Research Papers

Rancho La Brea stable isotope biogeochemistry and its implications for the palaeoecology of late Pleistocene, coastal southern California

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Abstract

We sampled 143 individuals from Rancho La Brea (RLB) large faunal collections for bone collagen stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope ratios. These collections were recovered from asphalt seeps in the Los Angeles Basin, California, USA, and date from ∼ 40 to 12 ka. Our findings indicate that despite a slight reduction in collagen nitrogen content, RLB skeletal remains are relatively well preserved and most yield proteins diagnostic of diet. Herbivore δ^{13}C and δ^{15}N values covary with rumination and are consistent with changes in late Pleistocene vegetation reconstructed from pollen profiles. We find no evidence for reliance on C_4 grasses at RLB, despite low atmospheric CO_2 concentrations. Carnivore δ^{15}N values indicate *Canis dirus*, *Smilodon fatalis* and *Panthera leo atrox* competed for similar prey sets and were equally reliant on ruminant and nonruminant prey types. The δ^{15}N values of *Mammut americanum* indicate partial reliance on vegetation with lower δ^{15}N values (such as nitrogen-fixing taxa), distinguishing them from the remainder of the study population. A comparison of RLB and European faunal δ^{15}N values from the late Pleistocene suggests that coastal southern California experienced greater aridity.
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1. Introduction

Several extinct medium- to large-bodied mammalian taxa are abundant in late Pleistocene faunal assemblages recovered from asphalt seeps at Rancho La Brea (RLB), California, USA, and have been extensively studied to reconstruct the ecology of late Pleistocene faunal communities. Canine sexual dimorphism and dental breakage patterns and microwear have provided information on carnivore killing and feeding behavior (Van Valkenburgh and Ruff, 1987; Van Valkenburgh et al., 1990; Van Valkenburgh and Hertel, 1993; Anyonge, 1996; Binder et al., 2002; Van

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Valkenburgh and Sacco, 2002). Dental impacta and calculus from RLB herbivores as well as digesta and DNA in coprolites from elsewhere have been analyzed to identify feeding preferences (Whitehead et al., 1982; Akersten et al., 1988; Lepper et al., 1991; Webb et al., 1992; Laub et al., 1994; Mihlbachler, 1998; Hofreiter et al., 2000; Gobetz and Bozarth, 2001). Here we report the results of bone collagen stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope analysis of RLB fauna to address a similar set of ecological issues including: (1) climate-induced temporal variation in herbivore diets, (2) isotope signatures associated with ruminant versus nonruminant digestive physiologies and browsing versus grazing strategies, (3) the potential abundance of C$_4$ grasses and (4) trophic level relationships and their implications for resource choice. We also explore a subset of methodological issues unique to the RLB depositional environment.

2. Study site

2.1. RLB asphalt seeps

Asphalt seeps provide an unusual opportunity to examine the palaeoecology of plant and animal communities. Located in the Los Angeles Basin south of the Santa Monica Mountains, RLB seeps are fed by petroleum originating in vertically tilted oil sands. Since ~ 40 ka, methane pressure has moved trapped asphalt to the surface through fissures in Pleistocene alluvium, forming seeps that can reach several square meters in area and 9–11 m in depth (Stock and Harris, 1992, pp. 11–13). The flow of seepage is episodic and a temporary reduction in pressure can cause surface asphalt to regress down the chimney from which it exuded. Once pooled, asphalt develops a viscous crust which is ''stickier'' during warm months and diurnal hours, increasing the potential for entrapment. Excavations at RLB began early in the 20th century and a collection in excess of 2 million skeletal elements is housed at the George C. Page Museum of La Brea Discoveries in Los Angeles. With few exceptions, skeletal remains are disarticulated indicating significant postmortem disturbance.

Samples were taken from Pits 3, 60, 61, 67 and 91. Pits 60 and 91 (28–26 ka) date to the end of oxygen-

isotope stage 3 (OIS 3, 59–24 ka). Pit 3, at ~ 20 ka, dates to last glacial maximum (LGM); and Pits 61 and 67 were active during the glacial–interglacial transition (GIT, 14–12 ka). Radiocarbon dates on fossil wood and bone show a gross temporal correlation with depth in major pits (Berger and Libby, 1968; Ho et al., 1969) supported by unpublished studies of Pit 91 taphonomy (Gust, personal communication). Yet, it should not be assumed that samples recovered from the same horizontal or vertical provenience within a pit or the same depth between pits are contemporaneous (see also Woodard and Marcus, 1973).

2.2. Coastal southern California late Pleistocene vegetation

Terrestrial pollen profiles from coastal southern California (south of 36°N) indicate that OIS 3 and LGM were cooler and more mesic than present (Heusser, 1998). At terminal OIS 3, oak and chaparral declined in abundance as pines increased creating open parklands similar to modern, coastal montane/juniper woodlands; mean annual temperature decreased from 11 to 5 °C at LGM (modern ~ 16 °C), and annual precipitation declined from 100 to 45 cm (modern ~ 38 cm) (Heusser, 1995; Heusser and Sirocko, 1997). At the GIT, conifers retreated and modern coastal plant communities (oak woodland, chaparral and coastal sage scrub) expanded reaching near-Holocene distributions by 10 ka.

Plant macrofossils from Pit 91 indicate that at 28–26 ka, the Santa Monica Plain was still dominated by coastal sage scrub with pines and cypress at slightly higher elevations (Warter, 1976; Harris and Jefferson, 1985; Shaw and Quinn, 1986; Stock and Harris, 1992). A chaparral community grew on the slopes of the Santa Monica Mountains with isolated coast redwood (*Sequoia sempervirens*) and dogwood (*Cornus californica*) in protected canyons and a riparian community that included willow (*Salix lasiolepis*), red cedar (*Juniperus* sp.) and sycamore (*Platanus racemosa*). These plant communities suggest a winter precipitation regime similar to the modern Mediterranean climate of coastal southern California. However, the presence of coast redwood, now distributed 600 km to the north in the summer fog belt, corroborates the pollen record, indicating a cooler, more mesic and less seasonal climate at terminal OIS 3 than present.

3. Sample description

3.1. Carnivores

Carnivores vastly dominate the RLB faunal assemblage, more than half of which are canids, a third felids and the remainder bears and mustelids (Stock and Harris, 1992). The abundance of canids and felids markedly exceeds that of modern savanna habitats and seeps formed a carnivore trap in which several were attracted to a single prey item. In keeping with this, tooth breakage patterns consistent with bone crushing indicate that large RLB carnivores more fully consumed their prey than extant wolves and felids, implying higher levels of resource stress leading to increased competition for carcasses (Van Valkenburgh and Hertel, 1993; Binder et al., 2002; but see Duckler and Van Valkenburgh, 1998).

(1) *Canis dirus* (dire wolf, *n* = 25) was widespread across North America below the subarctic (Dundas, 1999) and is the most common of the RLB canids (Stock and Harris, 1992, pp. 27). Their relative abundance and low levels of canine dimorphism are suggestive of a pack-based, monogamous social structure similar to that of living wolves (*Canis lupus*) (Van Valkenburgh and Sacco, 2002). However, *C. dirus* was larger than modern timber wolves with a broad head and massive dentition more similar to modern hyenas than to hunting canids (Van Valkenburgh and Ruff, 1987), supporting early speculation that *C. dirus* was an adept scavenger (Merriam, 1912; Matthew and Stirton, 1930) and possibly accounting for the absence of true hyenas at RLB. The RLB subspecies *Canis dirus guildayi* had significantly shorter limbs than nominate *C. dirus* east of the continental divide; thus, RLB specimens were also less cursorial (Kurtén, 1984).

(2) *Smilodon fatalis* (sabertooth cat, *n* = 23) is the best represented of the felids (Janczewski et al., 1992) ranking next to *C. dirus* in abundance with a MNI (minimum number of individuals) of 2100 (Stock and Harris, 1992, pp. 32). With approximately twice the body mass of modern African lions (Anyonge, 1993), *S. fatalis* had heavier forelimbs and shorter hindlimbs leading to the inference that they preyed on "large, slow-footed animals" (Kurtén and Anderson, 1980, pp. 188). Low levels of canine dimorphism rule against high male–male competition for mating op-

portunity characteristic of modern lion prides; thus, *S. fatalis* may have been a solitary, ambush hunter (Van Valkenburgh and Sacco, 2002; but see Akersten, 1985). Dental microwear patterns are unique to *S. fatalis* (Akersten, 1985; Van Valkenburgh and Ruff, 1987; Van Valkenburgh et al., 1990; Anyonge, 1996; Biknevicius and Van Valkenburgh, 1996; see also Duckler, 1997), suggesting that the cat killed with shallow, canine shear-bites (Bryant, 1996) which protected fragile upper canines from incidental contact with bone (Akersten, 1985; Van Valkenburgh and Ruff, 1987; Van Valkenburgh et al., 1990). The lack of microwear indicative of repetitive bone consumption further demonstrates that *S. fatalis* left large, edible portions of their kills behind, possibly supporting a co-evolutionary relationship with *C. dirus* (Van Valkenburgh et al., 1990).

(3) *Panthera leo atrox* (American lion, *n* = 8) was common in the Americas from Alaska to the Valley of Mexico. Larger but structurally similar to extant African lions (Anyonge, 1993), *P. leo atrox* was also more cursorial, with long slender limb proportions. Although the RLB sex ratio is male-biased calling into question a pride-based social structure (Jefferson, 1992), *P. leo atrox* shows marked canine dimorphism (Van Valkenburgh and Sacco, 2002) and a large brain relative to body size indicative of high levels of mating competition and gregarious behavior, respectively.

(4) *Canis latrans* (coyote, *n* = 9) is less well represented than *C. dirus* or *S. fatalis*, possibly less prone to entrapment or simply not as common. Their canines lack evidence for bone crushing as do the canines of two other small predators, *Puma concolor* and *Lynx rufus* (Van Valkenburgh and Hertel, 1993). Today *C. latrans* is the sole endemic canid in the Los Angeles Basin due at least in part to an eclectic dietary regime that includes invertebrates, plants, carrion, lagomorphs, rodents and other small mammals and birds (Kurtén and Anderson, 1980; Zeveloff and Collett, 1988, pp. 248).

3.2. Ruminant herbivores

(1) *Camelops hesternus* ("yesterday's" camel, *n* = 12) is common at RLB and thought to have been a browsing ruminant despite hypsodont cheek teeth characteristic of grazers. Modern camelids are opportunistic feeders with diverse diets based heavily on

dicots. RLB camelid dental impacta ($n = 15$) accordingly contain nearly 90% gymnosperm and dicot plant tissue, indicating a diet comparable to modern dromedaries (*Camelus dromedarius*) (Akersten et al., 1988).

(2) *Bison antiquus* (Pleistocene bison, $n = 17$) was more abundant in the Los Angeles Basin than long-horned *Bison latifrons* and is well represented at RLB. Although modern bison are nonselective grazers, the dental impacta of RLB specimens contain less than 15% monocots (Akersten et al., 1988). This may reflect the scarcity of grasses at RLB or a bias in the digestibility of plant fragments lodged in bison dentition, overrepresenting a winter diet high in dicots. Among 300 individuals at RLB, most are subadults and females are more than twice as common as males. Moreover, the subadult assemblage is represented by discrete age clusters, 2–4, 14–16 months, etc., rather than a continuous distribution of age classes; thus, females and subadults appear to have entered the Los Angeles Basin in late spring shortly after calving and overwintered and calved elsewhere (Jefferson and Goldin, 1989).

(3) *Capromeryx minor*, the "dwarf" pronghorn ($n = 1$), is a browsing ruminant standing < 60 cm at the shoulder and weighing ~ 10 kg. Long, light limbs and hypsodont teeth distinguished *C. minor* from most true Old World antelopes and African gazelle, respectively, while its horn core with forked sheath is reminiscent of extant pronghorn (*Antilocapra americana*).

3.3. Nonruminant herbivores

(1) Among the perissodactyls, tapirs are rare and *Equus occidentalis* (western horse, $n = 19$) is the dominant equid with an MNI of 120, nearly 100 of which are subadult and two out of three male (Stock and Harris, 1992, pp. 39). Unlike bison, they are represented by a continuous distribution of subadult age classes. Modern equids have mixed feeding strategies; while zebra (*Equus burchelli*) are considered hypergrazers, feral horses (*Equus caballus*) and burros (*Equus asinus*) in arid North American are heavily reliant on browse. Dental impacta recovered from a single RLB juvenile contained >50% dicots consistent with a browsing strategy (Akersten et al., 1988).

(2) *Paramylodon harlani* ($n = 10$), a "grazing" ground sloth native to North American grasslands, is the most common of the RLB sloths. *P. harlani* is considered a nonruminant based on the digestive physiology of modern sloths (Bradypodidea) which lack a caecum, or hindgut fermentation site characteristic of nonruminants but are not "true" ruminants (Cork, 1994, pp. 351) since they also lack a rumen, reticulum, abomasum and omasum and the protozoan microbial community responsible for foregut fermentation (Goffart, 1971, pp. 110–125). Naples (1989, pp. 21) argues that *P. harlani* was "…probably less efficient at ingesting grasses than other local grazers and is more accurately characterized as a mixed feeder," although the slow movement of ingesta through the gut may have facilitated survival on grasses when necessary.

(3) *Mammuthus columbi* (Columbian mammoth) and *Mammut americanum* (American mastodon) are rare at RLB. The former are poorly preserved suggesting they date to brief, cool, wet periods when waterborne sediments accumulated on the surface of highly viscous seeps. All mammoth samples available to us were noncollagenous.

The American mastodon ($n = 7$) was a browser (Koch et al., 1998) preferring moist, woody habitats (Laub, 1996). Their remains are common in open boreal forests such as spruce parklands south of the Great Lakes (Whitehead et al., 1982) and along the Atlantic seaboard (Kurtén and Anderson, 1980, pp. 344), but are also found in the Great Plains, Texas and Florida. Digesta from numerous specimens indicate an opportunistic, mixed foraging strategy and include twigs and cones of spruce (*Picea* sp.) and other conifers (Laub et al., 1994), leaves, coarse grasses, mosses (Gobetz and Bozarth, 2001) and riparian species [e.g., cypress (*Taxodium* sp.), sedges (*Carex* sp.), pondweed (*Potamogeton* sp.)] (Lepper et al., 1991; Webb et al., 1992; Mihlbachler, 1998).

4. Methods

4.1. Stable carbon isotopes

An animal's stable carbon isotope chemistry ($\delta^{13}C$) reflects the isotopic composition of its diet (Hobson and Schwarcz, 1986; Lovell et al., 1986; Metges et al.,

1990; Koch, 1998; Kelly, 2000). Fractionation between plant tissues and herbivore bone collagen approximates $+5‰$ and enrichment at higher trophic levels varies from $0‰$ to $2‰$ (Koch, 1998; Bocherens and Drucker, 2003). Herbivore diets can be distinguished by photosynthetic pathway type that covaries with discrimination against atmospheric $^{13}CO_2$ (Farquhar et al., 1989). Cool-season grasses and greater than 98% of dicots, virtually all trees and most shrubs and herbaceous plants, use C_3 photosynthetic mechanisms discriminating heavily against ^{13}C and expressing an average $\delta^{13}C$ value of $-26.7 \pm 2.7‰$ ($n = 370$) (Cerling et al., 1998). Warm-season grasses, and a small number of dicots (e.g., *Atriplex* sp.), now common to areas where daytime growing-season temperature exceeds 22 °C and precipitation exceeds 25 mm (Ehleringer et al., 1997), use C_4 photosynthesis, discriminating less against ^{13}C and expressing an average $\delta^{13}C$ value of $-12.5 \pm 1.1‰$ ($n = 455$) (Cerling et al., 1998). Modern averages are $\sim 1.5‰$ more negative than plants grown before fossil fuel depletion of atmospheric CO_2 (Bada et al., 1990; Marino and McElroy, 1991; Tieszen and Fagre, 1993). The Crassulacean acid metabolism (CAM) pathway in stem succulents (cacti) and epiphytes (e.g., orchids) produces $\delta^{13}C$ values characteristic of C_4 photosynthesis but is seldom a confounding factor since CAM plants rarely make a significant contribution to mammalian diets.

Several stress factors can affect photosynthetic rates and/or stomatal conductance, affecting plant $\delta^{13}C$. In general, $\delta^{13}C$ values are positively correlated with increases in salinity, light intensity and nutrient level and negatively correlated with water availability, as water use efficiency declines with increasing aridity (see Farquhar et al., 1989; Ehleringer et al., 1993 for reviews). The effects of environmental stress on intraspecific $\delta^{13}C$ is limited, however, by the range of conditions under which a particular species can grow before replacement by a better adapted species and is commonly $< \pm 2‰$. Factors other than stress also produce consistent offsets in $\delta^{13}C$. Woody plants typically have enriched $\delta^{13}C$ values relative to herbaceous forms growing in the same area, possibly a function of rooting depth. In closed forests, "canopy effect" produces $\delta^{13}C$ values depleted by $2-5‰$ versus open-site herbaceous plants and leaves depleted by $3-4‰$ near ground versus high in the canopy of a single tree in response to reduced light and uptake of recycled CO_2 (Heaton, 1999).

4.2. Stable nitrogen isotopes

Nitrogen isotope ratios ($\delta^{15}N$) increase systematically with trophic level in mammals as well as birds and fish; however, regulating mechanisms are not fully understood. Schoeller (1999) suggests that fractionation in transamination or deamination of amino nitrogen during urea synthesis produces an endogenous nitrogen pool $\sim 4‰$ heavier than dietary sources. If dietary and endogenous nitrogen mix equally in the gut, overall body nitrogen is enriched by $>2‰$. While controlled feeding experiments have produced conflicting results (e.g., Sponheimer et al., 2003), recent analyses of trophic level enrichment in a modern ecosystem, a prehistoric ecosystem and the Upper Paleolithic of Europe reported trophic level effects of $\sim 3-5‰$ (Bocherens and Drucker, 2003; Coltrain et al., 2004).

Most terrestrial plants derive nitrogen from soil ammonium (NH_4^+) or nitrate (NO_3^-), and their $\delta^{15}N$ values appear to be inversely correlated with precipitation in the absence of nitrogen-fixing mechanisms. While not well understood, this relationship is partially driven by the loss of isotopically depleted ammonia formed in arid soils by microbial activity (Heaton, 1987; Schwarcz et al., 1999; Robinson, 2001; see also Heaton et al., 1986; Sealy et al., 1987). In temperate and semiarid ecosystems, plant $\delta^{15}N$ commonly ranges from $3‰$ to $6‰$ (Pate, 1994; Evans and Ehleringer, 1994), while desert ecosystems can produce plant values $>12‰$ (Schwarcz et al., 1999). Conversely, values as depleted as $0‰$ to $-2‰$ have been reported for non-nitrogen-fixing plants in habitats where precipitation exceeds 100 cm/year (Heaton, 1987). $\delta^{15}N$ values near $0‰$ are typical of plants that fix atmospheric nitrogen (e.g., legumes, mosses and lichens) or grow in association with mycorrhizae, nitrogen-fixing fungi in the biological crust of arid soils (Evans and Ehleringer, 1994; Coltrain and Leavitt, 2002). Such plants have $\delta^{15}N$ values ranging from $-2‰$ to $2‰$ depending on the relative proportion of nitrogen extracted from the atmosphere versus soils (Evans and Ehleringer, 1994; Pate, 1994).

4.3. Procedures

A diamond core drill was used to remove cortical bone plugs from adult skeletal elements. Bone plugs were soaked 48 h in 2:1 toluene/methanol, decanted and replaced after 24 h, followed by 24 h of soxhlet extraction in 2:1 toluene/methanol. Plugs were then demineralized in 0.6N HCl at 4 °C followed by base extraction in 5% KOH and lyophilized. Samples were subjected to a second 48-h solvent soak in toluene/methanol and dried under vacuum. The resulting chemical fraction was gelatinized in 5 ml of acidified water (pH 3) for 24 h at 120 °C. Water-soluble and   -insoluble phases were separated by filtration and the water-soluble phase was lyophilized and weighed to obtain a collagen yield. Collagen $\delta^{13}C$ and $\delta^{15}N$ were determined by flash combustion to produce CO_2 and N_2 and subsequent gas isotope analysis on a Finnigan Delta Plus mass spectrometer coupled to a Carlo Erba EA118 CHN elemental analyzer. Both stable isotope measurements and sample weight percent carbon and nitrogen were obtained from a single combustion.

5. Results

5.1. Whole bone nitrogen content, collagen yields and atomic C/N ratios

RLB whole bone N content ($n = 143$) averaged 2.5 ± 0.9 wt.% and ranged from 0.3% in an *M. columbi* scapula (HC90558) to 4.0% in a small but beautifully preserved *P. leo atrox* innominate (X7098). Modern bone is ~ 4 wt.% N. Only 1 bone plug with N content < 1% (W589) yielded collagenous protein, whereas 12 plugs with an average N content of 0.4 ± 0.1% were noncollagenous. Collagen yields ranged from 21.1% to 0.1%, the former in the same well-preserved *P. leo atrox* innominate that produced a modern whole bone N value.

Atomic C/N ratios ranged from 3.1 to 4.0 and were normally distributed around a mean of 3.5 ± 0.2. C/N ratios between 2.9 and 3.6 are commonly considered indicative of well-preserved bone collagen (Ambrose, 1990; see van Klinken, 1999 for a review). Collagen C and N concentrations averaged 41.6 ± 4.6% and 13.9 ± 1.6% and ranged from 49.6% to 16.9% and

16.9% to 5.7%, respectively, with a *C. latrans* humerus (R11938) producing the anomalously low value in each range and a *S. fatalis* radius (HC35354) producing the high value. C and N concentrations were relatively consistent in samples with collagen yields greater than 2.5–3%, decreasing systematically below that threshold; however, the transition was neither abrupt nor erratic (Fig. 1a). C and N in samples with yields >2.5% averaged 43.2 ± 2.8% and 14.5 ± 0.9%; collagen yields between 2.5% and 1% averaged 38.6 ± 6.1% C and 12.5 ± 2.0% N,
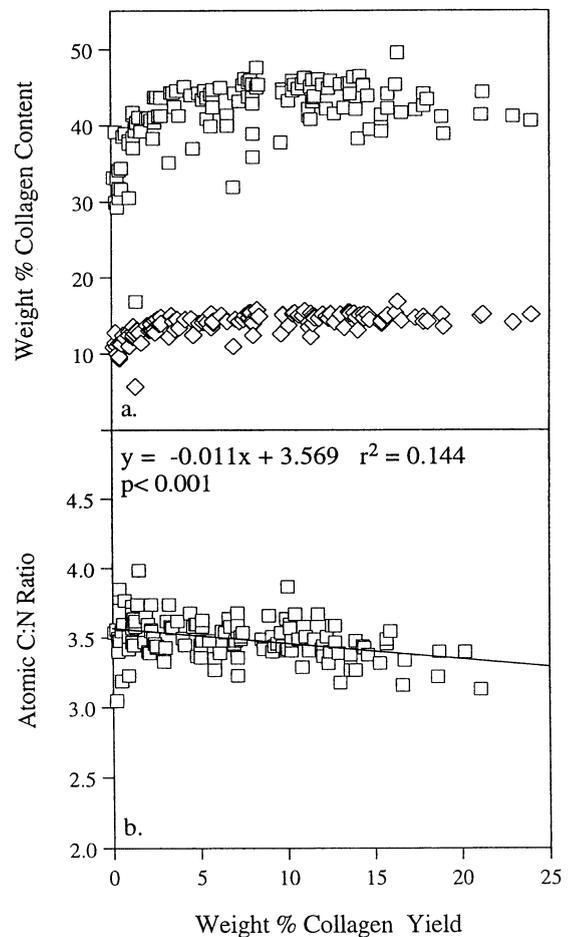
Fig. 1. (a) Collagen carbon (□) and nitrogen (◇) contents by weight percent plotted against collagen yields by weight percent for all collagenous faunal bone sampled from Rancho La Brea asphalt seeps. (b) Collagen atomic C/N ratios regressed against collagen yields for all collagenous samples.
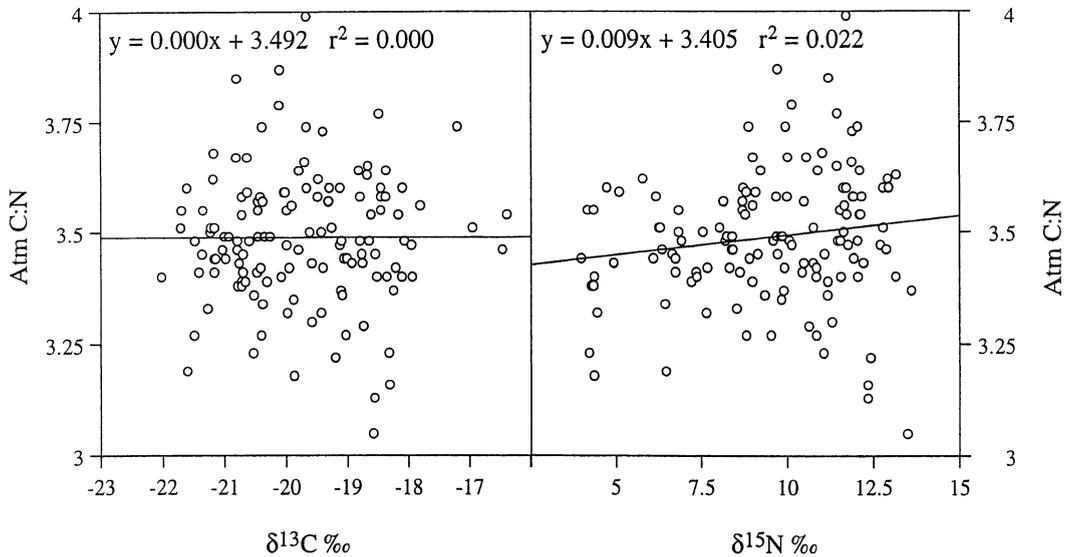
Fig. 2. Rancho La Brea atomic C/N ratios plotted against δ^{13}C and δ^{15}N values with correlation coefficients.

while samples that yielded < 1% collagen averaged 34.1 ± 3.6% C and 11.4 ± 1.1% N, the latter demonstrating that low collagen yields can be characterized by proportional C/N concentrations.

As collagen yields declined, C/N ratios increased slightly (Fig. 1b) and, although the correlation coefficient is low, the relationship is significant due to

sample size ($r^2 = 0.144$, $df = 130$, $p < 0.001$). Accordingly, C and N content in collagen samples with atomic C/N ratios between 2.9 and 3.6 averaged 41.7 ± 4.6% and 14.1 ± 1.5%, respectively; whereas collagen samples with "high" C/N ratios (3.6–4.0) averaged 41.3 ± 3.9% C and 13.0 ± 1.4% N. Thus a 1% decline in N content was responsible for "high"
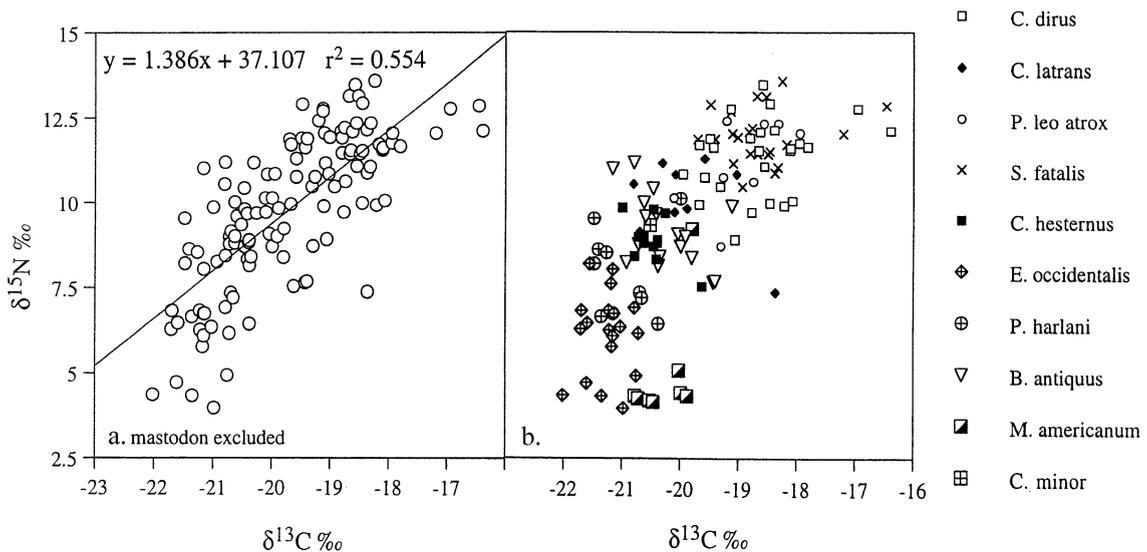
Fig. 3. (a) Rancho La Brea individual δ^{15}N values plotted against δ^{13}C (mastodon excluded), showing a positive correlation significant at $p > 0.0001$. (b) Individual δ^{15}N values plotted against δ^{13}C by species.
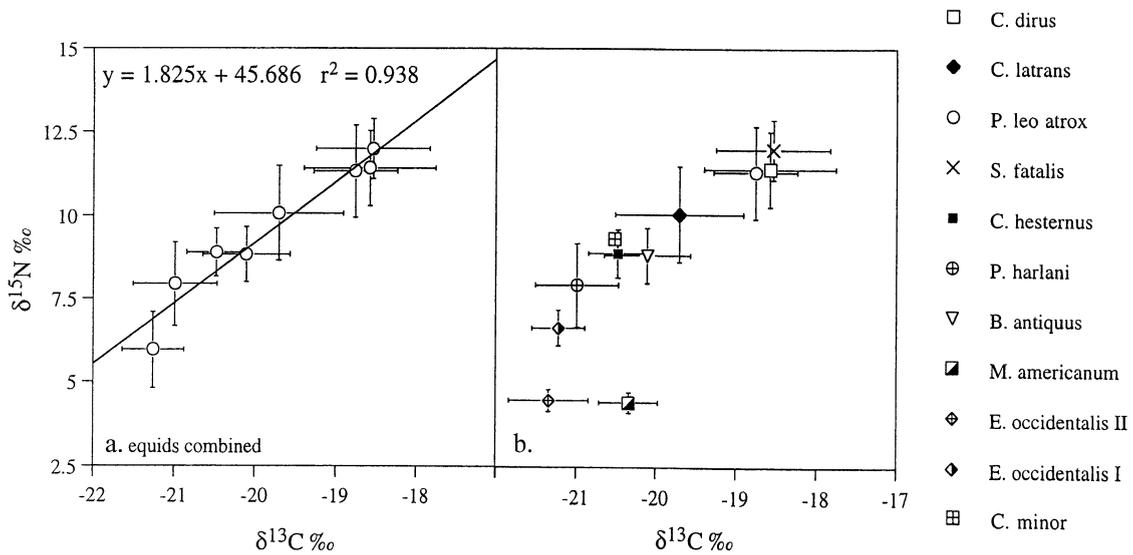
Fig. 4. (a) Rancho La Brea species mean $\delta^{15}N$ values plotted against mean $\delta^{13}C$ values at 1 standard deviation (equids combined, mastodon excluded), showing a strong positive correlation significant at $p > 0.0001$. (b) Mean $\delta^{15}N$ values plotted against $\delta^{13}C$ values by species, shown at 1 standard deviation, mastodon included and equids plotted in two groups.

C/N ratios and the difference is significant ($t = 3.29$, $df = 33$, $p = 0.002$). However, $\delta^{13}C$ and $\delta^{15}N$ values are not significantly correlated with collagen yields or C/N ratios (Fig. 2) and samples with "high" C/N ratios are included in figures discussed below.

5.2. Stable isotope ratios

Individual data are plotted in Fig. 3 and species means and standard deviations in Fig. 4. $\delta^{13}C$ and $\delta^{15}N$ values are positively correlated in individuals reliant on terrestrial source nitrogen (Fig. 3a, mastodon excluded) and in species with mean $\delta^{15}N$ values $> 5‰$ (Fig. 4a,

equids combined). $\delta^{15}N$ values $< 5‰$, in *M. americanum* and five equids (*E. occidentalis* II) (Fig. 4b), may be attributable to partial reliance on nitrogen-fixing taxa or the effects of increased precipitation on $\delta^{15}N$ values (Schwarcz et al., 1999; Amundson et al., 2003) and are discussed below. Large carnivores (*C. dirus*, *P. leo atrox* and *S. fatalis*) exhibited a mean $\delta^{13}C$ value of $-18.7 \pm 0.8‰$ and $\delta^{15}N$ value of $11.6 \pm 1.1‰$, the former $1.6‰$ and the latter $2.6‰$ greater than ruminant herbivore isotope values (*C. hesternus*, *B. antiquus*, and *C. minor*) and $2.4‰$ and $4.4‰$ greater than nonruminants with $\delta^{15}N$ values $> 5‰$ [*P. harlani* and 14 equids (*E. occidentalis* I)].

Table 1
Statistically significant differences in mean $\delta^{13}C$ and $\delta^{15}N$ values at $p = 0.05$

Carnivores	*P. leo atrox*	*S. fatalis*	*C. latrans*		
C. dirus	NS, NS	NS, NS	S, S		
P. leo atrox		NS, NS	S, NS		
S. fatalis			S, S		

Herbivores	*B. antiquus*	*P. harlani*	*E. occidentalis* I	*E. occidentalis* II	*M. americanum*
C. hesternus	NS, NS	S, S	S, S	S, S	NS, S
B. antiquus		S, S	S, S	S, S	NS, S
P. harlani			NS, S	NS, S	S, S
E. occidentalis I				NS, S	S, S
E. occidentalis II					S, NS

Average ruminant δ^{15}N was 2.3‰ greater than nonruminant δ^{15}N ($t = 7.049$, $df = 45$, $p < 0.001$), mastodon excluded, and 2.7‰ greater with their inclusion. Average ruminant δ^{13}C was 0.8‰ greater (excluding mastodon) significant at $p < 0.001$ ($t = -6.953$, $df = 56$).

Significant differences in the isotope chemistry of individual taxa are shown in Table 1. Large carnivore diets are statistically indistinguishable but significantly different from *C. latrans* with the exception of *P. leo atrox* δ^{15}N. *C. hesternus* and *B. antiquus* diets are indistinguishable yet significantly different from the

equids in both isotopes and mastodon in δ^{15}N. *P. harlani* diets are significantly different from equid δ^{15}N and mastodon in both isotopes. Equids differ between groups with respect to nitrogen, while *E. occidentalis* I varies significantly from mastodon in both isotopes and *E. occidentalis* II in carbon.

Fig. 5 plots isotope means and variances by radiocarbon years before present associated with sampled pits. Pits 60 and 91 date to terminal OIS 3 (28–26 ka), Pit 3 to LGM (20 ka) and Pits 61 and 67 to the GIT (14–12 ka). Species were relatively evenly distributed over the temporal span of the study with the exception of
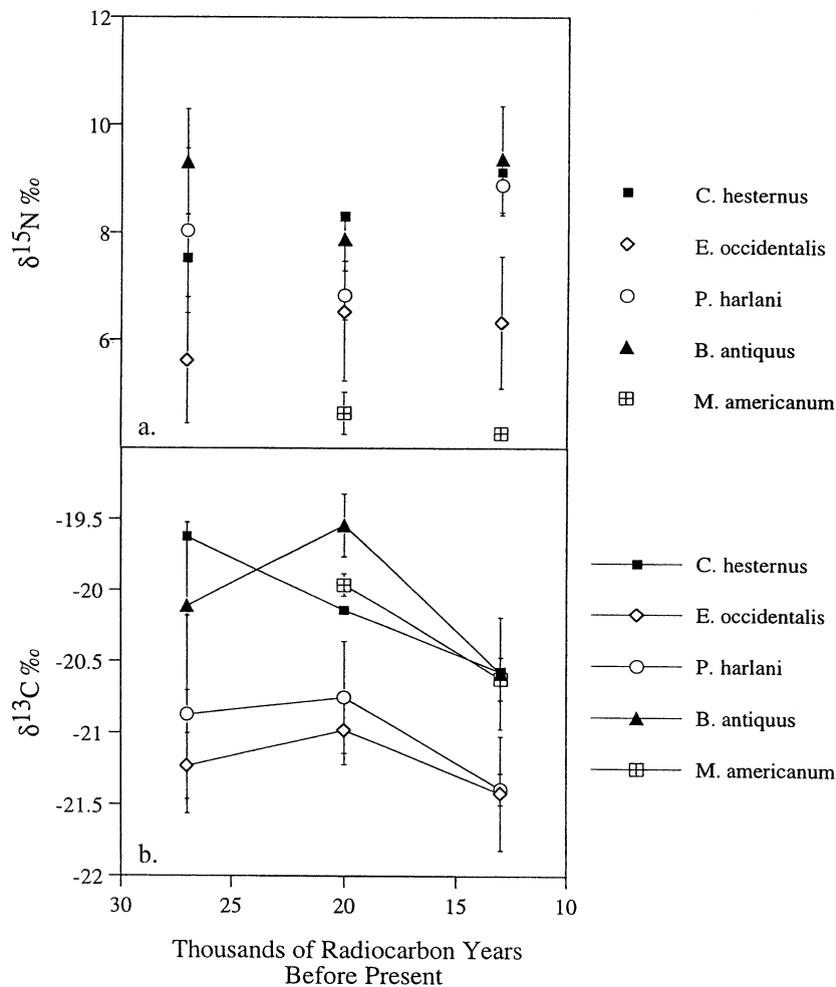
Fig. 5. (a–b) Rancho La Brea species mean δ^{15}N and δ^{13}C values shown at 1 standard deviation plotted against the age of pits, in radiocarbon years before present, from which samples were recovered. Samples dating to 28–26 ka (terminal OIS 3) are from Pits 60 and 91, samples dating to 20 ka, or last glacial maximum, from Pit 3 and samples dating to 14–12 ka, or the glacial–interglacial transition (GIT), from Pits 61 and 67.

camelids, represented by a single individual at OIS 3 and LGM. The isotopic separation between camelid/bison and equid $\delta^{15}N$ was maintained over time, although variances overlap at terminal OIS 3 and spacing is compressed by a decline in bison $\delta^{15}N$ values at LGM (Fig. 5a). In Fig. 5b, samples from LGM and the GIT sort by digestive physiology into ruminants and nonruminants with ruminant $\delta^{13}C$ values enriched by $1.0-1.5\%o$. Mastodons were the exception, sorting with the ruminants, but may not have been indigenous to RLB for reasons discussed below.

6. Discussion

6.1. Preservation criteria

Samples with collagen C/N ratios >3.6 (3.62–3.99, $n=23$) are included in species averages given the following conditions. However, in the past, it has been common to reject such samples based on preservation criteria established by Ambrose (1990), where samples outside the 2.9–3.6 range (range 1.5–19.1) were noncollagenous and exhibited low collagen yields, erratic carbon and nitrogen concentrations and stable isotope signatures inconsistent with known diets and samples of similar age and geographic context. RLB samples with atomic C/N ratios >3.6 did not exhibit the combined characteristics of noncollagenous protein reported by Ambrose (1990). Their C/N ratios did not vary erratically but represented the upper end of a normally distributed range. Although in some cases yields were low, collagen C and N concentrations were greater than 50% modern in all but one sample and did not vary randomly but declined systematically with yields (Fig. 1). The average carbon concentration in samples with high C/N ratios was statistically indistinguishable from that of samples with C/N ratios between 2.9 and 3.6. While nitrogen contents were slightly reduced, isotope ratios were consistent with the remainder of the study population. When these samples were added to the RLB dataset, the average difference in species means was within the analytical precision of both isotopes [$\pm 0.2\%o$ carbon and $\pm 0.3\%o$ nitrogen, i.e., average difference in $\delta^{13}C = -0.10 \pm 0.07\%o$ (range -0.04 to $-0.17\%o$); average difference in $\delta^{15}N = 0.01 \pm 0.16\%o$ (range 0.27 to $-0.15\%o$)]. Moreover, $\delta^{13}C$ and $\delta^{15}N$ values for

samples with C/N ratios above 3.6 did not covary with collagen yields ($r^2 = 0.071$, $df = 22$, $p = 0.220$; $r^2 = 0.008$, $p = 0.686$, respectively) or C/N ratios ($r^2 = 0.001$, $p = 0.901$; $r^2 = 0.023$, $p = 0.490$, respectively), similar to the collection as a whole.

The inclusion of these samples does not constitute a rejection of the statistic as a useful measure of protein preservation. Instead, we concur with previous work (e.g., Ambrose, 1990; van Klinken, 1999) and suggest that a suite of measures is necessary to evaluate collagen preservation. Whole bone nitrogen content was a highly useful predictor of preservation. All but one sample with N content less than 1% were noncollagenous. We also found that some samples with collagen yields <1 wt.% retained C and N concentrations proportionally similar to samples with higher yields but caution that this finding may be an artifact of the depositional environment at RLB and not applicable in all settings.

6.2. $\delta^{15}N$, herbivore diets and ruminant versus nonruminant digestive physiology

Time-averaged ruminant $\delta^{15}N$ (bison, camelids and dwarf pronghorn) was enriched 2.3‰ relative to nonruminants [ground sloth, equids (mastodon excluded)]. Isotopic enrichment in ruminants represents a near trophic level increase in the isotope signature of ingested, terrestrial nitrogen and/or endogenous nitrogen used in synthesis of nonessential amino acids. Temporal patterning evident in Fig. 5a suggests that isotopic spacing was maintained in part by resource partitioning since at LGM, ruminant and nonruminant diets were more similar than during terminal OIS 3 or the GIT. Compression of herbivore diets is consistent with a decline in primary productivity and shift in the distribution of plant communities characteristic of glacial maxima (Heusser, 1998; Cowling, 1999; Petit et al., 1999). Accordingly, terrestrial pollen profiles from coastal southern California record a decline in herbaceous plants, oaks, chaparral and coastal sage scrub accompanied by an increase in pine and juniper/cypress at LGM (Heusser, 1998). While it is not clear how herbivore diets were partitioned to distinguish equids, nonruminants relying on either grass or browse, from both ruminant browsers (camelids) and grazers (bison) [although RLB bison may be better categorized as mixed feeders (Akersten et al., 1988)],

the simplest approach would argue that equids were heavily reliant on C_3 taxa with similar $\delta^{15}N$ values over the course of the study. At LGM, with a decline in the primary productivity of other vegetation, camelids and bison were forced to rely more heavily on conifers.

Digestive physiology may also have contributed to time-averaged and episodic variation in herbivore $\delta^{15}N$ values. Autoenzymatic digestion of microbial bodies active in foregut fermentation (Langer, 1986; Alexander, 1993) should have a moderate trophic level effect on ruminants, enriching their endogenous nitrogen pool relative to nonruminants. Equids (*E. caballus*) from several sites in late Pleistocene Europe have mean $\delta^{15}N$ values ranging from 5.0‰ to 6.8‰ [Bocherens et al., 1991, 1995, 2001; Fizet et al., 1995; Iacumin et al., 1997 (EPSL Online Background Dataset)]; complementary data on bovids are available from three sites. A mean value of 6.7‰ for Marillac cave (France) bison (*Bos priscus*) is 1.6‰ greater than equids from the same site, and Marillac wild ox (*Bos primigenius*) exhibit a mean $\delta^{15}N$ value 1.0‰ greater than the equids (Fizet et al., 1995). In keeping with this pattern, wild ox from Paglicci cave (Italy) are enriched 1.1‰ relative to equids (Iacumin et al., 1997). The pattern is reversed at Kent's cavern (England) where equid tooth collagen $\delta^{15}N$ values ($n = 15$) range from 2.2‰ to 8.5‰ with a mean of $6.5 \pm 1.7‰$, while a single *Bos* M_3 produced a value of 5.6‰ (Bocherens et al., 1995). However, the *Bos* sample was the only ruminant in the Kent's cavern dataset providing no context for assessing its $\delta^{15}N$ value, whereas nonruminant $\delta^{15}N$ values for woolly rhinoceros (*Coelodonta antiquitatis*) and cervids cluster tightly around the equid mean.

Sealy et al. (1987) have argued that water-stressed ruminants have elevated $\delta^{15}N$ values due to recycling of urea, and Ambrose (1991, 1993) predicted a similar effect caused by increased fractionation during urea production; but RLB ruminant $\delta^{15}N$ decreased during LGM, the most arid episode in the sequence, discounting physiological water stress as a causal factor in enriched ruminant $\delta^{15}N$. Conversely, Ambrose (1991, 1993) has argued that protein-stressed herbivores conserve ^{15}N-depleted, urea nitrogen by recycling it through the gut, lowering tissue $\delta^{15}N$ values. The latter strategy may have contributed to depleted, bison $\delta^{15}N$ at LGM, whereas equids, whose diets were relatively uniform isotopically over the span of the study, do not show this effect.

Finally, variation in the soil/plant $\delta^{15}N$ values of specific plant communities cannot be entirely dismissed as a contributing factor, although a causal relationship is not immediately evident. Soil $\delta^{15}N$ increases as mg N/g soil decreases with depth (Evans and Ehleringer, 1994), implicating rooting depth as a potential mechanism. Schwarcz et al. (1999) have assembled compelling evidence for a negative correlation between precipitation and soil/plant $\delta^{15}N$, but this relationship is unlikely to account for the offset between ruminant and nonruminant $\delta^{15}N$ since arid soil conditions would elevate the $\delta^{15}N$ values of all herbivores not merely the ruminants.

Equids are plotted together in Fig. 5, but can be divided into two groups (Fig. 4b) based on a significant difference in mean $\delta^{15}N$ values (*E. occidentalis* I, 6.8‰; *E. occidentalis* II, 4.5‰). The former is 2.3‰ and the latter 4.5‰ less than ruminant $\delta^{15}N$ values. Individuals in the latter group are not restricted to a single time period; however, they may date to brief, wet episodes when high precipitation reduced plant $\delta^{15}N$ values.

We noted earlier that, although considered a "grazing" ground sloth, *P. harlani* is better classified as a mixed feeder based on its feeding mechanisms (Naples, 1989). *P. harlani* is also classified as a nonruminant based on the digestive physiology of sister species. When time-averaged (Fig. 4b), ground sloth $\delta^{15}N$ values are more positive than the equids or "true" nonruminants, but do not sort with the ruminants leading us to consider the effects of their "convergent" digestive physiology on endogenous $\delta^{15}N$ values. Modern sloths lack protozoa active in foregut fermentation and thus are not as well suited as ruminants to high cellulose diets, but compensate by retaining ingesta within their gut for as long as a week, defecating weekly rather than daily or several times a day common to herbivores (Goffart, 1971, pp. 117, 124). The slow movement of ingesta through the digestive tract is facilitated by extremely low rates of basal metabolism (Cork, 1994). The stomachs of living sloths are also very large, nearly filling their abdominal cavity and are always full or near full, even after fasting several days. Further, it has been demonstrated that bacteria isolated from sloth guts hydrolyze cellulose (Goffart, 1971, pp. 117). Accordingly, Cork (1994, Fig. 21.3) considers modern sloths "foregut fermenting nonruminant mammals." If so, sloths digest bacterial microbes in their short, small intestines

producing slight trophic level enrichment that might generally position them between ruminants and non-ruminants isotopically. In Fig. 5a, their $\delta^{15}N$ values covary with bison, enriched and sorting with ruminants at terminal OIS 3, depleted, sorting with equids at LGM and enriched again at the GIT. If our simple argument is valid, at LGM, ground sloths show nearly the same increase in reliance on conifers as bison.

By comparison, mastodon diets varied little over time and low $\delta^{15}N$ values suggest partial reliance on nitrogen-fixing taxa. At high latitudes, reindeer (*Rangifer tarandus*) rely nearly entirely on lichens for winter forage and expressed the highest $\delta^{13}C$ ($-18.5‰$ to $-17.2‰$) and lowest $\delta^{15}N$ values ($2.4–2.8‰$) among herbivores sampled in two recent studies (Iacumin et al., 2000; Coltrain et al., 2004). Reindeer from Marillac cave, France (Fizet et al., 1995), and Scladina cave, Belgium (Bocherens et al., 2001), have more enriched $\delta^{15}N$ values, $4.7‰$ and $4.5‰$, respectively, suggesting that lichens were important in but did not dominate European diets as might be expected at mid-latitudes, possibly providing an analog for RLB mastodon (mean $\delta^{15}N = 4.4 \pm 0.3‰$). We also suggest that mastodons were not indigenous to RLB. Their remains are rare and poorly preserved and their diets clearly distinguish them from other RLB nonruminants.

6.3. $\delta^{13}C$, herbivore diets and ruminant versus nonruminant digestive physiology

RLB $\delta^{13}C$ values indicate herbivores subsisted on C_3 vegetation growing in open environments. Canopy effect is not evident nor is there any indication that C_4 grasses proliferated at terminal OIS 3 or LGM, as might be expected given low atmospheric CO_2. At current CO_2 concentrations, C_4 grasses dominate in low-latitude, summer-wet habitats where growing-season temperature exceeds 22 °C (Ehleringer et al., 1997; Sage and Monson, 1999). $\delta^{13}C$ values for herbivore enamel from late Pleistocene sites in the American southwest (Connin et al., 1998) indicate that C_4 plants were dominant in areas characterized at LGM by reduced growing season temperature but a near-modern level of growing season moisture. These results suggest that at RLB during LGM growing seasons were arid.

Time-averaged, the mean ruminant $\delta^{13}C$ value was $0.8‰$ greater than that of the nonruminants (excluding mastodon), significant at $p < 0.001$. Enriched $\delta^{13}C$ in ruminants is consistent with increased methanogenesis characteristic of foregut fermentation if carbon for synthesis of nonessential amino acids derives from a common "energy" pool (Hedges, 2003; Metges et al., 1990; Hedges and van Klinken, 2000). Methane (CH_4), a byproduct of bacterial activity during rumination, is depleted $30–40‰$ relative to diet and apparently accounts for $\sim 10\%$ of the total carbon flux, given that Metges et al. (1990) reported expired CO_2 values for cows $3–4\%$ heavier than diet. Crutzen et al. (1986) estimated that the production of methane was several times greater in Serengeti ruminants than in nonruminants, and Cerling and Harris (1999) reported a mean enamel $\delta^{13}C$ value in zebra (*E. burchelli*) depleted by $1–2‰$ relative to ruminant hypergrazers. RBL ruminant $\delta^{13}C$ values were consistently enriched $\sim 1‰$ relative to nonruminants (Fig. 5b), a particularly interesting finding given that ruminant $\delta^{15}N$ values declined at LGM, indicating ruminant and nonruminant diets became more similar. Similarly, $\delta^{13}C$ was enriched by an average of $0.7 \pm 0.1‰$ in bison or wild ox (*Bos*) versus equids at three European sites dating to the late Pleistocene (Bocherens et al., 1995; Fizet et al., 1995; Iacumin et al., 1997).

Methanogenesis may not be solely responsible for heavy ruminant $\delta^{13}C$ at RLB and elsewhere but should have been a contributing factor (Hedges, 2003), particularly during periods of resource stress when endogenous carbon was routinely utilized for neAA synthesis. Ruminant forage may also have been consistently enriched over the study period but is difficult to reconstruct isotopically. Weighing the combined effects of marked fluctuations in precipitation, temperature and atmospheric CO_2 on the $\delta^{13}C$ values of specific late Pleistocene vegetation is beyond the scope of current research. Systematic enrichment in $\delta^{13}C$ values at LGM (Fig. 5b) is, however, consistent with a decline in plant water use efficiency, implicating water stress as a causal mechanism (Heaton, 1999). In keeping with this result, a recent study found that bone consumption based on tooth breakage in *C. dirus* declined from 15 to 12 ka (Binder et al., 2002), implying that food was more scarce shortly after LGM than at the GIT.

Temporal patterning in both isotopes across taxa (Fig. 5) can be read to indicate that Pits 3 and 61/67 are well dated and were active during discrete time

intervals, constraining the isotope signatures of herbivore forage, whereas camelid isotope values at OIS 3 did not follow the expected pattern suggesting an unresolved temporal discontinuity associated with Pit 60. Unfortunately, *C. hesternus* is represented by a single individual at terminal OIS 3, providing no context for determining if the oldest camelid isotope values are representative.

6.4. Trophic level relationships

Large carnivore $\delta^{15}N$ values were statistically indistinguishable, with an interspecific mean of $11.6 \pm 1.1\%o$, $2.6\%o$ greater than ruminants, $4.4\%o$ greater than nonruminants (*E. occidentalis* II and mastodon excluded) and $7.2\%o$ greater than low-nitrogen equids and mastodon, indicating relatively even reliance on ruminant and nonruminant prey excluding low-nitrogen equids and mastodon which appear unimportant in carnivore diets. Reliance on similar prey sets is consistent with dental evidence for high levels of competition (Van Valkenburgh and Hertel, 1993), while the lack of evidence for predation on mastodon and low-nitrogen equids supports the belief that they were not indigenous to RLB or were present during brief episodes. Species-specific, temporal variation in large carnivore $\delta^{15}N$ was not patterned.

C. latrans occupies the position of an omnivore in the RLB food web, with a mean $\delta^{15}N$ value $1.5\%o$ less than large carnivores and $2.0\%o$ greater than herbivores when the latter are averaged (mastodon and low-nitrogen equids excluded). Lacking data on small mammals, it is not possible to be more specific about coyote diets other than to note that the position *C. latrans* occupies accords well with the eclectic dietary regime of modern coyotes (Zeveloff and Collett, 1988).

S. fatalis exhibits the most enriched mean $\delta^{15}N$ value ($12.0 \pm 0.8\%o$), indicating that the cat may have preferentially targeted ruminant prey (mean ruminant $\delta^{15}N = 9.0 \pm 0.9\%o$) and calling into question the argument that they preferred "large, slow-footed animals" (Kurtén and Anderson, 1980, pp. 188). Two *C. dirus* and *S. fatalis* samples were distinguished by $\delta^{13}C$ values more positive than $-17.5\%o$ (Fig. 3), implicating either consumption of isotopically enriched animal tissues or higher than average fractionation between diet and bone collagen. The former is unlikely since virtually no evidence for C_4 enrichment is present at RLB, whereas the latter may be the consequence of resource stress.

6.5. Comparative data and their implications

RLB $\delta^{13}C$ values are typical of late Pleistocene, European fauna living in open environments and within the range of modern herbivores from temperate and cold climates (Tauber, 1986; Bocherens et al., 1994). Specifically, RLB mean equid and bison $\delta^{13}C$ values ($-21.3 \pm 0.4\%o$, $20.2 \pm 0.6\%o$, respectively) are within the range of European equids and bovids ($-21.7\%o$ to $-20.2\%o$, $-20.6\%o$ to $-19.5\%o$, respectively) [Fizet et al., 1995; Bochereet al., 1995, 2001; Iacuminet et al., 1997, ESPL, Online, Background Dataset], and mean carnivore $\delta^{13}C$ values are very similar (RLB = $-19.0 \pm 0.6\%o$, Europe = $-19.3 \pm 0.6\%o$) (Fizet et al., 1995; Bocherens et al., 1995, 2001). However, RLB bison $\delta^{15}N$ values ($9.1 \pm 1.0\%o$) are enriched nearly a trophic level relative to the mean for European bovids ($6.7 \pm] 1.2\%o$) and the upper end of the range for European equids ($\delta^{15}N$ range, $5.1–6.8\%o$) (Bocherens et al., 1991, 1995; Fizet et al., 1995, Iacumin et al., 1997; Bocherens et al., 2001) is the mean for *E. occidentalis* I. Accordingly, European wolf (*C. lupus*) and hyena (*Crocuta*) $\delta^{15}N$ values ($9.8 \pm 0.5\%o$) (Fizet et al., 1995; Bocherens et al., 1995, 1999, 2001) are more similar to RLB ruminants than carnivores.

An offset in $\delta^{15}N$ of this magnitude is difficult to attribute solely to physiological water stress and may indicate that coastal southern California was, on average, more arid during the growing season than western Europe, enriching soil/plant $\delta^{15}N$ values. This suggestion appears to contradict Heusser's argument that coastal southern California received substantially more annual precipitation during the late Pleistocene than it does at present; however, if a winter precipitation regime was in place, as indicated by Pit 91 (terminal OIS 3) macrofossils, summers may have been arid relative to western Europe.

6.6. Isotopic covariance

Strong interspecific covariance in the ratios of both isotopes was unexpected (Figs. 2a, 3a). Such correlations have been demonstrated among the tissues of a single sea bird ($r^2 = 0.85$; Mizutani et al., 1991), at the

intraspecific level, within food webs and across wider assemblages of animal taxa (see Kelly, 2000 for a review). Kelly (2000) notes that within and between species, this relationship is commonly a product of mixed diets in which groups relying more heavily on C_4 vegetation also have enriched $\delta^{15}N$ values since C_4 plants commonly grow in more arid habitats, characterized by enriched soil $\delta^{15}N$. Mixed marine/terrestrial food webs also produce a similar effect in which groups reliant on marine resources exhibit accordingly positive $\delta^{13}C$ values and $\delta^{15}N$ values enriched by the multiple trophic level structure of marine food webs (Coltrain et al., 2004). Kelly further argues that if these relationships are solely a function of trophic level enrichment, a slope of 1.5–4.0 is predicted given 3–4‰ trophic level enrichment in $\delta^{15}N$ divided by 1–2‰ enrichment in $\delta^{13}C$. Regressing mean $\delta^{15}N$ values for RLB species reliant on terrestrial source nitrogen against $\delta^{13}C$ produces a slope of 1.83, $r^2 = 0.938$ (Fig. 3a). Yet, clearly, these data do not conform to either well-understood context for such a relationship. Neither C_4 plants nor marine resources were present. While trophic level enrichment between RLB carnivores and herbivores is expected, the relationship between ruminant and nonruminant herbivores is more difficult to explain. This pattern is either strongly influenced by the correlated effects of methanogenesis and trophic level enrichment associated with ruminant digestive physiology or the result of a highly correlated and consistently maintained offset in the $\delta^{13}C$ and $\delta^{15}N$ values of ruminant versus nonruminant forage. Mechanisms necessary to maintain such an offset in C_3 plant communities under the varying growing conditions characteristic of this study are not well identified.

7. Conclusion

Most RLB skeletal remains were adequately preserved to yield in vivo stable carbon and nitrogen isotope values. Several criteria were used to accurately characterize protein preservation. Whole bone nitrogen content, atomic C/N ratios, collagen yields and carbon and nitrogen concentrations were highly useful in identifying samples with adequate protein preservation despite slightly elevated atomic C/N ratios.

We also found that ruminant and nonruminant digestive physiologies produced distinct carbon and nitrogen isotope signatures and suggest that isotope enrichment evident in ruminants is in part a function of methane production and microbial digestion. Accordingly, ground sloth isotope signatures suggest they were nonruminant foregut fermentors similar to modern sloths. However, these inferences require further validation through physiological experimentation. We found no evidence for the presence of C_4 grasses during the late Pleistocene but do report an approximate 1.0–1.5‰ enrichment in herbivore $\delta^{13}C$ at LGM and believe that it represents the response of plant communities to water stress.

Isotope signatures characteristic of the three large carnivores at RLB indicate they were essentially sympatric, competing for the same set of prey in keeping with other evidence for high levels of competition, although Smilodon appears to have preferentially targeted ruminant prey. Conversely, coyotes were not in competition with large carnivores and appear more omnivorous, although our understanding of coyote diets is hampered by the absence of data on small mammals. Mastodon were partially reliant on nitrogen-fixing plant taxa suggesting they occupied a unique foraging niche and were not indigenous to the study area. RLB $\delta^{13}C$ values are within the range of values for comparable European faunal assemblages, whereas $\delta^{15}N$ values are elevated suggesting soil/plant $\delta^{15}N$ values were arid enriched during the growing season. The interpretive potential of this study was somewhat limited by the lack of high-resolution temporal control over subsets of the study population such as the equids and mastodon.

Acknowledgements

Appendix A

Page Musm catalog no.	Species	Pit	Provenience	Skeletal element	Whole bone % N	% Weight loss	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	% Coll by weight	Coll wt.% carbon	Coll wt.% nitrogen	Atomic C/N
H1411	C. dirus	3	D4, 22′	rt tibia	3.04	8.83	−16.95	12.78	9.1	45.93	15.27	3.51
H1422	C. dirus	3	C4, 20.5′	rt tibia	3.02	6.15	−17.95	11.76	1.8	40.89	13.76	3.47
H1370	C. dirus	3	C4, 20.5′	rt tibia	2.94	7.96	−19.58	10.75	8.6	44.82	15.24	3.43
H1573	C. dirus	3	E3, 21′	rt tibia	2.73	8.45	−18.55	11.07	6.9	43.80	14.79	3.45
H1627	C. dirus	3	D4, 21′	rt tibia	3.17	5.65	−18.10	11.61	2.0	40.69	13.18	3.60
H1901	C. dirus	60	10−12′	lt tibia	3.07	9.92	−17.81	11.65	2.2	40.47	13.27	3.56
H1909	C. dirus	60	10−12′	lt tibia	2.55	9.61	−18.38	12.15	5.1	43.28	14.10	3.58
H1905	C. dirus	60	C10, 9−12′	lt tibia	2.79	6.86	−18.58	13.49	0.2	29.98	11.49	3.05
H1908	C. dirus	60	10−12′	lt tibia	2.74	9.24	−18.46	9.98	1.3	40.39	13.16	3.58
H1902	C. dirus	60	C10, 9−12′	lt tibia	2.69	7.65	−18.07	10.05	0.4	34.18	11.45	3.48
H1877	C. dirus	61	C9, 10−14′	lt tibia	3.48	7.87	−19.95	10.84	0.9	37.99	12.95	3.42
H1865	C. dirus	61	G15,11−14′	lt tibia	3.22	5.24	−18.80	11.91	6.7	46.19	15.06	3.58
H1809	C. dirus	61	D15, 14−17.5′	lt tibia	3.46	7.33	−19.49	11.89	4.6	43.43	14.17	3.58
H1870	C. dirus	61	C10, 12−15.5′	lt tibia	3.41	6.85	−19.13	12.78	4.7	44.63	14.48	3.60
H1766	C. dirus	61	E11, 15−18′	lt tibia	2.88	6.72	−19.43	11.63	2.3	43.79	14.59	3.50
H1872	C. dirus	61	E16, 12.5−16′	lt tibia	2.89	14.56	−19.67	9.94	1.4	41.11	12.81	3.74
H1732	C. dirus	67	none	lt tibia	2.62	11.71	−18.46	12.94	4.8	43.66	14.15	3.60
H1712	C. dirus	67	SE crnr, 16−19′	lt tibia	3.11	9.26	−19.31	10.47	3.4	41.34	13.46	3.57
H1801	C. dirus	67	SE crnr, 16−19′	lt tibia	2.85	8.51	−19.67	11.70	0.6	38.58	12.51	3.60
H1789	C. dirus	67	C6, 12−15.5′	lt tibia	3.16	9.28	−19.06	8.89	9.2	45.44	15.43	3.44
R18374	C. dirus	91	8.5′	rt tibia	2.94	4.43	−18.11	11.55	9.1	44.63	15.33	3.40
R18354	C. dirus	91	8′1″	rt tibia	3.01	6.25	−18.62	12.09	6.4	43.26	14.27	3.54
R24957	C. dirus	91	9′ 5″	rt tibia	2.27	5.22	−16.39	12.12	9.6	45.54	15.03	3.54
R24956	C. dirus	91	8′10″	rt tibia	2.92	7.09	−18.21	9.91	10.0	45.12	15.37	3.42
R27398	C. dirus	91	F11, 8′, 11.25″	rt tibia	2.40	28.88	−18.77	9.71	4.1	37.04	12.51	3.45
				Average	2.93	8.78	−18.62	11.35	4.6	41.85	13.91	3.51
				Std. dev.	0.30	4.72	0.85	1.15	3.3	3.93	1.19	0.13
W546	C. latrans	3	D4, 22	lt femur	2.56	6.38	−19.58	11.30	13.6	40.90	14.46	3.30
W9735	C. latrans	3	E4, 26	rt hum	2.84	9.59	−19.03	10.84	13.6	39.27	13.99	3.27
W5296	C. latrans	60	C13,13′	rib	3.06	14.07	−19.88	9.82	5.8	41.39	14.39	3.35
W573	C. latrans	61	C12, 17	lt femur	2.39	9.79	−20.08	10.83	12.4	38.37	13.15	3.40
W575	C. latrans	61	none	lt femur	1.84	10.87	−20.81	10.55	11.7	42.38	13.47	3.67
W589	C. latrans	67	none	lt femur	0.67	21.15	−20.31	11.17	6.1	31.95	11.01	3.39
W584	C. latrans	67	none	lt femur	3.36	8.15	−18.36	7.36	20.2	41.24	14.16	3.40
R11849	C. latrans	91	none	rt hum	1.94	9.55	−20.10	9.71	10	40.86	12.32	3.87
R11938	C. latrans	91	none	lt hum	1.85	6.18	−20.70	9.13	1.2	16.89	5.72	3.45
				Average	2.28	10.64	−19.87	10.08	10.5	37.03	12.52	3.46
				Std. dev.	0.81	4.60	0.79	1.25	5.6	8.16	2.78	0.19
X7061	P. leo atrox	3	E4, 21	lt innom	3.66	8.88	−17.94	12.05	18.7	44.39	15.21	3.40

Appendix A (*continued*)

Page Musm catalog no.	Species	Pit	Provenience	Skeletal element	Whole bone % N	% Weight loss	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	% Coll by weight	Coll wt.% carbon	Coll wt.% nitrogen	Atomic C/N
HC15241	P. leo atrox	3	D4, 20	lt innom	2.97	12.27	−18.74	10.62	10.8	42.21	14.98	3.29
X7096	P. leo atrox	60	E10, 12−15′	rt innom	3.94	12.50	−19.26	10.75	12.2	46.37	15.39	3.51
X7190	P. leo atrox	60	C10, 9−15′	rt innom	1.04	17.35	−20.11	10.13	0.4	30.53	9.39	3.79
X7113	P. leo atrox	61	south wall	rt innom	2.26	11.99	−19.30	8.70	10.1	43.19	14.01	3.60
X7098	P. leo atrox	61	A9, 20	rt innom	4.02	9.17	−18.56	12.34	21.1	40.67	15.17	3.13
X7117	P. leo atrox	67	SE, 16−19	rt innom	3.96	4.81	−19.20	12.42	18.6	41.43	15.00	3.22
R42380	P. leo atrox	91	F9, 8	lt innom	3.17	3.93	−18.31	12.34	16.6	41.16	15.18	3.16
				Average	3.13	10.11	−18.93	11.17	13.6	41.24	14.29	3.39
				Std. dev.	1.04	4.39	0.68	1.35	6.7	4.72	2.02	0.23
HC35353	S. fatalis	3	T4, 9′	rt radius	3.27	7.53	−19.01	11.93	12.0	45.62	15.48	3.44
HC35350	S. fatalis	3	none	rt radius	3.59	5.04	−18.93	10.47	3.0	44.37	15.10	3.43
HC35354	S. fatalis	3	F5, 9′	rt radius	3.49	7.42	−18.76	12.21	14.4	49.57	16.88	3.43
HC35349	S. fatalis	3	F3 and F5, 6.5′	rt radius	3.24	12.37	−19.10	12.04	7.0	46.01	15.42	3.48
HC35352	S. fatalis	3	5.75′	rt radius	3.43	34.49	−18.80	11.46	13.9	44.22	14.82	3.48
K2254	S. fatalis	60	D10, 12.5′	lt radius	2.89	10.59	−18.32	11.05	0.9	30.54	11.05	3.23
K2252	S. fatalis	60	C10, 11−13′	lt radius	3.24	5.15	−16.46	12.87	2.4	41.29	13.94	3.46
K2250	S. fatalis	60	C10, 11−13′	lt radius	2.60	15.90	−18.37	10.88	1.2	39.65	12.70	3.64
HC35770	S. fatalis	60	none	lt radius	2.08	13.81	−18.49	11.44	0.7	39.01	12.08	3.77
HC35771	S. fatalis	60	G12, 12−13′	lt radius	2.28	11.96	−18.67	11.43	1.9	41.05	13.13	3.65
HC35850	S. fatalis	61	A7, 18′	rt radius	3.51	10.82	−18.52	13.15	2.0	40.72	13.96	3.40
HC35847	S. fatalis	61	C11−12, 19−20′	rt radius	2.78	13.52	−18.68	13.16	5.1	44.72	14.37	3.63
K1807	S. fatalis	61	none	rt radius	3.37	7.85	−19.48	12.91	1.3	40.45	13.03	3.62
HC35846	S. fatalis	61	C15, 14−17′	rt radius	2.84	8.21	−18.82	12.10	6.6	45.36	14.53	3.64
HC35849	S. fatalis	61	F17, 13−15′	rt radius	1.38	13.17	−19.67	11.71	1.5	39.27	11.47	3.99
HC35905	S. fatalis	67	G10, 13−15′	lt radius	3.16	10.69	−19.09	11.16	5.0	44.13	15.32	3.36
HC35914	S. fatalis	67	G10, 13−15′	lt radius	2.71	15.14	−18.25	13.60	4.8	40.95	14.18	3.37
HC35915	S. fatalis	67	F8, 16−19′	lt radius	2.92	10.34	−19.13	12.70	12.7	45.44	15.26	3.47
HC35907	S. fatalis	67	none	lt radius	2.33	13.81	−19.70	11.87	8.9	43.28	13.78	3.66
HC35912	S. fatalis	67	G11, 13−17′	lt radius	3.01	6.41	−19.40	11.88	1.1	41.44	12.97	3.73
R17668	S. fatalis	91	8′	lt radius	3.11	9.75	−18.17	11.72	7.4	45.40	14.95	3.54
R12485	S. fatalis	91	5′11″	rt radius	2.62	7.01	−18.46	11.52	6.2	44.30	14.57	3.55
R18585	S. fatalis	91	8′1″	rt radius	1.31	8.28	−17.20	12.04	2.2	41.14	12.82	3.74
				Average	2.83	11.27	−18.67	11.97	5.3	42.52	13.99	3.55
				Std. dev.	0.62	5.95	0.73	0.79	4.4	3.72	1.42	0.17
Z1389	C. hesternus	3	E4, 21′	lt mt	3.10	12.29	−20.41	8.31	11.9	45.58	15.53	3.42
Z1117	C. hesternus	60	E12,12−13′	lt rad/ul	2.80	3.34	−19.62	7.53	4.0	44.01	14.67	3.50
Z1276	C. hesternus	61	B13, 14−18′	lt mt	3.51	4.79	−20.26	9.68	11.5	45.49	15.22	3.49
Z1273	C. hesternus	61	D13, 15′	lt mt	3.43	6.86	−20.72	8.97	12.9	43.93	15.14	3.39
Z1268	C. hesternus	61	none	lt mt	3.04	6.05	−21.00	9.85	8.5	37.85	12.66	3.49
Z1279	C. hesternus	61	D14, 14−18.5′	lt mt	1.01	23.48	−20.40	8.80	5.8	39.99	14.27	3.27
Z1281	C. hesternus	61	D7, 14−16′	lt mt	2.23	8.02	−20.63	8.99	1.1	38.46	12.24	3.67

none	*C. hesternus*	67	C15, 14.5–17.5′	rt hum	2.10	12.63	− 20.39	8.87	3.2	42.51	13.26	3.74
none	*C. hesternus*	67	D15–16, 8–10′	rt hum	2.27	18.61	− 20.46	9.79	7.3	44.99	15.04	3.49
none	*C. hesternus*	67	F4, 14–15′	rt hum	2.80	8.24	− 20.63	8.79	12.5	46.51	15.13	3.59
none	*C. hesternus*	67	F7, 14–20′	rt hum	2.60	6.70	− 20.79	8.41	9.4	44.85	15.12	3.46
none	*C. hesternus*	67	E8, 18.5–20′	rt hum	2.64	6.56	− 20.46	8.69	10.1	46.04	15.05	3.57
				Average	2.63	9.80	− 20.48	8.89	8.2	43.35	14.44	3.51
				Std. dev.	0.68	5.99	0.34	0.66	3.9	2.99	1.11	0.13
Z4629	*E. occidentalis*	3	E3, 20.5′	lt mt III	3.36	6.20	− 20.76	4.93	2.5	43.69	14.87	3.43
Z4628	*E. occidentalis*	3	E5, 22′	rt mt III	3.17	11.12	− 20.79	6.91	5.5	45.02	15.09	3.48
Z4642	*E. occidentalis*	3	E4, 21–27′	rt mt III	2.09	5.57	− 21.22	6.25	0.9	37.68	12.52	3.51
Z4561	*E. occidentalis*	3	E3, 21′	rt mt III	3.39	16.41	− 21.16	8.02	11.0	45.92	15.28	3.51
Z4719	*E. occidentalis*	60	8–9′	rt mc III	2.36	9.36	− 21.60	6.46	0.5	31.69	11.58	3.19
Z4800	*E. occidentalis*	60	E12, 12–14′	rt mc III	2.61	8.89	− 21.23	6.83	0.3	33.08	11.03	3.50
Z4591	*E. occidentalis*	61	C16, 13–18′	lt mt III	3.17	5.33	− 21.14	6.74	9.7	46.31	15.71	3.44
Z4599	*E. occidentalis*	61	D15, 14–17.5′	rt mt III	3.52	4.81	− 20.72	6.17	3.3	44.64	14.56	3.58
Z4602	*E. occidentalis*	61	E14, 14–16′	rt mt III	2.98	5.39	− 21.70	6.83	2.2	43.75	14.39	3.55
Z4612	*E. occidentalis*	61	F17, 13–16′	rt mt III	1.02	5.62	− 22.02	4.36	0.3	29.30	10.05	3.40
Z4620	*E. occidentalis*	67	none	rt mt III	3.14	3.72	− 21.16	6.09	14.3	45.44	15.43	3.44
Z4639	*E. occidentalis*	67	G11, 13–15′	rt mt III	3.38	4.41	− 21.71	6.29	7.3	47.63	15.83	3.51
Z4636	*E. occidentalis*	67	F7, 14–17′	rt mt III	3.02	5.37	− 21.61	4.72	1.2	39.31	12.73	3.60
Z4649	*E. occidentalis*	67	F7, 14–17′	rt mt III	3.04	5.80	− 21.19	7.61	3.1	44.33	14.27	3.62
Z4625	*E. occidentalis*	67	none	rt mt III	2.89	6.63	− 21.56	8.19	4.4	44.29	14.05	3.68
R37133	*E. occidentalis*	91	I11, 10′	rt mt III	2.61	6.23	− 21.18	5.78	3.7	45.14	14.56	3.62
R32957	*E. occidentalis*	91	9′	rt mt III	2.28	7.00	− 21.03	6.35	6.9	45.77	15.44	3.46
R28217	*E. occidentalis*	91	F11, 9′	lt mt III	2.17	4.95	− 20.98	3.98	2.5	41.30	14.02	3.44
R28300	*E. occidentalis*	91	F11, 9′	rt mt III	1.42	39.20	− 21.35	4.34	0.5	34.47	11.34	3.55
				Average	2.72	8.53	− 21.27	6.15	4.2	41.51	13.83	3.50
				Std. dev.	0.68	7.99	0.35	1.22	4.0	5.58	1.75	0.11
1713−L10	*P. harlani*	3	D4, 21–23	lt radius	3.21	5.51	− 20.70	7.34	10.2	43.70	14.97	3.41
none	*P. harlani*	3	D5, 21.5	rt radius	2.34	17.50	− 20.38	6.44	16.7	38.97	13.61	3.34
none	*P. harlani*	3	E5, 16–19	rt radius	2.41	11.84	− 21.16	6.74	11.2	41.60	14.23	3.41
1713−L29	*P. harlani*	60	E12, 12–13′	radius (ss)	2.37	9.80	− 20.66	7.20	2.1	38.32	13.18	3.39
1713−R25	*P. harlani*	60	D12, 16–18′	radius (ss)	1.75	17.88	− 19.99	10.12	1.1	37.08	12.47	3.47
1713−L25	*P. harlani*	61	none	lt radius	2.75	8.76	− 21.41	8.61	9.9	41.34	14.13	3.41
1713−R26	*P. harlani*	67	none	rt radius	3.06	7.17	− 21.49	9.52	13.9	42.31	15.09	3.27
none	*P. harlani*	67	none	rt radius	1.71	23.31	− 21.27	8.52	2.9	35.15	12.31	3.33
HC13872	*P. harlani*	91	none	lt radius	2.27	7.26	− 21.48	8.19	5.1	42.47	14.26	3.48
HC38414	*P. harlani*	91	none	lt radius	2.26	8.43	− 21.36	6.65	5.0	39.91	13.48	3.45
				Average	2.41	11.75	− 20.99	7.93	7.8	40.09	13.77	3.40
				Std. dev.	0.49	5.85	0.52	1.26	5.3	2.69	0.95	0.07
Y2450	*B. antiquus*	3	D5, 21.5	rt mc	2.65	4.79	− 19.40	7.67	8.6	44.34	15.13	3.42
Y2427	*B. antiquus*	3	E4, 18–22	rt mc	3.13	3.84	− 19.80	8.37	15.7	44.23	14.91	3.46
Y5507	*B. antiquus*	3	D5, 18	rt mc	2.71	6.07	− 19.43	7.64	12.3	42.20	14.83	3.32

Appendix A (*continued*)

Page Musm catalog no.	Species	Pit	Provenience	Skeletal element	Whole bone % N	% Weight loss	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	% Coll by weight	Coll wt.% carbon	Coll wt.% nitrogen	Atomic C/N
Y2260	*B. antiquus*	60	C12, 12.5′	lt mt	2.14	4.23	−20.38	8.13	1.1	41.77	13.66	3.57
Y2235	*B. antiquus*	60	8−9′	lt mt	1.57	16.40	−20.72	8.76	0.1	33.20	10.94	3.54
Y2313	*B. antiquus*	60	C10, 10−12′	lt mt	1.93	5.46	−19.91	8.98	0.2	39.20	12.84	3.56
Y5486	*B. antiquus*	61	F13, 14−16	lt mc	2.25	6.83	−19.99	8.69	7.1	43.67	14.36	3.55
HC23969	*B. antiquus*	61	A13, 14−18	lt mc	2.87	6.69	−20.93	8.23	15.7	42.64	14.24	3.49
Y5484	*B. antiquus*	61	B16, 14.5−18	lt mc	2.28	7.01	−20.60	9.58	10.2	43.87	14.70	3.48
HC23970	*B. antiquus*	61	G14, 4−5	lt mc	2.43	3.85	−20.63	10.00	10.4	46.11	14.68	3.67
HC23974	*B. antiquus*	67	none	rt mc	1.88	11.23	−21.17	11.01	7.1	45.48	14.41	3.68
Y2421	*B. antiquus*	67	H9, 15−18.5	rt mc	3.06	2.42	−20.35	8.39	10.6	45.44	15.21	3.49
Y2432	*B. antiquus*	67	H9, 15−18.5	rt mc	2.65	4.84	−20.42	9.66	10.9	44.97	14.67	3.58
HC36190	*B. antiquus*	91	L11	rt mt	1.11	12.46	−20.80	11.19	0.4	31.82	9.64	3.85
HC33276	*B. antiquus*	91	N11	lt mt	2.27	8.01	−19.79	9.21	9.9	42.21	13.54	3.64
HC46647	*B. antiquus*	91	I6	lt mt	1.88	6.89	−20.04	9.06	7.1	42.87	13.94	3.59
HC36876	*B. antiquus*	91	J11	lt mt	2.72	5.05	−19.11	9.89	12.0	44.21	15.29	3.37
				Average	2.33	6.83	−20.20	9.09	8.2	42.25	13.94	3.54
				Std. dev.	0.54	3.55	0.58	1.04	5.1	4.03	1.53	0.13
Z1078	*M. americanum*	3	8.5−9	dist radius	2.20	12.20	−20.02	5.09	12.7	45.26	14.72	3.59
HC60247	*M. americanum*	3	D4, 21−22	lt mt III	3.27	9.94	−19.98	4.44	15.3	42.08	14.78	3.32
HC60227	*M. americanum*	3	E3, 20−22	rt mt II	3.01	12.52	−19.87	4.35	13.0	39.55	14.51	3.18
HC85229	*M. americanum*	61	B11, 14−18	rt mt III	2.69	15.47	−20.53	4.21	7.1	38.96	14.06	3.23
HC85217	*M. americanum*	61	B11, 14−18	lt mt II	3.34	13.32	−20.46	4.16	15.9	43.47	14.28	3.55
HC85216	*M. americanum*	67	none	lt lunar	3.22	15.25	−20.72	4.27	14.6	41.71	14.41	3.38
HC85219	*M. americanum*	67	none	rt magnum	2.90	12.21	−20.78	4.34	13.6	41.45	14.29	3.38
				Average	2.95	12.99	−20.34	4.41	13.2	41.78	14.44	3.38
				Std dev	0.40	1.92	0.37	0.31	2.9	2.16	0.26	0.15
Z8573	*C. minor*	unkn	none	frags	not run	6.67	−20.52	9.33	7.1	35.91	12.47	3.36

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