preferred open habitats (Kurtén and Anderson, 1980; Christiansen and Harris, 2009). Our data instead show a preference for browsing herbivores and by proxy a more closed habitat.

Arctodus simus $\delta^{13}C$ values are consistent with diet based on C_3 resources. *Arctodus* has been considered an herbivore (Emslie and Czaplewski, 1985), scavenger (Gillette and Madsen, 1992) and hyper-

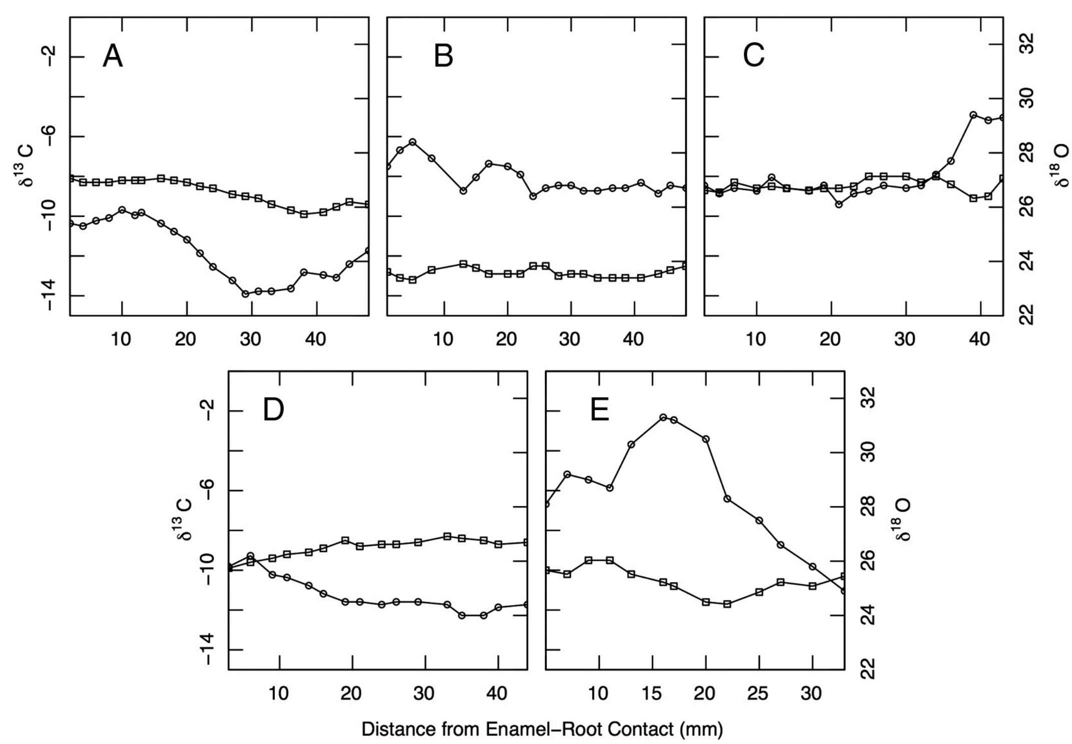

Fig. 4. Serial sampled teeth from Fairmead Landfill. $\delta^{13}C$ (squares) and $\delta^{18}O$ (circles). A) MCPC A1355a (*Equus*), B) MCPC A1902 (*Equus*), C) MCPC A579 (*Equus*), D) MCPC A282 (*Camelops*), E) UCMP 197567 (*Tetrameryx irvingtonensis*).

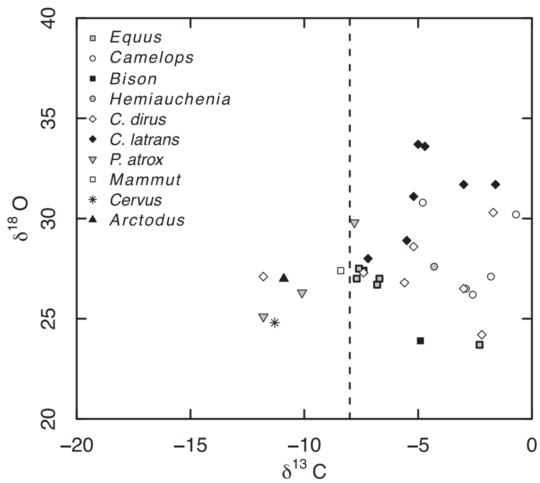

Fig. 5. $\delta^{13}C$ and $\delta^{18}O$ values for the McKittrick tar seeps. Faunal $\delta^{13}C$ significantly higher than Fairmead Landfill, and most McKittrick taxa have a mixed C_3–C_4 diet.

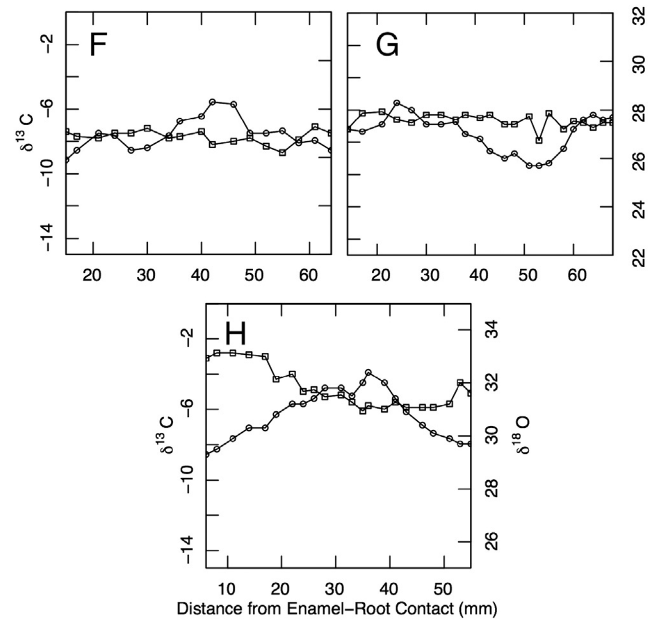

Fig. 6. Serial sampled teeth from the McKittrick tar seeps. $\delta^{13}C$ (squares) and $\delta^{18}O$ (circles). F) UCMP 212872 (*Equus*), G) UCMP 212874 (*Equus*), H) UCMP 2128 93 (*Camelops*).

carnivore (Matheus, 1995). Figueirido et al. (2010) instead suggests a highly variable, omnivorous diet which is consistent with extant *Ursus arctos* (Pasitschniak-Arts, 1993). If *Arctodus* was predominately a carnivore, its reliance on C_3 resources limit its diet to two taxa, *Cervus elaphus* and *Mammut americanum*.

5.3. Inter-locality isotopic differences

Comparing the Irvingtonian aged localities reveals that *Mammuthus*, *Camelops* and *Tetrameryx* $\delta^{13}C$ values differ significantly between Fairmead Landfill and Irvington (ANOVA, $p < 0.05$). These differences may arise from the shift from a wetter mixed woodland-grassland environment at Irvington a drier more open prairie of Fairmead Landfill.

Comparisons between the inland faunas reveal that all shared taxa between Fairmead Landfill and McKittrick exhibit significant differences (ANOVA, $p < 0.05$). The overall range of $\delta^{13}C$ values at McKittrick is approximately twice that of Fairmead Landfill, suggesting a more varied habitat or diverse flora. The shift towards C_4 consumption seen at McKittrick indicates the presence of a more arid grassland habitat, with some woodlands present.

Comparisons among the inland Rancholabrean McKittrick fauna and the coastal fauna of Rancho La Brea reveal significant differences (ANOVA, $p < 0.001$). Comparative data were selected from two published data sets. *Equus* and *Bison* were compared to data from Feranec et al. (2009). These authors report serial sampled $\delta^{13}C$ and $\delta^{18}O$ for both *Equus* and *Bison* tooth enamel. While Coltrain et al. (2004) report a larger data set for both taxa, their $\delta^{13}C$ data are from collagen, which averages over several years and may obscure some contributions to diet (Hedges et al., 2007). In the absence of published enamel data for Rancho La Brea, *Panthera atrox*, *Canis latrans*, *Canis dirus* and *Camelops hesternus* collagen data from Coltrain et al. (2004) were used for comparisons for these taxa. For these taxa, collagen data were corrected to dietary values using a $\delta^{13}C_{collagen-diet}$ offset of 5‰ (Koch, 1998). Values were then corrected to equivalence with enamel using the appropriate fractionation factors. *Camelops hesternus*, *Canis dirus* and *Canis latrans* are significantly different between localities (ANOVA, $p < 0.05$). *Panthera atrox* and *Equus* do not differ significantly (ANOVA, $p > 0.05$). The McKittrick *Bison* $\delta^{13}C$ falls within the observed range of $\delta^{13}C$ values, while McKittrick *Mammut americanum* falls outside the 2σ range of their Rancho La Brea analogs. Rancho La Brea was more mesic during the late Pleistocene, with a flora dominated by coastal sage scrub and chaparral (Stock and Harris, 1992). C_4 plant consumption at Rancho La Brea was broadly similar to McKittrick, with obligate grazers (*Bison*, *Equus*) from both localities feeding on a mix of C_3 and C_4 grasses.

While the individual $\delta^{13}C$ values for the presumed browser, *Mammut americanum*, are distinctly different between localities, both are consistent with a diet of C_3 browse. Curiously, McKittrick *Camelops hesternus* consumed far more C_4 plants than Rancho La Brea individuals. Dental boluses from Rancho La Brea *Camelops hesternus* indicate a browsing diet (Akersten et al., 1988). This likely reflects a greater abundance of saltbush (or its C_4 species) at McKittrick.

Unlike *Canis dirus* (Fox-Dobbs et al., 2007), there are no detailed dietary reconstructions of Rancho La Brea *Panthera atrox*, although the $\delta^{13}C$ values of the two taxa are statistically indistinguishable, suggesting a similar diet of C_3 ruminants (Coltrain et al, 2004).

Table 4
Statistical comparisons of McKittrick Tar Seep $\delta^{13}C$ values. Bold *p*-values indicate significant differences. Carnivore values were adjusted by 1.3‰ to correct for trophic level fractionation (Clementz et al., 2009). For taxa where n = 1, plus signs (+) indicates the $\delta^{13}C$ value fell within of the 2σ of the mean.

	Canis dirus	*Canis latrans*	*Panthera atrox*	*Camelops hesternus*	*Equus* sp.
Canis dirus		0.67	0.07	0.43	0.16
Canis latrans			<**0.01**	0.47	<**0.01**
Panthera atrox				<**0.01**	0.18
Camelops hesternus					<**0.01**
Arctodus simus	+	−	+	−	−
Bison sp.	+	+	−	+	+
Cervus elaphus	+	−	+	−	−
Hemiauchenia macrocephala	+	+	−	+	+
Mammut americanum	+	+	+	−	+

5.4. Seasonality and C_4 grasses in inland California

The magnitude of $\delta^{18}O$ seasonal variation in serial sampled teeth varies between taxa, possibly a result of taxon specific metabolic, migrational or seasonal dietary effects. At Fairmead Landfill, MCPC A1355a (*Equus*) displays the clearest seasonal variation. The remaining *Equus* individuals are more difficult to interpret; MCPC A579 appears to show a dampened seasonal cycle while MCPC A1902a does not exhibit an expected sinusoidal pattern. McKittrick *Equus* show slightly less variability in $\delta^{18}O$, although a seasonal cycle is apparent in both individuals (UCMP 212874, UCMP 212872). While the sampled McKittrick *Camelops hesternus* (UCMP 212893) shows clear evidence of seasonal variation, Fairmead Landfill *Camelops* (MCPC A282) exhibits less variation. *Tetrameryx irvingtonensis* has the highest variability in $\delta^{18}O$. With the exception of the McKittrick *Camelops hesternus,* the variation in $\delta^{13}C$ values of herbivore teeth from both localities is low, suggesting little dietary variation between summer and winter at both localities.

At Fairmead Landfill, the individual *Tetrameryx* tooth with the highest in $\delta^{18}O$ variation was recovered from a different bone bed than other serial sampled teeth and may have experienced greater seasonal variability than individuals recovered from other bone beds.

All serial sampled *Equus* teeth show relatively low variability in $\delta^{13}C$. We interpret as indicating that both McKittrick and Fairmead Landfill had a relatively stable diet and floral community with little turnover on a seasonal scale. Comparing $\delta^{13}C$ and $\delta^{18}O$ values between Fairmead Landfill and McKittrick *Equus* and *Camelops* reveals a negative correlation in both *Camelops* individuals. The inverse relationship in *Camelops* isotope values may be a result of seasonal shifts in the diet. Different parts of the same plant are expected to have different isotopic compositions, with woody tissues enriched in $\delta^{13}C$ (Dawson et al., 2002). A shift in diet for *Camelops* during the winter months to woodier browse or a heavier reliance on halophytes (Köhler-Rollefson, 1991; Vetter, 2007; Towhidi et al., 2011) would explain the observed relationship. Some species of *Atriplex* maintain high photosynthetic capability at low temperatures (Caldwell et al., 1977) which would make them a likely winter forage for *Camelops*. Compared to *Equus*, *Camelops* diets appear to have been more variable on a seasonal scale at both localities suggesting that while the proportion of grasses at each locality remained relatively constant, browse varied seasonally.

McKittrick and Fairmead Landfill $\delta^{13}C$ values show a clear shift in C_4 abundances from the middle to late Pleistocene. C_4 biomass abundance is related to mean annual temperature (MAT), MAP and atmospheric pCO_2 (Collatz et al., 1998; Connin et al., 1998). C_4 grasses are favored over C_3 at both higher MAT and higher growing season (summer) precipitation and also at lower pCO_2 (Ehleringer et al., 1997). Modern California is dominated by winter precipitation and abundances of C_4 grasses in California are low (~10%) (Teeri and Stowe, 1976; Teeri and Livingstone, 1980; Paruelo and Lauenroth, 1996). Likewise, the model of (Kohn and McKay, 2012) predicts no C_4 biomass for modern Fairmead Landfill or McKittrick. While temperatures were lower during the last glacial maximum, lower pCO_2 may have offset this effect and favored C_4 grasses (Collatz et al., 1998; Koch et al., 2004). The dominant C_4 signal from McKittrick comes from *Camelops* and may not accurately reflect C_4 grass abundances. Both grazing taxa (*Equus* and *Bison*) show a mixed C_3–C_4 diet suggesting that C_4 grasses were more common during the late Pleistocene, but were not the dominant grass type.

5.5. Meteoric waters and precipitation

We estimated mean annual precipitation (MAP) following the general methods of Kohn and McKay (2012) and Kohn (2010). Since this method relies on $\delta^{13}C$ values from C_3 plants it is not appropriate for ecosystems where C_4 plants are prevalent, therefore McKittrick was omitted from MAP calculations.

For the two remaining localities we used only herbivore $\delta^{13}C$ values. Enamel values were first corrected to plant values by subtracting 14.3‰ (Passey et al., 2005) and then correcting for changes in atmospheric $\delta^{13}C$ using an average pleistocene $\delta^{13}C_{atm}$ of −6.5‰ ($\delta^{13}C_{plant} = \delta^{13}C_{enamel} - 14.3‰ – 1.5‰$). Using an elevation of 75 m and latitude of 37° for Fairmead Landfill we calculate a MAP of 360 ± 130 mm (mean ± 2 S.E.). The average MAP today for the Fairmead area is ~280 mm. Accounting for the error in our MAP calculations we show no significant difference between modern MAP and the middle Pleistocene. In contrast, MAP for middle Pleistocene coastal California differs significantly from modern MAP. Modern MAP for Freemont, California is ~410 mm, whereas Irvington (34 m, 37.5°) yields a modeled Pleistocene MAP of 900 ± 220 mm, significantly higher than modern values. Both Fairmead Landfill and Irvington fossils were recovered over several meters of vertical section (Dundas et al., 1996; Firby, 1968). This suggests that MAP calculations from these assemblages represent an average over a prolonged time period.

Predicting surface water $\delta^{18}O$ values followed the approach of Kohn (1996), where $\delta^{18}O_{PO4} \sim 26.8 - 8.9\,h + 0.76\,\delta^{18}O_{surface\ water}$, for large herbivores. We adjusted enamel carbonate data to reflect phosphate values using a fractionation factor of $\alpha_{CO3\text{-}PO4} = 1.0086 \pm 0.0007$ (Bryant et al., 1996). For Fairmead Landfill we estimate meteoric water oxygen isotope values of −5.7 ± 0.9‰ (mean ± 2 S.E.). Inferred Irvington $\delta^{18}O$ values are −6.5 ± 1.1‰, lower than Fairmead Landfill but not significantly so. McKittrick $\delta^{18}O$ values are most similar to those of Fairmead Landfill (ANOVA, $p < 0.05$), with modeled surface water values of −5.3 ± 1.2‰. The oxygen isotope composition of seawater is expected to be ~1‰ higher than modern values during glacial cycles (Schrag et al., 2002). Accounting for this enrichment, the predicted surface water composition for Irvington is within the range of modern meteoric water compositions (i.e. −7.5‰ VSMOW; Kendall and Coplen, 2001). Conversely, the modeled compositions for the inland localities are ~2‰ higher than modern compositions. These high herbivore $\delta^{18}O$ values may reflect ^{18}O-enrichment of vegetation through increased evapotranspiration (Sternberg et al., 1984; Flanagan et al., 1991) or evaporative enrichment of local water sources, suggesting higher aridity.

6. Conclusions

The analysis of tooth enamel from three localities offers new insights into the paleoenvironment of Pleistocene California. Irvingtonian Fairmead Landfill was a C_3 dominated grassland, although with some scrub and tree cover as indicated by the palynological and faunal evidence. Herbivores exhibit little variability in $\delta^{13}C$ values, suggesting similar diets, but forms of partitioning that are not revealed using stable isotope analysis are possible (i.e. selective feeding, feeding at different times of day). Irvington $\delta^{13}C$ values are also indicative of a C_3 dominated environment, although likely with more wooded areas present. Carnivore carbon isotope values also reveal direct competition among felids, canids and ursids for similar prey species.

The late Rancholabrean McKittrick asphalt seeps preserve a mixed C_3–C_4 habitat with the presence of both woodlands and grasslands. Herbivore diets differed more significantly with a larger separation low $\delta^{13}C$ browsers and high $\delta^{13}C$ grazers. A large range in $\delta^{13}C$ among McKittrick canids suggests opportunistically feeding, while *Panthera atrox* retained a narrower range of $\delta^{13}C$ values, similar to that observed for the Fairmead Landfill felids. The abundance of data for the coastal Rancho La Brea fauna allowed comparison between it and inland McKittrick, revealing shifts in the diets of both canids and *Camelops hesternus*, while browsers and obligate grazers had similar diets.

Precipitation estimates reveal that Fairmead Landfill experienced a similar amount of rain during the middle Pleistocene, while coastal Irvington received twice the modern average. Serial sampled teeth from inland localities reveal resource partitioning between *Camelops* and *Equus* on a seasonal scale with the former favoring higher $\delta^{13}C$ plants during the winter. Similarly, C_4 grass abundances were higher during the late Pleistocene of California.

Acknowledgments

We would like to thank Patricia Holroyd at the University of California Museum of Paleontology for access to the Irvington, Fairmead Landfill and McKittrick collections. We also thank Samantha Evans at Boise State University for her assistance with isotopic analyses. Discussions with Matthew J. Kohn also greatly improved this paper. The College of Science and Mathematics and the Department of Earth and Environmental Sciences, California State University, Fresno funded this study.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2015.07.034.

References

Akersten, W.A., Foppe, T.M., Jefferson, G.T., 1988. New source of dietary data for extinct herbivores. Quaternary Research 30, 92–97.
Asami, R., Ibarra, Y., Scott, E., Dundas, R.G., 2011. *Equus* from the middle Irvingtonian Fairmead Landfill Locality, Madera County, California. Proceedings Supplement to the online Journal of Vertebrate Paleontology, Program and Abstracts, Society of Vertebrate Paleontology Annual Meeting, Las Vegas, NV, p. 64.
Ayliffe, L.K., Chivas, A.R., 1990. Oxygen isotope composition of the bone phosphate of Australian kangaroos: potential as a palaeoenvironmental recorder. Geochim. Cosmochim. Acta 54 (9), 2603–2609.
Bell, C.J., Bever, G.S., 2006. Description and significance of the *Microtus* (Rodentia: Arvicolinae) from the type Irvington fauna, Alameda County, California. J. Vertebr. Paleontol. 26 (2), 371–380.
Brooks, J.R., Flanagan, L.B., Buchmann, N., Ehleringer, J.R., 1997. Carbon isotope composition of boreal plants: functional grouping of life forms. Oecologia 110, 301–311.
Bryant, D.J., Koch, P.L., Froelich, P.N., Showers, W.J., Genna, B.J., 1996. Oxygen isotope partitioning between phosphate and carbonate in mammalian apatite. Geochim. Cosmochim. Acta 60 (24), 5145–5148.
Caldwell, M.M., Osmond, C.B., Nott, D.L., 1977. C4 pathway photosynthesis at low temperature in cold-tolerant Atriplex species. Plant Physiol. 60 (1), 157–164.
Cerling, T., Harris, J., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120 (3), 347–363.
Cerling, T.E., Hart, J.A., Hart, T.B., 2004. Stable isotope ecology in the Ituri Forest. Oecologia 138 (1), 5–12.
Chatters, J., Van De Water, P., 2013. Paleoecology of the Irvingtonan Fairmead Landfill Site, Madera County, California. Geol. Soc. Am. Abstr. Programs 45 (6), 9.
Christiansen, P., Harris, J.M., 2009. Craniomandibular morphology and phylogenetic affinities of *Panthera atrox*: implications for the evolution and paleobiology of the lion lineage. J. Vertebr. Paleontol. 29 (3), 934–945.
Clementz, M.T., Koch, P.L., 2001. Differentiating aquatic mammal habitat and foraging ecology with stable isotopes in tooth enamel. Oecologia 129, 461–472.
Clementz, M., Fox-Dobbs, K., Wheatley, P., Koch, P., Doak, D., 2009. Revisiting old bones: coupled carbon isotope analysis of bioapatite and collagen as an ecological and palaeoecological tool. Geol. J. 44 (5), 605–620.
Collatz, G.J., Berry, J.A., Clark, J.S., 1998. Effects of climate and atmospheric CO2 partial pressure on the global distribution of C4 grasses: present, past, and future. Oecologia 114 (4), 441–454.
Coltrain, J., Harris, J., Cerling, T., Ehleringer, J., Dearing, M., Ward, J., Allen, J., 2004. Rancho La Brea stable isotope biogeochemistry and its implications for the palaeoecology of late Pleistocene, coastal southern California. Palaeogeogr. Palaeoclimatol. Palaeoecol. 205 (3–4), 199–219.
Connin, S.L., Betancourt, J., Quade, J., 1998. Late Pleistocene C_4 plant dominance and summer rainfall in the Southwestern United States from isotopic study of herbivore teeth. Quat. Res. 50 (2), 179–193.
Davis, O.K., 1999. Pollen analysis of Tulare Lake, California: Great Basin-like vegetation in Central California during the full-glacial and early Holocene. Review of Palaeobotany and Palynology 107, 249–257.
Dawson, T.E., Mambelli, S., Plamboeck, A.H., Templer, P.H., Tu, K.P., 2002. Stable isotopes in plant ecology. Annu. Rev. Ecol. Syst. 507–559.
Diefendorf, A.F., Mueller, K.E., Wing, S.L., Koch, P.L., Freeman, K.H., 2010. Global patterns in leaf ^{13}C discrimination and implications for studies of past and future climate. Proc. Natl. Acad. Sci. 107 (13), 5738–5743.
Dreimanis, A., 1968. Extinction of mastodons in eastern North America: testing a new climatic-environmental hypothesis. Ohio J. Sci. 68 (6), 257–272.
Dundas, R.G., Chatters, J.C., 2013. The mid-Irvingtonian Fairmead Landfill fossil site, Madera County Paleontology Collection, and Fossil Discovery Center of Madera County, California. Geol. Soc. Am. Field Guid. 32, 63–78.
Dundas, R., Smith, R., Verosub, K., 1996. The Fairmead Landfill Locality (Pleistocene, Irvingtonian), Madera County, California: preliminary report and significance. PaleoBios 17 (2–4), 50–58.
Ehleringer, J.R., Cooper, T.A., 1988. Correlations between carbon isotope ratio and microhabitat in desert plants. Oecologia 76 (4), 562–566.
Ehleringer, J.R., Monson, R.K., 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. Annu. Rev. Ecol. Syst. 411–439.
Ehleringer, J., Phillips, S., Comstock, J., 1992. Seasonal variation in the carbon isotopic composition of desert plants. Funct. Ecol. 396–404.
Ehleringer, J.R., Cerling, T.E., Helliker, B.R., 1997. C4 photosynthesis, atmospheric CO2, and climate. Oecologia 112 (3), 285–299.
Emslie, S.D., Czaplewski, N.J., 1985. A new record of giant short-faced bear, *Arctodus simus*, from western North America with a re-evaluation of its paleobiology. Nat. Hist. Mus. Los Angel. Cty. Contrib. Sci. 371, 1–12.
Feranec, R.S., 2003. Stable isotopes, hypsodonty, and the paleodiet of *Hemiauchenia* (Mammalia: Camelidae): a morphological specialization creating ecological generalization. Paleobiology 29 (2), 230–242.
Feranec, R., 2004. Isotopic evidence of saber-tooth development, growth rate, and diet from the adult canine of *Smilodon fatalis* from Rancho La Brea. Palaeogeogr. Palaeoclimatol. Palaeoecol. 206 (3–4), 303–310.
Feranec, R., Hadly, E., Paytan, A., 2009. Stable isotopes reveal seasonal competition for resources between late Pleistocene bison (*Bison*) and horse (*Equus*) from Rancho La Brea, southern California. Palaeogeogr. Palaeoclimatol. Palaeoecol. 271 (1–2), 153–160.
Figueirido, B., Perez-Claros, J.A., Torregrosa, V., Martin-Serra, A., Palmqvist, P., 2010. Demythologizing *Arctodus simus*, the 'short-faced' long-legged and predaceous bear that never was. J. Vertebr. Paleontol. 30 (1), 262–275.
Firby, J.B., 1968. Revision of the Middle Pleistocene Irvington Fauna of California (M.A. Thesis), University of California, Berkeley (134 pp.).
Flanagan, L.B., Comstock, J.P., Ehleringer, J.R., 1991. Comparison of modeled and observed environmental influences on the stable oxygen and hydrogen isotope composition of leaf water in *Phaseolus vulgaris* L. Plant Physiol. 96 (2), 588–596.
Fox-Dobbs, K., Bump, J., Peterson, R., Fox, D., Koch, P., 2007. Carnivore-specific stable isotope variables and variation in the foraging ecology of modern and ancient wolf populations: case studies from Isle Royale, Minnesota, and La Brea. Canadian Journal of Zoology 85, 458–471.
Fox-Dobbs, K., Leonard, J.A., Koch, P.L., 2008. Pleistocene megafauna from eastern Beringia; paleoecological and paleoenvironmental interpretations of stable carbon and nitrogen isotope and radiocarbon records. Palaeogeogr. Palaeoclimatol. Palaeoecol. 261, 30–46.
Fox-Dobbs, K., Dundas, R.G., Trayler, R.B., Holroyd, P.A., 2014. Paleoecological implications of new megafaunal ^{14}C ages from the McKittrick tar seeps, California. J. Vertebr. Paleontol. 34 (1), 220–223.
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. Palaeogeogr. Palaeoclimatol. Palaeoecol. 126 (1), 91–99.
Friedli, H., Loetscher, H., Oeschger, H., Siegenthaler, U., Stauffer, B., 1986. Ice core record of the $^{13}C/^{12}C$ ratio of atmospheric CO_2 in the past two centuries. Nature 324 (6094), 237–238.
Gillette, D.D., Madsen, D.B., 1992. The short-faced bear *Arctodus simus* from the late Quaternary in the Wasatch Mountains of central Utah. J. Vertebr. Paleontol. 12 (1), 107–112.
Gillette, D.D., Madsen, D.B., 1993. The Columbian mammoth, Mammuthus columbi, from the Wasatch Mountains of central Utah. J. Paleontol. 669–680.
Guy, R.D., Reid, D.M., Krouse, H.R., 1980. Shifts in carbon isotope ratios of two C_3 halophytes under natural and artificial conditions. Oecologia 44 (2), 241–247.
Heaton, T.H., 1999. Spatial, species, and temporal variations in the $^{13}C/^{12}C$ ratios of C 3 plants: implications for palaeodiet studies. J. Archaeol. Sci. 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. Am. J. Phys. Anthropol. 133 (2), 808–816.
Henderson, A.K., Shuman, B.N., 2009. Hydrogen and oxygen isotopic compositions of lake water in the western United States. Geological Society of America Bulletin 121, 1179–1189.
Kendall, C., Coplen, T.B., 2001. Distribution of oxygen-18 and deuterium in river waters across the United States. Hydrol. Process. 15 (7), 1363–1393.
Koch, P.L., 1998. Isotopic reconstruction of past continental environments. Annu. Rev. Earth Planet. Sci. 26 (1), 573–613.
Koch, P.L., Fisher, D.C., Dettman, D.L., 1989. Oxygen isotopic variation in the tusks of extinct proboscideans; a measure of season of death and seasonality. Geology 17 (6), 515–519.
Koch, P., Tuross, N., Fogel, M., 1997. The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. J. Archaeol. Sci. 24 (5), 417–429.
Koch, P.L., Hoppe, K.A., Webb, S.D., 1998. The isotopic ecology of late Pleistocene mammals in North America Part 1. Florida. Chem. Geol. 152 (1–2), 119–138.
Koch, P.L., Diffenbaugh, N.S., Hoppe, K.A., 2004. The effects of late Quaternary climate and pCO2 change on C_4 plant abundance in the south-central United States. Palaeogeogr. Palaeoclimatol. Palaeoecol. 207, 331–357.
Köhler-Rollefson, I.U., 1991. Camelus dromedarius. Mamm. Species 375, 1–8.
Kohn, M.J., 1996. Predicting animal $\delta^{18}O$: accounting for diet and physiological adaptation. Geochim. Cosmochim. Acta 60 (23), 4811–4829.
Kohn, M., 2010. Carbon Isotope Composition of Terrestrial C_3 Plants as Indicators of (Paleo)Ecology and (Paleo) Climate. Proc. Natl. Acad. Sci. 107, 46.
Kohn, M.J., Cerling, T.E., 2002. Stable isotope compositions of biological apatite. Rev. Mineral. Geochem. 48 (1), 455–488.
Kohn, M.J., McKay, M.P., 2012. Paleoecology of late Pleistocene-Holocene faunas of eastern and central Wyoming, USA, with implications for LGM climate models. Palaeogeogr. Palaeoclimatol. Palaeoecol. 326–328, 42–53.
Kohn, M.J., Schoeninger, M.J., Valley, J.W., 1998. Variability in oxygen isotope compositions of herbivore teeth: reflections of seasonality or developmental physiology? Chem. Geol. 152 (1), 97–112.
Kohn, M.J., Miselis, J.L., Fremd, T.J., 2002. Oxygen isotope evidence for progressive uplift of the Cascade Range, Oregon. Earth Planet. Sci. Lett. 204 (1–2), 151–165.
Kohn, M.J., McKay, M.P., Knight, J.L., 2005. Dining in the Pleistocene—who's on the menu? Geology 33 (8), 649–652.
Kurtén, B., Anderson, E., 1980. Pleistocene Mammals of North America. Columbia University Press.
Lepper, B.T., Frolking, T.A., Fisher, D.C., Goldstein, G., Sanger, J.E., Wymer, D.A., Ogden, J.G., Hooge, P.E., 1991. Intestinal contents of a late Pleistocene mastodont from midcontinental North America. Quat. Res. 36 (1), 120–125.
Lindsay, E., Johnson, N., Opdyke, N., 1975. Preliminary correlation of North American land mammal ages and geomagnetic chronology. In: Smith, G.R., Friedland, N.E. (Eds.), Studies on Cenozoic Paleonology and Stratigraphy in Honor of Claude W. Hibbard, Volume Claude W. Hibbard MemorialPapers on Paleontology vol. 3. University of Michigan Museum of Paleontology, pp. 111–119.

Longinelli, A., 1984. Oxygen isotopes in mammal bone phosphate: a new tool for paleohydrological and paleoclimatological research? Geochim. Cosmochim. Acta 48 (2), 385–390.

Luz, B., Kolodny, Y., 1985. Oxygen isotope variations in phosphate of biogenic apatites, IV. Mammal teeth and bones. Earth Planet. Sci. Lett. 75 (1), 29–36.

Marchand, D., Allwardt, A., 1981. Late Cenozoic Stratigraphic Units, Northeastern San Joaquin Valley, California. Bull. US Geol. Surv. 1470, 1–70.

Mason, H., 1944. A Pleistocene flora from the McKittrick asphalt deposits of California. Proc. Calif. Acad. Sci. 4 (25), 221–234.

Matheus, P.E., 1995. Diet and co-ecology of Pleistocene short-faced bears and brown bears in eastern Beringia. Quat. Res. 44 (3), 447–453.

Minckley, T.A., Davis, O.K., Eastoe, C., Blinn, D.W., 1997. Analysis of environmental indicators from a mastodon site in the Prescott National Forest, Yavapai County, Arizona. J. Ariz. Nev. Acad. Sci. 23–29.

Paruelo, J.M., Lauenroth, W., 1996. Relative abundance of plant functional types in grasslands and shrublands of North America. Ecol. Appl. 1212–1224.

Pasitschniak-Arts, M., 1993. Ursus arctos. Mamm. Species 439, 1–10.

Passey, B.H., Cerling, T.E., 2002. Tooth enamel mineralization in ungulates: implications for recovering a primary isotopic time-series. Geochim. Cosmochim. Acta 66 (18), 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 CO2, and bioapatite in different mammals. J. Archaeol. Sci. 32 (10), 1459–1470.

Sarna-Wojcicki, A., Pringle, M., Wijbrans, J., 2000. New 40Ar/39Ar age of the Bishop Tuff from multiple sites and sediment rate calibration for the Matuyama-Brunhes boundary. J. Geophys. Res. 105 (B9) (p. 21,431-421,443).

Savage, D.E., 1951. Late Cenozoic vertebrates of the San Francisco Bay region. Univ. Calif. Publ. 28, 215–314.

Schrag, D.P., Adkins, J.F., McIntyre, K., Alexander, J.L., Hodell, D.A., Charles, C.D., McManus, J.F., 2002. The oxygen isotopic composition of seawater during the Last Glacial Maximum. Quat. Sci. Rev. 21 (1), 331–342.

Schultz, J.R., 1938. A Late Quaternary Mammal Fauna from the Tar Seeps of McKittrick. Carnegie Instutution of Washington Publication, California, pp. 111–215.

Semprebon, G.M., Rivals, F., 2010. Trends in the paleodietary habits of fossil camels from the Tertiary and Quaternary of North America. Palaeogeogr. Palaeoclimatol. Palaeoecol. 295 (1), 131–145.

Seymour, K.L., 1989. Panthera onca. Mamm. Species 340, 1–9.

Sternberg, L.O., Deniro, M.J., Johnson, H.B., 1984. Isotope ratios of cellulose from plants having different photosynthetic pathways. Plant Physiol. 74 (3), 557–561.

Stirton, R.A., 1939. Cenozoic mammal remains from the San Francisco Bay region. Bull. Dep. Geol. Sci. 24, 339–409.

Stock, C., Harris, J.M., 1992. Rancho La Brea: a record of Pleistocene life in California. Natural History Museum of Los Angeles.

Teeri, J., Livingstone, D., 1980. The distribution of C_4 species of the Cyperaceae in North America in relation to climate. Oecologia 47 (3), 307–310.

Teeri, J., Stowe, L., 1976. Climatic patterns and the distribution of C_4 grasses in North America. Oecologia 23 (1), 1–12.

Tipple, B.J., Meyers, S.R., Pagani, M., 2010. Carbon isotope ratio of Cenozoic CO_2: a comparative evaluation of available geochemical proxies. Paleoceanography 25 (3), PA3202.

Towhidi, A., Saberifar, T., Dirandeh, E., 2011. Nutritive value of some herbage for dromedary camels in the central arid zone of, Iran. Trop. Anim. Health Prod. 43 (3), 617–622.

Van Der Merwe, N.J., Medina, E., 1991. The canopy effect, carbon isotope ratios and foodwebs in Amazonia. J. Archaeol. Sci. 18 (3), 249–259.

Vetter, L., 2007. Paleoecology of Pleistocene Megafauna in Southern Nevada, USA: Isotopic Evidence for Browsing on Halophytic Plants (M.S. Thesis), University of Nevada, Las Vegas (182 pp.).