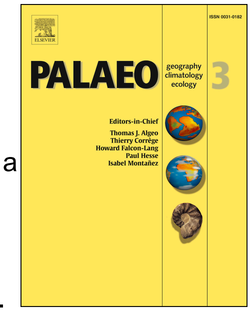
Journal Pre-proof



Pleistocene paleoecology and feeding behavior of terrestrial vertebrates recorded in a pre-LGM asphaltic deposit at Rancho La Brea, California

Benjamin T. Fuller, John R. Southon, Simon M. Fahrni, Aisling B. Farrell, Gary T. Takeuchi, Olaf Nehlich, Eric J. Guiry, Michael P. Richards, Emily L. Lindsey, John M. Harris

PII: S0031-0182(19)30513-9

DOI: https://doi.org/10.1016/j.palaeo.2019.109383

Reference: PALAEO 109383

To appear in: *Palaeogeography, Palaeoclimatology, Palaeoecology*

Received Date: 28 May 2019

Revised Date: 21 September 2019

Accepted Date: 23 September 2019

Pleistocene paleoecology and feeding behavior of terrestrial vertebrates recorded in a pre-LGM asphaltic deposit at Rancho La Brea, California

Benjamin T. Fuller[1,2,3*], John R. Southon[1], Simon M. Fahrni[1], Aisling B. Farrell[2], Gary T. Takeuchi[2], Olaf Nehlich[4], Eric J. Guiry[4], Michael P. Richards[5], Emily L. Lindsey[2], John M. Harris[2]

[1]*Department of Earth System Science, University of California, Irvine, Keck CCAMS Group, B321 Croul Hall, Irvine, California, 92697 USA*
[2]*La Brea Tar Pits and Museum, 5801 Wilshire Boulevard, Los Angeles, California 90036 USA*
[3]*Department of Archaeology and Heritage Studies, School of Culture and Society, Aarhus University, DK-8270, Højbjerg, Denmark*
[4]*Department of Anthropology, University of British Columbia, Vancouver, British Columbia V6T 1Z1 Canada*
[5]*Department of Archaeology, Simon Fraser University, Burnaby, British Columbia V5W 1S6 Canada*

KEY WORDS: stable isotopes; radiocarbon dating; megafauna; climate change; extinction

Running title: Pleistocene paleoecology in southern California

*Corresponding author:

B.T. Fuller
E-mail: fuller@cas.au.dk

Abstract

Sixteen taxa comprising extinct megafauna and extant species from a single asphalt deposit (Project 23, Deposit 1) at Rancho La Brea were isotopically analyzed ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) and ^{14}C dated to investigate paleoecology and feeding behavior of terrestrial vertebrates in southern California during the late Pleistocene. The large majority of the ^{14}C dates cluster between ~35-36 kyr BP, but a range of ages indicate this seep was active from ~30 to >43 kyr BP. Many of the *Smilodon fatalis* and *Canis dirus* as well as the *Canis latrans* have similar $\delta^{13}C$ (~ –19‰ to –18‰) and $\delta^{15}N$ (~ 11‰ to 12‰) results, indicating that these predators may have consumed similar prey species and possibly competed with each other through hunting and/or scavenging. The remains of contemporary potential prey species for these three predators include juvenile *Bison antiquus* and *Camelops hesternus*, and possibly adult *Paramylodon harlani* and *Capromeryx minor*. However, the $\delta^{15}N$ results of a single *C. dirus* (8.9‰) and the *Panthera atrox* (8.3‰) were significantly lower than the other large predators. Potential prey for this dire wolf and lion include *Nothrotheriops shastensis*, *Equus occidentalis* and possibly *Mammut americanum*. Many of the herbivores appear to have utilized broadly similar C_3 ecological environments. However, the adult *E. occidentalis* had isotopic results similar to the *Sylvilagus* sp. and *Spermophilus beecheyi* that have restricted home ranges, suggesting this horse was similarly local in its distribution or consumed a similar plant food selection. The isotopic values for extant taxa (*Actinemys marmorata, Crotalus* sp., *Mustela frenata*) suggest similar dietary patterns to their modern counterparts, indicating their ecological niches have remained relatively constant. The results presented here establish a foundation for future diachronic studies to better understand how the climate of the last ~50 kyr BP impacted biodiversity and ecological communities in southern California.

1. Introduction

Located in Los Angeles, California, the Rancho La Brea (RLB) tar pits (Figure 1), comprise numerous deposits formed by surficial asphalt seeps that have entrapped and preserved entire ecosystems (e.g. plants, insects, mollusks, reptiles, birds, mammals) from >50 kyr BP to the present (Marcus and Berger, 1984; Quinn, 1992; Stock and Harris, 1992; Ward et al. 2005; Holden et al., 2017). This vast collection of floral and faunal remains provides an unprecedented resource from which to investigate various research questions related to climate change and paleobiology during the late Pleistocene and Holocene. Unfortunately, past research efforts have been hampered by the fact that these specimens are impregnated with petroleum derivatives such as asphaltenes —contaminants that skew results for stable isotope ratio measurements and radiocarbon dating (Fuller et al. 2014). However, recent advances in collagen extraction methodology have overcome these problems and now permit the more rapid and cost-effective extraction of uncontaminated bone collagen from RLB specimens (Fuller et al. 2014; 2015; 2016).

To date, only a limited number of studies have published carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios of collagen combined with radiocarbon ages from RLB (Fox-Dobbs et al., 2006; Fuller et al 2014; 2016). While past work examined Pleistocene birds and large mammals from different time intervals as well as Holocene specimens, no studies have yet focused on investigating dietary patterns from within a single deposit – i.e., among animals that likely shared, and interacted on, the landscape.

Here we present $\delta^{13}C$ and $\delta^{15}N$ measurements directly paired with radiocarbon ages for 16 extant and extinct taxa (n = 28 individuals) from a single asphaltic deposit: Project 23 Deposit 1 (Figure 2). These results are combined with $\delta^{13}C$ measurements and radiocarbon dates from wood specimens (n = 2) as well as previously published results (n = 7; Fuller et al., 2014) for a total of 37 analyzed specimens. In addition, sulfur ($\delta^{34}S$) stable isotope ratios were measured for liquid tar and solid asphalt, as well as for a subset of these bone collagen samples (n = 22 individuals; where enough collagen was available). Our aim is to reconstruct the trophic ecology and paleobiology of organisms that represent a specific interval of entrapment during the late Pleistocene.

2. Materials and methods

During construction at the Los Angeles County Museum of Art in 2006, 16 new asphaltic deposits were discovered adjacent to RLB (Fuller et al., 2014; Holden et al., 2017). Due to time constraints, these deposits were not excavated in situ but were removed intact in 23 large wooden boxes (“Project 23”) so that they could be conserved and relocated for detailed analysis.

Here we focus only on Box 1 or Deposit 1 from Project 23. The main asphaltic vent of Deposit 1 is relatively small in size — approximately 2 m wide x 2 m long x 2 m deep (Figure 2). However, the section of sediment that was boxed measures 4 m wide x 5 m long x 2 m deep. Thus far, Deposit 1 has been found to contain over 25,000 specimens, although cataloging has not been completed. Previously, three extinct carnivorans: *Canis dirus* (n = 4); *Panthera atrox* (n = 1); *Smilodon fatalis* (n = 2) dated to ~35 kyr BP were studied (Fuller et al., 2014). The present study sampled additional *Canis dirus* (n = 3) and *Smilodon fatalis* (n = 6) and 13 additional taxa for stable isotopic analysis and radiocarbon dating: *Bison antiquus* (n = 2); *Camelops hesternus* (n = 1); *Canis latrans* (n = 1); *Capromeryx minor* (n = 1); *Actinemys marmorata* (n = 1); *Crotalus* sp. (n = 1); *Equus occidentalis* (n = 2); *Lepus* sp. (n = 1); *Mustela frenata* (n = 1); *Nothrotheriops shastensis* (n = 1); *Paramylodon harlani* (n = 1); *Spermophilus beecheyi* (n = 2); *Sylvilagus* sp. (n = 4).

Wood samples were treated to remove asphalt by sonication in solvents of increasing polarity: 2:1 toluene/methanol (repeat until colorless), methanol and ultra-pure Milli-Q water. Specimens were then prepared using an ABA protocol: 1N HCl, 1N NaOH repeat until colorless, 1N HCl at 75 ºC; bleached to holocellulose in 1:1 mixture of 1N HCl and 1M $NaClO_2$ at 75 ºC; rinse with Milli-Q water and air dried (UCI AMS Facility, 2011). Bone specimens (~150 mg) were sectioned at RLB using a handheld Dremel rotary tool and collagen was isolated at the UC Irvine, Keck Carbon Cycle AMS Laboratory using the procedure developed by Fuller et al. (2014) for asphalt impregnated bones from RLB.

Stable isotope ratios of carbon and nitrogen were measured on aliquots of 0.7 mg of collagen placed in tin capsules and combusted to CO_2 and N_2, using a Fisons NA 1500NC elemental analyzer/Finnigan Delta Plus isotope ratio mass spectrometer combination. For carbon and nitrogen, five working isotopic standards that are ultimately traceable to Vienna PDB and AIR are run with every batch of collagen. These are i) a mixture of USGS24 and IAEA N1 where the USGS24 (ammonium sulphate) and N1 (graphite) provide $\delta^{15}N$ and $\delta^{13}C$ values of +0.4‰ and –16.1‰, respectively; and ii) the NRC DORM2 standard ($\delta^{15}N$ +14.2‰, $\delta^{13}C$ –17.2‰); plus in-house standards of L-Cysteine ($\delta^{15}N$ –6.2‰, $\delta^{13}C$ –28.8‰), Tryptophan ($\delta^{15}N$ –3.4‰, $\delta^{13}C$ –12.4‰), and Adenosine Triphosphate (ATP2017) ($\delta^{15}N$ 0.0‰, $\delta^{13}C$ –21.2‰). These give multi-point calibrations for both $\delta^{15}N$ and $\delta^{13}C$, and while the Cysteine and Tryptophan standards return negative $\delta^{15}N$ values that are not directly relevant to collagen results, they strengthen the calibration by extending the linearity check over a larger range. In addition, several ATP aliquots of different sizes are run with each set, to check for and if necessary correct any dependence of the isotopic ratios on sample size. The measured calibration results are typically within ±0.2‰ of the literature values (or long-term averages for in-house standards) for δ^{15}N, and ± 0.1‰ for δ^{13}C, and those values are conservatively quoted as the 1 sigma uncertainties for the reported collagen results.

Sulfur isotope ratios were analysed using ~3 mg of collagen plus 1 mg of V_2O_5, using an Elementar vario MICRO cube coupled to an Isoprime 100 isotope ratio mass spectrometer in the Department of Anthropology at the University of British Columbia. Sulfur isotopic compositions were calibrated relative to VCDT using a two point calibration anchored with IAEA-S-1 (silver sulfide, δ^{34}S = –0.30‰) and NBS-127 (barium sulfate, δ^{34}S = 20.3‰). The following standards were used to monitor analytical accuracy and precision: methionine (δ^{34}S = 9.1 ± 0.6‰), NIST 1577c (bovine live, δ^{34}S = 1.7 ± 0.5‰), IAEA-S-3 (silver sulfide, δ^{34}S = –31.9 ± 0.6‰), and casein protein (δ^{34}S = 6.3 ± 0.6‰). The mean difference between duplicate δ^{34}S measurements on collagen samples (*n*=20) was 1.2‰ for δ^{34}S. Following Szpak et al. (2017), the standard uncertainty for δ^{34}S measurements was calculated to be ± 1.3‰. All isotopic results are presented as the ratio of the heavier isotope to the lighter isotope (^{13}C/^{12}C, ^{15}N/^{14}N, ^{34}S/^{32}S) and reported as δ values in in parts per 1,000 or "per mil" relative to internationally defined standards for δ^{13}C (VPDB), δ^{15}N (AIR) and δ^{34}S (VCDT).

Radiocarbon dates were measured using a National Electrostatics Corporation 0.5 MV 1.5SDH-1 Pelletron with a 60 sample modified MC-SNICS ion source (Southon and Santos, 2004), on graphitized CO_2 derived from 2 mg of collagen. The unknowns were analyzed with oxalic acid standards (OX1), plus known age bone standards, modern (19th century cow) and blanks that have no detectable amount of radiocarbon (Beaufort Sea whale, 60-70 kyr) that were prepared in the same manner as the unknowns. Unless otherwise noted, all radiocarbon dates reported in the text are uncalibrated.

3. Results

All sample information, isotopic results and radiocarbon dates for the specimens are listed in Supplementary Table 1. As expected, the extracted collagen was well preserved (with the ultrafiltered gelatin presenting a white color and fluffy texture) and all samples had collagen yields of >1% with C:N values between 3.2-3.5 (DeNiro, 1985). The δ^{13}C collagen values ranged from –23.3‰ to –18.0‰, indicating that these species consumed predominately C_3-based diets or prey that had such diets. The δ^{15}N values ranged from 5.7‰ to 12.1‰ and document different trophic levels or similar trophic levels in food webs starting with different nitrogen isotopic baselines. A single wood sample was measured for δ^{13}C; its value of –20.2‰ indicates a C_3 terrestrial tree (Cerling et al., 1997; Ward et al., 2005). Additional studies linking plant species with isotopic results for ecological reconstructions are planned. The radiocarbon results ranged between ~30 to >43 kyr BP, evidence that the Deposit 1 asphalt seep actively entrapped a variety of species in several different episodes (see Discussion).

In terms of the δ^{34}S measurements, the first such analysis on specimens from RLB, 15 of the 22 samples (68%), had collagen that was acceptable for isotopic analysis using the criteria set forth in Nehlich and Richards (2009). However, seven specimens were found to contain %S in excess of 0.35% and to have C:S (600 ± 300) and N:S (200 ± 100) values outside the normal range for modern mammalian collagen, suggesting sulfur contamination from the asphalt. This is not entirely surprising, as compared to the carbon and nitrogen content of bone collagen, the amount of organic sulfur is small (~5-7 residues/1000) and only found in the amino acid methionine (Nehlich and Richards, 2009). As crude oil contains a high percentage of sulfur (~1-2% in the Los Angeles Basin) in compounds bonded to the hydrocarbon molecules (Sheridan, 2006; Mullins et al., 2007), even a trace amount of hydrocarbon contamination in the bone collagen may be enough to skew the sulfur results while not significantly altering $\delta^{13}C$, $\delta^{15}N$ or ^{14}C ages. Thus, $\delta^{34}S$ measurements, while providing a valuable complement to $\delta^{13}C$ and $\delta^{15}N$ results, may be problematic for RLB specimens and further work is needed to investigate this potential resource. There was a large difference between the $\delta^{34}S$ measurements of the viscous tar (8.5 ± 0.7‰) and the hardened asphalt (–2.3 ± 0.9‰) (Supplementary Table 2). This may have been due to the loss of volatile organic compounds in the transition from a liquid to solid state, or could be related to a greater amount of organic and/or humic compounds in the asphalt (Fuller et al., 2014).

4. Discussion

4.1. Deposit 1 Periods of Entrapment

The $\delta^{13}C$ and $\delta^{15}N$ results are graphed in relation to their radiocarbon ages in Figure 3 (a,b). In addition, a reconstruction of Deposit 1 depicting the three-dimensional position of the specimens that were ^{14}C dated is shown in Figure 4. As was predicted based on past work (Fuller et al., 2014), the majority of the samples date between ~34 to 36 kyr BP. Further, multiple ^{14}C dates on the same specimens reveal that the main period of accumulation for this deposit occurred between ~35 and 36 kyr BP (Supplementary Table 1). However, the range of dates points to multiple additional entrapment events. For example, a horse (*E. occidentalis*) and the two pieces of wood dated much older than the majority of the other specimens, between ~40 to 42 kyr BP. To rule out the possibility that this older date could be related to asphalt contamination (although there were no signs from the collagen), we did a complete re-extraction of the collagen from the same *E. occidentalis* bone and ^{14}C-dated it again. The results confirmed that this horse was significantly older by approximately ~6 kyr than the rest of the dated specimens in the main deposit. Moreover, this *E. occidentalis* was found in the center of the Deposit 1 (Grid B-1, Level 3) and surrounded by younger specimens (Figure 4). Thus, this specimen acutely highlights the dangers of pit averaging and demonstrates why stratigraphy cannot be used to infer age at RLB (Fuller et al., 2015; 2016; Holden et al., 2017).

There also appear to be at least two smaller entrapment events represented in our sample—a California ground squirrel (*S. beecheyi*) was dated to ~31 kyr BP and a cottontail rabbit (*Sylvilagus* sp.) was dated at the limit of radiocarbon dating at >43 kyr BP. A western pond turtle (*Actinemys marmorata*) was determined to be much younger than all of the other specimens (~30 kyr BP). This turtle, located away from the main Deposit 1 asphaltic vent (Grid E-3, Level 2; Figure 4) in an ancient stream channel that ran along the northeast side of the main deposit, postdates all of the other results.

The major cluster of ^{14}C dates in Deposit 1 corresponds to calibrated ages of ~ 40-41 kyr cal BP using the IntCal13 dataset (Reimer et al., 2013), bracketing the brief warm Interstadial 10 event on the GICC05 Greenland ice core timescale (Svensson et al., 2008) but extending into cold periods before and after. It is important to note that calibration for ^{14}C dates in this time range is a work in progress: calibrated ages have shifted by as much as 1 kyr between successive versions of the IntCal calibration, and further significant shifts are anticipated.

4.2 Dietary Reconstruction

4.2.1. Herbivores and reptiles

In Deposit 1, the juvenile *B. antiquus*, *C. hesternus*, and *E. occidentalis* and the adult *P. harlani* and *C. minor*, generally cluster together in terms of their $\delta^{13}C$ and $\delta^{15}N$ results (Figure 5a). This is also the case for the *B. antiquus*, *C. hesternus* and *P. harlani* that were measured for $\delta^{34}S$ results (Figures 5b,c). The isotopic results suggest these animals were living and feeding in ecologically similar landscapes during the latest Pleistocene. In contrast the adult horse had significantly lower $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values and plots with the rabbits and squirrels. This difference could have a temporal component due to changing soil and vegetation conditions related to climate, as this adult *E. occidentalis* is significantly older than the other Deposit 1 specimens (~42 kyr BP). Or it could suggest that some horses were living and/or feeding in a different habitat than the artiodactyls and ground sloths. That this horse is isotopically similar to the small mammals with restricted home ranges suggests that its range was restricted to the vicinity of the Los Angeles Basin.

Previous examinations of migration patterns in bison and horses at RLB found that bison were more migratory and consumed a greater proportion of C_4 plants in their diet compared to the horses (Jefferson and Goldin, 1989; Feranec et al., 2009). In addition, dental mesowear analysis concluded that both *B. antiquus* and *C. hesternus* consumed woody vegetation and that *E. occidentalis* was a grazer (Jones and Desantis, 2017). Examination of the Coltrain et al. (2004) dataset indicates that many *E. occidentalis* specimens had ^{15}N-depleted results that were different from the other herbivores, supporting the argument that they were inhabiting a different, possibly local, ecological niche at RLB. Isotopic indications of different dietary preferences in Pleistocene bison and horses were also found in eastern Beringia (Fox-Dobbs et al., 2008). The high $\delta^{15}N$ value of the very young horse compared to the adult could also reflect a "nursing effect" (Fuller et al., 2006) as modern young foals can nurse up to a year after birth in the wild (Bennett, 1999). It would be interesting to see if stable isotope ratio analysis of late Pleistocene horses and bison from other localities showed similar ecological separation.

The *N. shastensis* specimen plots away from the other Deposit 1 species in terms of its $\delta^{13}C$ and $\delta^{15}N$ results (Figure 5a). However, it has similar $\delta^{34}S$ values to the adult *E. occidentalis* and the *Sylvilagus* sp., which suggests that it was a local resident and not migratory (Figures 5b,c). The ^{13}C-enriched value of this Shasta ground sloth could indicate it was inhabiting a more open C_3 landscape, and Pleistocene sloths with similar but highly variable isotopic results were found in the Pampean region of Argentina (Bocherens et al., 2016). Only one other *N. shastensis* has been isotopically analyzed and radiocarbon dated at RLB (Fuller et al., 2014). This specimen dates to a later interval (~28 kyr BP) and has a nearly identical $\delta^{13}C$ value (-19.6‰) to the Deposit 1 *N. shastensis* but a much higher $\delta^{15}N$ value (9.3‰) which is similar to a contemporary RLB bison (~29 kyr BP). Thus, just like the Pleistocene sloths of South America (Bocherens et al., 2016), the Shasta ground sloths appear to have highly variable $\delta^{15}N$ values that could be related to climate, ecology, or consumption of symbiotic organisms; analysis of a larger number of specimens from RLB is needed to help decipher its paleobiology in more detail.

The *Sylvilagus* sp., *Lepus* sp. and *S. beecheyi* plot isotopically near the adult *E. occidentalis* and below the main cluster of the megaherbivores (Figure 5a). Extant representatives of these small species have restricted home ranges and these specimens further confirm that the vegetation in the immediate vicinity of RLB was dominated by C_3 plant species at this time. Additional analysis of desert cottontail (*Sylvilagus audubonii*) and brush rabbits (*Sylvilagus bachmani*) from Deposit 1 found a similar distribution of ^{14}C ages but highly variable $\delta^{15}N$ values (Fox et al., 2017). This is not surprising as modern rabbits and those from archaeological contexts in Utah (Ugan and Coltrain, 2011) and Holocene rabbits from Idaho (Commendador and Finney, 2016) display a large range of $\delta^{15}N$ values. These $\delta^{15}N$ values can reflect the rabbit's diet, local soil conditions (such as salinity) and temperature (Somerville et al., 2018), demonstrating the challenges encountered when isotopically reconstructing the paleoecology of sites with small mammals.

The rattlesnake (*Crotalus* sp.) has a low $\delta^{13}C$ value (–22.6‰) and an elevated $\delta^{15}N$ value (9.6‰). This ^{13}C-depleted result contrasts with the other species studied and suggest its C_3 prey came from a more closed or wooded environment (Cerling et al., 2004). Based on the isotopic results, its potential prey could have included small rodents and birds, which were also recovered from Deposit 1 but were not analyzed. Such a diet is in agreement with that of extant rattlesnakes and indicates there has been little change in feeding patterns between the Pleistocene and today (Klauber, 1997).

The *A. marmorata* is the first freshwater species to be isotopically analyzed from RLB. Its ^{13}C-depleted result is in agreement with that of archaeological freshwater fish (Guiry et al., 2016), and its elevated $\delta^{15}N$ value, suggests it was feeding on other aquatic organisms, possibly small fish or amphibians. This is in agreement with the diets of extant western pond turtles, which are omnivores and consume fish, frogs, aquatic invertebrates, insects and plant foods (Rhodin et al., 2017). That this turtle produced the youngest ^{14}C date of all the specimens analyzed from Deposit 1 could be due to the fact that it was found in a stream channel away from the main asphalt vent. Its presence confirms that there were viable freshwater habitats in and around RLB during the Pleistocene as *A. marmorata* does not venture far (< 1 km) from water (Rhodin et al., 2017). This finding is consistent with RLB's location on a coastal plain; today water pools in and around the asphalt deposits and small ephemeral streams such as "Oil Creek" traverse the site (Stock and Harris, 1992).

4.2.2. Carnivores

The stable isotope ratio results ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) and radiocarbon dates allow investigation of the feeding behavior of extinct and extant species living in the Los Angeles Basin between ~30-40 kyr BP (Figures 5a,b,c). For the most part, the sabertooth cats (*S. fatalis*), dire wolves (*C. dirus*) and the coyote (*C. latrans*) cluster together isotopically, evidence that they all likely consumed prey that had nearly identical and predominately C_3-based terrestrial diets with little variation. This suggests these predators were relatively specialized in terms of diet and were potentially competing with each other through hunting and/or scavenging. Similarities in $\delta^{13}C$ enamel apatite values, reflecting likely dietary competition between *Smilodon* sp. and *C. dirus*, were also found at much older sites (> 550 kyr) from central California, suggesting that this behavior has a long history in North America (Trayler et al., 2015). These results also agree with a recent study from Argentina where *Smilodon populator* was found to be isotopically similar to the large canid *Protocyon*, again indicating direct competition for food sources between these two species (Bocherens et al., 2016). However, a recent study of $\delta^{13}C$ values in tooth enamel of *S. fatalis* and *C. dirus* at RLB found differences attributed to different feeding habits, with dire wolves argued to have had a preference for prey from more open environments (DeSantis et al., 2019). The reason(s) for the discrepancy between the collagen and carbonate isotopic results is currently unknown and additional research is needed to clarify these findings in the future.

Whereas only adult individuals of *C. dirus* and *C. latrans* are represented in this study, the *S. fatalis* specimens comprise two adults, two juveniles and four very juvenile individuals and there were no large dietary differences between individuals at differing stages of maturity (Figure 5a). Using the trophic level fractionation factors of ~1 to 2‰ for $\delta^{13}C$, ~3 to 5‰ for $\delta^{15}N$ and ~+1 to –1‰ for $\delta^{34}S$ (Kelly, 2000; Bocherens and Drucker, 2003; Richards et al., 2003; Fox-Dobbs et al., 2007; Krajcarz et al., 2019), the potential prey for this cluster of Deposit 1 predators include the juvenile bison (*B. antiquus*) and camel (*C. hesternus*). To a lesser extent, adult Harlan's ground sloths (*P. harlani*) and dwarf pronghorns (*C. minor*) (Figures 5a,b,c) could also have been consumed as the isotopic spacing for these individuals is only ~3‰ or below the 4.6 ± 0.7‰ calculated for modern North American gray wolves (*Canis lupus*) (Fox-Dobbs et al., 2007). However, lower collagen-to-collagen trophic level spacings (2.4‰ to 3.5‰) were determined for modern wolves feeding on a variety of prey species (see Table S1, Bocherens, 2015). Dire wolves from eastern Beringia had similar dietary habits but also included horses as an important prey species (Fox-Dobbs et al., 2008). The mammoth (*Mammuthus columbi*) from Deposit 11 was included in this project as it dates to a similar time interval (~36 kyr BP; (Fuller et al., 2014)) but mammoths do not appear to have been an important part of the diet of the local RLB carnivorans, and this is in agreement with the diets of *Homotherium* from the Alaska-Yukon region (Bocherens, 2015). However, *Homotherium* preferentially preyed upon juvenile mammoths at the Friesenhahn Cave site in Texas (Graham, 1976; Graham et al., 2013; DeSantis and Koch, 2017). Given the small sample sizes of the species analyzed here, these interpretations should be viewed with caution; additional research is needed to better delineate these predator-prey relationships. However, large carnivores targeting juvenile megaherbivores have been argued to play a critical role in limiting ecological impact during the Pleistocene (Van Valkenburg et al., 2016), and these isotopic results suggesting the consumption of young prey could lend some support to this possibility at RLB.

Interestingly, one *C. dirus* has $\delta^{13}C$ (-18.1‰) and $\delta^{15}N$ values (8.8‰) that plot below the main cluster of the large carnivores and near the American Lion (*P. atrox*) ($\delta^{13}C$ = -18.4‰; $\delta^{15}N$ = 8.3‰) (Figure 5a). Interpreting the $\delta^{13}C$ and $\delta^{15}N$ results from Deposit 1 as indicators of potential prey species for this dire wolf and lion is complicated by the small number of specimens that were sampled and only the Shasta ground sloth (*N. shastensis*) appears as a possible prey candidate. The $\delta^{34}S$ results confirm that this *N. shastensis* and possibly the adult *E. occidentalis* were potential prey for this *C. dirus* (Figures 5b,c). Unfortunately, the $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ results provide no match between the recovered prey species and this *P. atrox*.

As a result, we evaluate potential prey for this ^{15}N-depleted American lion using the dataset of Coltrain et al. (2004) without regard to chronology. In terms of $\delta^{15}N$ values, potential prey could have included *E. occidentalis* and/or mastodons (*Mammut americanum*) as was noted earlier (Fuller et al., 2014). However, the $\delta^{13}C$ values are elevated by >2‰ compared to the *E. occidentalis* and *M. americanum* which is higher than the carbon trophic level effect of 1.3 ± 0.6‰ calculated by Fox-Dobbs et al., (2007) for modern North American gray wolves but similar to trophic spacings of ~2-4‰ proposed by Bocherens (2015). Alternatively, the low $\delta^{15}N$ results could reflect differences related to time period, locality and/or climate. For example, it is possible these unique *C. dirus* and *P. atrox* were not local and traveled to RLB from distant habitats that were cooler and wetter such as the San Gabriel Mountains or further afield in northern California. Modern studies of wolves (*C. lupus*) and African lions (*Panthera leo*) indicate they can migrate large distances over time in search of food and new territory (Mech and Cluff, 2011; Kittle et al., 2016), and additional isotopic research is required to explore this possibility in detail. Nonetheless, the fact that the *C. dirus* plots isotopically with both the *S. fatalis* and *P. atrox* is evidence that dire wolves may have been competing with these other large feline predators in different ecological niches in southern California during the Pleistocene.

The Deposit 1 *C. latrans* has isotopic results similar to the *S. fatalis* and *C. dirus* specimens. This indicates that this particular coyote (~37 kyr BP) may have been scavenging from both of these predators kills whereas the coyotes analyzed by Coltrain et al. (2004) were feeding at a lower trophic level and on different foods. This supports an interpretation that *C. latrans* had dietary flexibility over the past ~50 kyr BP, which may have helped it survive the Pleistocene extinction event (Meachen and Samuels, 2012). Similar dietary flexibility has been suggested for the puma (DeSantis and Haupt, 2014).

A long-tailed weasel (*Mustela frenata*), recovered from Deposit 1 and radiocarbon dated to the main entrapment episode (~35 kyr BP), was also analyzed for $\delta^{13}C$ and $\delta^{15}N$ values. This extant species is found throughout North and South America and is an obligate carnivore that can consume a variety of prey such as insects, rodents, reptiles, small birds and rabbits (Schwartz and Schwartz, 2001). The *M. frenata* plots separately from the large predators for both $\delta^{13}C$ and $\delta^{15}N$ values and is closer to the herbivores (Figure 5a). The isotopic results suggest this *M. frenata* was consuming California ground squirrels and cottontail rabbits at RLB, which is in agreement with the dietary habits of extant individuals and suggests there has been little change in the dietary patterns of long-tailed weasels in the last 35 kyr.

5. Conclusions

Fossil specimens of extinct megafauna, extant small- and mid-sized vertebrates, and wood from a single asphalt deposit (Project 23 Deposit 1) at RLB were radiocarbon dated and analyzed for stable isotope ratios to investigate paleoecology and feeding behavior in southern California during a discreet interval of the Pleistocene. The ^{14}C ages for these specimens clustered around ~35-36 kyr BP, but a chronologically older adult *Equus occidentalis* and a wide range of dates for the smaller animals and wood samples indicate that multiple entrapment or accumulation events occurred from >43 to ~30 kyr BP at this location. This reinforces the point that the practice of “pit averaging” —where an average radiometric age is assigned to all specimens from an asphaltic deposit— is problematic and prone to error at RLB.

The habitats around RLB during this period of the Pleistocene were dominated by C_3 vegetation and none of the fauna showed evidence of consuming significant amounts of C_4 plants. While many of the megafaunal herbivores had similar stable isotopic results, the adult *E. occidentalis* specimen had a diet similar to *Sylvilagus* sp. and *Spermophilus beecheyi*. As these species have limited home ranges, this could suggest that the range of this particular horse was confined to the vicinity of RLB. All of the smaller animals studied here (*Mustela frenata*, *Sylvilagus* sp., *Spermophilus beecheyi*, *Crotalus* sp., *Actinemys. marmorata*) do not differ radically in dietary or ecological niche patterns from their modern counterparts. Sabertooth cats, dire wolves, and coyotes had isotopically similar results that could reflect predation of the same prey animals or the scavenging of their carcasses. The dietary flexibility of the coyotes may indicate that they weren’t primary predators of large prey animals. The coyotes’ post-Pleistocene size reduction may have several explanations including absence of large prey animals and competitive stress involving wolves and humans and climate change.

Of the 22 specimens measured for $\delta^{34}S$, nearly a third failed the collagen quality controls set forth for modern bone collagen. This high failure rate is in contrast to the $\delta^{13}C$ and $\delta^{15}N$ measurements, where all samples that produced sufficient collagen had acceptable atomic C:N ratios between 3.2-3.5. Given the high amount of sulfur in crude oil and the low organic content of sulfur in bone, a slight contamination of purified collagen with sulfur compounds bonded to hydrocarbon molecules could be enough to compromise $\delta^{34}S$ measurements in specimens from RLB. Thus, while these $\delta^{34}S$ results provide important complementary information to the $\delta^{13}C$ and $\delta^{15}N$ results, they should be treated with some caution but should also spur additional molecular research in this area. Nonetheless, isotopic analyses of Deposit 1 specimens based on $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$ and ^{14}C measurements permit an enhanced understanding of trophic level dynamics in southern California during the latest Pleistocene. This work serves as a starting point for future diachronic studies to better understand how the climate of the last 50 kyr impacted biodiversity and ecological communities in the Los Angeles Basin.

Acknowledgements

Chanda Bertrand, Hector Martinez and Shari Bush are thanked for assistance with collagen preparation. Bryn Letham is thanked for creating the map in Figure 1. BTF acknowledges the support of Marcello Mannino and the DEDiT (Danish and European Diets in Time) start-up project (n. 21276) funded by the Aarhus University Research Foundation (*Aarhus Universitets Forskningsfond*). Declarations of interest: None.

References

Bennett, D.G. 1999. From Breeding to Weaning. Western Horseman: Fort Worth, Texas pp. 35 ISBN-13:978-0911647518.

Bocherens H. 2015. Isotopic tracking of large carnivore palaeoecology in the mammoth steppe. Quaternary Science Reviews. 117:42-71.

Bocherens, H., Cotte, M., Bonini, R., Scian, D., Straccia. P., Soibelzon, L., Prevosti, F.J. 2016. Paleobiology of sabretooth cat Smilodon populator in the Pampean Region (Buenos Aires Province, Argentina) around the Last Glacial Maximum: Insights from carbon and nitrogen stable isotopes in bone collagen. *Palaeogeogr Palaeoclimatol, Palaeoecol* 449:463-474.

Bocherens, H., Drucker D. 2003. Trophic level isotopic enrichment of carbon and nitrogen in bone collagen: case studies from recent and ancient terrestrial ecosystems. International Journal of Osteoarchaeology 13:46-53.

Caldwell, R. J., Taylor, L.A., Eakins, B.W., Carignan, K.S., Grothe, P.R., Lim, E., Friday, D.Z., 2011. Digital Elevation Models of Santa Monica, California: Procedures, Data Sources and Analysis. NOAA Technical Memorandum NESDIS NGDC-46. Boulder: U.S. Department of Commerce.

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

Cerling, T.E., Hart, J.A., Hart, T.B. 2004. Stable isotope ecology in the Ituri Forest. *Oecologia* 138(1):5–12.

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. *Palaeogeogr Palaeoclimatol, Palaeoecol* 205:199-219.

Commendador, A.S., Finney, B.P. 2016. Holocene environmental change in the eastern Snake River Plain of Idaho, USA, as inferred from stable isotope analyses of small mammals. *Quat Res* 85(3):358-370.

DeNiro, M.J. 1985. Postmortem preservation and alteration of in vivo bone collagen isotope ratios in relation to palaeodietary reconstruction. *Nature* 317:806–809.

DeSantis, L.R.G., Haupt, R.J. 2014. Cougars' key to survival through the Late Pleistocene extinction: insights from dental microwear texture analysis. *Biology Letters* 10: 20140203.

DeSantis, L.R., Koch, P.L. 2017. Dietary ecology of the scimitar-toothed cat Homotherium Serium from Friesenhahn Cave as inferred from stable isotopes and dental microwear: A cheetah-like predator. Communication presented at the 77th Annual Meeting of the Society of Vertebrate Paleontology, Calgary, Canada.

DeSantis, L.R., Crites, J.M., Feranec, R.S., Fox-Dobbs, K., Farrell, A.B., Harris, J.M., Takeuchi, G. T., Cerling, T.E. 2019. Causes and consequences of Pleistocene megafaunal extinctions as revealed from Rancho La Brea Mammals. Current Biology 29(15):2488-2495.e2

Feranec, R.S., Hadly, E.A., 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* 271:153–160.

Fox, N.S., Southon, J.R., Fuller, B.T., Takeuchi, G.T., Farrell, A.B., Lindsey, E.L., Blois, J.L. 2017. A tale of two faunas: Small mammal paleoecology within and among Project 23 deposits at Rancho La Brea. *Communication presented at the 77th Annual Meeting of the Society of Vertebrate Paleontology, Calgary, Canada* Website: https://www.researchgate.net/publication/319311339_A_Tale_of_Two_Faunas_Small_Mammal_Paleoecology_within_and_among_Project_23_Deposits_at_Rancho_La_Brea?ev=auth_pub (accessed 18.03.2019).

Fox-Dobbs, K., Bump, J.K., Peterson, R.O., Fox, D.L., Koch, P.L., 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. *Can J Zool* 85:458-471.

Fox-Dobbs, K., Leonard, J.A., Koch, P.L. 2008. Pleistocene megafauna from eastern Beringia: Palaeoecological and paleoenvironmental interpretations of stable carbon and nitrogen isotope and radiocarbon records. *Palaeogeogr Palaeoclimatol, Palaeoecol* 261:30-46.

Fox-Dobbs, K., Stidham, T.A., Bowen, G.J., Emslie, S.D., Koch, P.L. 2006. Dietary controls of extinction versus survival among avian megafauna in the late Pleistocene. *Geology* 34(8):685-688.

Fuller, B.T., Fahrni, S.M., Harris, J.M., Farrell, A.B., Coltrain, J.B., Gerhart, L.M., Ward, J.K., Taylor, R.E., Southon, J.R. 2014. Ultrafiltration for asphalt removal from bone collagen for radiocarbon dating and isotopic analysis of Pleistocene fauna at the tar pits of Rancho La Brea, Los Angeles, California. *Quat. Geochronol.* 22:85-98.

Fuller, B.T., Fuller, J.L., Harris, D.A., Hedges, R.E.M. 2006. Detection of breastfeeding and weaning in modern human infants with carbon and nitrogen stable isotope ratios. *Am J Physl Anthropol* 129(2):279-293.

Fuller, B.T., Harris, J.M., Farrell, A.B., Takeuchi, G., Southon, J.R. 2015. Sample preparation for radiocarbon dating and isotopic analysis of bone from Rancho La Brea, Los Angeles, California. *La Brea and beyond: The paleontology of asphalt-preserved biotas*, ed. Harris JM. Natural History Museum of Los Angeles County, Science Series 42:151–167.

Fuller, B.T., Southon, J.R., Fahrni, S.M., Harris, J.M., Farrell, A.B., Takeuchi, G.T., Nehlich, O., Guiry, E., Richards, M.P., Taylor, R.E. 2016. Tar trap: No evidence of domestic dog burial with "La Brea Woman". *PaleoAmerica* 2(1):56-59.

Graham, R.W. 1976. Pleistocene and Holocene Mammals, Taphonomy and Paleoecology of the Friesenhahn Cave Local Fauna, Bexar County, Texas [Ph.D. thesis]: University of Texas at Austin, 233 pp.

Graham, R.W., Lundelius, E. L., Meissner, L. 2013. Friesenhahn Cave: Late Pleistocene paleoecology and predator-prey relationships of mammoths with an extinct scimitar cat. The Geological Society of America, Field Guide 30, pp 15-31

Guiry, E.J., Needs-Howarth, S., Friedland, K.D., Hawkins, A.L., Szpak, P., Macdonald, R., Courtemanche, M., Holm, E., Richards, M.P. 2016 Lake Ontario salmon (Salmo salar) were not migratory: A long-standing historical debate solved through stable isotope analysis. *Sci Rep* 6:36249.

Holden, A.R., Southon, J.R., Will, K., Kirby, M.E., Aalbu, R.L., Markey, M.J. 2017. A 50,000 year insect record from Rancho La Brea, Southern California: Insights into past climate and fossil deposition *Quat Sci Rev* 168:123-136.

Jefferson, G.T., Goldin, J.L. 1989. Seasonal migration of bison antiquus from Rancho La Brea, California. *Quat Res* 31(1):107-112.

Jones, D.B., Desantis, L.R.G. 2017. Dietary ecology of ungulates from the La Brea tar pits in southern California: A multi-proxy approach. *Palaeogeogr Palaeoclimatol, Palaeoecol* 466:110-127.

Kelly, J.F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Can J Zool* 78(1):1-27.

Kittle, A.M., Bukombe, J.K., Sinclair, A.R.E., Mduma, S.A.R., Fryxell, J.M. 2016. Landscape-level movement patterns by lions in western Serengeti: comparing the influence of inter-specific competitors, habitat attributes and prey availability. *Mov Ecol.* 4:17.

Klauber, L.M. 1997. Rattlesnakes: Their Habitats, Life Histories, and Influence on Mankind. (University of California Press, Berkeley) pp.1-1553 ISBN 0-520-21056-5

Krajcarz, M.T., Krajcarz, M., Drucker, D.G., Bocherens H. 2019. Prey-to-fox isotopic enrichment of $\delta^{34}S$ in bone collagen: Implications for palaeoecological studies. *Rapid Communications in Mass Spectrometry* 33(16):1311-1317.

Marcus, L.F., Berger R., 1984. The significance of radiocarbon dates for Rancho La Brea. *Quaternary Extinctions*, eds. Martin PS, Klein RG. (University of Arizona Press, Tucson, Arizona) pp. 159-188.

Meachen, J.A., Samuels, J.X. 2012. Evolution in coyotes (*Canis latrans*) in response to the megafaunal extinctions. *Proc Natl Acad Sci USA*. 109(11):4191-4196.

Mech, L.D., Cluff, H.D., 2011. Movements of Wolves at the Northern Extreme of the Species' Range, Including during Four Months of Darkness. *PLoS ONE* 6(10): e25328.

Muhs, D.R., Simmons, K.R., Schumann, R., Groves, L.T., Mitrovica, J.X., Laurel, D. 2012. Sea-level history during the Last Interglacial complex on San Nicolas Island, California: implications for glacial isostatic adjustment processes, paleozoogeography and tectonics. *Quat Sci Rev* 37:1-25.

Mullins, O.C., Sheu, E.Y., Hammami, A., Marshall, A.G. 2007. Asphaltenes, Heavy Oils, and Petroleomics. (Springer, New York) pp. 1-660.

Nehlich, O., Richards, M.P., 2009. Establishing collagen quality criteria for sulphur isotope analysis of archaeological bone collagen. *Archaeol Anthropol Sci* 1(1):59–75.

Quinn, J.P. 1992. Rancho La Brea: Geological setting, Late Quaternary depositional patterns and mode of fossil accumulation. *The regressive Pleistocene shoreline, southern California. Guidebook 20*, eds. Heath EG, Lewis WL (South Coast Geological Society, Santa Ana, California). pp. 221-232.

Reimer, P. J., E. Bard, A. Bayliss, J. W. Beck, P. G. Blackwell, C. B. Ramsey, C. E. Buck, H. Cheng, R. L. Edwards, M. Friedrich, P. M. Grootes, T. P. Guilderson, H. Haflidason, I. Hajdas, C. Hatte, T. J. Heaton, D. L. Hoffmann, A. G. Hogg, K. A. Hughen, K. F. Kaiser, B. Kromer, S. W. Manning, M. Niu, R. W. Reimer, D. A. Richards, E. M. Scott, J. R. Southon, R. Staff, C. S. M. Turney, and J. van der Plicht (2013). IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0-50,000 years cal BP. Radiocarbon, 55(4):1869–1887.

Rhodin, A.G.J., Iverson, J.B., Bour, R., Fritz, U., Georges, A., Shaffer, H.B., van Kijk, P.P. 2017. *Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status* (8th ed.) Turtle Taxonomy Working Group. pp. 1-292 ISBN: 978-1-5323-5026-9.

Richards, M.P., Fuller, B.T., Sponheimer, M., Robinson, T., Ayliffe, L., 2003. Sulfur isotopes in palaeodietary studies: a review and results from a controlled feeding experiment. *Int J Osteoarchaeol* 13:37–45.

Schwartz, C.W., Schwartz, E.R. 2001. The wild mammals of Missouri, (University of Missouri Press, Columbia) pp. 426 ISBN 0-8262-1359-6.

Sheridan, M., 2006. California crude oil production and imports. *California Energy Commission* pp. 1-14 website:http://www.energy.ca.gov/2006publications/CEC-600-2006-006/CEC-600-2006-006.PDF (accessed 01.05.2019).

Somerville, A.D., Froehle, A.W., Schoeninger, M.J. 2018. Environmental influences on rabbit and hare bone isotope abundances: Implications for paleoenvironmental research. Palaeogeography, Palaeoclimatology, Palaeoecology 497:91-104.

Southon, J.R., Santos, G.M. 2004. Ion source development at KCCAMS, University of California, Irvine. *Radiocarbon*. 46(1):33-39.

Stock, C, Harris, J.M. 1992. Rancho La Brea: A record of Pleistocene life in California. *Science Series* 37:1-113.

Svensson, A., Andersen, K. K., Bigler, M., Clausen, H. B., Dahl- Jensen, D., Davies, S. M., Johnsen, S. J., Muscheler, R., Parrenin, F., Rasmussen, S. O., Röthlisberger, R., Seierstad, I., Steffensen, J. P., and Vinther, B. M.: 2008 A 60 000 year Greenland stratigraphic ice core chronology, Clim. Past, 4, 47–57.

Szpak P., Metcalfe J.Z., Macdonald R.A. 2017. Best practices for calibrating and reporting stable isotope measurements in archaeology. Journal of Archaeological Science: Reports 13:609-616.

Trayler, R.B., Dundas, R.G., Fox-Dobbs, K., Van DeWater, P.K. 2015. Inland California during the Pleistocene—Megafaunal stable isotope records reveal new paleoecological and paleoenvironmental insights. *Palaeogeogr Palaeoclimatol, Palaeoecol*. 437:132–140.

UCI AMS Facility, 2011. Acid Base/Acid (ABA) Sample pre-treatment. Website: https://www.ess.uci.edu/group/ams/files/aba_protocol.pdf (accessed 02.05.2019).

Ugan, A., Coltrain, J. 2011. Variation in collagen stable nitrogen values in black-tailed jackrabbits (Lepus californicus) in relation to small-scale differences in climate, soil, and topography. *J Archaeol Sci* 38(7):1417-1429.

Van Valkenburgh, B., Hayward, M.W., Ripple, W.J., Meloro, C., Roth, V.L. 2016. The impact of large terrestrial carnivores on Pleistocene ecosystems. *Proc Natl Acad Sci USA* 113(4):862-867.

Ward, J.K., Harris, J.M., Cerling, T.E., Wiedenhoeft, A., Lott, M., Dearing, M.D., Coltrain, J.B., Ehleringer, J.R. 2005. Carbon starvation in glacial trees recovered from the La Brea tar pits, southern California. *Proc Natl Acad Sci USA* 102 (3):690-694.

Figure Legends:

Figure 1. Schematic map showing location of Rancho La Brea relative to past and present coastlines of the Santa Monica Basin. Dashed line represents approximate location of coast at 35 kyr BP (i.e., ~60 meters below current sea level). Muhs et al. (2012) estimate a RSL position of about -70 m asl for 35-40 kyr BP for the nearby San Nicolas Island; though tectonic uplift on the mainland would likely have yielded a slightly higher RSL in our study area. Map drawn with QGIS 2.18.16 using bathymetric and topographical digital elevation model data produced by NOAA's Tsunami Inundation Project and National Geographic Data Center (Caldwell et al., 2011).

Figure 2. View of Deposit 1 looking south. Archived with GUID 10862447-dc6c-4af1-998d-5b1040ae7763 (Photograph by Carrie M. Howard, La Brea Tar Pits Museum).

Figure 3a. Deposit 1 $\delta^{13}C$ values plotted against uncalibrated ^{14}C ages in years BP. While the main entrapment or accumulation event for Project 23 Deposit 1 occurred between ~35-36 kyr BP, there is evidence for multiple other smaller entrapment events between ~30 to >43 kyr BP. All specimens show evidence of consuming predominately C_3-based diets during this period.

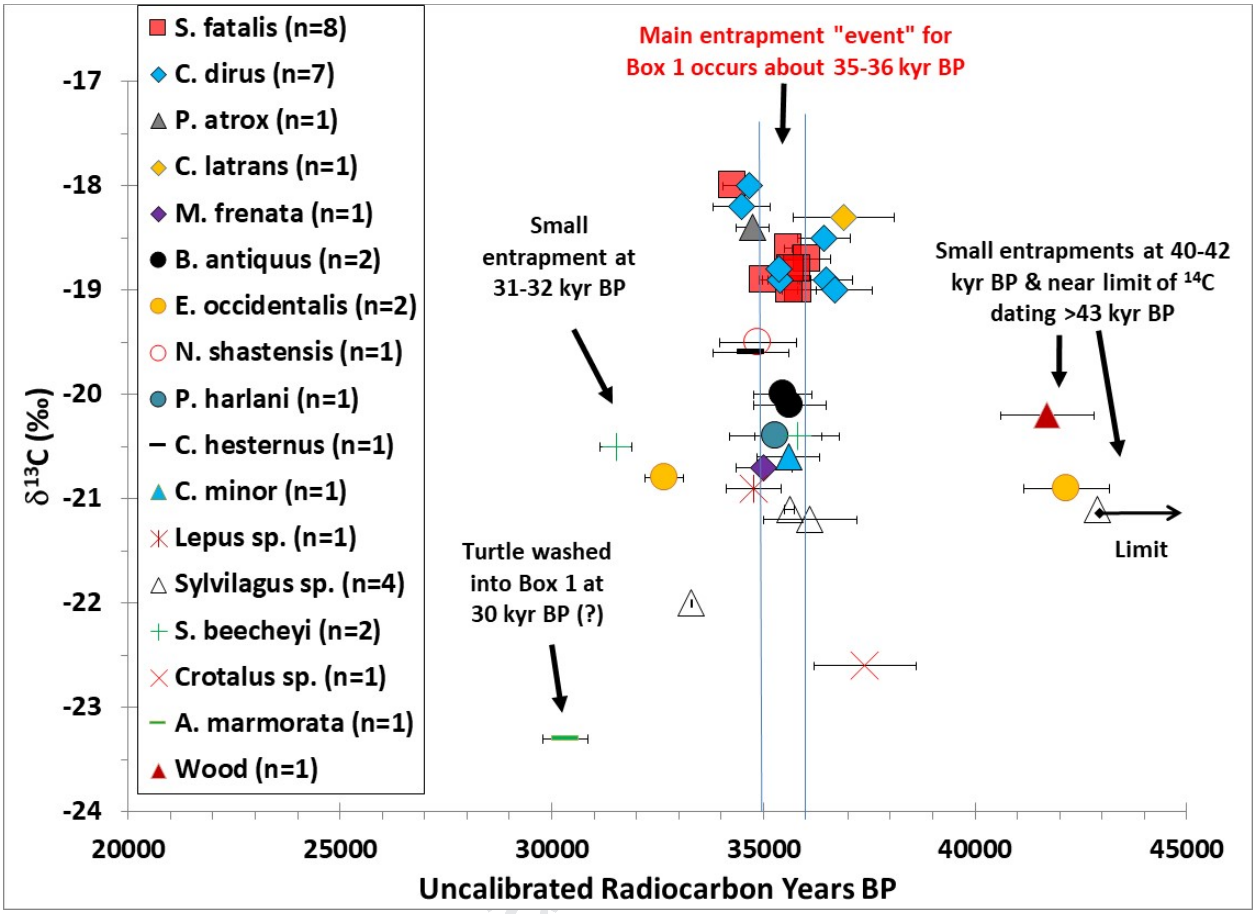
Figure 3b. Deposit 1 $\delta^{15}N$ values plotted against uncalibrated ^{14}C ages in years BP. While the main entrapment or accumulation event for Project 23 Deposit 1 occurred between ~35-36 kyr BP, there is evidence for multiple other smaller entrapment events between ~30 to >43 kyr BP.

Figure 4. Reconstruction of Deposit 1 showing the three-dimensional position of radiocarbon-dated specimens. Shapes denote different trophic or ecological groups: Triangles = Large Carnivores; Squares = Large Herbivores; Circles = Small Vertebrates (small mammals and reptiles); Diamonds = Plants. Periods of deposition more than 1,000 years apart are separated by color: Red < 31,000 RCYBP; Orange 31,000 - 33,000 RCYBP; Green 33,000 - 37,500 RCYBP; Blue 37,500 - 41,500 RCYBP; Purple 41,500 - 43,000 RCYBP.

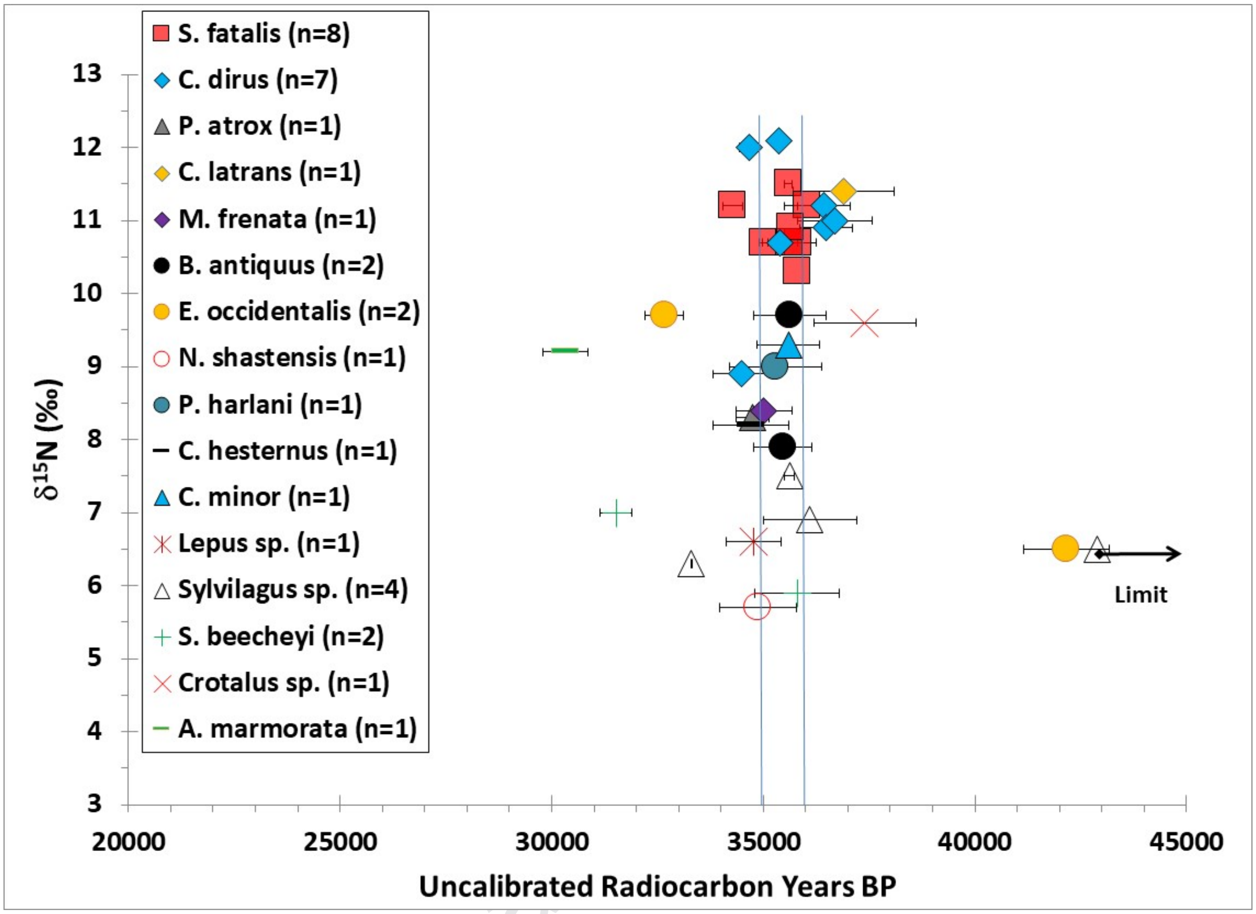
Figure 5a. $\delta^{13}C$ and $\delta^{15}N$ results from Project 23 Deposit 1 at RLB. Note: the *M. columbi* is from Deposit 11 but is included here as it has a ^{14}C-measurement (36,770 ± 750 BP) which dates near the main cluster of the Deposit 1 specimens (Fuller et al., 2014).

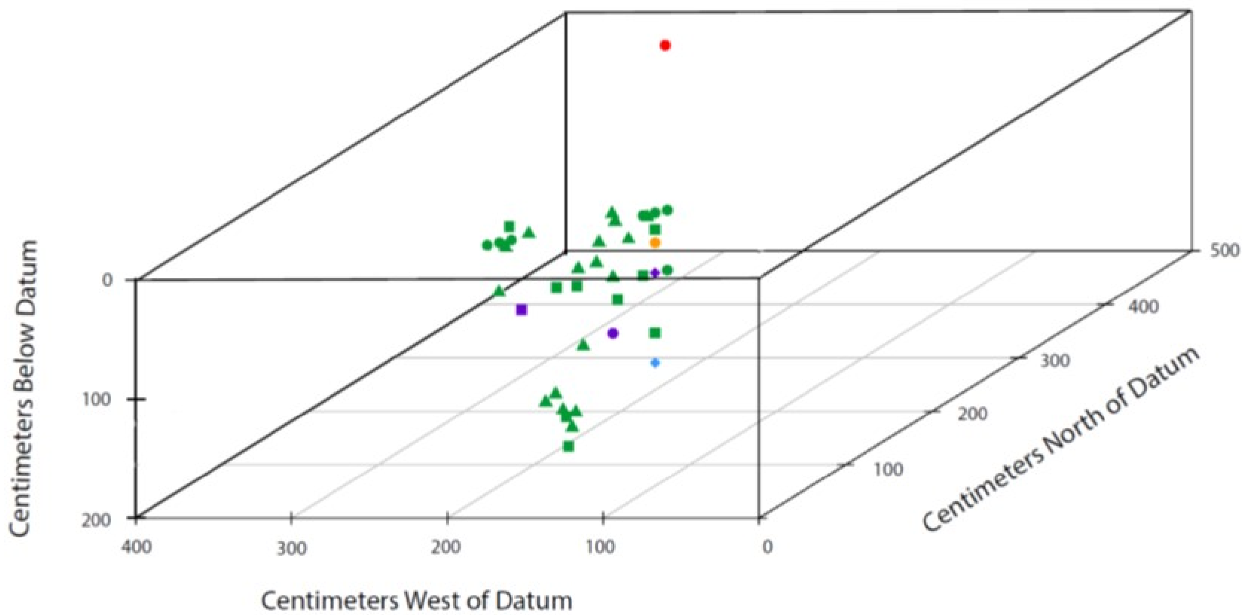
Figure 5b. $\delta^{13}C$ and $\delta^{34}S$ results from Deposit 1 at RLB.

Figure 5c. $\delta^{34}S$ and $\delta^{15}N$ results from Deposit 1 at RLB.

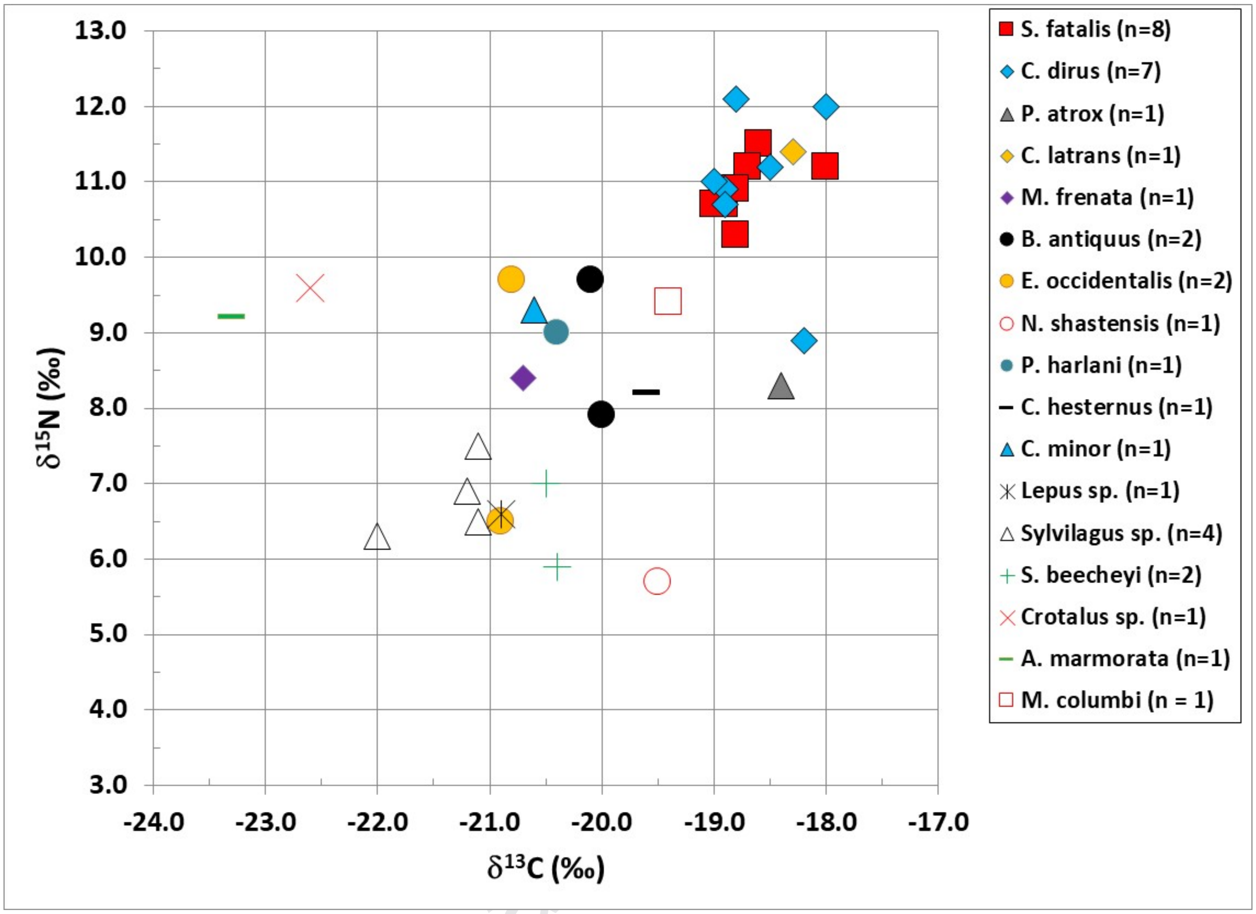


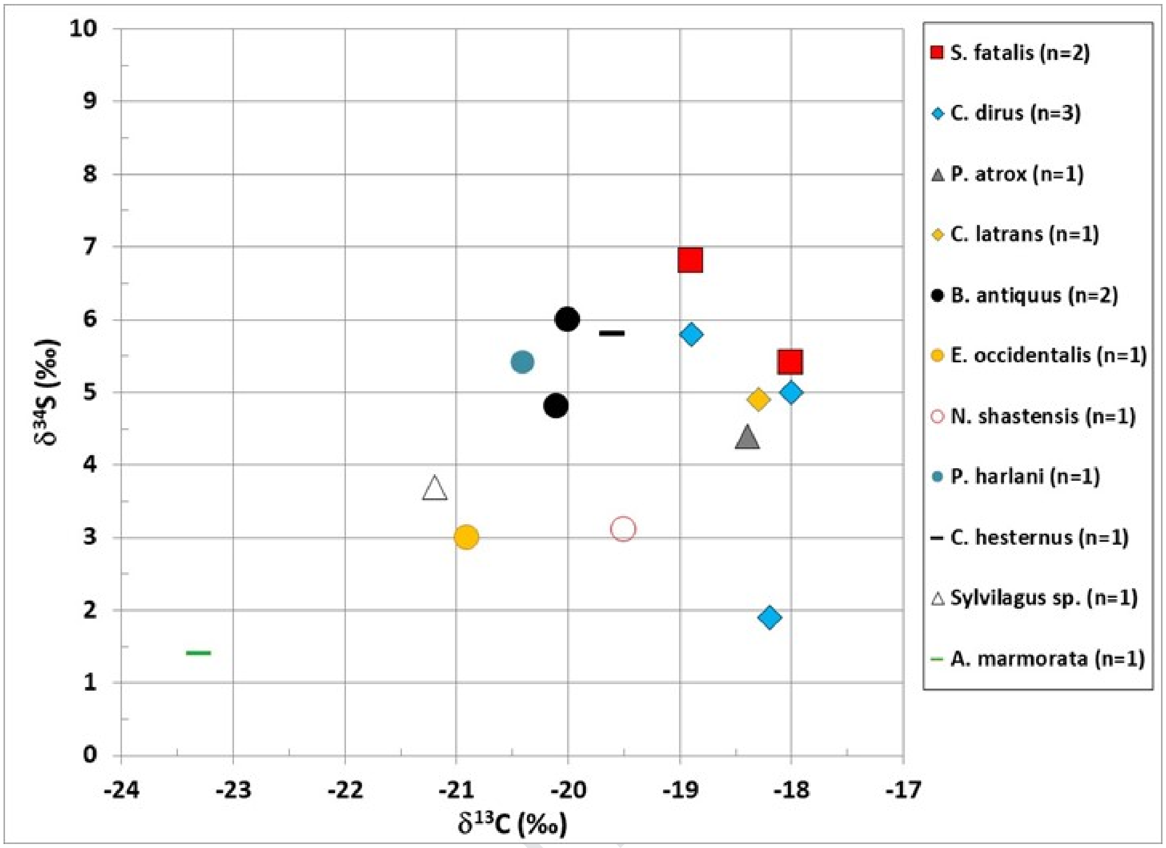
S. fatalis (n=8)
C. dirus (n=7)
P. atrox (n=1)
C. latrans (n=1)
M. frenata (n=1)
B. antiquus (n=2)
E. occidentalis (n=2)
N. shastensis (n=1)
P. harlani (n=1)
C. hesternus (n=1)
C. minor (n=1)
Lepus sp. (n=1)
Sylvilagus sp. (n=4)
S. beecheyi (n=2)
Crotalus sp. (n=1)
A. marmorata (n=1)
Wood (n=1)
Main entrapment "event" for
Box 1 occurs about 35-36 kyr BP
Small
entrapment at
31-32 kyr BP
Small entrapments at 40-42
kyr BP & near limit of 14C
dating >43 kyr BP
Limit
Turtle washed
into Box 1 at
30 kyr BP (?)
δ13C (‰)
-17
-18
-19
-20
-21
-22
-23
-24
20000
25000
30000
35000
40000
45000
Uncalibrated Radiocarbon Years BP


S. fatalis (n=8)
C. dirus (n=7)
P. atrox (n=1)
C. latrans (n=1)
M. frenata (n=1)
B. antiquus (n=2)
E. occidentalis (n=2)
N. shastensis (n=1)
P. harlani (n=1)
C. hesternus (n=1)
C. minor (n=1)
Lepus sp. (n=1)
Sylvilagus sp. (n=4)
S. beecheyi (n=2)
Crotalus sp. (n=1)
A. marmorata (n=1)
Limit
δ15N (‰)
13
12
11
10
9
8
7
6
5
4
3
20000
25000
30000
35000
40000
45000
Uncalibrated Radiocarbon Years BP

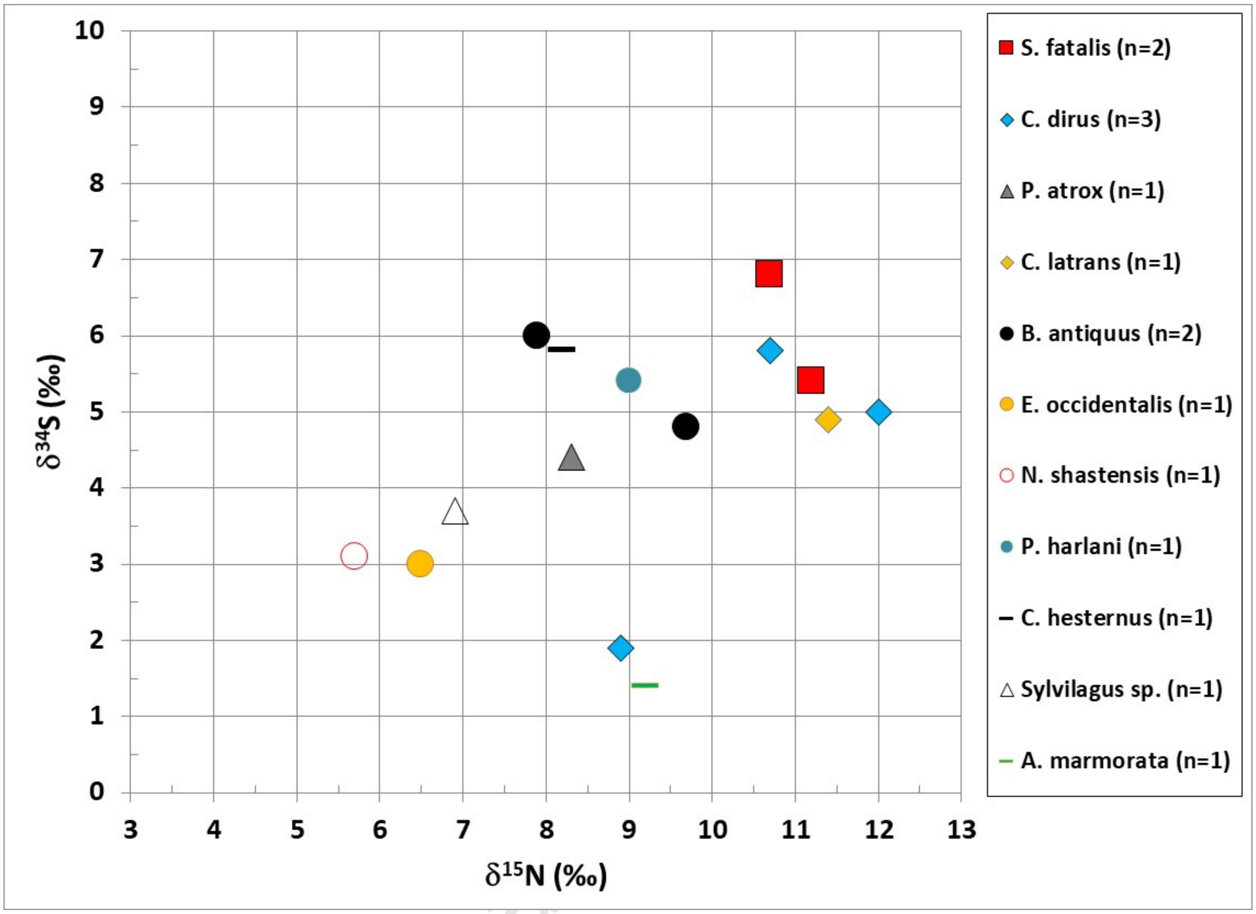


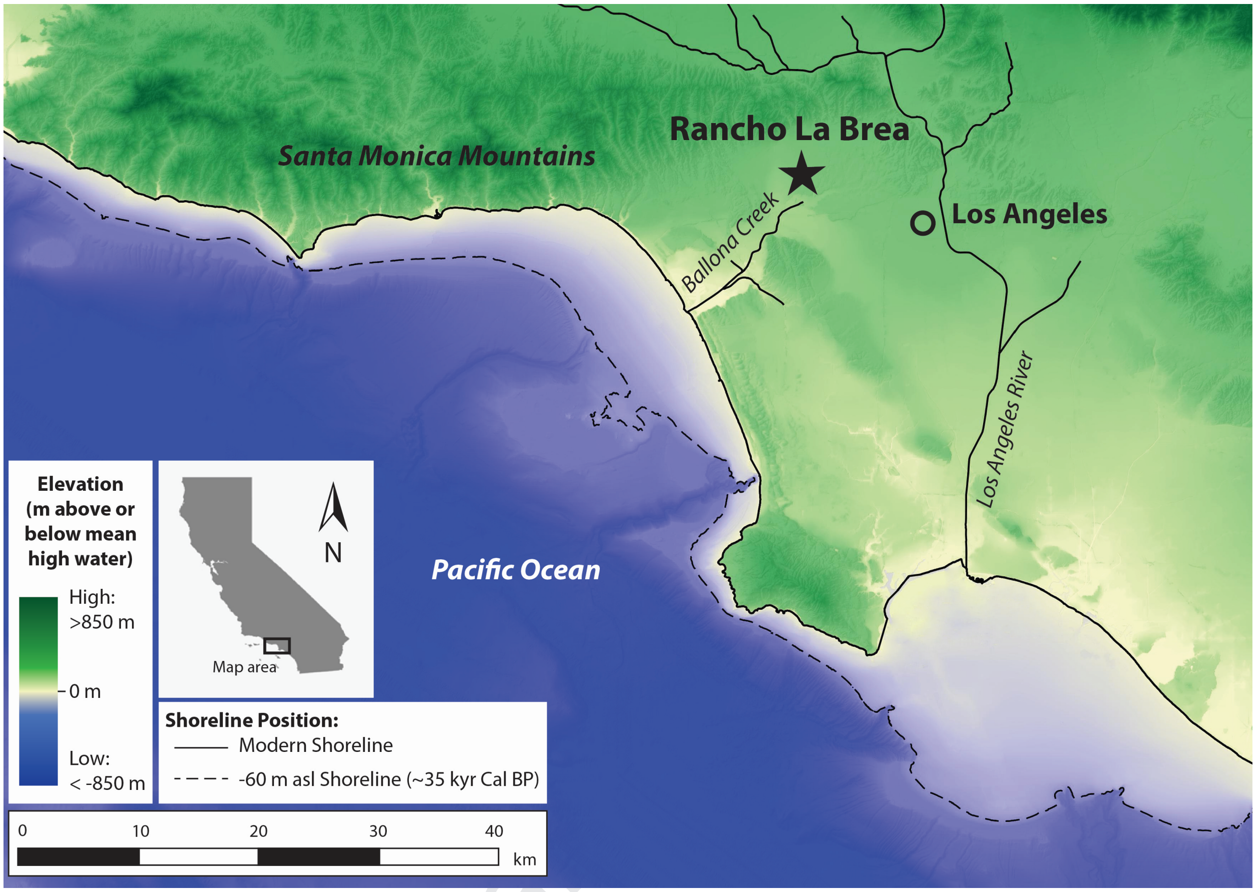
Centimeters Below Datum
0
100
200
400
300
200
100
0
Centimeters West of Datum
500
400
300
200
100
Centimeters North of Datum


13.0
12.0
11.0
10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
δ15N (‰)
-24.0
-23.0
-22.0
-21.0
-20.0
-19.0
-18.0
-17.0
δ13C (‰)
S. fatalis (n=8)
C. dirus (n=7)
P. atrox (n=1)
C. latrans (n=1)
M. frenata (n=1)
B. antiquus (n=2)
E. occidentalis (n=2)
N. shastensis (n=1)
P. harlani (n=1)
C. hesternus (n=1)
C. minor (n=1)
Lepus sp. (n=1)
Sylvilagus sp. (n=4)
S. beecheyi (n=2)
Crotalus sp. (n=1)
A. marmorata (n=1)
M. columbi (n = 1)



10
9
8
7
6
5
4
3
2
1
0
δ34S (‰)
-24
-23
-22
-21
-20
-19
-18
-17
δ13C (‰)
S. fatalis (n=2)
C. dirus (n=3)
P. atrox (n=1)
C. latrans (n=1)
B. antiquus (n=2)
E. occidentalis (n=1)
N. shastensis (n=1)
P. harlani (n=1)
C. hesternus (n=1)
Sylvilagus sp. (n=1)
A. marmorata (n=1)


10
9
8
7
6
5
4
3
2
1
0
δ34S (‰)
3
4
5
6
7
8
9
10
11
12
13
δ15N (‰)
S. fatalis (n=2)
C. dirus (n=3)
P. atrox (n=1)
C. latrans (n=1)
B. antiquus (n=2)
E. occidentalis (n=1)
N. shastensis (n=1)
P. harlani (n=1)
C. hesternus (n=1)
Sylvilagus sp. (n=1)
A. marmorata (n=1)



Rancho La Brea
Santa Monica Mountains
Los Angeles
Ballona Creek
Los Angeles River
Pacific Ocean
Elevation (m above or below mean high water)
High: >850 m
0 m
Low: < -850 m
N
Map area
Shoreline Position:
Modern Shoreline
-60 m asl Shoreline (~35 kyr Cal BP)
0
10
20
30
40
km

- Project 23 Deposit 1 main entrapment ^{14}C dated to ~35-36 kyr BP
- Wide range of ^{14}C ages indicate seep was active from ~30 to >43 kyr BP
- Sabertooth cats, dire wolves, and coyotes had isotopically similar diets
- Extant taxa had similar dietary patterns to their modern counterparts
- First reported $\delta^{34}S$ measurements on specimens from RLB