Dietary ecology of Pleistocene camelids: Influences of climate, environment, and sympatric taxa

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ABSTRACT

Wild members of Camelidae live in some of the most arid environments, including North Africa, Arabia, the Gobi Desert of China and Mongolia and high elevation environments in the Andes Mountains. A better understanding of the paleoecology of the three most abundant Pleistocene camelids (*Camelops*, *Hemiauchenia*, and *Palaeolama*) may clarify modern adaptations to arid environments. Mammalian tooth enamel δ^{13}C values were used to compare diets of co-occurring species in California, Texas, and Florida and δ^{18}O values were used to investigate climate. Carbon isotope analysis suggests *Camelops* was likely an opportunistic browser that consumed both C_3 and C_4 browse/CAM plants, potentially consuming C_4 browse (e.g., saltbush). *Hemiauchenia* had an opportunistic and highly generalized diet, while *Palaeolama* was a specialized forest browser. Stable oxygen isotopes and aridity index values suggest that Ingleside was warmer than McKittrick Brea, but there are no significant differences in aridity between the two sites. Co-occurrence data from the Paleobiology Database suggest that *Palaeolama* was restricted to forested environments as it occurred with two browsers, *Tapirus* and *Odocoileus,* at 90.5% of all sites. *Camelops* and *Hemiauchenia* both co-occurred with a broader range of taxa, further suggesting these camelids lived in diverse habitats. The generalized diet of *Hemiauchenia*, the likely ancestor of modern South American camelids, allowed for the adaptations of extant *Lama* and *Vicugna* to survive in the arid environments of the Andes Mountains. Collectively, these data clarify the dietary ecology of extinct camelids and provide insight into the potential importance of generalist diets for increased resilience to changing environments and/or climates.

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1. Introduction

Modern camelids are the last survivors of a more diverse group of late Neogene camelids that had a much broader geographic distribution in the Americas. A reliance on low quality vegetation and water acquired from their diet allows camelids to live where few other large animals could survive (Bas and Bonacic, 2003). Understanding the paleoecology of recently extinct camelids may reveal how these extant animals adapted to arid environments and may provide insights for their conservation in the face of changing climates. During the Pleistocene, *Camelops*, *Hemiauchenia*, and *Palaeolama* were the three most abundant camelid genera in North America (Honey et al., 1998; Paleobiology Database 18 March, 2013). Although many studies have looked at the paleoecology of multiple genera (e.g., Dompierre and

Churcher, 1996; Meachen, 2003; Kohn et al., 2005; DeSantis et al., 2009; Semprebon and Rivals, 2010; Yann and DeSantis, 2014), there are no direct comparisons of the stable isotope ecology of *Camelops*, *Hemiauchenia*, and *Palaeolama*.

Here, we aim to clarify the paleoecology of Pleistocene camelids by investigating the diets of *Camelops*, *Hemiauchenia*, and *Palaeolama* and co-occurring herbivores. These results will be used to address the following questions: 1) How does a camelid's dietary strategy, which may be generalized or specialized, influence the dietary ecology and/or co-occurrence of genera from the same family?; 2) Can we predict the occurrence of camelids based on the occurrence of other mammalian taxa, including the presence/absence of inferred obligate browsers or obligate grazers?; and, 3) Has the feeding ecology of Pleistocene camelids influenced the modern distributions of Lamini camelids?

1.1. Stable isotopes for dietary and environmental reconstructions

Diets and regional climates can be assessed using stable isotope values from mammalian tooth enamel (e.g., Koch, 1998; MacFadden, 2000; Kohn and Cerling, 2002). Stable carbon isotopes in tooth enamel

track the isotope composition of herbivorous diets with a 14.1 ± 0.5‰ enrichment between the tooth enamel of medium- to large-bodied herbivorous mammals (i.e., ungulates and proboscideans) and vegetation consumed (DeNiro and Epstein, 1978; Cerling and Harris, 1999). Enamel is primarily inorganic and is less prone to diagenesis than other tissues like bone or dentin, thus it is ideal for isotopic analysis (Wang and Cerling, 1994; MacFadden et al., 2010). Further, when whole communities are sampled, it is possible to reconstruct dietary partitioning and available habitat types (e.g., Cerling et al., 1997; DeSantis et al., 2009).

Before reconstructing diets from tooth enamel isotope values, the regional abundance of C_3, C_4, and CAM vegetation must be considered. C_3 grasses typically grow in areas with cooler and wetter growing seasons, such as higher latitude sites in North America, and $\delta^{13}C$ values range from −33‰ to −22‰ with a mean of −27‰ (e.g., Paruelo and Lauenroth, 1996; Cerling et al., 1997). C_4 grasses typically dominate in areas with high growing season temperatures and $\delta^{13}C$ values range from −19‰ to −9‰ with a mean of −13‰ (e.g., Paruelo and Lauenroth, 1996; Cerling et al., 1997). While most shrubs use the C_3 photosynthetic pathway, the distribution of C_4 shrubs, such as *Atriplex* (saltbush), and CAM plants can also influence diet and regional environmental interpretations.

Data presented in this study are from sites in Florida (Haile 8A, Tri-Britton, Inglis 1A, and Leisey Shell Pit 1A, hereafter referred to as Leisey 1A; DeSantis et al., 2009; Yann and DeSantis, 2014), the Gulf Coast of Texas (Ingleside), and the southern portion of the San Joaquin Valley in California (McKittrick Brea). A mean $\delta^{13}C$ value of −0.7‰ from *Bison* enamel (a morphologically inferred grazer; e.g., Janis and Ehrhardt, 1988) suggests C_3 grasses were likely rare at Ingleside and Haile 8A (consistent with the model in Paruelo and Lauenroth, 1996). This suggests tooth enamel $\delta^{13}C$ values of ≤ −8‰ are indicative of a predominately C_3 tree or shrub diet and values between −8‰ and −2‰ suggest a mixed feeding diet with varying proportions of C_3 and C_4 vegetation. Carbon values of ≥ −2‰ suggest reliance on C_4 grasses. These values are not cutoff points for pure C_3 and C_4 diets, but instead represent diets that are dominated by one particular photosynthetic pathway after taking into account the ^{13}C-enrichment between plants and tooth enamel (Friedli et al., 1986; Marino and McElroy, 1991; Marino et al., 1992; Cerling et al., 1997; Passey et al., 2005).

In California, C_3 grasses like *Nassella pulchra* (purple needlegrass) dominated the San Joaquin Valley prior to the peak of heavy grazing between the 1840s and 1860s (Burcham, 1961), while C_4 grasses dominated the Sonoran and Chihuahuan deserts (e.g., Woodward, 2008). In addition to C_4 grass, there is also the possibility that C_4 shrubs like *Atriplex* (saltbush), or CAM plants, contributed to Pleistocene diets.

Modern camels prefer *Atriplex*, *Acacia*, and *Salsola* (saltwort; Williamson and Payne, 1978), and will even choose dried out pasture over dense succulent vegetation (Yagil, 1986). Camels are able to eat these salty plants and drink brackish water due to their ability to concentrate urine (Ayoub and Saleh, 1998). *Atriplex* is one of the few salt tolerant C_4 shrubs that are common in the United States. Molecular evidence suggests that *Atriplex* arrived in North America between 9.8 and 8.8 million years ago (Kadereit et al., 2010), and is still found in North America. Of the 113 modern species, 71 species are native to the United States and Canada; only one species is found in Florida, 15 species in Texas (predominately west Texas), and 37 species in California (USDA and NRCS, 2014). Only a few studies have assessed Pleistocene distributions of *Atriplex*, but there is evidence of *Atriplex* in the Mojave Desert 20,000 years ago and potentially even older specimens have been found in the Great Basin (~25–30 Ka) and at McKittrick Brea (~30–5.2 Ka; *Atriplex lentiformis*; Mason, 1944; Thompson, 1979; Van Devender and Spaulding, 1979). There also appears to be an increase in *Atriplex* abundance during the early Holocene, as suggested by pollen records (Louderback and Rhode, 2009).

As it has been hypothesized that succulents and megafauna coevolved (Janzen, 1986), CAM plants must be considered when discussing the diets of Pleistocene camelids. A modern example of a succulent used as forage by livestock is *Opuntia*, or prickly pear, which is the state plant of Texas. While succulents make up ≤2% of relative biomass at 93% of 73 grassland and shrubland sites in temperate North America, at 3 of these sites they made up between 7% and 38% relative biomass, with the latter occurring at Black Gap Wildlife Management Area in western Texas (just outside Big Bend National Park; Paruelo and Lauenroth, 1996). However, modern, cold winters in the Great Basin, Mojave, and Chihuahuan deserts limit the abundance of succulents (e.g., Dimmit, 2000); suggesting their abundance may have been further limited during glacial times.

While $\delta^{13}C$ values track an animal's diet, stable oxygen isotope values track the water consumed by an animal either through active drinking or through the consumption of leafy vegetation (Longinelli, 1984; Luz et al., 1984; Bryant and Froelich, 1995; Kohn, 1996). Stable oxygen isotope values are influenced by an animal's physiology, the region's climate, elevation, continentality, and the original water source (Dansgaard, 1954, 1964; Longinelli, 1984; Luz et al., 1984; Kohn, 1996; Kohn and Cerling, 2002; Levin et al., 2006). Taxa that drink surface water track changes in meteoric water and are referred to as evaporation insensitive (or less sensitive), as their $\delta^{18}O$ values are less affected by changes in aridity. In contrast, $\delta^{18}O$ values of taxa that get most of their water from plants are affected by increased evaporation in leaf water during periods of water deficit and are termed evaporation sensitive.

Perhaps the strongest link between environmental conditions and mammalian $\delta^{18}O$ values relates to the observation that meteoric water $\delta^{18}O$ values are positively correlated with mean annual temperature across space and through time (Dansgaard, 1964). Therefore, mammals have lower $\delta^{18}O$ values in colder locations (or time periods) and higher $\delta^{18}O$ values in warmer locations (or time periods) (Dansgaard, 1964; Luz et al., 1984; Ayliffe et al., 1992). As water deficits can affect the $\delta^{18}O$ values of some mammals, by careful choice of taxa for analysis, the effects of local temperature and aridity can be disentangled. For example, proboscideans have been hypothesized to be evaporation insensitive due to their need to drink large quantities of water and this has been verified by the lack of significant changes in $\delta^{18}O$ values with increased water deficits in modern Africa (Levin et al., 2006). Average proboscidean $\delta^{18}O$ values can be used as a baseline for meteoric water and a relative aridity index for each site can be established by calculating $\Delta^{18}O_{ES-EI}$ values (equal to $\delta^{18}O_{evaporation\ sensitive} - \delta^{18}O_{evaporation\ insensitive}$; $\delta^{18}O_{evaporation\ insensitive}$ = site-specific proboscidean value, Yann et al., 2013).

1.2. Camelid distribution and diet

Camelidae, the family containing extant Camelini camels (true camels; Bactrian and dromedary camels) and Lamini camelids (vicuñas, guanacos, llamas, and alpacas), provides an interesting opportunity to investigate successful adaptations to arid environments. Wild members of Camelidae are found in some of the most arid environments, including the Gobi Desert of China and Mongolia and high elevation environments in the Andes Mountains of Argentina, Bolivia, Chile, and Peru (e.g., Baldi et al., 2008; Hare, 2008; Lichtenstein et al., 2008). The unique ability of all extant camelids to survive in arid conditions may have significant evolutionary and conservation implications (e.g., Aranguren, 1930; Cabrera, 1932; Webb, 1965, 1974; Harrison, 1979, 1985). Camelidae evolved in North America during the middle Eocene and the ancestor of true camels migrated to Eurasia and Africa during the mid/late Miocene (e.g., Pickford, 1993; Pickford et al., 1995; van der Made et al., 2002; Vislobokova et al., 2003; Titov and Logvynenko, 2006). Another major immigration event within Camelidae occurred when *Hemiauchenia* migrated to South America during the latest Pliocene or early Pleistocene (Webb, 1974; Marshall et al., 1982). North American members of Camelidae, lamini *Hemiauchenia* and *Palaeolama* and camelini *Camelops*, went extinct at the end of the Pleistocene, while