DIET AND WATER SOURCE OF PLEISTOCENE LAMINI CAMELIDS BASED ON STABLE ISOTOPES OF TOOTH ENAMEL: IMPLICATIONS FOR NORTH AMERICAN VEGETATION AND PALEOCLIMATE

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To

Melissa Talley,

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and my family for supporting me

when many did not.

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Chapter 1

INTRODUCTION

Climate change is currently occurring at an unprecedented rate and is having profound effects on organisms across the globe (e.g., Gellesch et al., 2013). Past and current changes have been documented as alterations of diversity, abundance, dietary niches, speciation, and extinction (e.g. Barnosky et al., 2004; Koch and Barnosky, 2006; DeSantis et al., 2009; Blois et al, 2010; Figueirido et al., 2012). However, it is particularly challenging to predict how organisms will respond to climatic changes (e.g. Brown et al., 1997; Araujo and Rahbek, 2006; Schloss et al., 2012).

To better understand how future climatic changes may influence mammals and their floral and faunal communities, paleoenvironmental and paleoecological research often looks back to periods of geologically rapid warming such as the Paleocene Eocene Thermal Maximum (e.g. Gingerich, 2003; McInerney and Wing, 2011; Secord et al., 2012) or to periods of cyclic change like the Pleistocene glacial and interglacial periods (e.g. Barnosky, 2005; Lister and Stuart, 2008; DeSantis et al., 2009). Although Pleistocene communities are non-analogous when compared to modern ecosystems and communities, most Pleistocene taxa belong to families with modern descendants. While these modern taxa are often not found in the same regions as their Pleistocene ancestors, Pleistocene fossil assemblages are invaluable to the understanding of mammalian responses to climate change. Further, glacial and interglacial periods also provide the opportunity to investigate the consistency of mammalian adaptations to changing climates or environments (Koch et al., 1998; DeSantis et al., 2009).

1.1. Stable isotopes as a tool for inferring past environments and climates

A variety of mammalian tissues, including hair, bone, and teeth, have been used for modern, archeological, and paleontological reconstructions (e.g. Ayliffe and Chivas, 1990; O'Connell et al., 2001; Kohn and Cerling, 2002; Crawford et al., 2008). Specifically, mammalian tooth enamel allows for paleoecological reconstructions of diet, climate, and relative aridity during the Pleistocene. Mammalian tooth enamel is often used to reconstruct the environment and the climate of Pleistocene fossil sites as the crystals are larger, more densely packed, and contain less organic matter, as compared to tissues such as bone and dentin which are more prone to diagenetic alteration (e.g. Ayliffe et al., 1994, Bryant et al., 1994; Fricke et al., 1996). Additionally, enamel represents discrete intervals of growth and can be used to infer average dietary and climate information or seasonal variability. Typically, two sampling strategies are used, bulk and serial sampling (Figure 1). Bulk samples are taken parallel to the growth axis and provide an average value for the whole tooth. Serial samples are taken perpendicular to the growth axis and provide values for distinct periods during the mineralization of the tooth. The inclusion of multiple samples per tooth allows investigations into changes in climate and diet over the time it takes a tooth to mineralize. Depending on the taxon sampled, one tooth can represent a few months to a year or more of time. The incorporation of both bulk and serial samples allow for investigations into the diet, ecology, and seasonality of the sites being sampled.

1.1.1. Stable Carbon isotopes

Stable carbon isotope ($\delta^{13}C$) values from mammalian tooth enamel can be used to clarify our understanding of past environments as $\delta^{13}C$ values reflect the photosynthetic pathway of vegetation consumed (e.g. DeNiro and Epstein, 1978; Krueger, 1991; Lee-Thorp and van der Merwe, 1991; Cerling et al., 1997; Cerling and Harris, 1999). C_4 vegetation includes warm season grasses and some shrubs, like saltbush, with $\delta^{13}C$ values ranging from -20‰ to -10‰ (Bender, 1971). C_3 vegetation includes cool season grasses, trees, and most shrubs with $\delta^{13}C$ values that range from -33‰ to -22‰, and denser forests have more negative values (e.g. Bender, 1971; van der Merwe and Medina, 1991). Tooth enamel $\delta^{13}C$ values record the relative proportion of C_3 and C_4 vegetation in an animal's diet, but there is also enrichment between an animal's diet and the tooth enamel values (e.g. DeNiro and Epstein, 1978; Cerling and Harris, 1999). Tooth enamel values of medium to large bodied ungulates are enriched by ~14.1‰, as compared to dietary $\delta^{13}C$ values, which means that tooth $\delta^{13}C$ values of about -2‰ to +4‰ indicate a diet dominated by C_4 vegetation and -19‰ to -8‰ indicate a diet dominated by C_3 vegetation (Cerling and Harris, 1999). Incorporation of both C_3 and C_4 vegetation will result in tooth enamel values between -8‰ and -2‰ (Cerling et al., 1997).

The abundances of C_3 and C_4 grasses in modern environments are based on growing season temperatures and precipitation (Teeri and Stowe, 1976; Connin et al., 1998; Holmgren, 2007). In the United States, C_3 grasses dominate the west coast and much of the mid and northern part of the country (Teeri and Stowe, 1976). Exceptions include a dominance of C_4 grass in the Sonoran and Chihuahuan deserts, the Gulf Coast region, and Florida, where they make up 80%+ of the grasses present (Long and Lakela, 1971; Teeri and Stowe, 1976; Woodward, 2008). Typically, trees and shrubs utilize the C_3 photosynthetic pathway, but in the western United States C_4 shrubs, like *Atriplex* (saltbush), can also play a substantial role in the diet of herbivores (Vetter, 2007; USDA, NRCA, 2014).

1.1.2. Stable oxygen

Stable oxygen ($\delta^{18}O$) isotope values from mammalian tooth enamel reflect water consumption, be it through active drinking or through the consumption of plant water (Longinelli, 1984; Luz et al., 1984; Bryant and Froelich, 1995; Kohn, 1996). Additionally, $\delta^{18}O$ values are influenced by geographic and climatic variables, including elevation, continentality, temperature, and precipitation (e.g. Dansgaard, 1964; Ayliffe and Chivas, 1990). Increasing elevation decreases $\delta^{18}O$ values by 2.0±1.0‰ per kilometer and increasing latitude decreases $\delta^{18}O$ values by 0.002±0.001‰ per kilometer (Dansgaard, 1964; Criss, 1999; Poage and Chamberlain, 2001). Decreases in $\delta^{18}O$ values also occur as you move inland, while the effect is more variable, the average is 0.002±0.002‰ per kilometer (Criss, 1999). Stable oxygen isotope values also vary due to changes in ambient temperature and interactions between temperature and precipitation known as the "amount effect" (Dansgaard, 1964). In regions that typically experience temperatures below 20ºC, temperature has the greatest influence on $\delta^{18}O$ values, causing a 0.7‰ increase per degree centigrade of temperature increase (Dansgaard, 1964). At lower latitudes with temperatures above 20ºC, $\delta^{18}O$ values are influenced by the amount of precipitation ("amount effect"), with higher humidity and rainfall contributing to lower $\delta^{18}O$ values (Dansgaard, 1964; Higgins and MacFadden, 2004). The original source of water also influences $\delta^{18}O$ values as different water sources are subjected to differing amounts of precipitation and evaporation (Dansgaard, 1964).

The influence of evaporation can also be seen in the water found in leafy vegetation, with greater evaporation leading to more positive $\delta^{18}O$ values (e.g. Ayliffe and Chivas, 1990; Kohn et al., 1996; Levin et al., 2006). These evaporative increases are then transferred to the organisms eating the vegetation, and therefore can be used to better understand the aridity of a site or region

(Levin et al., 2006). An aridity index can be used to separate the influences of temperature and aridity/precipitation on $\delta^{18}O$ values (Levin et al., 2006).

1.2. The Importance and Evolution of Camelidae

Camelidae, the family containing modern Bactrian camels, dromedary camels, vicunas, guanacos, lamas, and alpacas, provides an interesting opportunity to investigate successful adaptations to arid environments. Wild members of Camelidae are found in some of the driest and harshest environments including the Gobi Desert of China and Mongolia and high elevation environments in the Andes Mountains in Argentina, Bolivia, Chile, and Peru (e.g. Baldi et al., 2008; Hare, 2008; Lichtenstein et al., 2008). While modern wild camels are restricted to South America and Asia, the unique ability of all extant camelids to adapt to harsh conditions may have significant evolutionary and conservation implications (e.g. Aranguren, 1930; Cabrera, 1932; Webb, 1965, 1974; Harrison, 1979, 1985). Camelidae, as a family, originated in North America during the middle Eocene where it remained until the late Miocene when true camels (*Camelus*) immigrated to Eurasia, and eventually to Africa (Pickford et al., 1993, 1995). The family further migrated into South America during the late Pliocene or early Pleistocene (Webb, 1974; Marshall et al., 1982). Interestingly, North American members of Camelidae went extinct with many other large bodied mammals at the end of the Pleistocene while modern representatives are found in South America and Asia (Webb, 1974).

Modern members of Camelidae only represent one subfamily, Camelinae (Miocene-Present), but past subfamilies also included Stenomylinae (Oligocene-Miocene), Floridatragulinae (Eocene-Miocene), Miolabinae (Miocene), and Protolabinae (Miocene; Honey et al., 1998). Camelinae can be further subdivided to separate modern old world camels from modern new world camelids

(Honey et al., 1998). Dromedary and Bactrian camels belong to the tribe (taxonomic unit between family and genus) Camelini, which is represented by *Camelus* during the Pleistocene (Honey et al., 1998). South American taxa are referred to as camelids and belong to the tribe Lamini. Pleistocene Lamini camelids include *Blancocamelus*, *Camelops*, *Hemiauchenia*, and *Palaeolama* (Honey et al., 1998). One phylogenetic tree created using cranial, dental, and postcranial characters, illustrates the relationship of the modern genera (*Camelus*, *Lama*, *Vicugna*) to Pleistocene genera (*Camelus*, *Camelops*, *Hemiauchenia*, *Palaeolama*; Figure 2; Scherer, 2013). Other trees, based on similar characteristics, show a similar relationship, but also include *Blancocamelus* (Honey et al., 1998). Regardless of differences in the phylogenetic relationships within Lamini camelids, this work can provide insight into the diet and ecology of this tribe of camelids. This dissertation focuses on the well-represented Pleistocene genera, including *Camelops*, *Hemiauchenia*, and *Palaeolama*, to better understand the paleoecological history of the ancestors of modern South American camelids.

Modern camelids, including wild vicunas and guanacos, have evolved the ability to live in harsh environments of the arid, high elevation Andes Mountains through modifications to their use of body water, the ability to acquire the majority of their water from the food they eat, and their reliance on low quality forage (Kay and Maloiy, 1989; San Martin and Bryant, 1987; Bas and Bonacic, 2003; Gonzalez et al., 2006; Borgnia et al., 2010). Members of Camelidae are able to concentrate their waste products more efficiently than other medium- to large-bodied mammals (Kay and Maloiy, 1989). Another adaptation that allows camelids to live in harsh environments is their ability to use plant water to fulfill their water requirements, which allows them to go much longer without actively drinking (Borgnia et al., 2008). While camelids are opportunistic feeders that will consume high quality vegetation when available, their ability to utilize low quality vegetation allows them to survive in areas where many other large animals cannot (Bas and Bonacic, 2003; Gonzalez et al., 2006; Borgnia et al., 2010). It is also suggested that more efficient digestion means that camelids can consume less vegetation than other animals of similar size (San Martin and Bryant, 1987). While the diet and environment of modern camelids is well understood, it is not clear how the Pleistocene ancestors transitioned from more hospitable environments in North America to the high elevation deserts of South America.

1.3. Objectives and Research Questions

While previous studies have looked at the diet of individual camelids, little work has focused on the dietary modifications of the Pleistocene camelids in response to changing climates and environments (exceptions include Feranec, 2003; DeSantis et al., 2009). This dissertation provides a better understanding of the isotopic ecology of Lamini camelids and their modifications and responses to past climates and environments by addressing the following questions:

- Are camelids sensitive to changes in climatic conditions?
- Can camelids document changing climatic regimes in paleontological records?
- How are dietary niches of camelids and other co-occurring mammals impacted by increasing evaporative conditions and competition?
- How is the dietary breadth of Pleistocene camelids impacted by coexisting camelids and sympatric taxa?
- Can the suite of taxa at a given site be used to predict the presence of camelids?

- How has the feeding ecology of Pleistocene camelids potentially played a role in the modern distribution of Lamini camelids?

Previous work has suggested that camelids may be sensitive to environmental change, but this has not been directly tested. Thus, chapter 2 aims to assess if members of Camelidae, specifically Lamini camelids, are sensitive to changing environmental and climatic conditions. Subsequently, this method was also applied to all sites examined in chapters 3 and 4. Chapter 2 uses previously published stable oxygen isotope values to further develop an aridity index for North American Pleistocene taxa. This work identifies Pleistocene taxa that track changing environmental conditions, which are then used to quantify the regional environmental and climatic conditions for the southwestern and southeastern United States. The second chapter also investigates the influences of a taxon's diet on their sensitivity to changing environmental conditions. The focus of chapter 3 is to explore the influences of increasing evaporative conditions and changing environments on the diet of Pleistocene camelids and their fossil communities in Florida. Stable carbon and oxygen isotope values are used to characterize two Pleistocene community sites, including comparing the paleoenvironmental conditions and relative aridity to two previously published Florida sites. Collectively, the examination of four fossil localities in Florida can provide insights regarding camelid ecology, especially throughout the Pleistocene and when occurring during potentially different climatic regimes. Chapter 4 aims to clarify the isotope ecology of the three most common Pleistocene Lamini camelids, while investigating how the presence of a second camelid influences a camelid's dietary strategy. Using data from the Paleobiology Database, chapter 4 also aims to investigate which taxa co-occur with each camelid; this may identify a suite of taxa that are indicative of the preferred environmental conditions of each of the camelids.

As a whole, this dissertation aims to improve understandings of Pleistocene Lamini camelid ecology, while potentially providing insight into the influences of their paleoecology on distributions of modern taxa. Using stable carbon and oxygen isotopes, this work aims to determine the influences of climate, environmental change, and sympatric taxa on the diet and dietary modifications of *Camelops*, *Hemiauchenia*, and *Palaeolama*. Additionally, this work develops a method to identify changes in relative aridity through time in North America, and globally. Collectively, the integration of geochemical tools from Pleistocene sites aims to provide a better understanding of the ancestors of modern South American camelids and of changing climates during the Pleistocene.

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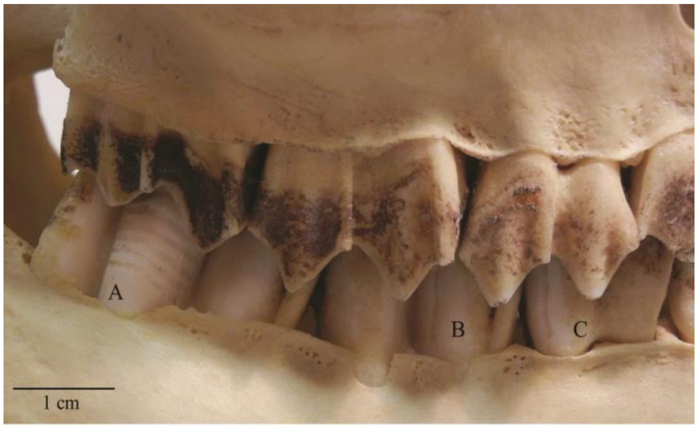

Figure 1.1. Examples of sampling techniques on a modern camelid, *Lama guanacoe*. A. serial samples; B and C. bulk samples.

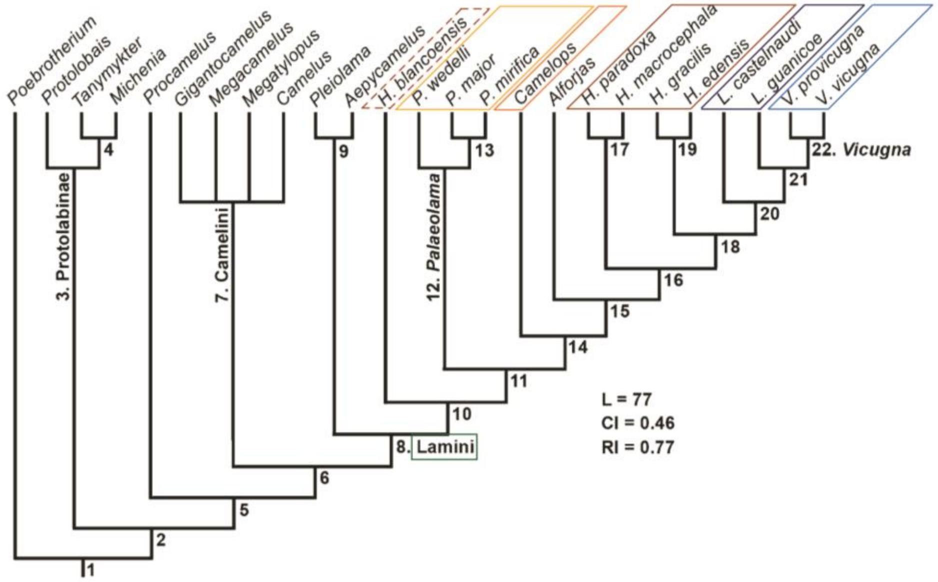

Figure 1.2. Relationships of Camelidae based on cranial, dental, and postcranial characteristics. Modified from Scherer, 2012. Modern Lamini camelids are outlined in cool colors (blue) and Pleistocene taxa included in this study are in warm colors (orange, yellow).

Chapter 2

THE APPLICATION OF AN OXYGEN ISOTOPE ARIDITY INDEX TO TERRESTRIAL PALEOENVIRONMENTAL RECONSTRUCTIONS IN PLEISTOCENE NORTH AMERICA

2.1. Introduction

Global climates during the Pleistocene were generally colder than in all previous Cenozoic epochs and were characterized by the presence of cyclical climatic regimes and permanent ice sheets in both the Northern and Southern Hemispheres (Zachos et al. 2001). Antarctic ice cores record cyclical glacial and interglacial periods over the past 800,000 years (Lambert et al. 2008); however, these conditions have likely been occurring since the onset of the Pleistocene ~2.6 Myr ago (Zachos et al. 2001; Walker and Geissman 2009). The presence of both boreal vegetation and mammals in the southeastern United States during the Pleistocene suggests cooler periods, especially during the Last Glacial Maximum (Voorhies 1974; Graham 1976; Delcourt 2002). During other periods in the Pleistocene (i.e., early to mid-Wisconsin, prior to 22 Ka) the vegetation and vertebrate remains from the Southeast indicate a temperate climate (e.g., Russell et al. 2009), possibly even warmer than today (e.g., Holman 1980). Precipitation estimates for the Pleistocene also vary throughout North America and suggest both wetter and drier precipitation regimes, relative to today (e.g., Leigh and Feeney 1995; DeSantis et al. 2009; LaMoreaux et al. 2009). In the southwestern United States, soil data suggest drier yet monsoonal climates during the early Pleistocene (Smith et al. 1993). Southwestern climates were cooler than today, possibly typified by cooler summers and milder winters (Van Devender and Spaulding 1979; Zachos et al. 2001) with highly variable precipitation (e.g., Metcalfe et al. 2002). Given the stark contrasts with modern regional climates and environments, a detailed understanding of biotic responses to past climate changes requires a comprehensive understanding of regional climates through time.

Although little is known about the variability of Pleistocene regional climates or the consequent effects on biotic communities, quantifying relative climatic and environmental differences between the southeastern and southwestern United States can clarify driving mechanisms for floral and faunal abundances. Stable carbon and oxygen isotope values from mammalian tooth enamel carbonate can be used to investigate regional paleoclimates and paleoenvironments. When reconstructing paleoenvironments from mammalian tooth enamel we are interested in relative abundances of plants that use the C_4 photosynthetic pathway (i.e., warm-season grasses) and those that use the C_3 photosynthetic pathway (i.e., cool-season grasses, shrubs, and trees) which can be interpreted from $\delta^{13}C_{enamel}$ values. Modern C_4 vegetation is typified by $\delta^{13}C$ values that range from −22‰ to −33‰ (Bender 1971). Carbon isotope values of modern C_3 vegetation instead range from −10‰ to −20‰ (Bender 1971), with more negative values often indicative of closed forest environments (e.g., van der Merwe and Medina 1991). In a given environment, there is typically a difference of 12–14‰ between plants photosynthesizing via the two different pathways (Bender 1971).

The distribution of C_3 and C_4 plants is often linked to atmospheric carbon dioxide levels, temperature, aridity, or season of precipitation (e.g., Kemp 1983; Paruelo and Lauenroth 1996; Connin et al. 1998; Holmgren 2007). C_4 grasses today are typically abundant in warmer and/or drier climates. However, it is unclear whether aridity, temperature, or season of precipitation was a greater driver of C_4 abundance during the Pleistocene. Lower $p\mathrm{CO}_2$ levels during glacial periods have been suggested to promote increased C_4 abundance in Texas (Koch et al. 2004), but it has also been suggested that C_4 abundance in the western United States was likely influenced by warm-season precipitation (Connin et al. 1998; Holmgren 2007).

A study of temperate shrubs and grasslands in North America (Paruelo and Lauenroth 1996) indicates that there is a positive correlation between the distribution of C_4 grasses and mean annual precipitation, the percent of summer season precipitation, and mean annual temperature, which explains 66% of the variability. Of the 66%, mean annual temperature contributes 25% of the total variability and mean annual precipitation plus season of precipitation contributes 75% of the total variability (Paruelo and Lauenroth 1996). Thus, both the amount and season of precipitation may play a significant role in C_4 abundance.

The same trend is seen in the Chihuahuan desert, which experiences distinct summer (June to September, 61%) and winter (October to March, 34%) seasons of precipitation (Kemp 1983). The photosynthetic pathway of the dominant vegetation type corresponds to the temperature during these periods of abundant precipitation, with C_3 plants growing during the colder, winter-precipitation season and C_4 plants dominating during the hotter, summer-precipitation season (Kemp 1983). Previous work also indicates that warm regions with insufficient summer precipitation have limited C_4 vegetation (e.g., Kemp 1983) and that a change in the season of abundant rainfall from summer to spring can cause a shift from C_4 to C_3 plants, in simulated conditions (Epstein et al. 1999).

Carbon isotope values in tooth enamel can reveal dietary food sources by capturing the relative proportion of C_3/C_4 plants consumed regionally. By characterizing climatic regimes and C_4 consumption by resident mammalian herbivores, we can begin to assess driving mechanisms for C_4 abundance in the past. For medium- to large-bodied herbivores, $\delta^{13}C$ values recorded in their tooth enamel have an enrichment factor of ~14.1‰ relative to their diet (Cerling and Harris 1999). Accounting for this enrichment, $\delta^{13}C_{enamel}$ values ≤ −8‰ reflect a predominantly C_3 diet, whereas values ≥ −2‰ indicate a predominantly C_4 diet (Cerling et al. 1997).

Whereas carbon isotope values can be used to examine vegetation, stable oxygen isotopes, which are influenced by climatic and geographic variables such as temperature, precipitation, and humidity, can be analyzed to characterize regional climates (e.g., Dansgaard 1954, 1964; Ayliffe and Chivas 1990). Oxygen isotope values can also serve as a proxy for regional terrestrial temperature and precipitation, with greater $\delta^{18}O$ values indicative of warmer and/or drier conditions (e.g., Dansgaard 1964; Luz et al. 1984; Kohn 1996).

Below 20°C, there is a positive correlation between mean annual air temperature and the $\delta^{18}O$ value of precipitation (Dansgaard 1954, 1964). This temperature effect, which is approximately 0.7‰ per degree centigrade, is the dominant control on high latitude precipitation $\delta^{18}O$ values year round and dominates at midlatitudes during the winter months (Dansgaard 1964; Criss 1999). At lower latitudes, and midlatitudes during the summer, when temperatures are above 20°C and there is abundant precipitation or high humidity, the "amount effect" becomes a dominant control on $\delta^{18}O$ values of precipitation (Dansgaard 1964)—that is, an increase in the amount of precipitation leads to lower $\delta^{18}O$ values. If precipitation/humidity is limited in a particular region, the influence of temperature will have the greatest effect (Dansgaard 1964).

Original water sources also affect the resulting precipitation. Continental sources of water result in precipitation with lower $\delta^{18}O$ values than precipitation derived from a marine source, owing to continuous evaporation of isotopically light water (Dansgaard 1964). Seasonal changes in the source of moisture can also influence $\delta^{18}O$ values (Dansgaard 1964). The southwestern United

States experiences seasonal monsoons with varying sources of moisture (e.g., Douglas et al. 1993). The Southwest receives its largest proportion of annual precipitation during the summer (e.g., Kemp 1983; Douglas et al. 1993), when it is on the edge of a larger phenomenon—the Mexican Monsoon—that forms during the summer months over the northwestern portion of Mexico (Douglas et al. 1993). In the United States, the effects of the monsoon are greatest in New Mexico and Arizona and extend into Colorado, Kansas, Nevada, Oklahoma, Texas, Utah, and southeastern California (Douglas et al. 1993). During May, winds from the west largely bring moisture inland from the Pacific Ocean, with only a small influx from the Gulf of California (Douglas et al. 1993). By July, the winds are coming from the west over the Pacific Ocean and the Gulf of California, as well as from the east over the Caribbean and Gulf of Mexico (Douglas et al. 1993). Despite changing wind patterns, previous work suggests that the Caribbean and Gulf of Mexico are not providing abundant low-level warm-season precipitation during the monsoon (Douglas et al. 1993; Higgins et al. 1997). Instead, convection over the tropical Pacific Ocean and Gulf of California appears to provide the moisture needed for abundant summer rains (Douglas et al. 1993; Higgins et al. 1997). Effects of these monsoons were likely weaker or nonexistent during full glacial times (e.g., Spaulding and Graumlich 1986; Connin et al. et al. 1998; Metcalfe et al. 2000), but may have been stronger between 12 and 9 Ka (e.g., Spaulding and Graumlich 1986). In Florida, precipitation is derived from the Atlantic Ocean and the Gulf of Mexico with little to no change in seasonal moisture sources; however, there is a dry season between November and April (e.g., Biedinger and Lushine, 1993).

In addition to varying climatic and source-water controls, geographic variables such as elevation, latitude, and continentality affect $\delta^{18}O$ precipitation values. Increasing elevation causes a depletion of ^{18}O, which leads to a decrease in $\delta^{18}O$ values at a rate of about 2.0 ± 1‰ per kilometer (Dansgaard 1964; Criss 1999; Poage and Chamberlain 2001). Extreme elevations (>5000 m) have different lapse rates and can affect δ^{18}O values (Dansgaard 1954, 1964), but because all sites in this study are well below the 5000-m threshold, elevation is less likely a contributor to δ^{18}O values. Latitude also plays a role in the δ^{18}O values of precipitation and on average; the effect is 0.002 ± 0.001‰ per kilometer (Criss 1999). As with extreme elevation, δ^{18}O values at extreme polar latitudes (>70°) also deviate from global lapse rates. All sites in this study are between 25° and 45° N, so the effect of extreme latitudes does not significantly influence δ^{18}O values. At temperatures greater than 5°C, there is also an influence of continentality, where δ^{18}O values become more negative as you move inland; this is due to the rain-out of heavier ^{18}O and continuous evaporation of isotopically depleted freshwater as you move away from the source (Dansgaard 1964). Globally, the influence of continentality is highly variable, but if the effect of elevation is removed, the average longitudinal effect is 0.002 ± 0.002‰ per kilometer (Criss 1999). Thus, increasing elevation, latitude, and continentality leads to precipitation with lower δ^{18}O values (Dansgaard 1964).

Fresh surface water will also have varying δ^{18}O values (e.g., Epstein and Mayeda 1953). Epstein and Mayeda (1953) included snow in Chicago (mean value, −17.0‰), rain in Bermuda (−6.6‰) and Chicago (−7.1‰), Mississippi River water in St. Louis (−8.9‰) and Baton Rouge (−4.9‰), and water from Lake Michigan (−6.1‰) and the Great Salt Lake (−7.4‰). Each of these bodies of water has a different value due to the amount of evaporation that has occurred and the Rayleigh distillation processes (Dansgaard 1964). The value of source water also affects the δ^{18}O values from tooth enamel, which can vary at a given fossil locality if there are numerous sources of fresh water (e.g., Longinelli 1984; Luz et al. 1984). The isotopic composition of leaf water can also influence δ^{18}O values during the formation of tooth enamel (e.g., Kohn et al. 1996).

Increased aridity causes greater evaporation of leaf water and results in more evaporative (i.e., positive) δ^{18}O values (e.g., Ayliffe and Chivas 1990).

Oxygen isotope values in tooth enamel are also affected by a host of other factors. Among these are physiological characteristics such as diet, metabolic rates, and water turnover (Longinelli 1984; Luz et al. 1984; Kohn 1996), with the dominant control being body water (Kohn and Cerling 2002). Controls affecting δ^{18}O tooth enamel values of an individual organism are dependent on specific inputs (e.g., breathing, leaf water, and drinking) and outputs (e.g., exhaled CO_2 and water vapor, sweat, waste excretion) and consequently require an understanding of the physiology of disparate organisms (Kohn and Cerling 2002). Seasonal changes in the environment or behavior can also influence δ^{18}O values (Kohn and Cerling 2002).

Influences of temperature versus precipitation are difficult to disentangle, but there are multiple terrestrial aridity proxies including those that utilize plant macrofossils (Wilf 2000), carbonate nodules (Retallack 2007), bone collagen (Cormie et al. 1994), bone phosphate (Ayliffe and Chivas 1990), enamel carbonate (Levin et al. 2006), and microfossil paleocommunities (Patnaik 2003). Geochemical proxies (e.g., bone collagen, bone phosphate, enamel carbonate) and paleocommunities are directly associated with vertebrate faunas and are likely of greatest value when examining biotic responses to climate change. To better understand and separate out the influences on oxygen isotope values, taxa with differing drinking water requirements, and therefore different sensitivities to aridity, need to be examined (Kohn 1996). Previous work on modern mammals has shown that oxygen isotopic enrichment of tooth enamel relative to meteoric water values can be used as an aridity index to separate the influences of temperature and precipitation by examining taxa with demonstrated sensitivity to water deficits, i.e., evaporation-sensitive taxa (Levin et al. 2006). Evaporation-sensitive taxa get most of their water from leafy plant material whereas evaporation-insensitive taxa derive most of their water by actively drinking (Levin et al. 2006). The work of Levin et al. (2006) suggests that African elephants can be used as a baseline evaporation-insensitive taxon because they drink water multiple times a day when there is abundant surface water (Owen-Smith 1988). The seasonal abundance and distribution of this surface water controls the abundance and distribution of elephants (Stokke and du Toit 2002). During the wet season, elephant groups are typically found within 5 km of surface water, but during the dry season, they have more limited ranges and are often found within 3.5 km of a water source (Stokke and du Toit 2002). This need to drink water, as opposed to getting it from their food, supports the identification of proboscideans as evaporation-insensitive animals.

Levin et al. (2006) also identified giraffids, dikdiks, and oryxes as evaporation-sensitive taxa, given their significant positive relationships between $\delta^{18}O_{enamel}$ values and increasing water deficits, but these taxa are not present in the United States today. Thus, identifying North American taxa capable of tracking climatic changes (i.e., relative aridity) can help clarify regional climatic differences during historic and prehistoric times (e.g., Cook et al. 2004).

Here, we further developed an aridity index and show how stable oxygen and carbon isotopes can be used to quantify regional climatic and environmental conditions in the southeastern and southwestern United States during the Pleistocene. We determine which mammals are most sensitive to aridification by assessing the magnitude and frequency of aridity index values (i.e., the difference between oxygen isotope values of each taxon and a site-specific evaporation-insensitive proboscidean $\delta^{18}O$ value). Using carbon isotope values, we also investigated the influence of diet on evaporation-sensitivity. Once evaporation-sensitive taxa are identified, we then test the following hypotheses: (1) the Southeast was warmer and wetter than the Southwest during the Pleistocene, and (2) C_4 abundance in the Southwest was driven by greater aridity, rather than temperature.

2.1.1. Site Information

Basic information about each site was collected from previously published literature and has been included in Table 1 and Figure 1. When available, we also mention isotopically inferred environments. Spring-fed and riverine deposits that range in age from >40,000 to 7000 years old dominate in the Southwest. These sites have an average elevation of ~1170 m. Most sites in the Southwest have been interpreted as glacial sites, but the remaining sites were classified by age. If sites extended past the last glacial period, they were identified as glacial/transitions. No interglacial sites from the Southwest were included, because published isotopic data are lacking. Southwestern sites are likely dominated by C4 vegetation in basins at lower elevations, but possibly have more C3 vegetation at higher elevations.

Sinkholes and other freshwater and shallow marine environments dominate in the Southeast. Leisey 1A (1.6 to 1.3 Ma) and Inglis 1A (2.0 to 1.6 Ma) are the oldest sites included in this study, but the remaining seven sites in the Southeast are Rancholabrean in age. Estimates from Google Earth indicate that all sites in the Southeast have elevations of <20 m. Seven of the nine sites are identified as glacial or are inferred to be glacial/transition, but Leisey 1A and Waccasassa River were identified as interglacial sites. Inglis 1A was identified as a C3 dominated site, but mosaics of C3 and C4 vegetation characterize the others.

2.2. Methods

2.2.1. Data Collection

We compiled previously published mammalian tooth enamel stable isotope values from Pleistocene fossil sites with a minimum of two taxa. Our search terms in Web of Science, Google Scholar, and GeoRef included combinations of the following: stable isotopes, mammal, Pleistocene, Quaternary, carbon, oxygen, diet, climate, United States, and North America. Data were included from sites based on location, the reporting of carbon and oxygen isotope values, the presence of an evaporation-insensitive proboscidean (Levin et al. 2006), and the age of Pleistocene. All papers used comparable chemical methodologies, including sodium hypochlorite or hydrogen peroxide, acetic acid, and phosphoric acid reactions, following the procedures in Koch et al. (1997). Neither sodium hypochlorite nor hydrogen peroxide affect the isotopic signature of tooth enamel (Koch et al. 1997), making these studies comparable. Notable deviations include the use of 1.0 M acetic acid by Connin et al. (1998), Koch et al. (1998), Feranec and MacFadden (2000), and Hoppe (2004), as opposed to 0.1 M acetic acid used by DeSantis et al. (2009), and Nunez et al. (2010). Feranec and MacFadden (2000) further modified their procedures and used 0.1 M acetic acid for serial samples, as suggested by Koch et al. (1997). Connin et al. (1998) also used a phosphoric acid reaction temperature of 50°C whereas the other studies used 90°C. Not all studies specified whether a single vessel or a common acid bath was used during the phosphoric acid reaction. Despite small deviations, the methods used in these studies are comparable, thus making the stable isotope values comparable.

Definitions of the Southeast and Southwest are modified after Karl and Koss (1984) (Fig. 1). The Southwest includes Nevada, Utah, Colorado, Arizona, New Mexico; however, one site from north central Sonora, Mexico was included because of its proximity (less than ~250 km) to sites in Arizona and New Mexico (Fig. 1). The southeast includes Virginia, North Carolina, South Carolina, Georgia, Alabama, and Florida; however, the need for oxygen isotope values and the presence of evaporation-insensitive proboscideans limited all southeastern sites to Florida (Fig. 1). Our searches yielded 17 sites with 311 specimens. Nine sites are in Florida (*n* = 220) and eight sites are in the Southwest (*n* = 91). Because $\delta^{18}O$ values from three-quarters of the sites (12 of 16) and almost half of the specimens (144 of 311) were based on V-SMOW, all V-PDB values were converted to V-SMOW by using the following equation $\delta_{SMOW} = 1.03086\ \delta_{PDB} + 30.86$ (Friedman and O'Neil 1977).

2.2.2. Data Analysis

Evaporation-sensitivity was determined by calculating the difference between each sample and a known evaporation-insensitive taxon, i.e., proboscideans. As previously stated, proboscideans were used as an evaporation-insensitive baseline because of their need to drink water (Owen-Smith 1988) and their documented insensitivity to water deficits in Africa (Levin et al. 2006). To determine aridity index values, $\delta^{18}O$ values for proboscideans at each site were averaged to create a site-specific value that was subtracted from all remaining mammalian isotope values from that same site. Individuals with greater $\delta^{18}O$ values than proboscideans have positive aridity index values whereas individuals with lower $\delta^{18}O$ values have negative values. All aridity index values were calculated separately for each site in the Southeast and Southwest and were subsequently used to create frequency histograms (Fig. 2). These histograms and average family aridity index values were then used to determine evaporation-sensitive/less-sensitive classifications. All families with mean aridity index values greater than 0.5‰ were classified as evaporation-sensitive. This cutoff, although arbitrary, separates groups that typically have more positive values from those with typically zero to negative values, and is further supported by family means and standard errors of mean values. Alternatively, a cutoff value of 1‰ could also be used; however, because all southeastern taxa would have been categorized as less sensitive (including the most sensitive camelids, see Results), this more conservative cutoff is likely inappropriate for global comparisons or studies that includes less arid regions. Additional applications of this aridity index will require calibration of an appropriate cutoff value based on the site- or region-specific isotope values before additional families can be identified as evaporation-sensitive or insensitive. We tested each variable for normality using the Shapiro-Wilk test and all subsequent statistical tests were done using parametric two-sample Student's *t*-tests and nonparametric Mann-Whitney *U*-tests (XLSTAT-Pro), when appropriate. To address the potential influences of comparing sites from different climatic regimes we reanalyzed the data after removing the older localities of Leisey 1A (1.6–1.3 Ma) and Inglis 1A (2.0–1.6 Ma) from the Southeast. Thus, the second analyses included two sites of Rancholabrean age and 12 sites less than 45,000 cal yr B.P.

2.3. Results

2.3.1. Stable Oxygen Isotopes

Family aridity index values are noted in the frequency histograms (Fig. 2) and in Table. Although taxa are grouped by family, each of the following families is only represented by one genus: Bovidae, Cervidae, Equidae, and Tapiridae. There are two genera represented by Antilocapridae, Camelidae, and Tayassuidae, but there is no statistical difference between the aridity index or oxygen isotope values from *Mylohyus* and *Platygonus* (Tayassuidae) or *Hemiauchenia* and *Palaeolama* (Camelidae) in the Southeast. Because of differences in available taxa, we used two different genera of Antilocapridae and Camelidae for comparisons between the Southeast and Southwest, but both antilocaprids are from the same tribe, Stockoceratini (Janis and Manning 1998), and both of the camelids are from the same tribe, Lamini (Honey et al. 1998). Thus, we posit that family classifications are sufficient for the scope of this study.

In the southeast, Camelidae has the greatest mean aridity index value, 0.8‰, followed by Bovidae, 0.5‰; Cervidae, 0.5‰; Equidae, 0.5‰; Antilocapridae, 0.3‰; Tayassuidae, −0.1‰; and Tapiridae, −1.7‰. In the Southwest, Antilocapridae has the greatest mean aridity index value, 6.6‰, followed by Tayassuidae, 5.7‰ (only one specimen was analyzed); Camelidae, 2.7‰; Cervidae, 1.4‰; Equidae, 1.3‰; and Bovidae, 0.3‰. Aridity index values of sensitive taxa are greatest in the Southwest ($p < 0.01$). When all values from the Southeast and the Southwest are averaged, families have the following mean aridity index values: Antilocapridae, 4.1‰; Camelidae, 1.4‰; Equidae, 0.9‰; Cervidae, 0.6‰; Bovidae, 0.4‰; Tayassuidae, 0.1‰; and Tapiridae, −1.7‰. Given our cutoff for sensitive taxa of 0.5‰, which represents a threshold above which most specimens in a particular family have greater aridity index values than insensitive taxa, we categorized Antilocapridae, Camelidae, Equidae, and Cervidae as evaporation-sensitive families, in contrast to the less sensitive families of Bovidae, Tayassuidae, and Tapiridae. Further, Camelidae is consistently one of the most sensitive families in both the Southeast and the Southwest, with the greatest and second greatest mean aridity index values, respectively.

Mean δ^{18}O values of all combinations of taxa (i.e., sensitive, less sensitive, proboscideans, and all taxa; Table 3, Fig. 3) in the southeastern United States are greater than those in the southwestern United States. Mean δ^{18}O values of evaporation-sensitive taxa are greater than less sensitive taxa in both the Southeast and Southwest (Table 3). The same comparisons of aridity index values and $\delta^{18}O$ values hold even when early to mid-Pleistocene sites are removed.

2.3.2. Stable Carbon Isotopes

All interregional comparisons (e.g., sensitive, proboscideans, and all taxa) demonstrate greater $\delta^{13}C$ values in the Southwest than the Southeast (Table 3, Fig. 3). In the Southwest, less sensitive taxa have greater mean $\delta^{13}C$ values than the evaporation-sensitive taxa; however, mean differences are indistinguishable in the Southeast (Table 3). Again, when the earlier Pleistocene sites are removed there are no changes in the statistical significance of any comparisons.

2.4. Discussion

2.4.1. Identifying Climate-Sensitive Families

The identification of taxa capable of tracking climate change is important for determining climatic regimes both regionally and through time. Although "shotgun blast" analyses of fossil taxa (i.e., sampling all herbivorous taxa in a fauna) have been used to characterize climates without identifying evaporation-sensitive taxa a priori (e.g., DeSantis et al. 2009; Secord et al. 2012), it is difficult to determine if more homogenous $\delta^{18}O$ values are indicative of lower aridity rather than the lack of "aridity tracking" evaporation-sensitive taxa in a given fauna. Previous research on paleoclimatic reconstructions has focused on equids (Bryant et al. 1994) and cervids (Cormie et al. 1994); however, our data suggest that they may not be the best taxa for tracking aridity. Much like giraffids, dikdiks, and oryxes in Africa (Levin et al. 2006) and kangaroos in Australia (Ayliffe and Chivas 1990; Murphy et al. 2007), camelids and antilocaprids may be important taxa for assessing changes in relative humidity. Further, families such as Camelidae can be used to track changes in aridity since the middle Eocene in North America (Honey et al. 1998) and early Pleistocene in South America (e.g., Marshall et al. 1982), and antilocaprids can be used to track more evaporative conditions in North America since the Miocene (Janis and Manning 1998). The methods outlined in this study can be used to identify evaporation-sensitive taxa through time and globally.

Although carbon isotope values have been suggested as a possible metric of determining evaporation-sensitivity (Levin et al. 2006), our results question the utility of using dietary niches based on δ^{13}C values to identify evaporation-sensitivity. In the Southeast, the sensitivity of taxa cannot be determined from mean δ^{13}C values, and in the Southwest, δ^{13}C values are lower for evaporation-sensitive taxa than for less sensitive taxa (Table 3). This pattern of lower δ^{13}C values in less sensitive taxa is particularly interesting considering that δ^{13}C values in the Southwest are greater overall. Taxa most sensitive to changes in evaporation, possibly because they rely on plant matter as a water source rather than drinking, may not be able to consume greater amounts of C_4 resources if the region is too dry. Although this is speculative, further work examining the relationship between evaporation-sensitivity and dietary niches is necessary for clarifying the paleobiology of extinct mammals. Aridity index values are a better predictor of evaporation-sensitivity than average carbon or oxygen isotope values alone.

2.4.2. Identifying Regional Climatic Regimes

Although modern meteoric water δ^{18}O values are not analogous to Pleistocene meteoric water values, modern precipitation δ^{18}O values are lower in the Southwest than in the Southeast (Bowen and Revenaugh 2003; Bowen 2013). This may be due to differing temperatures, aridity, elevation, continentally, and/or sources of moisture. Because these variables are difficult to disentangle we do not draw conclusions about relative differences in temperature between the

Southwest and southeast during the Pleistocene, but we can use an aridity index to interpret the relative aridity of the southeastern and southwestern United States.

Lower aridity index values suggest wetter conditions in the Southeast relative to the Southwest during the Pleistocene. Although the robustness of climate interpretations from time-averaged sites spanning the Pleistocene may be a cause for question, analysis of only latest Pleistocene sites (i.e., middle to late Rancholabrean, ~200 to 9 Ka) results in identical trends and interpretations. This indicates that the time-averaging of fossil localities analyzed here does not alter regional climate interpretations for Pleistocene sites. These results provide compelling evidence for regionally variable climates, specifically, significant differences in aridity between the Southwest and Southeast during the late Pleistocene, much as we see today. This research demonstrates how integrating stable isotope analyses with an aridity index improves our understanding of past climates, the first step to understanding potential biotic responses to changing climates.

Comparisons of oxygen isotope values between extinct mammals and modern taxa can also inform our understanding of climatic conditions in the two regions. Oxygen isotope values of Pleistocene evaporation-sensitive horses (27.0‰) in the Southwest are approximately equivalent to values seen in horses today (~27.2±1.9‰; Hoppe et al. 2005), suggesting that conditions in the Southwest during the Pleistocene were similar to present-day conditions. In contrast, feral horses from Shackleford Banks off the coast of North Carolina have tooth enamel oxygen isotope values of 27.3±1.5‰ (Hoppe et al. 2004) versus average values of 30.7‰—or 31.1‰ if only the late Pleistocene equids are averaged—for Pleistocene horses from Florida. Thus, Pleistocene Florida appears to have been warmer and/or drier than modern coastal North Carolina. However, further examination of the geochemistry of modern animals throughout

Florida and the Southwest is needed to make more specific comparisons between regional climates during the Pleistocene and today.

The application of an aridity index allows for large-scale comparisons of relative aridity despite complex effects of climatic and geographic variables on precipitation $\delta^{18}O$ values. For example, the aridity index can also be used to examine intraregional differences in relative aridity. Modern conditions at Leisey 1A and Inglis 1A are similar—both sites have mean annual precipitation between 127 and 178 cm per year (National Climatic Data Center 2005a), mean annual temperatures greater than 21ºC (National Climatic Data Center 2005b), and similar modern precipitation $\delta^{18}O$ values (−3.7‰ and −3.9‰, respectively [Bowen and Revenaugh 2003; Bowen 2013]). Both sites are approximately ≤3 m in elevation and are located <30 km from the Gulf of Mexico. For the Pleistocene, however, mean sensitive aridity index values are greater at Leisey 1A than at Inglis 1A (Table 2). This indicates drier conditions at Leisey 1A, a conclusion also supported by the geology and palynology (e.g., DeSantis et al. 2009). Collectively, these data suggest that Leisey 1A and Inglis 1A were deposited during differing climatic conditions (DeSantis et al. 2009).

This aridity index can be expanded to investigate geographically or temporally disparate sites beyond North America and the Pleistocene. Evaporation-insensitive proboscideans could be used from sites dating from the Miocene to today (Lambert and Shoshani 1998). Sites older than Miocene in age, or sites that lack proboscideans, will require additional research to identify an evaporation-insensitive baseline. Levin et al. (2006) also identified the hippopotamus, rhinoceros, and warthog as modern African taxa that are not sensitive to changes in water deficit, indicating that they, or their fossil equivalents, may be reasonable candidates for evaporation-insensitive baselines. This would allow for an increase in the number of sites that could be examined globally.

Identifying other evaporation-insensitive taxa requires understanding the physiology of a given taxon well enough to suggest it was dependent on meteoric water. One example includes a study of the Paleocene-Eocene Thermal Maximum in which the hippo-like *Coryphodon* was used as an evaporation-insensitive taxon (Clementz et al. 2008; Secord et al. 2012) and *Sifrhippus* was identified as an evaporation-sensitive taxon (Secord et al. 2012). Using morphology and oxygen isotopes to determine evaporation-sensitivity may be more difficult during more humid times in the geologic past, and may require changes in the calibration of the aridity index.

With the identification of evaporation-insensitive taxa, this aridity index could also be useful in Australia, despite the near absence of placental taxa. For example, kangaroos such as *Macropus* have been identified as aridity indicators and are capable of tracking relative humidity (e.g., Ayliffe and Chivas 1990; Murphy et al. 2007). Additionally, koalas, which get most of their water from the leaves they eat, may be good candidates for evaporation-sensitive taxa. Because of its large body size and inferred higher drinking requirements, *Diprotodon* (Price and Piper 2009) may be a candidate for an evaporation-insensitive taxon during the Pleistocene.

In addition to using modern temperature and precipitation data to characterize regions, aridity index values could be used to further investigate modern taxa, specifically the influences of changing climates on local mammals. A better understanding of the modern record may also allow for more informed interpretations of the fossil record.

2.4.3. Drivers of C_4 Abundance

The absence of forest indicator taxa such as *Tapirus* (DeSantis and MacFadden 2007), paired with greater $\delta^{13}C$ values, indicates a more open landscape with abundant C_4 vegetation (typically, warm-season grasses, although CAM plants may have also been consumed in the Southwest [Ehleringer 1989; van der Merwe and Medina 1991; Cerling et al. 1997]) in the Southwest sites examined. C_4 vegetation is typically dominant when temperatures are higher and/or pCO_2 levels are lower (Monson et al. 1982; Jordan and Ogren 1984; Koch et al. 2004). However, the amount of precipitation and the season of precipitation also influence the abundance of C_4 vegetation today (e.g., Paruelo and Lauenroth 1996; Murphy and Bowman 2007). Specifically, C_4 abundance in North America is positively correlated with mean annual temperature, mean annual precipitation, and the proportion of precipitation falling during the summer (Paruelo and Lauenroth 1996). In Australia, seasonal water availability is a better predictor of relative C_4 abundance than is mean annual temperature (Murphy and Bowman 2007).

Although aridity and season of precipitation are thought to be the main drivers of C_4 abundance today, pCO_2 has been suggested as a possible driver in the past (Huang et al. 2001; Koch et al. 2004). Our findings cast doubt on this. DeSantis et al. (2009) showed greater consumption of C_4 resources at the interglacial Leisey 1A locality, and although no direct measurements of CO_2 coincident with this ~1.5 Ma site are possible (ice core data do not exceed ~800,000 years; Lambert et al. 2008), CO_2 levels were likely higher at the interglacial site than at the glacial site Inglis 1A, which is instead typified by C_3 consumers and the near absence of C_4 consumption (DeSantis et al. 2009). During the Pleistocene, greater aridity is coincident with increased C_4 consumption in the Southwest—despite possibly lower inferred mean temperatures based on mean $\delta^{18}O$ values. Carbon dioxide is unlikely to be the sole determinant of C_4 abundance during the Pleistocene (Huang et al. 2001), and the associations we observed between C_4 abundance and $p\mathrm{CO}_2$ levels suggest that aridity or seasonal aridity may have been a greater driver than temperature or $p\mathrm{CO}_2$ in influencing C_4 abundance during the Pleistocene.

2.5. Conclusions

1. Oxygen isotope aridity index values can be used to better understand regional aridity, and Camelidae and Antilocapridae may be more useful for tracking changing climatic conditions, including aridity, than taxa that have been used in the past (e.g., horses).
2. Based on aridity index values, this work suggests that the southwestern United States was drier than the southeastern United States during the Pleistocene.
3. C_4 consumption was greater in the Southwest than in the wetter Southeast during the Pleistocene. Thus, aridity or seasonal precipitation may have been a more important driver than temperature or $p\mathrm{CO}_2$ of regional C_4 abundance at this time.
4. The applicability of this aridity index extends beyond North America and the Pleistocene. With the identification of an evaporation-insensitive taxon, the aridity index can be used both globally and through time.

Collectively, the methods described here can be used to identify evaporation-sensitive taxa, (including those lacking modern analogues) through time and globally. Further, the identification and subsequent study of evaporation-sensitive and less sensitive taxa can improve our understanding of regional climate change and potential drivers for C_4 abundance.

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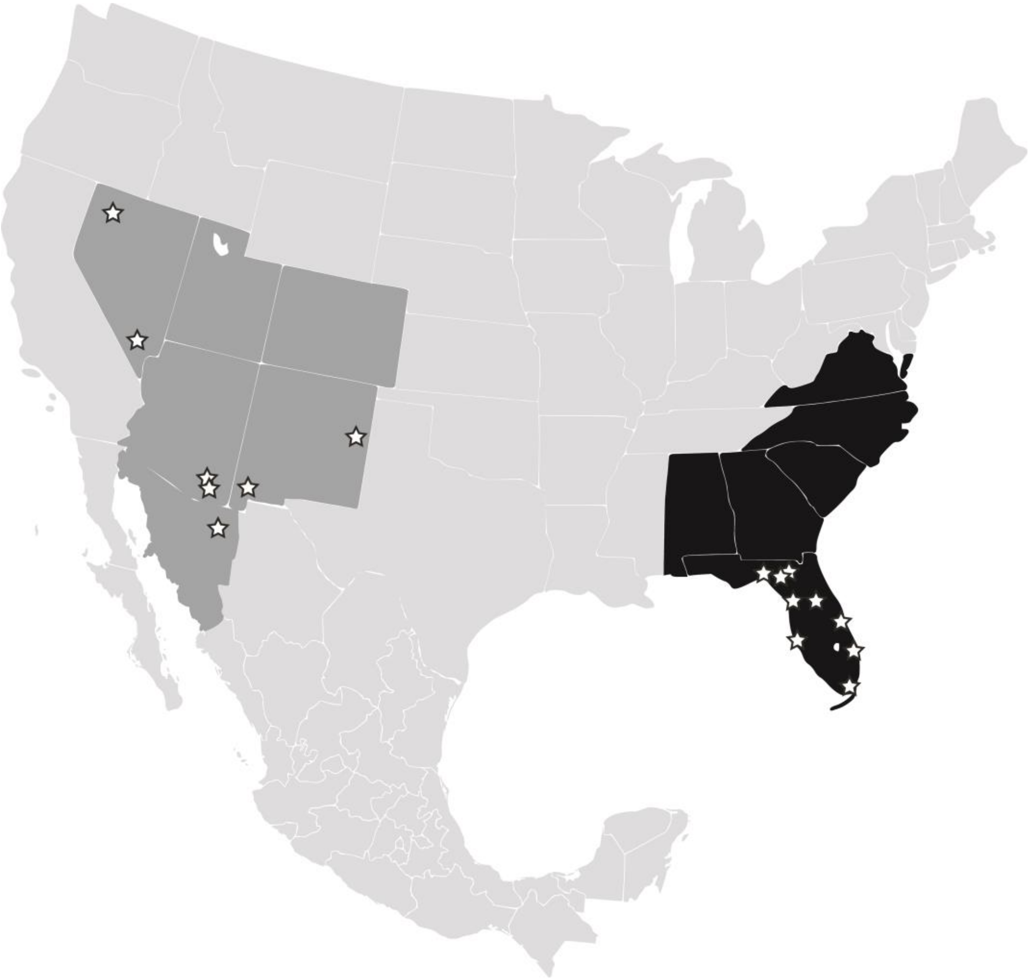

Figure 2.1 North American sites analyzed from the southeastern (black) and the southwestern (dark gray) United States.

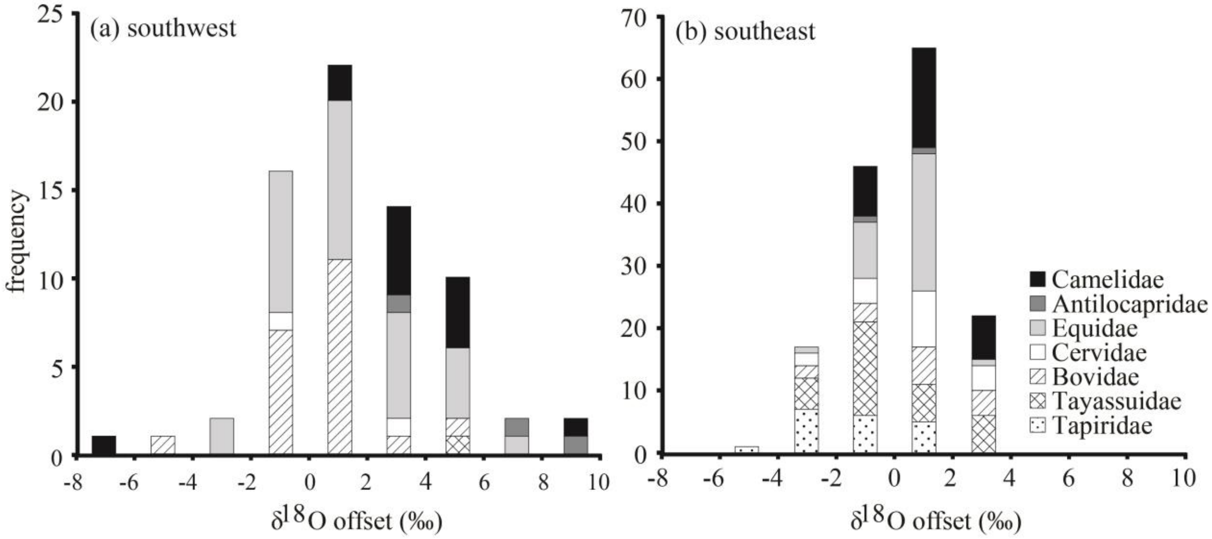

Figure 2.2. Aridity index values from the southwestern and the southeastern United States. Each bin encompasses a 2‰ aridity index value. Values for each bin are greater than or equal to the left end-member, and less than the right-end member (e.g., $0 \leq x < 2$). Evaporation-sensitive families (solid) and less sensitive families (patterned).

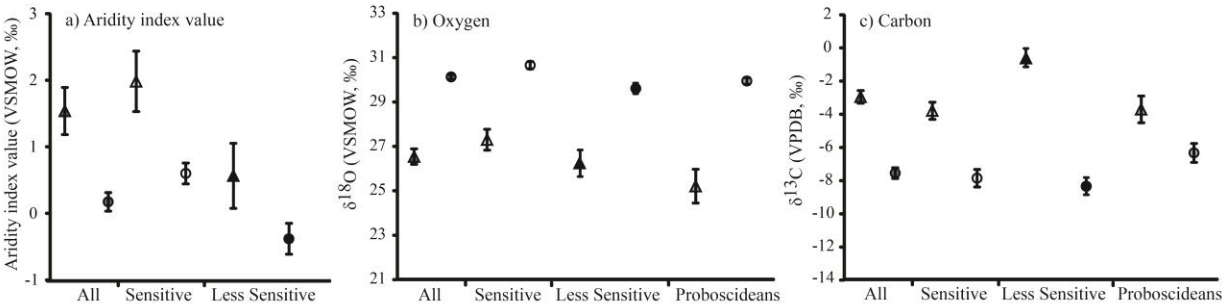

Figure 2.3. Mean isotopic values of all taxa, evaporation-sensitive tax), less sensitive, and proboscideans. ▲ = Southwest, ● = southeast, error bars indicate standard errors of the means.

Table 2.1. Site Characteristics.

State	Site	Latitude	Longitude	Elevation (m)	Estimated age (10^3 yr B.P.)	Site type	Glacial or interglacial	Inferred landscape
Florida	Cutler Hammock[a]	25.617*	-80.317*	3*	11.0-9.5	sinkhole	glacial	mosaic environment with C_3 and C_4 vegetation, C_4 abundance ~80-90%
Florida	Hornsby Springs[a]	29.85*	-82.593*	11*	12.3-10.75	sinkhole	glacial/transitional[†]	mosaic environment with C_3 and C_4 vegetation, C_4 abundance ~50-80%
Florida	Inglis 1A[b]	29	-82.683	3*	2000-1600	sinkhole	glacial	forested with low abundance of C_4 vegetation
Florida	Leisey 1A[a,b]	27.7	-82.5	1*	1600-1300	shell bed	interglacial	mosaic environment with C_3 and C_4 vegetation
Florida	Page Ladson[a]	30.233*	-83.917*	7*	15.08-14.2	sinkhole	glacial	mosaic environment with C_3 and C_4 vegetation, C4 abundance ~80-90%
Florida	Rock Springs[a]	28.75*	-81.5*	15*	Rancholabrean	bed of spring run	glacial	C_3 and C_4 vegetation present[‡]
Florida	Vero Beach[a]	27.633*	-80.383*	3*	>30.0-9.0	pond or marsh	glacial/transitional[†]	mosaic environment with C_3 and C_4 vegetation, C_4 abundance ~50-80%
Florida	Waccasassa River[c]	29.5*	-82.7*	15*	middle Rancholabrean	river deposit	interglacial	C_3 and C_4 vegetation present[‡]
Florida	West Palm[a]	26.667*	-80.067*	6*	25	coastal marsh	glacial	mosaic environment with C_3 and C_4 vegetation, C_4 abundance ~80-90%
Arizona	Murray Springs[d]	31.567*	-110.167	1270	31.0-10.2	spring fed ponds and marshes	glacial/transitional[†]	basin C_4 grasslands/wetlands, possibly more C_3 plants at higher elevations
Arizona	Seff[d]	31.967*	-110.3	1130	12.0-10.0	not reported	glacial/transitional[†]	basin C_4 grasslands/wetlands, possibly more C_3 plants at higher elevations
New Mexico	Blackwater Draw[d,e]	34.433*	-103.2	1280	20.0-0.7	spring fed pond/drainage	glacial	basin C_4 grasslands/wetlands, possibly more C_3 plants at higher elevations
New Mexico	Howell's Ridge Cave[d]	31.917*	-108.5	1680	14.0-12.0	cave	glacial[†]	basin C_4 grasslands/wetlands, possibly more C_3 plants at higher elevations
Nevada	Rye Patch[d]	40.467*	-118.3	1260	29.0-22.0	riverine	glacial[†]	C_3 dominated environment[‡]
Nevada	Tule Springs[d]	36.317*	-115.183	970	≥40.0-11.5	spring deposit	glacial/transitional[†]	C_3 dominated environment with some C_4 vegetation[‡]
Mexico	Terapa[f]	29.683*	-109.65	605	43.0-40.0	riverine	glacial[†]	mosaic environments with marsh and grasslands

Source: [a] Koch et al. 1998; [b] DeSantis et al. 2009; [c] Feranec and MacFadden 2000; [d] Connin et al. 1998; [e] Hoppe 004; [f] Nunez et al. 2010 *not published, estimated using Google Earth; [†]the interpretation was not published, inferred from age, [‡]the interpretation was not published, inferred from limited published $\delta^{13}C$ values.

Table 2.2. Site-specific mean δ^{18}O values and aridity index values for proboscideans, less sensitive taxa (LS), and sensitive taxa (S). Aridity index = site-specific mean δ^{18}O value minus site-specific mean proboscidean value.

State	Site	*n*	Proboscidean δ^{18}O (‰)	SD	*n*	LS δ^{18}O (‰)	SD	LS aridity index (‰)	SD	*n*	S δ^{18}O (‰)	SD	S aridity index (‰)	SD
Florida	Cutler Hammock[a]	6	30.7	1.2	4	29.2	1.4	-1.5	1.4	2	31.4	1.7	0.7	1.7
Florida	Hornsby Springs[a]	6	30.9	0.8	1	29.8	--	-1.1	--	2	29.4	1.6	-1.6	1.6
Florida	Inglis 1A[b]	1	29.6	--	14	29.0	1.0	-0.6	1.0	19	29.7	0.9	0.1	0.9
Florida	Leisey 1A[a,b]	16	29.9	1.4	28	29.6	2.4	-0.3	2.4	37	31.1	1.4	1.2	1.4
Florida	Page Ladson[a]	6	30.0	0.9	2	28.4	1.6	-1.6	1.6	3	27.1	1.4	-2.9	1.4
Florida	Rock Springs[a]	7	29.9	1.2	2	27.8	1.4	-2.1	1.4	2	31.7	0.1	1.8	0.1
Florida	Vero Beach 2[a]	7	29.8	0.9	4	28.3	1.0	-1.5	1.0	4	31.0	1.0	1.2	1
Florida	Waccasassa River[c]	5	30.8	0.7	10	31.8	1.1	1.0	1.1	18	31.3	0.9	0.5	0.9
Florida	West Palm[a]	12	29.0	0.9	2	30.2	1.0	1.6	1.0	0	--	--	--	--
Arizona	Murray Springs[d]	2	26.6	0.8	5	26.9	1.3	0.3	1.3	22	27.4	2.2	0.8	2.2
Arizona	Seff[d]	1	27.1	--	0	--	--	--	--	1	29.4	--	2.3	--
New Mexico	Blackwater Draw[d,e]	9	26.5	3.0	11	26.3	2.3	-0.2	2.3	1	27.5	--	1.0	--
New Mexico	Howell's Ridge Cave[d]	1	30.1	--	0	--	--	--	--	1	22.9	--	-7.2	--
Nevada	Rye Patch[d]	1	18.8	--	1	19.8	--	1.0	--	2	18.8	0.3	0.0	0.3
Nevada	Tule Springs[d]	4	20.8	1.5	2	22.7	3.3	1.9	3.3	8	25.5	2.3	4.7	2.3
Mexico	Terapa[f]	3	26.1	0.7	3	29.1	2.4	3.0	2.4	13	29.8	2.6	3.7	2.6

Source: [a] Koch et al. 1998; [b] DeSantis et al. 2009; [c] Feranec and MacFadden 2000; [d] Connin et al. 1998; [e] Hoppe 2004; [f] Nunez et al. 2010. δ^{13}C values are based on the VPDB standard and δ^{18}O values are based on the VSMOW standard.

Table 2.3. Means and p-values from two sample t-tests and Mann-Whitney U-tests for $\delta^{13}C$ and $\delta^{18}O$ values from the southeastern (SE) and southwestern (SW) United States. Abbreviations: S, evaporation-sensitive; LS, less sensitive; P, proboscidean.

Comparisons			$\delta^{13}C$ (‰)		$\delta^{18}O$ (‰)	
SW (S,LS,P)	vs.	SE (S,LS,P)	-3.0 > -7.6	$p < 0.0001$*	26.5 < 30.1	$p < 0.0001$*
SW (S,LS)	vs.	SE (S,LS)	-2.8 > -8.2	$p < 0.0001$*	26.9 < 30.2	$p < 0.0001$*
SW (P)	vs.	SE (P)	-3.8 > -6.4	$p = 0.006$*	25.2 < 29.9	$p < 0.0001$*
SW (LS)	vs.	SE (LS)	-2.1 > -7.4	$p < 0.0001$*	25.7 < 29.8	$p < 0.0001$*
SW (S)	vs.	SE (S)	-3.9 > -7.9	$p < 0.0001$*	27.3 < 30.7	$p < 0.0001$*
SE (S)	vs.	SE (LS)	-7.9 < -7.4	$p = 0.179$	30.7 > 29.8	$p = 0.0002$*
SW (S)	vs.	SW (LS)	-3.9 < -2.1	$p = 0.005$*	27.3 > 25.7	$p = 0.038$*

$\delta^{13}C$ values are based on the V-PDB standard and $\delta^{18}O$ values are based on the V-SMOW standard. * =significant result.

Chapter 3

EFFECTS OF PLEISTOCENE CLIMATE ON DIETARY NICHES AND ENVIRONMENTAL HETEROGENEITY IN FLORIDA

3.1. Introduction

Pleistocene glacial and interglacial cycles have substantially affected past climates and biotic communities (e.g. Graham et al., 1996). Previous research indicates that Pleistocene plant and animal assemblages are more complex and non-analogous when compared to the assemblages that we see today (e.g. Leopold, 1967; Graham and Lundelius, 1989). Understanding how relatively rapid glacial and interglacial fluctuations affected medium to large bodied mammals and their communities may help clarify the consequences of changing climates on modern mammalian communities.

Globally, glacial and interglacial climatic changes are reconstructed using proxies such as ice cores (e.g. Lambert et al., 2008), lake sediments (e.g. Brigham-Grette et al., 2007; Nakagawa et al., 2012), and mammalian tooth enamel (e.g. Connin et al., 1998; Gaboardi et al., 2005; Tutken et al., 2007), in addition to many others. In Florida, the state with the richest Pleistocene fossil record of terrestrial mammals east of the Mississippi river, Pleistocene climate and sea level reconstructions have largely been based on pollen from lake cores that only record the past ~62,000 years (e.g. Watts, 1980; Grimm and Jacobson, 2003; Huang et al., 2006; Grimm et al., 2006). Multiproxy analyses of coral have also been used further back in the Pleistocene (e.g. Gischler et al., 2009; Muhs et al., 2011), but they provide little information about terrestrial environments and mammalian communities. Stable isotope analyses of mammalian tooth enamel have also been used to characterize climate and environmental conditions in Florida (e.g. Koch et al., 1998; DeSantis et al., 2009), but these analyses are also limited during the early and middle Pleistocene. This paucity of data leaves the early and middle Pleistocene without compelling evidence of terrestrial climates or environmental reconstructions for Florida.

Despite limited early to middle Pleistocene climatic reconstructions, Florida still provides an interesting backdrop for understanding the impact of changing climatic conditions on large herbivorous mammals throughout the Pleistocene. As sea level changes are recorded on the relatively narrow peninsula, it is possible to use the geology and the paleontology of fossil sites located close to the present coast line to identify them as glacial or interglacial (Morgan and Hulbert, 1995; Emslie, 1998). Unfortunately, many sites in Florida lack geologic evidence allowing for classifications of glacial or interglacial.

Previous work on a known glacial site, Inglis 1A, and a known interglacial site, Leisey Shell Pit 1A (hereafter referred to as Leisey 1A), used stable oxygen and carbon isotopes to further clarify the climates and environments and document dietary niche modification of mammals between these two sites (DeSantis et al., 2009; Feranec and DeSantis, 2014). The isotopic characterization of each site was consistent with geologic evidence indicating glacial and interglacial designations at Inglis 1A and Leisey 1A, respectively (DeSantis et al., 2009). Further, these sites can be used as a “Rosetta stone” for comparison to additional Pleistocene sites in Florida. In order to understand the causes of dietary niche modification, stable oxygen and carbon isotope ratios from sympatric taxa at two additional sites in Florida are here used to quantify relative differences in climatic regimes and dietary niches of mammalian taxa. Specifically, we test the hypothesis that more evaporative conditions supported more heterogeneous vegetation, leading to an increase in more disparate dietary niches during the Pleistocene in Florida.

3.1.1. Stable Isotopes and Paleoenvironmental Reconstructions

Stable isotope values from mammalian tooth enamel can be used to assess past climates and environments. Bulk samples, taken parallel to the growth axis of a tooth, provide an average oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) isotope value over the time the tooth was mineralizing. $\delta^{18}O$ values can be used to investigate the climate of a site or region (e.g. Longinelli, 1984; Luz et al., 1990; Bryant and Froelich, 1995; Bocherens et al., 1996). Specifically, $\delta^{18}O$ values reflect the isotopic signature of water consumed through drinking meteoric water and/or the consumption of leaf water (e.g. Dansgaard, 1964; Kohn, 1996; Levin et al., 2006). Taxa that get the majority of their water by actively drinking track changes in meteoric water and are termed "evaporation insensitive" (Levin et al., 2006). In contrast, taxa that get the majority of their water from the food they eat record evaporative conditions and are referred to as "evaporation sensitive" (Levin et al., 2006).

Under more evaporative conditions (i.e., warmer and/or drier) oxygen isotope values increase, especially in leafy vegetation (Dansgaard, 1964; Luz et al., 1984; Ayliffe et al., 1992). Additionally, increases in $\delta^{18}O$ values during more evaporative conditions result in a disparity between the oxygen isotope values from evaporation sensitive and evaporation insensitive taxa (Levin et al., 2006). Differences between evaporation sensitive and insensitive taxa can subsequently be used as an aridity index to compare the relative aridity of sites or regions (Levin et al., 2006; Yann et al., 2013).

Stable carbon isotopes ($\delta^{13}C$) from plant material are incorporated into the tooth enamel of medium and large bodied ungulates with an enrichment factor of 14.1‰ (Cerling and Harris, 1999). Stable carbon isotope values can therefore be used to reconstruct diet and changes in dietary niches, specifically the relative proportion of C_3 and C_4 vegetation consumed (e.g. Cerling et al., 1997; Cerling and Harris, 1999; DeSantis et al., 2009). C_4 grass and C_3 trees and shrubs dominate modern environments in Florida, while C_3 grass, C_4 dicots, and CAM plants are rare (Teeri and Stowe, 1976; Stowe and Teeri, 1978). Based on the dominant vegetation, tooth enamel $\delta^{13}C$ values greater than -2‰ are indicative of a C_4 grass dominated diet, and $\delta^{13}C$ values less than -8‰ indicate a diet dominated by C_3 browse (Cerling et al., 1997; Cerling and Harris, 1999). Mixed feeders are characterized by $\delta^{13}C$ values between -8‰ and -2‰ (Cerling et al., 1997; Cerling and Harris, 1999).

In addition to bulk isotope samples that reflect an animal's average diet and/or climatic regime, serial samples can classify the climate and the environment of each site and investigate relative seasonality. Serial samples taken perpendicular to the growth axis of a tooth record intervals of time during which the tooth was mineralizing (e.g. a few months). While Equus teeth are typically sampled from fossil sites to facilitate comparisons with previously published work (e.g. Higgins and MacFadden, 2004; Hoppe et al., 2004; DeSantis et al., 2009; Feranec et al., 2009), camelids may be better trackers of environmental conditions, specifically changes in relative aridity (Yann et al., 2013). The combination of Equus and camelid serial samples will likely allow for more detailed interpretations of the climate, the environment, and relative seasonality at Pleistocene sites.

3.1.2. Fossil sites

Two previously published Pleistocene sites from Florida, Leisey 1A and Inglis 1A, were discussed by DeSantis et al. (2009). Here, we examine two additional Pleistocene sites in Florida, Haile 8A and Tri-Britton (Figure 1, Table 1), and combine all data to assess past climates, ecology, and mammalian paleobiology during the Pleistocene of Florida. All sites in this study are primarily dated using vertebrate biochronology, which does not allow for correlation with oxygen isotope stages, but the inclusion of multiple proxies allows for the interpretation of climatic conditions at each site.

The two oldest sites, Inglis 1A (2.0-1.6 Ma) and Leisey 1A (1.6-1.0 Ma), can respectively be assigned to glacial and interglacial climates based on the local geology and the fossils present (Morgan and Hulbert, 1995). Inglis 1A (2.0 to 1.6 Ma) is a sinkhole deposit in the Eocene Inglis Formation and contains terrestrial fossils found approximately 5 meters below modern sea level. This indicates they were deposited at a much lower sea level stand when the sinkhole was located further from the Pleistocene coast (Morgan and Hulbert, 1995). The lack of a marine fossil component, plus the presence of cool adapted muskrat and pronghorn, contributes to the identification of Inglis 1A as a glacial site. Further work characterized the glacial site using stable oxygen isotopes and found that Inglis 1A had a smaller range in $\delta^{18}O$ values and lower mean $\delta^{18}O$ values, all consistent with a glacial interpretation (DeSantis et al., 2009).

Leisey 1A (~1.6 to 1.0 Ma) is part of a bone bed found in the Belmont Formation that is dominated by marine shell material that was being excavated when the deposit was discovered (Morgan and Hulbert, 1995). The intermixed warm adapted alligators and marine invertebrates suggest the material was deposited during a high sea level stand during an interglacial period (Morgan and Hulbert, 1995). Further, greater $\delta^{18}O$ values at Leisey 1A as compared to Inglis 1A, suggest warmer and/or drier conditions during an interglacial climatic regime (DeSantis et al., 2009).

Tri-Britton (0.5-0.4 Ma) is a collection of vertebrate fossils from a shelly, quartz sand deposit (Meers and Hulbert, 2002). Within the original deposit there were no obvious signs of unconformities, and there were no indications of mixing (pers. comm., Hulbert, 2014) While the deposit is dominated by terrestrial and freshwater species, there are also marine vertebrate and invertebrate fossils that were likely reworked during periods of relatively low sea level (Meers and Hulbert, 2002). As the site is found inland with little geologic evidence to support extremely low sea levels, it is possible that the deposit indicates sea levels lower than the previous extreme interglacial. Sea levels during the previous interglacial are thought to be six to nine meters higher than modern conditions (Kopp et al., 2009). The presence of gopher tortoises and two species of *Hesperotestudo* tortoises at Tri-Britton also suggest xeric environments and according to one study, there are no additional upland vertebrate taxa that suggest mesic hardwoods, pine flatwoods, or coastal marine environments (Franz and Quitmyer, 2005).

Haile 8A (0.3-0.13 Ma) is a Pleistocene sinkhole deposit in the Ocala Limestone that is located approximately 24 meters above modern sea level (Webb, 1974). The assemblage of box turtles present at Haile 8A, as well as the transition between highly organic deposits at the base of the sinkhole to truncated lateritic beds at the top, suggest rising sea level, potentially transitioning from a glacial (Illinonian) to an interglacial (Sangamonian) period (Auffenberg, 1967). The presence of gopher tortoises, two species of *Hesperotestudo* tortoises, pocket gophers (*Geomys*) and additional faunal components suggest the presence of xeric, pine flatwoods, and freshwater environments (Franz and Quitmyer, 2005).

3.2. Methods

Samples for stable carbon and oxygen isotope analysis were collected from mammalian tooth enamel using a low speed rotary drill and carbide bits. We preferentially selected late erupting teeth when available to reduce the effects of weaning on isotope values (Bryant et al., 1996); however, earlier erupting teeth were used when late erupting teeth were not available. A total of 96 enamel samples were collected from two sites in Florida, 46 from Tri-Britton and 50 from Haile 8A, and they were compared to previously published values from Leisey 1A (81 samples; DeSantis et al., 2009) and Inglis 1A (34 samples; DeSantis et al., 2009). Both bulk samples (samples taken parallel to a tooth's growth axis) and serial samples (a series of samples taken perpendicular to the growth axis of an individual tooth) were taken from fossil specimens housed in the Florida Museum of Natural History Vertebrate Paleontology collections located in Gainesville, Florida, USA. In addition to one *Equus* tooth from each site, a *Hemiauchenia* tooth from Haile 8A and a *Palaeolama* tooth from Tri-Britton were serially sampled. Also, one *Hemiauchenia* and one *Palaeolama* tooth from Leisey 1A and one *Hemiauchenia* tooth from Inglis 1A were sampled for comparison, and *Equus* serial samples were taken from DeSantis et al. (2009). Serial sample spacing of *Equus* was based on DeSantis et al. (2009) to increase comparability of taxa across localities and was approximately 2.5 mm between the start of each sample.

Two to three milligrams of powdered enamel was collected from each specimen, placed in microcentrifuge vials, and pretreated with 30% hydrogen peroxide for 24 hours to remove organics and 0.1 N acetic acid for 18 hours to remove secondary carbonates (similar to DeSantis et al., 2009). These samples were analyzed at the Department of Geological Sciences at the University of Florida where they were run on a Finnigan-MAT 252 isotope ratio mass spectrometer coupled with a Kiel III carbonate preparation device. All results are reported using the delta notation, $\delta = [(R_{sample}/R_{standard} - 1)*1000]$ (Coplen, 1994). For oxygen isotope values,

$R={}^{18}O/{}^{16}O$ and values are reported against V-SMOW (Coplen, 1994). All V-PDB values were converted using the following equation: $\delta_{VSMOW}=1.03086*\delta_{VPDB}+30.86$ (Friedman and O'Neil, 1977). For carbon isotope values, $R={}^{13}C/{}^{12}C$ and all values are reported against V-PDB (Coplen, 1994). All stable isotopes are from the carbonate portion of tooth enamel hydroxyapatite. Using replicate analyses of the standard NSB-19 and of the samples, the analytical precision is better than ±0.1‰. All statistical analyses were conducted using XLSTAT Pro. Shapiro-Wilk tests were used to determine normality and appropriate parametric (two-sample t-test or ANOVA) or non-parametric (Mann-Whitney U or Kruskal-Wallis) tests were used to compare resulting geochemical data.

3.3. Paleoenvironmental interpretations of sites in Florida

3.3.1. Climate

Using methods described in Yann et al. (2013), all taxa were categorized as "sensitive" or "less sensitive." Evaporation sensitive taxa include members of Antilocapridae, Camelidae, Cervidae, and Equidae. Less sensitive families include Bovidae, Tapiridae, and Tayassuidae, while the proboscideans include Elephantidae, Gomphotheriidae, and Mammutidae. Mean bulk $\delta^{18}O$ values of sensitive taxa and camelids are greatest at Tri-Britton followed by Leisey 1A, Haile 8A, and Inglis 1A ($p < 0.01$, Table 2, 3; Figure 2; DeSantis et al., 2009). The rank order of mean and maximum $\delta^{18}O$ values of sensitive taxa and camelids follow the same trend (Table 4). Based on mean and maximum $\delta^{18}O$ values of sensitive taxa and camelids, Tri-Britton is the warmest and/or driest of the four sites. Both Tri-Britton and the known interglacial, Leisey 1A, are warmer and/or drier than the known glacial site, Inglis 1A. There are no significant differences in bulk $\delta^{18}O$ values between Haile 8A and Leisey 1A (interglacial) or between Haile 8A and Inglis 1A (glacial).

Extant proboscideans are known to drink a significant portion of water and are insensitive to changes in evaporative conditions (Levin et al., 2006); thus, they can be used to assess changes in meteoric water, both today and in the past. However, as proboscideans are also known to travel long distances, their $\delta^{18}O$ values may or may not reflect meteoric water from their last site. Today, African elephants can travel more than 500 km during seasonal movement (Leggett, 2006). Individual fossil proboscidean specimens from Florida have strontium isotope ratios suggestive of movements of 150 km or more into Georgian environments, with some repeatedly traveling approximately 250 km to the Appalachian Mountains (Hoppe and Koch, 2006, 2007). To overcome the potential problems associated with seasonal migration of proboscideans, both proboscideans and peccaries (an evaporation "less sensitive" taxon based on Yann et al., 2013, which is also fairly abundant at all sites examined) were used to examine meteoric water.

Proboscidean mean $\delta^{18}O$ values are greatest at Haile 8A, followed by Tri-Britton, Leisey 1A (29.9‰), and Inglis 1A (29.6‰; Table 2; DeSantis et al., 2009). Further, proboscideans from Tri-Britton have a greater mean $\delta^{18}O$ value than those at Leisey 1A ($p = 0.0001$; Inglis 1A and Haile 8A cannot be compared due to small sample sizes; Table 2). The greater mean $\delta^{18}O$ proboscidean value at Haile 8A may be an artifact of a small sample size, or it may be complicated by the fact that modern proboscideans often have large home ranges and can seasonally migrate (Leggett, 2006). Due to limited peccaries at Tri-Britton, the site was not included in statistical comparisons; however, the greatest mean $\delta^{18}O$ value for peccaries is from Tri-Britton (n=3, 32.5‰). When comparing just peccaries, Inglis 1A has a lower mean $\delta^{18}O$ value (28.5‰) than Haile 8A (29.8‰, $p = 0.029$) and Leisey 1A (30.7‰, $p \leq 0.001$), but Leisey

1A and Haile 8A are not significantly different from one another. As $\delta^{18}O$ values of meteoric water are influenced by temperature, with lower $\delta^{18}O$ values occurring during periods of colder temperatures (e.g. Dansgaard, 1964), Inglis 1A (the known glacial site) likely experienced the coldest temperatures, while Tri-Britton was likely the warmest.

Since Pleistocene proboscideans from Florida may have migrated (Hoppe et al., 1999; Hoppe and Koch, 2007), both a proboscidean and a peccary offset was used to determine relative aridity for the four sites analyzed. Mean proboscidean oxygen offset values of camelids and evaporation sensitive taxa indicate that Tri-Britton has significantly greater mean offset values than both Inglis 1A and Haile 8A ($p < 0.01$, Table 3), suggesting greater evaporative conditions at Tri-Britton. Camelids and sensitive taxa from Leisey 1A have significantly greater mean values than camelids and sensitive taxa from Inglis 1A and Haile 8A ($p < 0.01$ and $p < 0.0001$, respectively), and Inglis 1A has greater mean values than Haile 8A ($p < 0.001$; Table 4); mean peccary oxygen offset values for camelids follow the same trend. Further, Tri-Britton has a significantly greater mean peccary offset value than Haile 8A ($p = 0.016$). Both the proboscidean and the peccary offset values indicate that Tri-Britton was the driest site followed by Leisey 1A and Inglis 1A, with Haile 8A being the wettest site analyzed.

Comparisons of mean $\delta^{18}O$ values of serially sampled teeth follow the same rank order as mean $\delta^{18}O$ values of all taxa. Specifically, mean $\delta^{18}O$ values for both equids and camelids were greatest at Tri-Britton followed by Leisey 1A, Haile 8A, and Inglis 1A (Table 5, Figure 3). As $\delta^{18}O$ values are greater during the summer as compared to the winter (e.g. Ayliffe et al., 1992; Dutton et al., 2005), the total range of serial samples from a given tooth can provide an estimate of relative seasonality with greater ranges suggestive of increased seasonality. All individual camelid oxygen ranges are $\leq 1.2‰$ while *Equus* serial samples are $\leq 2.7‰$ (Table 5). Low variability in the serially sampled camelids and horses likely indicates relatively low seasonality at all sites, with Inglis 1A and Leisey 1A potentially experiencing slightly more seasonally variable temperatures and/or precipitation (due to more pronounced ranges in *Equus* teeth at these sites). Another cause for small ranges in the serially sampled teeth could be due to migration, specifically the movement of animals south (or to warmer environments) during colder periods and further north during warmer periods; thus, dampening a seasonal signal in δ^{18}O values. While proboscideans are known to migrate today and in the past (Hoppe et al., 1999; Leggett, 2006; Hoppe and Koch, 2007), there is evidence that at least some of the equids found in Florida also migrated 150 km or more (Hoppe and Koch, 2007). It is unclear if Pleistocene camelids also migrated, but some of the specimens, especially those from Leisey 1A and Tri-Britton, suggest either mild seasonal changes or seasonal migration resulting in isotopic dampening. Alternatively, some of the fossil specimens analyzed were acquired from sinkhole localities that may have provided more homogenized drinking water. Specifically, sinkholes can contain both precipitation water and groundwater; thus, Haile 8A may have the most pronounced dampening of δ^{18}O values due to the mixing of both new and old water sources (Gat, 1971).

Collectively, the incorporation of δ^{18}O values, offset values, and other proxies can be used to characterize relative climates at each site (e.g. Auffenberg, 1967; Webb, 1974; Franz and Quitmyer, 2005; DeSantis et al., 2009; Kopp et al., 2009; Yann et al., 2013). The greatest camelid δ^{18}O values, the greatest camelid offset values, and the arid assemblage of tortoises and other vertebrates indicate that Tri-Britton is the warmest and driest of the four sites (this study; Franz and Quitmyer, 2005). Relatively high δ^{18}O and offset values, paired with the presence of warm adapted taxa and the geology of the site, indicate that Leisey 1A was a warm and dry interglacial site (DeSantis et al., 2009). Lower δ^{18}O and offset values, the geology of the site, and the presence of cool adapted taxa suggest Inglis 1A was a cooler and potentially wetter glacial site (DeSantis et al., 2009). *Odocoileus* and peccary $\delta^{18}O$ values at Haile 8A were indistinguishable from Leisey 1A, Haile 8A *Odocoileus* $\delta^{18}O$ values were indistinguishable from Inglis 1A, and *Hemiauchenia* $\delta^{18}O$ values were intermediate between Leisey 1A and Inglis 1A; therefore, Haile 8A has been identified as a transitional site. The assemblages of box turtles and changing soil types support a transition from cooler climates to warmer climates with increasing sea level (Auffenberg, 1967); while the lowest offset values indicate Haile 8A was the wettest of the four sites examined.

3.3.2. Environment

At Tri-Britton, $\delta^{13}C$ values suggest that *Equus* and *Mammuthus* were primarily C_4 grazers, and *Mammut*, *Palaeolama,* and *Tapirus* were primarily C_3 browsers (Table 6). Taxa with sample sizes of five or more (*Equus*, *Mammuthus*, *Mammut*, *Palaeolama*, and *Tapirus*) were used for intra-site comparisons at Tri-Britton (Table 7). *Palaeolama* has a mean value that is significantly lower than both *Mammuthus* and *Equus* ($p \leq 0.001$), and *Tapirus* and *Mammut* have significantly lower mean values than *Equus* ($p \leq 0.016$; Table 7). There are no statistical differences between browsers, but $\delta^{13}C$ values suggest that *Mammuthus* may be a mixed feeder. *Mammuthus* mean $\delta^{13}C$ values are indistinguishable from all taxa (browsers or grazers) with the exception of *Palaeolama* (Table 7), which has the most negative $\delta^{13}C$ value of all taxa at Tri-Britton.

Based on $\delta^{13}C$ values at Haile 8A, *Bison* and *Equus* were primarily C_4 grazers, *Hemiauchenia* was a mixed feeder, and *Mylohyus* and *Odocoileus* were primarily C_3 browsers (Table 6). Due to small sample sizes, *Mammuthus* and *Platygonus* were not included in the intra-site comparisons at Haile 8A (Table 8). At Haile 8A *Hemiauchenia* had significantly greater $\delta^{13}C$ values than the

C_3 browsing *Odocoileus* ($p = 0.019$) and significantly lower $\delta^{13}C$ values as compared to *Bison* and *Equus* ($p < 0.001$; Table 8). Additionally, both *Bison* and *Equus* had significantly greater $\delta^{13}C$ values than each of the inferred browsers (*Mylohyus* and *Odocoileus*) and the mixed feeding *Hemiauchenia* ($p \leq 0.028$; Table 8).

Comparisons of taxa across sites indicate that *Equus* was fairly common at both Tri-Britton and Haile 8A, with mean values of -0.1‰ and -2.5‰, respectively (Table 6, Figure 4). The same applies to Leisey 1A (-3.1‰), but at Inglis 1A, *Equus* was likely less common and $\delta^{13}C$ values for the two specimens are -4.8‰ and -4.6‰ (Figure 4; DeSantis et al., 2009). *Equus* from Tri-Britton had a diet of C_4 grass, while *Equus* from Haile 8A, Leisey 1A, and Inglis 1A had a diet of predominantly C_4 grass but consumed some C_3 resources (DeSantis et al., 2009). Inglis 1A has too few *Equus* specimens to be included in statistical comparisons, but *Equus* specimens from Tri-Britton have significantly greater mean $\delta^{13}C$ values than specimens from Haile 8A or Leisey 1A ($p < 0.05$); there is no difference between Haile 8A and Leisey 1A, and Inglis 1A has the lowest mean $\delta^{13}C$ value. Statistical comparisons indicate that *Equus* from Tri-Britton may have consumed a greater proportion of C_4 resources than individuals from any other site and/or C_4 grass values may have been more enriched in ^{13}C due to greater evaporative conditions. Specimens from Haile 8A and Leisey 1A suggest that *Equus* consumed fewer C_4 resources and/or C_4 grasses were more deplete in ^{13}C due to climatic conditions. Although Inglis 1A specimens were not included in statistical comparisons, *Equus* is the only taxon at Inglis 1A to consume C_4 recourses; thus, C_4 grasses were likely fairly limited.

Palaeolama, *Tapirus*, and *Odocoileus* are all present at Tri-Britton and Leisey 1A, but *Palaeolama* is not present at Inglis 1A or Haile 8A, and *Tapirus* is not present at Haile 8A. Mean $\delta^{13}C$ values of *Palaeolama*, *Tapirus*, and *Odocoileus* are greatest at Tri-Britton (Table 6), followed by Leisey 1A (-13.0‰, -12.7‰, -11.5‰, respectively). Based on $\delta^{13}C$ values ≤-10.5‰, *Palaeolama*, *Tapirus*, and *Odocoileus* are obligate browsers at all sites examined. Ranges of $\delta^{13}C$ values for these obligate browsers are less than or equal to 2.4‰, 2.8‰, and 1.5‰, respectively, indicating a relatively narrow dietary niche. *Palaeolama* from Tri-Britton has a significantly greater mean $\delta^{13}C$ value than from Leisey 1A ($p = 0.027$). *Tapirus* from Tri-Britton also had a significantly greater mean $\delta^{13}C$ value than at Leisey 1A or Inglis 1A ($p < 0.01$). Of these three taxa, *Odocoileus* is the only one present at all four sites, but due to small sample sizes of *Odocoileus* at Tri-Britton, statistical comparisons between all sites could not be made. *Odocoileus* specimens from Leisey 1A have a greater mean $\delta^{13}C$ value than Haile 8A or Inglis 1A ($p \leq 0.023$), but Haile 8A and Inglis 1A are indistinguishable.

In addition to determining dietary strategies, $\delta^{13}C$ values from *Tapirus* and other obligate browsers can be used to interpret the presence of forests and relative canopy density (van der Merwe and Medina, 1991; DeSantis and MacFadden, 2007). Tapirs have been used to track forested environments through time (DeSantis and MacFadden, 2007), thus they can be used to make interpretations about the presence of forested environments at Tri-Britton, Haile 8A, Leisey 1A, and Inglis 1A. Additionally, modern studies have shown that lower $\delta^{13}C$ values occur in denser canopy environments (van der Merwe and Medina, 1989, 1991), which can be used to compare relative canopy density between the four sites. The presence of *Tapirus* at Tri-Britton, Leisey 1A, and Inglis 1A indicates that these three sites had forested environments. Based on mean $\delta^{13}C$ values of *Tapirus*, Tri-Britton likely had more open forests than Leisey 1A or Inglis 1A. The absence of *Tapirus* at Haile 8A does not necessarily indicate the absence of forested environments, especially as *Odocoileus* is present and interpreted to be a C_3 browser.

Although *Tapirus* has been shown to track forested environments (DeSantis and MacFadden, 2007), some of the most negative δ^{13}C values are from *Odocoileus*. There is only one *Odocoileus* specimen from Tri-Britton, but the mean δ^{13}C value from Leisey 1A is significantly greater than the mean δ^{13}C values at Haile 8A and Inglis 1A. Thus, *Odocoileus* δ^{13}C values indicate that Leisey 1A likely had more open forests than Haile 8A and Inglis 1A and suggest the presence of even denser forests at the latter two sites than indicated by *Tapirus*. *Palaeolama* also has a more negative mean δ^{13}C value at Leisey 1A and Tri-Britton than *Tapirus* (although not statistically significant), suggesting denser forests than indicated by *Tapirus*. As evidenced by greater mean δ^{13}C values at Tri-Britton as compared to Leisey 1A, *Palaeolama* like *Tapirus*, indicates the presence of more open forests at Tri-Britton.

Mean δ^{13}C values of serially sampled equids follow the same trend as the δ^{18}O and offset values of bulk and serially sampled taxa, with Tri-Britton having the greatest mean value followed by Leisey 1A, Haile 8A, and Inglis 1A (Table 5). The largest range in δ^{13}C values is from Inglis 1A (2.3‰), but the three other sites have ranges between 1.1‰ and 1.7‰ (Table 5). Serially sampled *Equus* teeth indicate there is no substantial seasonal change in the diet of equids at all sites examined, but it suggests that the δ^{13}C values of the C_4 resources consumed are influenced by increasing evaporative conditions, recorded in δ^{18}O values. *Hemiauchenia* mean δ^{13}C values are greatest at Leisey 1A followed by Inglis 1A and Haile 8A. *Palaeolama* mean δ^{13}C values are greater at Tri-Britton than at Leisey 1A (Table 5). The greatest camelid ranges are from *Hemiauchenia* at Leisey 1A (3.0‰) and *Palaeolama* at Tri-Britton (2.5‰). The other camelid ranges are between 1.0‰ and 1.4‰ (Table 5). Based on the range of δ^{13}C values of *Hemiauchenia* from Leisey 1A (3.0‰), there may have been seasonal variation in diet, but there is no clear seasonal pattern in the tooth sampled (Figure 3).

As all medium to large bodied ungulates were sampled at all sites, assessing the total range of $\delta^{13}C$ values can provide insights to floral composition, including evaluating the presence of dense forests and/or open grasslands. Tri-Britton has the greatest total range in $\delta^{13}C$ values from -13.3‰ to +1.5‰ (range: 14.8‰) with many browsers, a few mixed feeders, and several obligate grazers (Table 2, Figure 4). Haile 8A has the second largest range in $\delta^{13}C$ values (14.4‰) from -14.2‰ to +0.2‰, but lacks mixed feeders (Table 2, Figure 4). Previously published $\delta^{13}C$ values from Leisey 1A range from -14.3‰ to -1.7‰ (12.6‰) with several browsers, grazers, and mixed feeders (DeSantis et al., 2009). Inglis 1A has the smallest range in $\delta^{13}C$ values from -15.3‰ to -4.6‰ and is dominated by browsers, with only grazing equids (10.7‰; Figure 4; DeSantis et al., 2009). Based on total ranges, taxa present, and the presence of obligate browsers and grazers at each site, Tri-Britton contained grassland environments and the most open forests of the four sites. Leisey 1A had moderately closed forests with available C_4 grasses, and Haile 8A was similar to both Tri-Britton and Leisey 1A, but with potentially fewer C_4 grass resources. Inglis 1A was the most homogeneous site and was dominated by denser canopied forests and limited C_4 resources.

Tri-Britton, the most open site with fairly open forests and the presence of grasslands, was also the warmest and driest of the four sites. As the climate cooled, some environments may have become more homogeneous with the presence of primarily forests and fewer C_4 grasslands. While there are limited reconstructions of the environment and climate of Florida during the early and middle Pleistocene, and climates of the late Pleistocene are interpreted as being out of phase with the North Atlantic (Grimm et al., 2006), the stable isotope analyses from Tri-Britton and Haile 8A may be used to improve previous environmental and climatic interpretations. In comparison with modern climates, the stable oxygen isotope values from Tri-Britton support previous interpretations of a more arid environment (Franz and Quitmyer, 2005). Despite the interpretation of no mesic hardwoods or pine flatwoods based on smaller vertebrates at Tri-Britton (Franz and Quitmyer, 2005), δ^{13}C values suggest a fairly heterogeneous environment with forests and open grasslands. Tortoises and other small vertebrates from Haile 8A suggest a more heterogeneous environment than Tri-Britton with pine flatwoods and freshwater environments (Franz and Quitmyer, 2005), but the range of δ^{13}C values at Haile 8A is not significantly different from that at Tri-Britton. While Haile 8A δ^{18}O values discussed above do not suggest the presence of xeric environments, as supported by the smaller vertebrates (Franz and Quitmyer, 2005), it is possible that xeric environments occurred on a much smaller scale.

Modern Florida is characterized by a diversity of ecoregions and ecotones, often including a variety of smaller or patchier scale microenvironments (e.g. Griffith et al., 2002; Dee and Menges, 2014). Due to the lack of floral reconstructions associated with the Pleistocene sites included in these analyses, it is challenging to separate the specific causes of floral diversity. Other interpretations for changes in δ^{13}C values could include influences of smaller scale differences in the local hydrology, the presence of or proximity to an ecotone with mixed environments, changes in fire regimes, topography, or soil type (e.g. Stephenson, 1990; Menges and Hawkes, 1998; Obeysekera et al., 1999; Boughton et al., 2006; DeSantis et al., 2007). Changes in the fire regime may have influenced the floral environment and stand structure, with less frequent fires allowing for the development of forested environments while an increase in fire frequency could have favored more open grasslands and/or the presence of smaller shrubs (e.g., Veno, 1976; Menges et al., 1993; Peterson and Reich, 2008).

It is compelling that the driest sites (Tri-Britton, Leisey 1A) have a high number of C_4 grazers and many C_3 browsers, indicating both open grasslands and forests. Further, the coolest site

(Inglis 1A) is dominated by C_3 browsing taxa, while Haile 8A shows intermediate conditions. While it is difficult to estimate the extent of forested and grassland environments at any of these sites, the resources had to have been abundant enough to support multiple taxa as well as their local, reproducing populations. However, additional work that assesses relationships between floral diversity and paleoclimates could help clarify the mechanisms driving environmental changes.

Identifying the specific sources driving differences in $\delta^{18}O$ values from Pleistocene tooth enamel can also be difficult. Groundwater from different modern aquifers in Florida can have distinctive isotopic signatures from at least -6.75‰ to 3.23‰, and can be used to identify the source and percent mixing of surface and ground water (e.g. Meyers et al., 1993; Katz et al., 1995; Ewe et al., 1999; Gremillion and Wanielista, 2000; Price and Swart, 2006). While identifying $\delta^{18}O$ values and the extent of groundwater mixing is possible in modern systems, it is difficult to interpret the effects of groundwater on $\delta^{18}O$ values in past systems. The medium to large bodied mammals included in this study, and other similar studies, were likely not consuming pure groundwater, but instead a mixture of rainwater, evaporated surface water, and more isotopically homogeneous groundwater (Koch et al., 1998; Hoppe et al., 2004). Greater influence of groundwater could lead to less seasonal signals in serial sampled teeth, similar to what we see in the serially sampled *Equus* teeth from Tri-Britton and Haile 8A and serially sampled *Hemiauchenia* teeth from Inglis 1A and Haile 8A. This dampened (or lack of) seasonal signal could alternatively suggest a less seasonal climate, especially at Haile 8A and Tri-Britton. Although the *Hemiauchenia* specimen from Inglis 1A shows no clear seasonal signal, the serially sampled *Equus* tooth from Inglis 1A shows the greatest seasonal variability (Figure 3, Table 5). Despite both specimens being recovered from a sinkhole, within a groundwater and rainwater fed larger karst environment, there was likely some real differences in the water sources consumed by these two taxa.

In addition to animals that actively drink water, taxa that consume large quantities of plant water may also be influenced by the δ^{18}O values of local groundwater and surface water. A study of modern hammock and pineland forest environments in southern Florida showed that different vegetative communities utilize different water sources (Ewe et al., 1999). For example, the pineland forests maintained high groundwater usage (78-100%), while the hammock vegetation had seasonally varied reliance on groundwater (0.8-86%; Ewe et al., 1999). Additionally, δ^{18}O values of plants can also vary in response to the local hydrology including access to various water sources and/or coastal flooding (e.g. DeSantis et al., 2007). This variation likely also occurred during the Pleistocene and may have influenced δ^{18}O values of plant water consumed by the mammals analyzed. Comparisons of taxa that typically consume vegetation from different environments (forests versus open grass/shrubland) can be complicated by the fact that plants in more open settings experience greater evaporation than plants growing in a denser forest (Kelliher et al., 1993; van der Merwe and Medina, 1989). While *Hemiauchenia* had greater δ^{18}O values than *Palaeolama* at Leisey 1A, consistent with the latter consuming less evaporative leaf water from relatively dense forests, there were no significant difference between browsing *Odocoileus* and mixed feeding *Hemiauchenia* at Leisey 1A, Inglis 1A, or Tri-Britton. Additionally, there were no significant differences between browsing *Mammut* and mixed feeding *Mammuthus* at Leisey 1A or Haile 8A, although that may be expected as these proboscideans were likely primarily drinking from local water sources and less influenced by differences in plant water.

3.3.3. Dietary Niche Modification

Bison, *Capromeryx*, and *Cuvieronius* are only found at one site, so they are not included in inter-site comparisons of dietary niches. Browsing *Palaeolama* and *Tapirus* and grazing *Equus* do not appear to significantly modify their dietary niches at the four sites included in this study. Specifically, they maintain their presence and their respective consumption of either denser forest vegetation or more open grassland resources regardless of environmental and/or climatic conditions. Significantly greater mean $\delta^{13}C$ values of *Tapirus* and *Palaeolama* at Tri-Britton, as compared to Leisey 1A ($p \leq 0.046$), may indicate more ^{13}C enriched plant values in response to increasing temperature and/or aridity (Cerling et al., 1997; Passey et al., 2005; Murphy et al., 2007; Fraser et al., 2008) and/or their consumption of plants within more open forests (van der Merwe and Medina, 1989). *Odocoileus* maintains a C_3 browsing niche at all sites present, but shifts from having the most negative $\delta^{13}C$ values at Inglis 1A and Haile 8A to more positive $\delta^{13}C$ values than both *Tapirus* and *Palaeolama* at Leisey 1A; this suggests a shift from a denser forest browser to a more open forest or edge browser at the more evaporative Leisey 1A site (as previously suggested by DeSantis et al., 2009). This pattern may also occur at Tri-Britton; however, as there is only one *Odocoileus* tooth, it is difficult to know if this trend is further supported. Consistent with previous work, *Equus* also maintains its niche as an obligate grazer during the Pleistocene (MacFadden and Cerling, 1994; Feranec and MacFadden, 2000); the significant increase in $\delta^{13}C$ values at Tri-Britton may represent an increase in the availability of C_4 grasses at the warmest and driest site.

Despite the lack of *Mammut* specimens from Haile 8A and only one specimen from Tri-Britton, mean $\delta^{13}C$ values of *Mammut* indicate all specimens have $\delta^{13}C$ values more negative than -6‰. Only one specimen from Tri-Britton had a mixed feeding diet (-6.3‰), all other specimens have

$\delta^{13}C$ values indicative of a browsing diet (≤ -10.0‰, Table 6). A predominately browsing diet is consistent with results from low-magnification stereomicroscopy and stable isotope analysis (e.g. Koch et al., 1998; Green et al., 2005), while opal phytoliths from tooth calculus have suggested they consumed some grasses (Gobetz and Bozarth, 2001). Although one specimen from Tri-Britton suggests that *Mammut* consumed a substantial amount of C_4 resources, additional work is needed to determine the extent to which *Mammut* was a mixed feeder at other Pleistocene localities in Florida and throughout North America.

The two *Mammuthus* specimens from Halie 8A have $\delta^{13}C$ values of 0.1‰ and 0.2‰ which are more positive than the mean $\delta^{13}C$ values from Leisey 1A (-2.9‰) and Tri-Britton (-7.6‰; Table 6; DeSantis et al., 2009). While there is no significant difference between Leisey 1A and Tri-Britton, Tri-Britton has a broader isotopic range (7.5‰) than Leisey 1A (2.6‰; Table 6; DeSantis et al., 2009). Previous work suggested that *Mammuthus* from sites in northern Florida had more negative $\delta^{13}C$ values than those from southern sites, indicating *Mammuthus* tracked the proportion of C_3 and C_4 grass (Koch et al., 1998). Data included here do not support this conclusion, as the most negative *Mammuthus* $\delta^{13}C$ values are found at the most southern site, which is the warmest and driest of those examined. While it seems counterintuitive for *Mammuthus* to consume more C_3 vegetation at the warmest and driest site, they may have altered their diets in response to the presence of other herbivores, or those values may have recorded their diet while present in other regions (e.g., migration). Collectively, geochemical data suggest that *Mammuthus* maintained a C_4 grazing diet at Haile 8A and Leisey 1A, but incorporated more C_3 vegetation at Tri-Britton.

Hemiauchenia $\delta^{13}C$ values are more variable than the other taxa previously discussed. The two specimens from Tri-Britton have $\delta^{13}C$ values of -6.3‰ and -13.1‰, but they were not included in the statistical analysis due to small sample sizes. The 11 specimens at Haile 8A have a mean $\delta^{13}C$ value of -9.2‰ and a range of 9.7‰ (Table 6). The 10 specimens from Leisey 1A have a mean $\delta^{13}C$ value of -6.4‰ and a range of 5.5‰ (DeSantis et al., 2009). The *Hemiauchenia* specimens from Leisey 1A have a significantly greater mean $\delta^{13}C$ value than those at Haile 8A ($p < 0.01$) or Inglis 1A ($p < 0.0001$), but there is no significant difference between mean $\delta^{13}C$ values at Haile 8A and Inglis 1A. The two specimens from Tri-Britton have a much larger range (11.1‰), but the mean value falls between Haile 8A and Leisey 1A (Table 6). Increased $\delta^{13}C$ ranges have been documented in *Hemiauchenia*, suggesting a change in dietary behavior from an obligate browser to a mixed feeder (with increased consumption of C_4 grasses; Feranec and MacFadden, 2000; Feranec, 2003; DeSantis et al., 2009). Floral changes across the Blancan-Irvingtonian boundary have been suggested to explain the increase in $\delta^{13}C$ values (Feranec, 2003), and this study further supports that changing environments and/or warmer and drier conditions may contribute to increased C_4 consumption (DeSantis et al., 2009).

Like *Hemiauchenia*, peccaries at these four sites also have more variable $\delta^{13}C$ values. *Platygonus*, the only peccary at Inglis 1A, has a mean $\delta^{13}C$ value of -11.4‰ and a range of 3.1‰ (DeSantis et al., 2009). Both *Platygonus* and *Mylohyus* are present at Haile 8A and their mean $\delta^{13}C$ values are -10.7‰ and -10.2‰ and their ranges are 2.8‰ and 4.3‰, respectively, indicative of a browsing diet (Table 6). Both peccaries are also present at Leisey 1A, but *Platygonus* has a mean of -6.2‰ and a range of 5.7‰ (suggestive of mixed feeding) and *Mylohyus* has a mean of -8.6‰ and a range of 7.3‰ (indicative of browsing; DeSantis et al., 2009). At Tri-Britton there are only two specimens of *Platygonus* (-7.8‰ and -7.5‰) and one specimen of *Mylohyus* (-9.9‰; Table 6); thus, statistical comparisons between peccaries at Tri-Britton were not possible. *Mylohyus* $\delta^{13}C$ values are not significantly different from those present at Haile 8A and Leisey 1A. *Platygonus* $\delta^{13}C$ values at Leisey 1A are significantly greater than those at both Haile 8A ($p < 0.05$) and Inglis 1A ($p < 0.001$), and there are no significant differences between mean $\delta^{13}C$ values from Haile 8A and Inglis 1A.

Previous work suggested that *Mylohyus* was a smaller forest browser while *Platygonus* had longer limbs and a grazing diet, which may have allowed for the co-occurrence of closely related taxa (Martin, 1974; Kurten, 1980). Dental microwear analysis of *Platygonus* from Indiana suggested a browsing to mixed feeding diet, and further comparisons suggested a faunivorous diet (Schmidt, 2008). Stable carbon isotope values from a *Mylohyus* and a *Platygonus* specimen in Florida show an overlap in $\delta^{13}C$ values (-8.0‰ and -8.3‰, respectively) suggesting a diet of C_3 or CAM vegetation (MacFadden and Cerling, 1996). Later work on the $\delta^{13}C$ values from *Platygonus* suggest a change from mixed feeding in the early Irvingtonian to a browsing diet in the late Irvingtonian (Feranec and MacFadden, 2000). Contrary to previous work, *Platygonus* had a browsing diet during glacial (Inglis 1A, early Irvingtonian; DeSantis et al., 2009) or potentially transitional sites (Haile 8A, early Rancholabrean), but was a mixed feeder during interglacial (Leisey 1A, early Irvingtonian; DeSantis et al., 2009) or more evaporative conditions (Tri-Britton, late Irvingtonian).

3.4. Conclusions

Collectively, this research further supports the idea that increasing evaporative conditions may have contributed to the existence of for more heterogeneous environments. These environments may have subsequently allowed for the co-occurrence of closely related taxa (e.g. the co-existence of taxa from the same family) at Tri-Britton, similar to Leisey 1A (DeSantis et al., 2009). Although Haile 8A represents a potential transitional site, it still documents an increase in taxa with more disparate dietary niches and greater heterogeneity than the glacial site, Inglis 1A. Dietary niche modification occurs in the dietary generalists (*Hemiauchenia*, *Platygonus*, and *Mylohyus*), potentially in response to changing climates and/or more heterogeneous environments. The lack of significant dietary niche modification in *Equus*, *Mammut*, *Palaeolama*, and *Tapirus* suggests that these taxa are dietary specialist and their diet was less impacted by changing climatic and/or environmental conditions. Thus, dietary niches are conserved in only the most specialized mammals. Further, this work demonstrates that aridity indices and stable oxygen isotope values can be used to determine relative temperature and aridity in Florida fossil sites that lack geologic evidence of glacial or interglacial designations.

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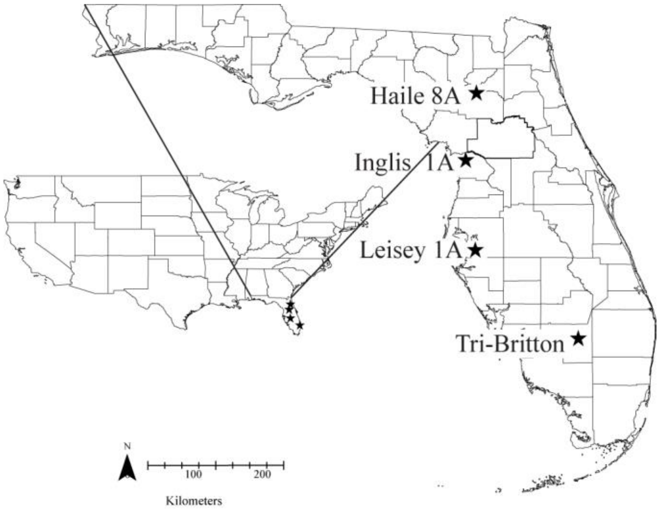

Figure 3.1. Site map of all Pleistocene fossil sites examined.

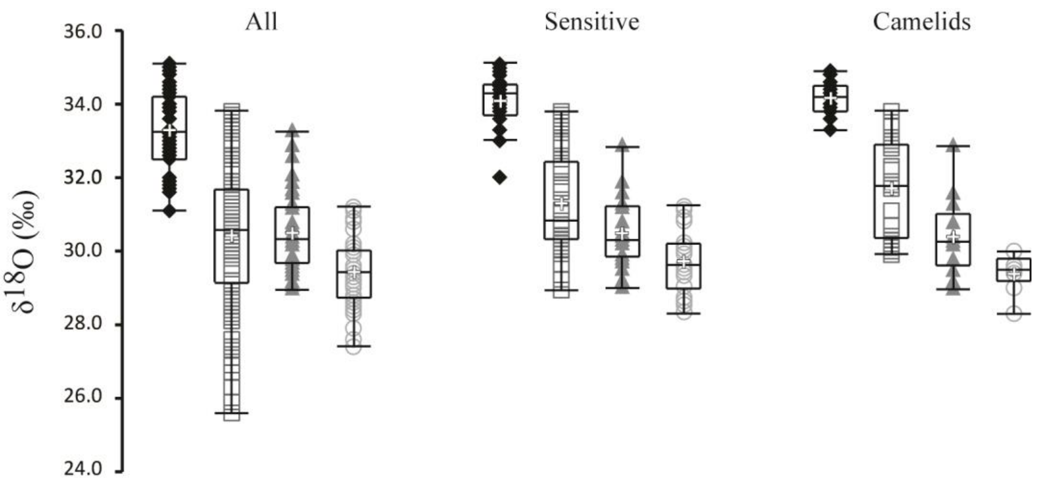

Figure 3.2. Box plots of δ^{18}O values for all taxa, sensitive taxa, and camelids from Tri-Britton (closed diamonds), Leisey 1A (open squares), Haile 8A (closed triangles), and Inglis 1A (open circles).

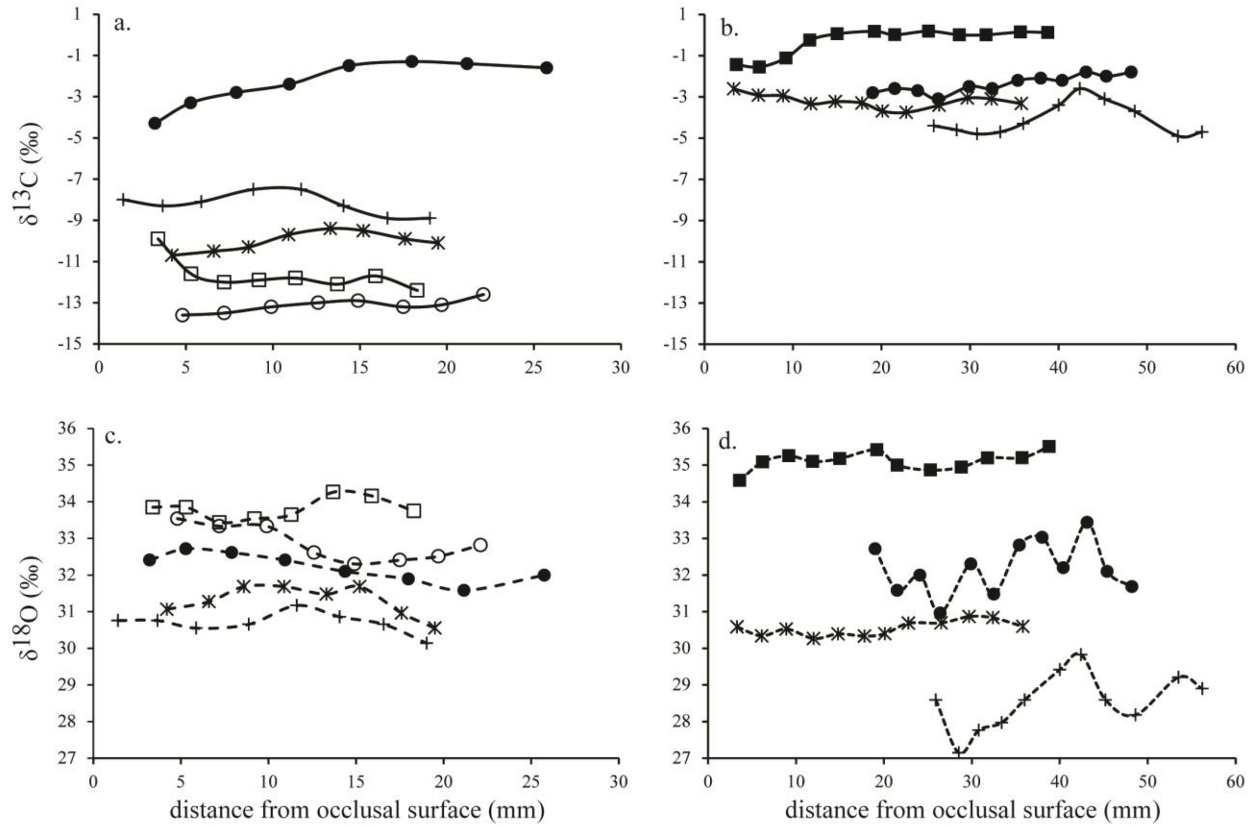

Figure 3.3. $\delta^{13}C$ and $\delta^{18}O$ serial samples from camelids (a and c) and equids (b and d). Each line represents one tooth from Hemiauchenia (solid symbol), Palaeolama (open symbol) or Equus (solid symbol) from Tri-Britton (square), Haile 8A (asterisk), Leisey 1A (circle), and Inglis 1A (plus sign).

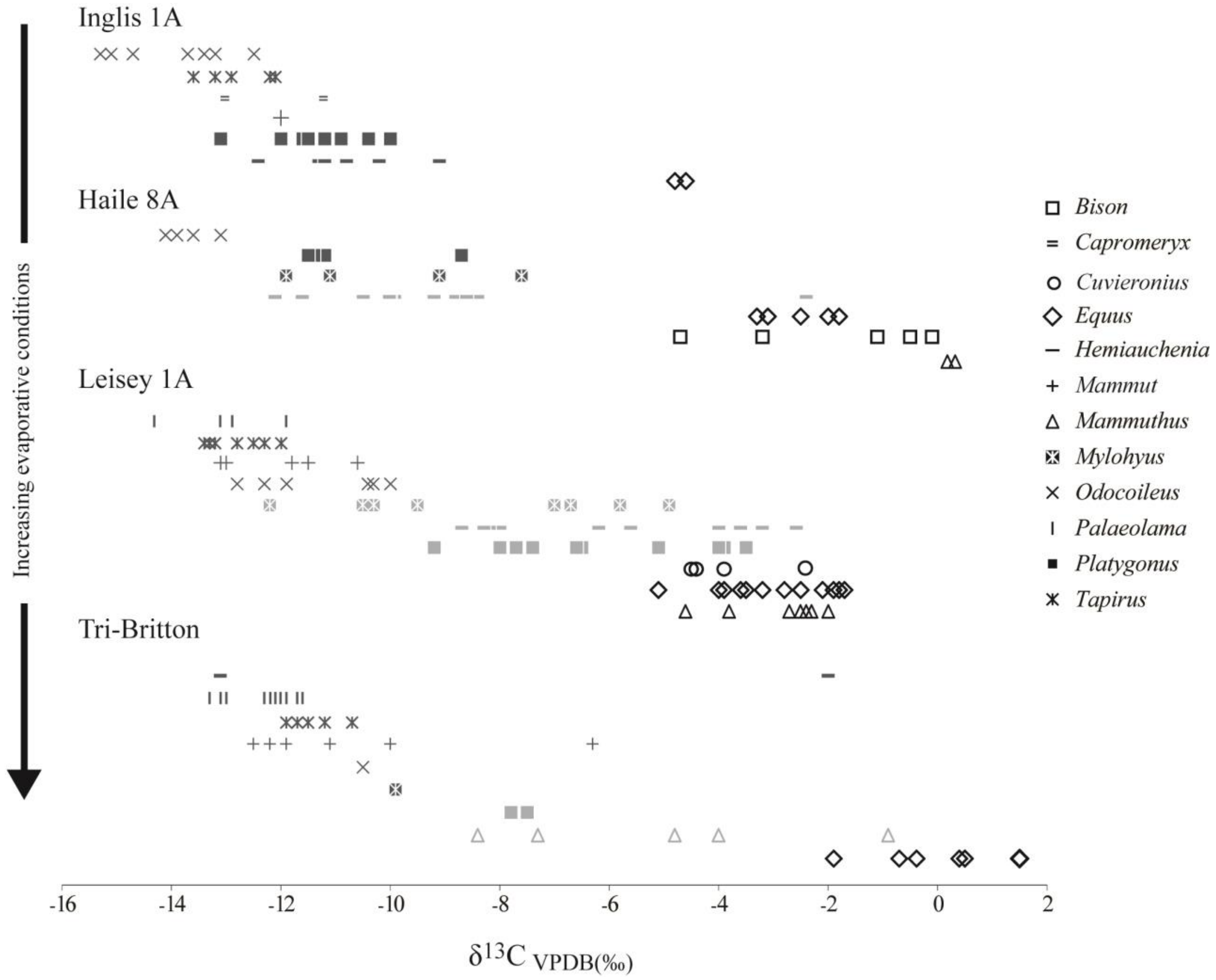

Figure 3.4. δ^{13}C values and dietary niche partitioning of herbivores from all sites examined. Sites are arranged based on increasing mean δ^{18}O values of sensitive taxa, from top to bottom. Within each site, taxa are ordered by increasing mean δ^{13}C values, including from left to right, browsers (taxa with mean values less than -8‰, dark gray), mixed feeders (taxa with mean values greater than or equal to -8‰ and less than or equal to -2‰, light gray), and grazers (taxa with mean values greater than -2‰, black).

Table 3.1. Site descriptions for all fossil sites examined.

site	mammals analyzed	other vertebrates present	depositional environment	inferred environment	rationale for inferred environment	age (NALMA)	age (Ma)
Haile 8A[1,2]	bison, camelids, deer, horses, mammoths, peccaries	felids, canids, ursid, pampatheres, mustelids, small mammals birds, lizards, snakes, tortoises, turtles, frogs	sinkhole	intermediate climate, transitional between glacial and interglacial	assemblages of box turtles and transitioning of soil types	early Rancholabrean	0.3 - 0.13
Tri-Britton[3,4]	camelids, deer, horses, mammoths, mastodons, peccaries, tapirs	tortoises, turtles, fish, alligator	fluvial	arid	assemblage of tortoises	late Irvingtonian	0.5 - 0.4
Leisey 1A[1,5]	camelids, deer, gomphotheres, horses, mammoths, mastodons, peccaries, tapirs	felids, canids, ursid, small mammals, xenarthrans birds, reptiles, freshwater fish, marine fish	coastal mangrove bay	interglacial	higher sea level, intermixed marine invertebrates and terrestrial vertebrates, warm adapted taxa, more positive $\delta^{18}O$ values	early Irvingtonian	1.6 - 1.0
Inglis 1A[1,5]	antilocaprids, camelids, deer, horses, mastodon, peccaries, tapirs	felids, canids, small mammals, xenarthrans birds, reptiles	sinkhole	glacial	lower sea level, deposit is 5 m below modern sea level, no marine fossils, presence of cool adapted taxa, lower $\delta^{18}O$ values	early Irvingtonian	2.0 - 1.6

[1] Morgan and Hulbert, 1995; [2] Auffenberg, 1967; [3] Meers and Hulbert, 2002; [4] Franz and Quitmyer, 2005; [5] DeSantis et al., 2009

Table 3.2. Descriptive statistics of stable oxygen isotopes ($\delta^{18}O$), carbon isotopes ($\delta^{13}C$), and oxygen ($\delta^{18}O$) offset values from Haile 8A and Tri-Britton.

		Haile 8A				Tri-Britton			
		All	S	LS	P	All	S	LS	P
$\delta^{18}O$	*n*	37	21	14	2	39	20	8	11
	mean	30.5	30.6	30.2	33	33.2	34.0	32.7	32.2
	max	33.3	32.9	32.1	33.3	35	35.0	33.2	33.8
	min	29	29.0	29.1	32.6	31.1	32.0	31.9	31.1
	range	4.3	3.9	3.0	0.7	3.9	3.0	1.3	2.7
	SD	1.1	1	0.9	0.5	1.1	0.7	0.7	0.7
	skewness	0.8	0.6	1.1	--	-0.1	-1.1	-0.8	0.8
	SEM	0.2	0.2	0.2	0.3	0.2	0.2	0.2	0.2
$\delta^{13}C$	*n*	38	21	14	3	39	20	8	11
	mean	-7.5	-8.6	-7.4	-0.3	-8.5	-8.1	-10.3	-8.1
	max	0.2	-1.8	-0.1	0.2	1.5	1.5	-7.5	-0.9
	min	-14.2	-14.2	-11.9	-1.3	-13.3	-13.3	-11.9	-12.5
	range	14.4	12.4	11.8	1.5	14.8	14.8	4.4	11.6
	SD	4.7	4.3	4.5	0.8	4.7	5.9	1.7	3.8
	skewness	0.4	0.5	0.6	-1.7	0.9	0.7	1	0.6
	SEM	0.8	0.9	1.2	0.5	0.8	1.3	0.6	1.2
$\delta^{18}O$ offset	*n*	35	21	14	--	28	20	8	--
	mean	-2.6	-2.4	-2.8	--	1.4	1.8	0.5	--
	max	-0.1	-0.1	-0.9	--	2.8	2.8	1	--
	min	-4	-4	-3.9	--	-0.3	-0.2	-0.3	--
	range	3.9	3.9	3	--	3.1	3	1.3	--
	SD	0.9	1	0.9	--	0.9	0.7	0.4	--
	skewness	0.7	0.6	1.1	--	-0.3	-1.1	-0.8	--
	SEM	0.2	0.2	0.2	--	0.2	0.2	0.2	--

All=all taxa except proboscideans, S=evaporation sensitive taxa, LS=less sensitive taxa, P=proboscideans, *n*=number of individuals, max=maximum value, min=minimum value, range=maximum-minimum, SD=standard deviation (n-1), SEM=standard error of the mean.

Table 3.3. Means and *p*-values from Kruskall-Wallis tests for stable oxygen isotopes ($\delta^{18}O$) and oxygen offset values from all sites examined.

	Sites			Camelids				Sensitive				Less Sensitive				Peccaries			
$\delta^{18}O$	Tri-Britton	vs	Inglis 1A	34.1	>	29.4	**<0.0001**	34.0	>	29.7	**< 0.0001**	32.7	>	29.0	**< 0.0001**	--		--	--
	Tri-Britton	vs	Haile 8A	34.1	>	30.5	**<0.0001**	34.0	>	30.6	**< 0.0001**	32.7	>	30.2	**0.005**	--		--	--
	Tri-Britton	vs	Leisey 1A	34.1	>	31.7	**0.0010**	34.0	>	31.3	**< 0.0001**	32.7	>	29.6	**0.0001**	--		--	--
	Leisey 1A	vs	Inglis 1A	31.7	>	29.4	**0.004**	31.3	>	29.7	**0.001**	29.6	>	29.0	0.289	30.7	>	28.5	**0.001**
	Leisey 1A	vs	Haile 8A	31.7	>	30.5	0.109	31.3	>	30.6	0.164	29.6	<	30.2	0.364	30.7	>	29.8	0.282
	Haile 8A	vs	Inglis 1A	30.5	>	29.4	0.175	30.6	>	29.7	0.067	30.2	>	29.0	0.088	29.8	>	28.5	**0.043**
Proboscidean	Tri-Britton	vs	Inglis 1A	1.9	>	-0.2	**0.005**	1.8	>	0.1	**0.0004**	0.5	>	-0.6	0.170	--		--	--
offset	Tri-Britton	vs	Haile 8A	1.9	>	-2.5	**<0.0001**	1.8	>	-2.4	**< 0.0001**	0.5	>	-2.8	**< 0.0001**	--		--	--
	Tri-Britton	vs	Leisey 1A	1.9	>	1.8	0.817	1.8	>	1.4	0.206	0.5	>	-0.3	0.196	--		--	--
	Leisey 1A	vs	Inglis 1A	1.8	>	-0.2	**0.006**	1.4	>	0.1	**0.005**	-0.3	>	-0.6	0.783	--		--	--
	Leisey 1A	vs	Haile 8A	1.8	>	-2.5	**<0.0001**	1.4	>	-2.4	**< 0.0001**	-0.3	>	-2.8	**0.0001**	--		--	--
	Haile 8A	vs	Inglis 1A	-2.5	<	-0.2	0.174	-2.4	<	0.1	**0.001**	-2.8	<	-0.6	**0.002**	--		--	--
Peccary	Tri-Britton	vs	Inglis 1A	1.6	>	0.9	0.087	1.5	>	1.2	0.352	-0.1	<	1.4	**0.008**	--		--	--
offset	Tri-Britton	vs	Haile 8A	1.6	>	0.7	**0.016**	1.5	>	0.8	**0.024**	-0.1	<	1.6	**0.011**	--		--	--
	Tri-Britton	vs	Leisey 1A	1.6	>	1.0	0.091	1.5	>	0.6	**0.002**	-0.1	>	-1.8	**0.036**	--		--	--
	Leisey 1A	vs	Inglis 1A	1.0	>	0.9	0.674	0.6	<	1.2	0.055	-1.8	<	1.4	**<0.0001**	--		--	--
	Leisey 1A	vs	Haile 8A	1.0	>	0.7	0.328	0.6	<	0.8	0.635	-1.8	<	1.6	**<0.0001**	--		--	--
	Haile 8A	vs	Inglis 1A	0.7	<	0.9	0.7	0.8	<	1.2	0.196	1.6	>	1.4	0.82	--		--	--

Bold values indicate significance. Less sensitive proboscidean offset values do not include proboscideans, and less sensitive peccary offset values do not include peccaries.

Table 3.4. Rank order of $\delta^{18}O$ values for sensitive taxa and camelids from all sites examined.

		Sensitive		Camelids	
	site	$\delta^{18}O$	rank	$\delta^{18}O$	rank
mean	Tri-Britton	34.0	1	34.1	1
	Leisey 1A	31.3	2	31.7	2
	Haile 8A	30.6	3	30.5	3
	Inglis 1A	29.7	4	29.4	4
maximum	Tri-Britton	35.0	1	34.2	1
	Leisey 1A	33.8	2	33.8	2
	Haile 8A	32.9	3	30.5	3
	Inglis 1A	31.2	4	30.0	4

Table 3.5. Descriptive statistics of serial samples from camelids and *Equus*.

			$\delta^{18}O$				$\delta^{13}C$			
		n	mean	max	min	range	mean	max	min	range
Equus	Haile 8A	12	30.5	30.9	30.3	0.6	-3.2	-2.6	-3.8	1.1
Equus	Inglis 1A	11	28.6	29.8	27.1	2.7	-4.1	-2.6	-4.9	2.3
Equus	Leisey 1A	12	32.2	33.4	31.0	2.5	-2.4	-1.8	-3.1	1.3
Equus	Tri-Britton	12	35.1	35.5	34.6	0.9	-0.3	0.2	-1.5	1.7
Hemiauchenia	Haile 8A	8	31.3	31.7	30.6	1.1	-10.0	-9.4	-10.7	1.3
Hemiauchenia	Inglis 1A	8	30.7	31.2	30.1	1.0	-8.2	-7.5	-8.9	1.4
Hemiauchenia	Leisey 1A	8	32.2	32.7	31.6	1.1	-2.3	-1.3	-4.3	3.0
Palaeolama	Leisey 1A	8	32.9	33.5	32.3	1.2	-13.1	-12.6	-13.6	1.0
Palaeolama	Tri-Britton	8	33.8	34.3	33.4	0.8	-11.7	-9.9	-12.4	2.5

n=number of samples per tooth, max=maximum, min=minimum, range=max-min

Table 3.6. Descriptive statistics of mammalian isotope values for Tri-Britton and Haile 8A.

			Carbon						Oxygen						Proboscidean Offset					
site	taxa	n	mean	min	max	range	SD	SEM	mean	min	max	range	SD	SEM	mean	min	max	range	SD	SEM
Tri-Britton	*Equus*	6	-0.1	-1.9	1.5	3.4	1.2	0.5	33.5	32.0	34.5	2.5	0.9	0.4	1.3	-0.2	2.3	2.5	0.9	0.4
	Hemiauchenia	2	-7.6	-13.1	-2.0	11.1	7.8	5.6	33.7	33.3	34.0	0.7	0.5	0.4	1.5	1.1	1.8	0.7	0.5	0.4
	Mammut	6	-10.7	-12.5	-6.3	6.2	2.3	0.9	32.2	31.6	32.8	1.2	0.5	0.2	--	--	--	--	--	--
	Mammuthus	5	-5.1	-8.4	-0.9	7.5	2.9	1.3	32.2	31.1	33.8	2.7	1.0	0.5	--	--	--	--	--	--
	Mylohyus	1	-9.9	--	--	--	--	--	32.5	--	--	--	--	--	0.3	--	--	--	--	--
	Odocoileus	1	-10.5	--	--	--	--	--	35.0	--	--	--	--	--	2.8	--	--	--	--	--
	Palaeolama	11	-12.3	-13.3	-11.6	1.7	0.6	0.2	34.2	33.6	34.9	1.3	0.5	0.1	2.0	1.4	2.7	1.3	0.5	0.1
	Platygonus	2	-7.7	-7.8	-7.5	0.3	0.2	0.2	32.5	31.9	33.1	1.2	0.8	0.6	0.3	-0.3	0.9	1.2	0.8	0.6
	Tapirus	5	-11.4	-11.9	-10.7	1.2	0.5	0.2	32.9	32.5	33.2	0.7	0.3	0.1	0.7	0.3	1.0	0.7	0.3	0.1
Haile 8A	*Bison*	5	-1.9	-4.7	-0.1	4.6	2.0	0.9	30.8	30.4	32.1	1.7	0.7	0.3	-2.2	-2.6	-0.9	1.7	0.7	0.3
	Equus	5	-2.5	-3.3	-1.8	1.5	0.7	0.3	30.7	30.2	31.2	1.0	0.4	0.2	-2.3	-2.8	-1.8	1.0	0.4	0.2
	Hemiauchenia	11	-9.2	-12.1	-2.4	9.7	2.5	0.8	30.5	29.0	32.9	3.9	1.2	0.3	-2.5	-4.0	-0.1	3.9	1.2	0.3
	Mammuthus	2	0.2	0.1	0.2	0.1	0.1	0.1	33.0	32.6	33.3	0.7	0.5	0.3	--	--	--	--	--	--
	Mylohyus	5	-10.2	-11.9	-7.6	4.3	1.8	0.8	29.9	29.1	31.7	2.6	1.0	0.5	-3.1	-3.9	-1.3	2.6	1.0	0.5
	Odocoileus	5	-13.4	-14.2	-12.3	1.9	0.7	0.3	30.7	29.7	31.9	2.2	1.0	0.4	-2.3	-3.3	-1.1	2.2	1.0	0.4
	Platygonus	4	-10.7	-11.5	-8.7	2.8	1.3	0.7	29.6	29.4	29.9	0.5	0.2	0.1	-3.4	-3.6	-3.1	0.5	0.2	0.1

n=number of individuals, max=maximum value, min=minimum value, range=maximum-minimum, SD=standard deviation (n-1), SEM=standard error of the mean.

Table 3.7. Intra-site comparisons of stable carbon isotope values from taxa at Tri-Britton. Taxa ordered by increasing mean values.

	Tapirus	*Mammut*	*Mammuthus*	*Equus*
Palaeolama	0.116	0.196	**0.001**	**< 0.0001**
Tapirus		0.750	0.159	**0.016**
Mammut			0.074	**0.004**
Mammuthus				0.344

Bold *p*-values indicate significant comparisons.

Table 3.8. Intra-site comparisons of stable carbon isotope values from taxa at Haile 8A. Taxa ordered by increasing mean values.

	Mylohyus	*Hemiauchenia*	*Equus*	*Bison*
Odocoileus	0.102	**0.019**	**0.000**	< **0.0001**
Mylohyus		0.675	**0.026**	**0.012**
Hemiauchenia			**0.028**	**0.012**
Equus				0.781

Bold *p*-values indicate significant comparisons.

Chapter 4

DIETARY NICHES OF PLEISTOCENE LAMINI CAMELIDS: INFLUENCES OF CLIMATE, ENVIRONMENT, AND SYMPATRIC TAXA

4.1. Introduction

With current and projected climate change, high elevation environments, like those in the Andes Mountains, are predicted to be some of the most severely affected (e.g. Bradley et al., 2004). Of the three extant arid adapted genera in Camelidae (*Camelus*, *Lama*, *Vicugna*), two of the wild species live exclusively in South America and occupy these harsh environments. The wild South American vicuna (*Vicugna vicugna*) and guanaco (*Lama guanicoe*) are part of the tribe Lamini, which is a rank between family and genus (Honey et al., 1998), as are the domesticated llama (*Lama glama*) and alpaca (*Lama pacos* or *Vicugna pacos* as suggested by Kadwell et al, 2001; Honey et al., 1998). These animals typically survive on low quality vegetation in the high-elevation Andes Mountains (Bas and Bonacic, 2003). In these arid environments, heavy reliance on the water contained in their food allows them to live where few other large animals could survive (Bas and Bonacic, 2003). Understanding how these extant animals have survived in the harsh environments of the Andes may provide insight for their conservation in the face of changing climates.

A more detailed examination of the dietary habits and paleoecology of Pleistocene ancestors may help to understand the dietary characteristics that support the harsh lifestyle of modern Lamini camelids. During the Pleistocene, there were four Lamini camelid genera in North America including *Blancocamelus*, *Camelops*, *Hemiauchenia*, and *Palaeolama* (Honey et al., 1998; PBDB, 2013). Many studies have looked at the paleoecology of multiple genera of Lamini camelids (e.g. Dompierre and Churcher, 1996; Meachen, 2003; Kohn et al., 2005; DeSantis et al., 2009; Semprebon and Rivals, 2010; Yann et al., in prep), but there has been no direct comparison of the stable isotope dietary ecology of the three most abundant North American genera during the Pleistocene (i.e. *Camelops, Hemiauchenia,* and *Palaeolama*).

Here, we aim to clarify the paleoecology of Pleistocene camelids by asking the following questions: 1) how does a camelid's dietary strategy (i.e. more generalized or more specialized) influence the dietary ecology and/or presence of confamilies (i.e. genera from the same family)?; 2) can we predict the occurrence of camelids based on the occurrence of other mammalian taxa, including the presence or absence of inferred "obligate browsers" or "obligate grazers"?; and, 3) how has the feeding ecology of Pleistocene camelids potentially played a role in influencing modern distributions of Lamini camelids?

4.1.1. Stable Isotopes for Dietary and Environmental Reconstructions

Stable isotopes from mammalian tooth enamel have been used to reconstruct diets and climates (Koch, 1998; MacFadden, 2000; Kohn and Cerling, 2002); when whole communities are sampled, it allows for reconstructions of dietary niche partitioning and environmental heterogeneity (e.g., DeSantis et al., 2009). An organism's diet is recorded in its tooth enamel through the incorporation of stable carbon isotopes ($\delta^{13}C$). Specifically, tooth enamel values track the proportion of C_3 and C_4 vegetation in the diet of herbivores with a 14.1‰ enrichment between tooth enamel and vegetation consumed (DeNiro and Epstein, 1978; Cerling and Harris, 1999). Before reconstructing diets inferred from tooth enamel, the regional abundance of C_4 grasses and shrubs should be consider. C_4 grasses typically dominate in areas with high growing season temperatures whereas C_3 grasses are typically found in areas that are cooler and wetter, such as higher latitude sites in North America (Teeri and Stowe, 1976). C_4 grasses make up more than 50% of all grasses in the Gulf Coast states, New Mexico, Arizona, and Oklahoma (Teeri and Stowe, 1976, MacFadden et al., 1999). In south Florida and the Gulf Coast of Texas C_4 grasses make up 70% to 100% of all the grasses (Teeri and Stowe, 1976, MacFadden et al., 1999).

Data presented in this study are from sites in Florida (i.e. Leisey 1A, Inglis 1A, Haile 8A, and Tri-Britton; DeSantis et al., 2009; Yann and DeSantis, in prep), the Gulf Coast of Texas (Ingleside), and a site in the southern portion of the San Joaquin Valley in California (McKittrick Brea). Where C_3 grasses are rare today (i.e. the four sites in Florida and Ingleside in Texas), tooth enamel $\delta^{13}C$ values of -8‰ or less are indicative of a diet consisting of mostly C_3 tree or shrub browse, values between -8‰ and -2‰ suggest a mixed feeding diet with varying proportions of C_3 and C_4 vegetation, and $\delta^{13}C$ values of -2‰ or greater suggest reliance on C_4 grasses.

In California, C_3 grasses like *Nassella pulchra* (the state grass, commonly referred to as purple needlegrass) dominated the San Joaquin Valley prior to heavy grazing, and C_4 grasses dominate the Sonoran and Chihuahuan deserts (e.g. Woodward, 2008). While Florida is currently dominated by C_4 grass and C_3 trees/shrubs (and this was likely also the case during the Pleistocene; e.g. Teeri and Stowe, 1976; Stowe and Teeri, 1978; Koch et al., 1998, DeSantis et al., 2009), the potential presence of C_3 grass and C_4 shrubs in California, and potentially Texas, complicates dietary interpretations during the Pleistocene. Molecular evidence suggests that *Atriplex* arrived in North America between 9.8 and 8.8 million years ago (Kadereit et al., 2010), making it a viable food source during the Pleistocene. Additionally, 71 species of *Atriplex* are native to the United States and Canada (of 113 modern species), with only one species found in

Florida, 15 species in Texas (mostly west Texas), and 37 species in California (USDA, NRCA, 2014). While there are only a few studies that have assessed the distribution of *Atriplex* throughout the United States during the Pleistocene, there is evidence of *Atriplex* in the Mojave Desert 20,000 years ago and potentially even older specimens (between 25,000 and 30,000 years old) have been found in the Great Basin and at McKittrick Brea (< 50 Ka, likely between 30 and 5.2 Ka; *Atriplex lentiformis*; Mason, 1944; Thompson, 1979; Van Devender and Spaulding, 1979). There also appears to be an increase in saltbush abundance during the early Holocene (Louderback and Rhode, 2009), as suggested by pollen records. Further, it has been suggested based on stable carbon isotopes and vegetation records that C_4 saltbush (*Atriplex*) may have been a significant part of the diet of *Camelops* (Vetter et al., 2007, 2008). Thus, in California, $\delta^{13}C$ values around -2‰ may indicate consumption of C_4 browse such as *Atriplex* and should be considered when making dietary interpretations.

Stable oxygen isotope ($\delta^{18}O$) values track the water consumed by an animal, either through actively drinking water or through the consumption of leafy vegetation (Longinelli, 1984; Luz et al., 1984; Bryant and Froelich, 1995; Kohn, 1996). Thus, $\delta^{18}O$ values can be used to reconstruct relative climates (e.g. Longinelli, 1984; Luz et al., 1990; Bryant and Froelich, 1995; Bocherens et al., 1996). Additionally, not all animals record climate information in the same way, which provides the opportunity to infer relative temperature separate from relative aridity (Levin et al., 2006; Yann et al., 2013). For example, animals that get the majority of their water by actively drinking track changes in meteoric water and typically do not have highly enriched $\delta^{18}O$ tooth enamel values during periods of increased aridity; this group of animals is considered to be "evaporation insensitive" (Levin et al., 2006). For example, proboscideans have been identified as evaporation insensitive due to their need to drink large quantities of water and evinced 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 therefore be used to roughly infer relative meteoric water values at a given site (Yann et al., 2013). In contrast, animals that get the majority of their water from plants that are subjected to greater amounts of evaporation are better able to record evaporative conditions and are considered as "evaporation sensitive" (Levin et al., 2006). Thus, using a proboscidean baseline, $\delta^{18}O$ values from "evaporation sensitive" taxa can be used to calculate $\delta^{18}O$ offset values and serve as a relative aridity index to separate the influence of temperature and precipitation on mammalian tooth enamel $\delta^{18}O$ values (Yann et al., 2013).

4.1.2. Camelid Diet and Distributions

The diets for Pleistocene camelids have been interpreted using many different proxies including, but not limited to, morphological characteristics, isotopic studies, dental bolus analysis, and microwear studies. Previous isotopic and morphological work suggests that the three Pleistocene camelids in this study consumed at least some C_3 vegetation; however, the proportion of C_4 vegetation consumed is more variable (e.g. Akersten et al., 1988; MacFadden et al., 1994; Dompierre and Churcher, 1996; Feranec, 2003; DeSantis et al., 2009).

Camelops has been interpreted as having a variety of feeding strategies based on different proxies, including a mixed feeder based on premaxilla shape (Dompierre and Churcher, 1996), and mostly a browser with some mixed feeding based on SEM microwear (Dompierre, 1995). Other studies suggest little to no reliance on grasses based on dental bolus and stable isotope analyses (Akersten et al., 1998; Coltrain et al., 2004). A combination of hypsodonty, mesowear, and microwear suggest *Camelops* had a browsing diet with differing amounts of grit (Semprebon and Rivals, 2010). Stable carbon isotopes and independent vegetation records also indicate that

Camelops may have had an affinity for C_4 halophytic shrubs such as *Atriplex* (saltbush), which can still be found in areas like the Mojave Desert (Vetter et al., 2007, 2008).

Palaeolama has the lowest crowned teeth of the Lamini camelids (Honey et al., 1998) and has been interpreted as a browser based on stable isotope, microwear, morphology, and coprolite analysis (e.g. MacFadden et al., 1994; Meachen, 2003; Kohn et al., 2005; MacFadden and Shockey, 1997; DeSantis et al., 2009; Semprebon and Rivals, 2010; Marcolino et al., 2012). Based on $\delta^{13}C$ values, *Palaeolama* has been interpreted as dwelling in denser, closed canopy forests (Meachen, 2003; Kohn et al., 2005; DeSantis et al., 2009), and it is possible that *Palaeolama* may have tracked forest environments much like *Tapirus* (DeSantis and MacFadden, 2007).

Hemiauchenia has a greater diversity of interpretations, including grazing, mixed feeding, and browsing (e.g. Janis, 1988; Dompierre and Churcher, 1996; Feranec, 2003; DeSantis et al., 2009). The shape of the premaxilla suggests that *Hemiauchenia* was likely a browser or specialized mixed feeder (Janis, 1988; Dompierre and Churcher, 1996). Carbon isotope studies similarly suggest a diet of browse or mixed vegetation and further indicate that *Hemiauchenia* had the ability to alter its diet in response to competition (e.g. the presence of *Palaeolama*; DeSantis et al., 2009) or environmental change (e.g. Feranec, 2003; DeSantis et al., 2009).

The distribution of these three camelids covers much of the western half of the United Sates and Florida (PBDB, 2013) (Fig. 1). While all three camelids can be found from the west to east coast of North America, *Camelops* has predominately been found in the western portion of North America while *Palaeolama* has predominately been found in Florida, and *Hemiauchenia* overlaps the range of both *Camelops* and *Palaeolama*. According to the Paleobiology Database

(2013), there are 171 unique camelid sites in the United States, 34 contain both *Camelops* and *Hemiauchenia*, 12 have *Hemiauchenia* and *Palaeolama*, and 3 have *Camelops* and *Palaeolama* (Figure 2). In addition to the three sites on the Paleobiology Database, Ingleside in Texas also had *Camelops* and *Palaeolama* (Lundelius, 1972). Of all potential sites with multiple camelids, Ingleside (TX, Lundelius, 1972), McKittrick Brea (CA, Schultz, 1938), and Haile 8A, Tri-Britton, Leisey 1A, and Inglis 1A (FL, Auffenberg, 1967; Webb, 1974; Meers and Hulbert, 2002; DeSantis et al., 2009; Yann and DeSantis, in prep) were examined or reviewed here. These sites were selected due to the high abundance of at least one camelid, the co-occurrence of certain camelids, and the ability to geochemically sample the herbivorous mammalian fauna to better understand respective environments. Specifically, we examined Ingleside in Texas to compare the dietary niches of *Palaeolama* and *Camelops*, McKittrick Brea in California to compare *Camelops* and *Hemiauchenia*, and previously published isotopic data from Haile 8A, Tri-Britton, Leisey 1A, and Inglis 1A in Florida were used to compare *Hemiauchenia* and *Palaeolama*.

4.2. Site Descriptions

Site descriptions of Ingleside in Texas and McKittrick Brea in California are summarized here. As all Florida sites are extensively discussed in prior work (DeSantis et al., 2009; Yann and DeSantis, in prep), we only briefly summarize site descriptions.

McKittrick Brea consists of multiple late Pleistocene asphalt deposits occurring in lenses of different ages (Schultz, 1938). Deposits range in age from about 30,000 to 5,255 ^{14}C years BP, with a questionable date of 38,000±2,500 ^{14}C years BP (Berger and Libby, 1966; Miller and Peck, 1979; France, 2008; Fox-Dobbs et al., 2014). It has been suggested that the McKittrick Brea fauna lived in a cold, harsh environment during the last glacial period (France, 2008);

however, Schultz (1938) suggested that the Pleistocene climate was similar to modern conditions in the San Joaquin Valley, based on plants, rodents, and birds present. Some of these deposits do contain aquatic and semiaquatic species suggesting seeps of water and muddy terrain near intermittent bodies of water (Miller, 1922), but the bodies of water were likely surrounded by dry areas that were slightly higher in elevation (~1 meter) and well drained (Miller, 1935). The presence of *Atriplex lentiformis*, a hydrophyte that occurs in both wetland and non-wetland environments (Mason, 1944; USDA, NRCS, 2014), also suggests the presence of seeps or bodies of water.

The Ingleside locality is located on Live Oak Ridge, a barrier island that is thought to have formed during a sea level stand 25 feet higher than modern levels. This high sea level stand dates to approximately 120,000 years ago and appears to be correlative with the Sangamonian interglacial (Ericson et al., 1964; Zeuner, 1959; Otvos and Howat, 1996). The fresh-water pond deposits, which contained the fossil bones, overlie the lagoonal deposits that formed behind the Ingleside barrier and are thus younger. The pond deposits apparently accumulated in an aolian deflation depression. The fauna indicates a late Pleistocene age for the deposit. The bison is the *Bison antiquus* morphotype, the common *Bison* in late Pleistocene deposits. An electron spin resonance (ESR) date on mastodon teeth indicates middle to late Wisconsinan age (Otvos and Howat, 1996). The presence of abundant large tortoise (*Geochelone* sp.) remains suggests a climate without severe winters.

The four sites in Florida are Pleistocene in age and include Inglis 1A (2.0-1.6 Ma), Leisey 1A (1.6-1.0 Ma), Tri-Britton (0.5-0.4 Ma), and Haile 8A (0.3-0.13 Ma) (Webb, 1974; Morgan and Hulbert, 1995; Meers and Hulbert, 2002). Leisey 1A was identified as an interglacial site based on the presence of marine fossils, the presence of warm adapted taxa, and high $\delta^{18}O$ values, indicating warm climates with high sea level (Morgan and Hulbert, 1995; DeSantis et al., 2009). Inglis 1A was identified as a glacial site based on the presence of fossils approximately 5 meters below current sea level, the presence of cool adapted taxa such as pronghorns and muskrats, the lack of marine fossils, and lower δ^{18}O values than Leisey 1A (Morgan and Hulbert, 1995; DeSantis et al., 2009). Unlike Leisey 1A and Inglis 1A, Haile 8A and Tri-Britton cannot be characterized as glacial or interglacial based on their geology alone. Instead, stable oxygen isotope values and aridity index values were used to further characterize the climate of these two sites (Yann and DeSantis, in prep). Tri-Britton has greater δ^{18}O and aridity index values than Leisey 1A, suggesting Tri-Britton was warmer and drier than Leisey 1A (Yann and DeSantis, in prep). δ^{18}O values of evaporation sensitive taxa at Haile 8A are not statistically different from Leisey 1A or Inglis 1A and suggest it was intermediate in climate and the combination of δ^{18}O values and aridity index values suggest Haile 8A was a moderately warm site that was wetter than the other three sites examined in Florida (Yann and DeSantis, in prep). Assessments of climate based on geochemical data are in agreement with previous data suggesting that Tri-Britton was warm and dry based on the tortoises present and Haile 8A was an intermediate site with a warm and wetter climate based on transitions in soils and the fauna present (Auffenberg, 1967; Franz and Quitmyer, 2005).

4.3. Methods

4.3.1. Stable Isotopes

Bulk enamel samples (n=133) were collected from medium to large herbivorous mammals from McKittrick Brea (CA) and Ingleside (TX) using a low speed rotary tool with carbide bits. Approximately 2 to 5 milligrams of tooth enamel were pretreated with 30% hydrogen peroxide or bleach to remove organic material and 0.1 N acetic acid or acetic acid/calcium acetate buffered solution to remove secondary carbonates. After chemical pretreatment, samples were either sent to the University of Florida's Department of Geological Sciences and run on a Finnigan-MAT 252 isotope ratio mass spectrometer coupled with a Kiel III carbonate preparation device or to Princeton Universitiy's Department of Geosciences lab where a VG Optima gas source mass spectrometer with an ISOCARB automated system was used. Results are reported using the standard delta notation, $\delta=[(R_{sample}/R_{standard})-1)*1000]$, with carbon ($R={}^{13}C/{}^{12}C$) reported against V-PDB and oxygen ($R={}^{18}O/{}^{16}O$) reported against V-SMOW (Coplen, 1994). To convert oxygen values from V-PDB to V-SMOW we used the following formula: $\delta_{VSMOW}=1.03086*\delta_{VPDB}+30.86$ (Friedman and O'Neil, 1977).

Of the 133 samples, 40 are bulk samples from McKittrick Brea and 93 are bulk samples from Ingleside. To allow for a comparison across six sites, we combined these data with previously published work from Florida (n=188; DeSantis et al., 2009; Yann and DeSantis, in prep) for a total of 321 bulk samples. To examine seasonality and strengthen climatic interpretations, one molar from *Camelops*, *Equus*, and *Hemiauchenia* were sampled from specimens at McKittrick Brea (28 total samples; 8, 12, and 8, respectively). Additionally, molars from *Camelops*, *Equus*, *Mammuthus, and Palaeolama* (36 total samples; 8, 12, 8, and 8, respectively) were sampled from specimens at Ingleside. Previously published serial samples of *Equus* molars from Inglis 1A, Leisey 1A, Haile 8A, and Tri-Britton (47 total samples; 11, 12, 12, and 12, respectively; DeSantis et al., 2009; Yann and DeSantis, in prep) were included. As camelids may better record relative seasonality (Yann et al., 2013), camelid teeth from all Florida sites were selected and serially sampled. Specifically, we sampled *Hemiauchenia* and *Palaeolama* teeth from Leisey 1A (16 samples; 8 and 8, respectively), a *Hemiauchenia* tooth from Inglis 1A (8 samples), a *Palaeolama* tooth from Tri-Britton (8 samples), and a

Hemiauchenia tooth from Haile 8A (8 samples; DeSantis et al., 2009; Yann and DeSantis, in prep; Supplemental Table 2). In addition to the above mentioned 472 samples here mentioned, a literature search using Web of Science, Google Scholar, and GeoRef (using search terms including camelid, *Camelops*, carbon, enamel, *Hemiauchenia*, *Palaeolama*, Paleolama, stable isotope, and tooth) resulted in an additional 135 geochemical samples from the camelids *Camelops, Hemiauchenia*, and *Palaeolama* (total of 62, 110, and 44 samples, respectively; MacFadden and Cerling, 1996; MacFadden and Shockey, 1997; Connin et al., 1998; Feranec and MacFadden, 2000; Feranec, 2003; Kohn et al., 2005; Ruez, 2005; Feranec and MacFadden, 2006; Hoppe and Koch, 2006; Vetter, 2007; Higgins and MacFadden, 2009; Nunez et al., 2010; Domingo et al., 2012; Kohn and McKay, 2012; Perez-Crespo et al., 2012; Trayler, 2012; Kita et al., 2014).

To examine relative aridity between the six sites, we also used a δ^{18}O aridity index (Levin et al., 2006; Yann et al., 2013). To calculate the aridity index, we subtracted average δ^{18}O values of evaporation sensitive taxa (e.g., camelids) from site-specific average proboscidean values, using the methods described in Yann et al. (2013). To further characterize the climate of each site, we combined aridity index values and mean δ^{18}O values to classify sites as warm and wet, cold and wet, warm and dry, or cold and dry. We also used δ^{13}C values to clarify the types of flora present at a site, including identifying the presence of dense forests (van der Merwe and Medina, 1989, 1991; Cerling et al., 1997; DeSantis and Wallace, 2008).

For all statistical comparisons of geochemical data, we used the Shapiro-Wilk test to determine normality and then used the appropriate parametric (two sample Student's *t*-test or ANOVAs with Tukey HSD and/or Fisher LSD comparisons) or nonparametric (Mann-Whitney *U*- or Kruskal Wallis) tests to compare isotopic values of taxa between and among sites. Bonferroni corrections, used to decrease the likelihood of Type I error (false positive), were not used for any of the multiple comparisons we ran as it also increases the likelihood of Type II error (false negative) (Cabin and Mitchell, 2000; Nakagawa, 2004). We conducted all analyses in Excel using XLSTAT-Pro.

4.3.2. Faunal Analysis

To determine which medium to large mammalian taxa commonly occurred with each of the camelids, all localities with *Camelops*, *Hemiauchenia*, or *Palaeolama* were downloaded from the Paleobiology Database on 18 March 2013 (PBDB, 2013). All sites with a minimum age greater than 2.6 million years were removed to limit the search to the Pleistocene. To ensure that only well sampled sites were included in the analyses, all sites with less than 10 mammalian taxa and all sites with less than 5 genera from the orders Artiodactyla, Perissodactyla, or Proboscidea were removed. Presence/absence data for all genera within the families Antilocapridae, Bovidae, Camelidae, Cervidae, Elephantidae, Equidae, Gomphotheriidae, Mammutidae, Tapiridae, and Tayassuidae, were then tabulated. Using the Paleobiology Database, the presence/absence of 32 genera was recorded and the percentage of sites where each genus co-occurred with each camelid was calculated. These percentages were used to determine if each camelid co-occurred most often with obligate grazers (i.e. *Mammuthus, Bison*), obligate browsers (i.e. *Odocoileus, Tapirus*), or other combinations of taxa.

4.4. Results

4.4.1. Dietary and Environmental Characterization

All taxa at Ingleside have δ^{13}C values that range from -13.2‰ to 1.8‰ (Figure 3) with a mean of -6.4‰. *Bison*, *Equus*, and *Mammuthus* have mean δ^{13}C values $\geq$-2.1‰, consistent with a diet of primarily C_4 vegetation (likely grass based on the rarity of C_4 shrubs along the Gulf Coast of Texas; Table 1, Figure 3). *Mammut*, *Palaeolama,* and *Tapirus* have mean δ^{13}C values $\leq$-11.1‰, consistent with primarily C_3 vegetation (likely browse, due to the presence of primarily C_4 grasses in this region today and δ^{13}C values suggestive of some forest cover; Table 1, Figure 3). *Camelops* specimens have the greatest range in δ^{13}C values from -12.0‰ to 1.0‰, suggesting consumption of C_3 and C_4 resources (Figure 3). Comparisons of all taxa with a sample size of $n \geq 5$ at Ingleside indicate that *Bison*, *Mammuthus*, and *Equus* (interpreted as grazers) have significantly greater δ^{13}C values than *Mammut*, *Palaeolama*, and *Tapirus* (interpreted as browsers; $p \leq 0.001$; Table 2). *Camelops* δ^{13}C values are significantly less than those of the inferred grazers ($p < 0.05$) and indistinguishable from the inferred browsers noted above (Table 2). A tooth from *Equus*, *Camelops*, and *Palaeolama* were also serially sampled from Ingleside. The greatest intra-tooth δ^{13}C value range (3.2‰) is from the *Equus* tooth (Figure 4). Both *Camelops* and *Palaeolama* have low variability in δ^{13}C values, with intra-tooth ranges of $\leq$1.0‰ (1.0‰ and 0.9‰, respectively; Figure 4).

All taxa at McKittrick Brea have δ^{13}C values that range from -9.5‰ to -2.6‰ (Figure 5) with a mean δ^{13}C value of -6.4‰. Taxa identified as grazers at Ingleside (*Equus*, *Bison*) have δ^{13}C values between -8.1‰ and -3.3‰ (Table 1). The most negative mean δ^{13}C value is from the *Antilocapra* specimens (-7.7‰, Table 1, Figure 5). Much like *Camelops* specimens from

Ingleside, *Camelops* specimens from McKittrick Brea have the greatest range in $\delta^{13}C$ values, from -9.5‰ to -2.6‰ (Table 1, Figure 5). At McKittrick Brea, the only significant differences in $\delta^{13}C$ values are between *Antilocapra* and three other taxa, *Camelops*, *Hemiauchenia*, and *Bison* (Table 3; $p < 0.05$). At McKittrick Brea, one tooth was serially sampled from *Equus*, *Camelops*, and *Hemiauchenia* (Figure 4). *Equus* has an intra-tooth range in $\delta^{13}C$ values of 3.2‰ (Figure 4). The samples from *Camelops* at McKittrick Brea have a range in $\delta^{13}C$ values of 3.3‰, but the samples from *Hemiauchenia* have low variability (total range of 0.5‰; Figure 4).

4.4.2. Climate Characterization

At Ingleside, $\delta^{18}O$ values of all taxa range from 26.1‰ to 34.3‰ (mean: 30.2‰). Families identified as "evaporation sensitive" (Camelidae, Cervidae, Equidae; Yann et al., 2013) range from 26.1‰ to 34.3‰ (Table 1). "Less sensitive" families (Bovidae, Tayassuidae, Tapiridae; Yann et al., 2013) have $\delta^{18}O$ values that range from 29.4‰ to 32.9‰ (Table 1). Proboscidean (*Cuvieronius, Mammut*, *Mammuthus*) $\delta^{18}O$ values range from 28.0‰ to 31.7‰ (Table 1). Three teeth were also serial sampled and *Equus* has an intra-tooth range in $\delta^{18}O$ values of 0.8‰, *Camelops* $\delta^{18}O$ values have a range of 0.7‰, and *Palaeolama* $\delta^{18}O$ values have a range of 1.1‰ (Figure 4).

Aridity index values at Ingleside range from -4.0‰ to 4.2‰ (Table 1). Of the taxa with $n \geq 5$, the maximum aridity index value is from *Equus,* followed by *Bison, Palaeolama,* and *Camelops/Tapirus* (Table 1). Mean aridity index values are greatest for *Palaeolama*, followed by *Bison, Camelops*/*Tapirus*, and *Equus* (Table 1).

At McKittrick Brea, $\delta^{18}O$ values from all taxa range from 22.1‰ to 32.0‰ (mean: 27.7‰). Families typically identified as "evaporation sensitive" (Antilocapridae, Camelidae, Equidae;

Yann et al., 2013) have $\delta^{18}O$ values that range from 23.3‰ to 32.0‰, while the only less sensitive taxon (*Bison*) ranges from 22.1‰ to 28.3‰ (Table 1). "Less sensitive" *Bison* has the lowest mean $\delta^{18}O$ value followed by *Camelops*, *Equus*, *Hemiauchenia*, and *Antilocapra* (Table 1). The lack of proboscidean samples prohibits the calculation of aridity index values. Serial samples of *Equus*, *Camelops*, and *Hemiauchenia* were highly variable; *Equus* $\delta^{18}O$ values have a total range of 3.5‰, *Camelops* $\delta^{18}O$ values have a total range of 2.3‰, and *Hemiauchenia* $\delta^{18}O$ values have a total range of 3.8‰ (Figure 4).

4.4.3. Camelid Diets

When *Palaeolama* (n=10) and *Camelops* (n=9) co-occur at Ingleside, camelid $\delta^{13}C$ values are never lower than -12.4‰ (Table 1, Figure 5). While *Palaeolama* has a maximum $\delta^{13}C$ value of -10.4‰, *Camelops* has a much larger range (total range of 13.0‰, from -12.0‰ to 1.0‰; Table 1). Additionally, two *Camelops* specimens have $\delta^{13}C$ values ≥-2.0‰, while the remaining seven specimens have $\delta^{13}C$ values ≤-9.8‰.

Hemiauchenia (n=8) and *Camelops* (n=5) co-occur at McKittrick Brea where all camelid $\delta^{13}C$ values are between -9.5‰ and -2.6‰ (Table 1, Figure 5). Of these two camelids, *Camelops* has a larger range in $\delta^{13}C$ values (-9.5‰ to -2.6‰, total range of 6.9‰) as compared to *Hemiauchenia* (-6.9‰ to -5.2‰, total range of 1.7‰; Table 1).

Hemiauchenia and *Palaeolama* both co-occur at Leisey 1A (n=10 and 6, respectively; DeSantis et al., 2009) and Tri-Britton (n=2 and 11, respectively; Yann and DeSantis, in prep). At Leisey 1A, *Hemiauchenia* $\delta^{13}C$ values range from -8.7‰ to -3.2‰ with a mean $\delta^{13}C$ value of -6.4‰, and *Palaeolama* $\delta^{13}C$ values range from -14.3‰ to -11.9‰ with a mean $\delta^{13}C$ value of -13.0‰ (DeSantis et al., 2009). At Tri-Britton, the two *Hemiauchenia* specimens have $\delta^{13}C$ values of -

13.1‰ and -2.0‰, while *Palaeolama* $\delta^{13}C$ values range from -13.3‰ to -11.6‰ with a mean $\delta^{13}C$ value of -12.3‰ (Yann and DeSantis, in prep).

At Haile 8A and Inglis 1A, *Hemiauchenia* is the only camelid present (DeSantis et al., 2009; Yann and DeSantis, in prep). At Haile 8A (n=11), $\delta^{13}C$ values range from -12.1‰ to -2.4‰ with a mean $\delta^{13}C$ value of -9.2‰ (Yann and DeSantis, in prep). At Inglis 1A (n=7), $\delta^{13}C$ values range from -12.4‰ to -9.1‰ with a mean $\delta^{13}C$ value of -10.9‰ (DeSantis et al., 2009).

Previously published $\delta^{13}C$ values for *Camelops* and all data included here (n=62 individual specimens) range from -12.0‰ to 1.0‰ with a mean $\delta^{13}C$ value of -6.0‰ (Connin et al., 1998; Vetter, 2007; Higgins and MacFadden, 2009; Perez-Crespo et al., 2012; Kohn and McKay, 2012; Trayler, 2012; Kita et al., 2014; Yann and DeSantis, in prep; Figure 6). Published *Hemiauchenia* $\delta^{13}C$ values and all data included here (n=110) range from -14.7‰ to 2.1‰ with a mean $\delta^{13}C$ value of -7.6‰ (MacFadden and Cerling, 1996; MacFadden and Shockey, 1997; Feranec and MacFadden, 2000; Feranec, 2003; Kohn et al., 2005; Feranec and MacFadden, 2006; Hoppe and Koch, 2006; DeSantis et al., 2009; Nunez et al., 2010; Yann and DeSantis, in prep; this work; Figure 6). Published *Palaeolama* $\delta^{13}C$ values and all data included here (n=44) range from -15.7‰ to -7.2‰ with a mean $\delta^{13}C$ value of -12.0‰ (MacFadden and Shockey, 1997; Hoppe and Koch, 2006; Kohn et al., 2005; Ruez, 2005; DeSantis et al., 2009; Domingo et al., 2012; Yann and DeSantis, in prep; this work; Figure 6).

4.4.4. Faunal Analysis

Occurrence data from the Paleobiology Database (2013) identified 65 sites with *Hemiauchenia*, 62 sites with *Camelops*, and 21 sites with *Palaeolama* that fit the requirements discussed in the methods (minimum age ≤ 2.6 Ma, presence of ≥ 10 mammalian taxa, presence of ≥ 5 genera from Artiodactyla, Perissodactyla, or Proboscidea). The presence data associated with each site indicates that *Equus* co-occurs with *Hemiauchenia*, *Camelops*, and *Palaeolama* at 98.5%, 98.4%, and 95.2% of all sites, respectively (Figure 7). *Hemiauchenia* most often co-occurs with *Odocoileus* (66.2%), *Camelops* (64.6%), and *Platygonus* (50.8%). At 20% to 50% of sites, *Hemiauchenia* co-occurs with *Tapirus* (44.6%), *Mammuthus* (43.1%), *Capromeryx* (38.5%), and *Mammut* (20%; Figure 7). *Camelops* most commonly occurs with *Hemiauchenia* (67.7%), *Odocoileus* (66.1%), and *Mammuthus* (54.8%). At 20% to 50% of all sites, *Camelops* also co-occurs with *Capromeryx* (43.5%), *Platygonus* (38.7%), *Bison* (30.6%), *Tapirus* (24.2%), and *Antilocapra* (21.0%; Figure 7). *Palaeolama* co-occurs with either *Tapirus* or *Odocoileus* at 100% of the sites included, and 81.0% of the sites contain both *Tapirus* and *Odocoileus*. Looking at *Tapirus* and *Odocoileus* individually, each co-occurs with *Palaeolama* at 90.5% of all sites (Figure 7). *Palaeolama* also commonly co-occurs with *Mammuthus* (71.4%) and *Mammut* (52.4%; Figure 7). At 20% to 50% of the sites, *Palaeolama* also co-occurs with *Hemiauchenia* (47.6‰), *Platygonus* (42.9%), *Mylohyus* (38.1%), and *Bison* (38.1%; Figure 7).

4.5. Discussion

4.5.1. Climate and Environmental Characterization of Sites

The range in $\delta^{13}C$ values at Ingleside (-13.2‰ to 1.8‰) indicates the presence of both C_3 and C_4 vegetation (Figure 3). The occurrence of *Tapirus* with a mean $\delta^{13}C$ value of -11.5‰, suggests that forests were present and fairly open (van der Merwe and Medina, 1991; DeSantis and MacFadden, 2007; DeSantis and Wallace, 2008). The presence of open C_4 grasslands is indicated by the occurrence of morphologically inferred grazers like *Bison*, *Mammuthus*, and *Equus*, with mean $\delta^{13}C$ values indicative of predominately C_4 diets (0.1‰, -1.4‰, -2.1‰, respectively).

While mean $\delta^{13}C$ values of morphologically inferred grazers (e.g. Janis, 1995) demonstrates the presence of C_4 vegetation (probably grass as C_4 shrubs were likely not consumed in any abundance by *Bison*, *Mammuthus*, and *Equus*), C_3 grasses were also likely present (Silvens, 1933; Teeri and Stowe, 1976). In addition to the known forest browser *Tapirus*, other inferred browsers at Ingleside (*Odocoileus*, *Palaeolama*, *Mammut*) have mean $\delta^{13}C$ values indistinguishable from *Tapirus* (Table 1, 2) suggesting enough C_3 forest resources to support a variety of browsing taxa, which is consistent with previous interpretations (Lundelius, 1972). In addition to these browsers, the mean $\delta^{13}C$ value of *Camelops* is indistinguishable from *Tapirus* (Table 1, 2), and previous studies have suggested that *Camelops* is a browser (e.g. Akersten et al., 1988; Coltrain et al., 2004). However, two individuals have $\delta^{13}C$ values that suggest they consumed substantial proportions of C_4 vegetation. While C_4 shrubs are less common, saltbush has been hypothesized as a vegetation source for *Camelops* (Vetter et al., 2007, 2008). As modern *Atriplex* is found relatively close to Ingleside (USDA, NRCA, 2014) it may have been a potential food source for *Camelops* and other herbivores at Ingleside.

Serial samples from *Equus* (total range of 2.1‰) at Ingleside indicate a seasonally variable diet, but a small range in $\delta^{18}O$ values (0.8‰) suggests little to no climate seasonality (Figure 4). Serial samples from *Camelops* and *Palaeolama* also indicate little to no climatic seasonality. The lack of high seasonal variability could be due to migration (e.g., ungulates moving to cooler regions during the summer and vice versa), or it is possible that the climate was less seasonally variable than today. Previous work on large tortoises (*Gopherus hexagonata* and *Geochelone crassicutata*) suggests potentially warmer winters or a more seasonal climate (Hibbard, 1960; Brattstrom, 1961; Lundelius, 1972); however, the age distribution of *Palaeolama* at Ingleside suggests seasonal reproduction or migration among the smaller camelid (Lundelius, 1972).

Unlike Ingleside, the majority of mammals examined from McKittrick Brea suggest they consumed a mixture of C_3 and C_4 vegetation, with no mammals browsing primarily in dense forests or consuming primarily C_4 vegetation (Figure 5). At McKittrick Brea, both *Equus* and *Bison* $\delta^{13}C$ values (-6.6‰ and -6.1‰, respectively) suggest greater consumption of C_4 resources than those found at Rancho La Brea (-8.6‰ and -7.4‰, respectively; Feranec et al., 2009), another Late Pleistocene tar seep (with pits ranging in age from ~35,000-11,000 years ago; O'Keefe et al., 2009) located ~220 km southeast of McKittrick Brea in Southern California. As both *Equus* and *Bison* (morphologically inferred grazers; Tieszen, 1994; Coppedge et al., 1998; Janis and Ehrhardt, 1988) have $\delta^{13}C$ values indicative of a mixed C_3-C_4 diet, this suggests the presence of both C_3 and C_4 grasses within the vicinity of McKittrick Brea. Additionally, ~40% of *Antilocapra* specimens suggest a diet dominated by C_3 vegetation (i.e., $\delta^{13}C$ values ≤ -8.3‰; Figure 5); however, the mean $\delta^{13}C$ value still suggests a mixed C_3-C_4 diet. While one elk tooth (*Cervus elaphus*) from a different McKittrick Brea collection (University of California Museum of Paleontology, UCMP) suggests the potential of forested environments (-11.3‰; Trayler, 2012), it is unclear if the collections are identical in age. *Camelops* has the greatest mean $\delta^{13}C$ of all taxa at McKittrick Brea suggesting the greatest percent of C_4 resources consumed. While C_4 resources could be from grasses, prior studies have suggested that *Camelops* was a browser (i.e. dental bolus studies; Akersten et al., 1988), even potentially consuming C_4 shrubs such as saltbush (i.e. *Atriplex*) in Nevada (Vetter et al., 2007, 2008). At McKittrick Brea, the most common fossil plant material has been identified as *Atriplex lentiformis* (also known as big saltbush), a C_4 shrub native to the area today (Mason, 1944; USDA, NRCA, 2014). While *Camelops* $\delta^{13}C$ values suggest the consumption of C_3 and C_4 resources, they may have been predominately browsers consuming both C_3 and C_4 trees and shrubs. Additional proxies, such as dental microwear texture analysis, may be necessary to parse out differences between browsing and grazing of *Camelops* and other mammalian taxa from McKittrick Brea.

While all taxa at McKittrick Brea have mean $\delta^{13}C$ values indicative of mixed C_3-C_4 diets, serial samples suggest seasonally variable diets and climates (Figure 4). While *Hemiauchenia* does not have a highly variable diet, it has the greatest range in $\delta^{18}O$ values (3.8‰); collectively, this suggests that even though there may have been a seasonally variable climate at McKittrick Brea, *Hemiauchenia* maintained similar proportions of C_3 and C_4 vegetation in its diet. Serial samples from *Camelops* and *Equus* both suggest the possibility of seasonally variable diets and climates. *Camelops* suggests the consumption of more C_3 resources during warmer and/or drier times and more C_4 resources during cooler and/or wetter periods. This same trend is also recorded in another serially sampled *Camelops* tooth from the UCMP collection from McKittrick Brea (Trayler, 2012). *Equus* shows the same pattern with the lowest $\delta^{13}C$ values corresponding with the greatest $\delta^{18}O$ values; however, this pattern was not observed by Trayler (2012) from the UCMP collection. Similar seasonal patterns are also seen in both *Bison* and *Equus* from Rancho La Brea (Feranec et al., 2009); however, previous work from Rancho La Brea suggests that seasonal signals in $\delta^{13}C$ values may reflect seasonal migration between areas dominated in C_3 vegetation and other dominated by C_4 vegetation (Feranec et al., 2009). The amount of variation in the McKittrick Brea specimens is smaller than those from Rancho La Brea and may represent seasonal differences within McKittrick Brea, as opposed to migrations to different environments with differing proportions of C_3 and C_4 vegetation.

In contrast to Rancho La Brea where carbon isotopes of mammalian herbivores do not suggest the presence of significant C_4 plant resources (Coltrain et al., 2004; Feranec et al., 2009), with the potential exception of *Bison* (Feranec et al., 2009), mammals at McKittrick Brea consumed a greater proportion of C_4 resources. For example, *Bison* from McKittrick Brea have a greater mean $\delta^{13}C$ value (-6.1‰) than those at Rancho La Brea (-7.4‰, Feranec et al., 2009).

4.5.2. Camelid Dietary Strategies

While *Hemiauchenia* samples from McKittrick Brea have a limited total range of 1.7‰ (n=8), suggestive of a mixed C_3 and C_4 diet, comparisons to material in Florida (Leisey 1A, Inglis 1A, Haile 8A, and Tri-Britton; i.e., $\delta^{13}C$ values that range from -13.1‰ to -2.0‰; DeSantis et al., 2009; Yann and DeSantis, in prep) suggest that *Hemiauchenia* was an opportunistic generalist and consumed a range of plant resources from predominately C_3 vegetation to predominately C_4 vegetation. The ability of *Hemiauchenia* to modify its diet does not appear to change through time. For example, $\delta^{13}C$ values indicative of a browsing diet are recorded at Inglis 1A (2.0-1.6 Ma), Tri-Britton (0.5-0.4 Ma), and Haile 8A (0.3-0.13 Ma) while Leisey 1A (1.6-1.3 Ma), Haile 8A (0.3-0.13 Ma) and McKittrick Brea (0.03-0.005 Ma) specimens indicate some degree of C_4 consumption. Thus, the diet of *Hemiauchenia* is fairly broad and may instead be influenced by climatic and/or environmental changes.

In Florida, C_3 grasses and C_4 shrubs were rare or absent from the environments so predominately C_3 values is indicative of browsing on C_3 trees and shrubs, while $\delta^{13}C$ values suggestive of primarily C_4 resources suggest grazing on predominately C_4 grass. At McKittrick Brea, C_3 grasses and C_4 shrubs were likely a larger part of the ecosystem. Thus, *Hemiauchenia* had the ability to consume both C_3 browse and C_4 grass in Florida, and at McKittrick Brea, *Hemiauchenia* likely consumed C_3 and C_4 resources. Additional work is needed to determine the extent to which *Hemiauchenia* utilized C_3 grass and C_4 shrubs at McKittrick Brea and will necessitate additional tools such as dental microwear.

The incorporation of additional geochemical data expands the total range of $\delta^{13}C$ values for *Hemiauchenia* to -14.7‰ to 2.1‰ (n=110; Figure 6; MacFadden and Cerling, 1996; MacFadden and Shockey, 1997; Feranec and MacFadden, 2000; Feranec, 2003; Kohn et al., 2005; Feranec and MacFadden, 2006; Hoppe and Koch, 2006; DeSantis et al., 2009; Nunez et al., 2010; Yann and DeSantis, in prep; this work), suggesting *Hemiauchenia* could feed in nearly every habitat from closed forests to open C_4 grasslands. This great range in $\delta^{13}C$ values (16.8‰) suggests *Hemiauchenia* is a dietary generalist that is able to opportunistically feed on the vegetation available in an environment, but the mean $\delta^{13}C$ value of -7.6‰ does suggest a preference for browse, as suggested by Feranec (2003).

Palaeolama specimens from Ingleside have a greater mean $\delta^{13}C$ value than samples from Florida (Leisey 1A and Tri-Britton), but samples from all three sites suggest a C_3 dominated diet (DeSantis et al., 2009; Yann and DeSantis, in prep). At both Leisey 1A and Tri-Britton, this suggests a diet consisting of forest browse, and a higher mean $\delta^{13}C$ value at Ingleside suggests the presence of potentially more open forests. Although the mean $\delta^{13}C$ value is greater at Ingleside, the overall range in $\delta^{13}C$ values (2.0‰) falls intermediate between Leisey 1A (2.4‰; DeSantis et al., 2009) and Tri-Britton (1.7‰, Yann and DeSantis, in prep), suggesting that *Palaeolama* has fairly constrained diets (dominated by C_3 resources) at a given site. The incorporation of previously published $\delta^{13}C$ values (total of 44 specimens; MacFadden and Shockey, 1997; Hoppe and Koch, 2006; Kohn et al., 2005; Ruez, 2005; DeSantis et al., 2009; Domingo et al., 2012; Yann and DeSantis, in prep; this work) indicates a diet dominated by C_3 browse, and all but four specimens suggest a denser forest diet. This supports previous interpretations and is consistent with other proxies (MacFadden et al., 1994; Dompierre and

Churcher, 1996; DeSantis et al., 2009), but the limited range in $\delta^{13}C$ values suggests that *Palaeolama* was a specialized forest browser.

At McKittrick Brea, *Camelops* has a larger total range in $\delta^{13}C$ values (from -9.5‰ to -2.6‰), than co-occurring *Hemiauchenia* (-6.9‰ to -5.2‰). Other McKittrick Brea material from the UCMP extends the maximum range of *Camelops* to include a value of -0.7‰ (Trayler, 2012). While the geochemical data of *Camelops* suggests a mixed C_3-C_4 diet to a predominately C_3 diet, the addition of material from Trayler (2012) suggests that some individuals relied more heavily on C_4 resources. Further, C_4 resources consumed by *Camelops* likely included C_4 shrubs such as saltbush, both at McKittrick Brea (as discussed above) and in Nevada (Vetter et al. 2007, 2008).

Camelops specimens from Ingleside have a greater range in $\delta^{13}C$ values then those from McKittrick Brea. Seven of the specimens have $\delta^{13}C$ values indicative of a predominately C_3 diet, but two suggest a heavy reliance on C_4 resources. Much like *Camelops* from California, individuals at Ingleside may have also consumed C_4 shrubs. Modern distributions of some species of saltbush (*Atriplex canescens*) can be found relatively close to the Ingleside site, today (efloras, 2014), and it is possible that this shrub or other C_4 shrubs made up substantial portions of *Camelops*'s diet.

Previous isotopic studies indicate *Camelops* $\delta^{13}C$ values ranged from -12.0‰ and 1.0‰ (mean: -6.0‰; n=62; Connin et al., 1998; Vetter, 2007; Higgins and MacFadden, 2009; Perez-Crespo et al., 2012; Kohn and McKay, 2012; Trayler, 2012; Kita et al., 2014; Yann and DeSantis, in prep). Previous work using stable isotopes from bone collagen and dental bolus studies at Rancho La Brea suggest that *Camelops* consumed little to no grass (~90% dicots and gymnosperms; Akersten et al., 1988; Coltrain et al., 2004). Microwear and mesowear of *Camelops* teeth from

New Mexico, Nevada, and Mexico also support a browsing diet (Semperbon and Rivals, 2010). This suggests that *Camelops* may not be a true dietary generalist, but instead an opportunistic browser. While the opportunistic generalist *Hemiauchenia* was able to immigrate to South America, *Camelops* failed to extend into "Beringia," potentially due to the lack of trees and shrubs compounded by limited access to winter forage (Guthrie, 2001; Szpak et al., 2010).

When *Hemiauchenia* is present as the only camelid (Inglis 1A and Haile 8A), all but one individual suggests a C_3 dominated diet with statistically indistinguishable mean $\delta^{13}C$ values. In the presence of another camelid, *Hemiauchenia* has a greater mean $\delta^{13}C$ value. At Leisey 1A, *Hemiauchenia* and *Palaeolama* co-occur and *Palaeolama* is a closed forest browser while *Hemiauchenia* becomes a mixed feeder; there is no overlap in $\delta^{13}C$ values at Leisey 1A. At Tri-Britton *Palaeolama* again has a closed forest browsing diet, but there were fewer *Hemiauchenia* specimens available to sample (n=2). While there are too few samples to make any strong conclusions, one sample overlaps with *Palaeolama*, consistent with a C_3 browsing diet, while the other sample indicates significant consumption of C_4 grass.

At McKittrick Brea, *Hemiauchenia* and *Camelops* are statistically indistinguishable from one another. The presence of C_4 *Atriplex* (saltbush; Mason, 1944) and the previous interpretations of browsing in *Camelops* (Akersten et al., 1998; Coltrain et al., 2004; Semprebon and Rivals, 2010) suggest that *Camelops* was likely browsing at McKittrick Brea. The mixed C_3-C_4 signal in *Hemiauchenia* may indicate greater consumptions of grass (as seen in the samples from Leisey 1A and Haile 8A) or it may also indicate the consumption of C_4 shrubs. *Camelops* and *Hemiauchenia* may be able to co-exist either because Hemiauchenia is more of a mixed feeder, potentially eating both browse and grass or body size differences allowed these taxa to eat different plant resources. *Palaeolama* and *Camelops* co-occurred at Ingleside where *Palaeolama* maintains a narrow range of $\delta^{13}C$ values, suggesting a forest browsing diet. All but two of the *Camelops* specimens have $\delta^{13}C$ values that overlap with *Palaeolama*, suggesting the consumption of C_3 forest browse in *Camelops*. As these taxa were likely consuming similar resources, *Camelops*'s large body size may have played a larger role in allowing these closely related taxa to co-occur at Ingleside.

4.5.3. Faunal Occurrences

While *Hemiauchenia* samples from McKittrick Brea have a limited total range of 1.7‰ (n=8), suggestive of a mixed C_3 and C_4 diet, comparisons to material in Florida (Leisey 1A, Inglis 1A, Haile 8A, and Tri-Britton; i.e., $\delta^{13}C$ values that range from -13.1‰ to -2.0‰; DeSantis et al., 2009; Yann and DeSantis, in prep) suggest that *Hemiauchenia* was an opportunistic generalist and consumed a range of plant resources from predominately C_3 vegetation to predominately C_4 vegetation. The ability of *Hemiauchenia* to modify its diet does not appear to change through time. For example, $\delta^{13}C$ values indicative of a browsing diet are recorded at Inglis 1A (2.0-1.6 Ma), Tri-Britton (0.5-0.4 Ma), and Haile 8A (0.3-0.13 Ma) while Leisey 1A (1.6-1.3 Ma), Haile 8A (0.3-0.13 Ma) and McKittrick Brea (0.03-0.005 Ma) specimens indicate some degree of C_4 consumption. Thus, the diet of *Hemiauchenia* is fairly broad and may instead be influenced by climatic and/or environmental changes.

In Florida, C_3 grasses and C_4 shrubs were rare or absent from the environments so predominately C_3 values is indicative of browsing on C_3 trees and shrubs, while $\delta^{13}C$ values suggestive of primarily C_4 resources suggest grazing on predominately C_4 grass. At McKittrick Brea, C_3 grasses and C_4 shrubs were likely a larger part of the ecosystem. Thus, *Hemiauchenia* had the ability to consume both C_3 browse and C_4 grass in Florida, and at McKittrick Brea, *Hemiauchenia* likely consumed C_3 and C_4 resources. Additional work is needed to determine the extent to which *Hemiauchenia* utilized C_3 grass and C_4 shrubs at McKittrick Brea and will necessitate additional tools such as dental microwear.

The incorporation of additional geochemical data expands the total range of $\delta^{13}C$ values for *Hemiauchenia* to -14.7‰ to 2.1‰ (n=110; Figure 6; MacFadden and Cerling, 1996; MacFadden and Shockey, 1997; Feranec and MacFadden, 2000; Feranec, 2003; Kohn et al., 2005; Feranec and MacFadden, 2006; Hoppe and Koch, 2006; DeSantis et al., 2009; Nunez et al., 2010; Yann and DeSantis, in prep; this work), suggesting *Hemiauchenia* could feed in nearly every habitat from closed forests to open C_4 grasslands. This great range in $\delta^{13}C$ values (16.8‰) suggests *Hemiauchenia* is a dietary generalist that is able to opportunistically feed on the vegetation available in an environment, but the mean $\delta^{13}C$ value of -7.6‰ does suggest a preference for browse, as suggested by Feranec (2003).

Palaeolama specimens from Ingleside have a greater mean $\delta^{13}C$ value than samples from Florida (Leisey 1A and Tri-Britton), but samples from all three sites suggest a C_3 dominated diet (DeSantis et al., 2009; Yann and DeSantis, in prep). At both Leisey 1A and Tri-Britton, this suggests a diet consisting of forest browse, and a higher mean $\delta^{13}C$ value at Ingleside suggests the presence of potentially more open forests. Although the mean $\delta^{13}C$ value is greater at Ingleside, the overall range in $\delta^{13}C$ values (2.0‰) falls intermediate between Leisey 1A (2.4‰; DeSantis et al., 2009) and Tri-Britton (1.7‰, Yann and DeSantis, in prep), suggesting that *Palaeolama* has fairly constrained diets (dominated by C_3 resources) at a given site. The incorporation of previously published $\delta^{13}C$ values (total of 44 specimens; MacFadden and Shockey, 1997; Hoppe and Koch, 2006; Kohn et al., 2005; Ruez, 2005; DeSantis et al., 2009; Domingo et al., 2012; Yann and DeSantis, in prep; this work) indicates a diet dominated by C_3

browse, and all but four specimens suggest a denser forest diet. This supports previous interpretations and is consistent with other proxies (MacFadden et al., 1994; Dompierre and Churcher, 1996; DeSantis et al., 2009), but the limited range in $\delta^{13}C$ values suggests that *Palaeolama* was a specialized forest browser.

At McKittrick Brea, *Camelops* has a larger total range in $\delta^{13}C$ values (from -9.5‰ to -2.6‰), than co-occurring *Hemiauchenia* (-6.9‰ to -5.2‰). Other McKittrick Brea material from the UCMP extends the maximum range of *Camelops* to include a value of -0.7‰ (Trayler, 2012). While the geochemical data of *Camelops* suggests a mixed C_3-C_4 diet to a predominately C_3 diet, the addition of material from Trayler (2012) suggests that some individuals relied more heavily on C_4 resources. Further, C_4 resources consumed by *Camelops* likely included C_4 shrubs such as saltbush, both at McKittrick Brea (as discussed above) and in Nevada (Vetter et al. 2007, 2008).

Camelops specimens from Ingleside have a greater range in $\delta^{13}C$ values then those from McKittrick Brea. Seven of the specimens have $\delta^{13}C$ values indicative of a predominately C_3 diet, but two suggest a heavy reliance on C_4 resources. Much like *Camelops* from California, individuals at Ingleside may have also consumed C_4 shrubs. Modern distributions of some species of saltbush (*Atriplex canescens*) can be found relatively close to the Ingleside site, today (efloras, 2014), and it is possible that this shrub or other C_4 shrubs made up substantial portions of *Camelops*'s diet.

Previous isotopic studies indicate *Camelops* $\delta^{13}C$ values ranged from -12.0‰ and 1.0‰ (mean: -6.0‰; n=62; Connin et al., 1998; Vetter, 2007; Higgins and MacFadden, 2009; Perez-Crespo et al., 2012; Kohn and McKay, 2012; Trayler, 2012; Kita et al., 2014; Yann and DeSantis, in prep). Previous work using stable isotopes from bone collagen and dental bolus studies at Rancho La

Brea suggest that *Camelops* consumed little to no grass (~90% dicots and gymnosperms; Akersten et al., 1988; Coltrain et al., 2004). Microwear and mesowear of *Camelops* teeth from New Mexico, Nevada, and Mexico also support a browsing diet (Semperbon and Rivals, 2010). This suggests that *Camelops* may not be a true dietary generalist, but instead an opportunistic browser. While the opportunistic generalist *Hemiauchenia* was able to immigrate to South America, *Camelops* failed to extend into “Beringia,” potentially due to the lack of trees and shrubs compounded by limited access to winter forage (Guthrie, 2001; Szpak et al., 2010).

When *Hemiauchenia* is present as the only camelid (Inglis 1A and Haile 8A), all but one individual suggests a C_3 dominated diet with statistically indistinguishable mean $\delta^{13}C$ values. In the presence of another camelid, *Hemiauchenia* has a greater mean $\delta^{13}C$ value. At Leisey 1A *Hemiauchenia* and *Palaeolama* co-occur and *Palaeolama* is a closed forest browser while *Hemiauchenia* becomes a mixed feeder; there is no overlap in $\delta^{13}C$ values at Leisey 1A. At Tri-Britton *Palaeolama* again has a closed forest browsing diet, but there were fewer *Hemiauchenia* specimens available to sample (n=2). While there are too few samples to make any strong conclusions, one sample overlaps with *Palaeolama*, consistent with a C_3 browsing diet, while the other sample indicates significant consumption of C_4 grass.

At McKittrick Brea, *Hemiauchenia* and *Camelops* are statistically indistinguishable from one another. The presence of C_4 *Atriplex* (saltbush; Mason, 1944) and the previous interpretations of browsing in *Camelops* (Akersten et al., 1998; Coltrain et al., 2004; Semprebon and Rivals, 2010) suggest that *Camelops* was likely browsing at McKittrick Brea. The mixed C_3-C_4 signal in *Hemiauchenia* may indicate greater consumptions of grass (as seen in the samples from Leisey 1A and Haile 8A) or it may also indicate the consumption of C_4 shrubs. *Camelops* and *Hemiauchenia* may be able to co-exist either because Hemiauchenia is more of a mixed feeder, potentially eating both browse and grass or body size differences allowed these taxa to eat different plant resources. *Palaeolama* and *Camelops* co-occurred at Ingleside where *Palaeolama* maintains a narrow range of $\delta^{13}C$ values, suggesting a forest browsing diet. All but two of the *Camelops* specimens have $\delta^{13}C$ values that overlap with *Palaeolama*, suggesting the consumption of C_3 forest browse in *Camelops*. As these taxa were likely consuming similar resources, *Camelops*'s large body size may have played a larger role in allowing these closely related taxa to co-occur at Ingleside.

4.5.4. Implications for Extant Camelids

Hemiauchenia has the largest range of $\delta^{13}C$ values of the three common Pleistocene Lamini camelids, indicating the ability to utilize different vegetation types and different environments. Their ability to modify their diet may have allowed *Hemiauchenia* to exist in areas with highly variable environments, including arid climates. While *Hemiauchenia* was able to immigrate to South America and *Palaeolama* immigrated back to North America (e.g. Wheeler, 1995), *Camelops* was unable to emigrate out of North America (Guthrie, 2001). Specialized browsing taxa are relatively rare on the mammoth steppes of areas like Beringia, which could be due to a combination of a grassland-dominated environment and limited access to winter forage (Guthrie, 2001). The lack of appropriate food sources (abundant browse) may have limited the movement of animals like *Camelops* out of North America (Guthrie, 2001).

Hemiauchenia is hypothesized as the most common ancestor to the modern Lamini camelids (*Lama* and *Vicugna*; e.g. Wheeler, 1995; Honey et al., 1998; Scherer, 2013), all of which are adapted to cold, arid environments. Fecal samples from modern vicunas indicate that they are able to take advantage of all plant functional types (e.g. grasses and shrubs, C_3 and C_4 resources) from all habitats within their range, but grasses do make up a large proportion of their diet (Borgnia et al., 2010). Based on isotopic analyses of grass and teeth, coupled with fecal analysis and degree of browsing, modern guanacos are also identified as generalist feeders (Cavieres and Fajardo, 2005; Gonzalez et al., 2006). Extant South American camelids are opportunistic feeders, allowing them to survive in high elevation, arid Andean environments (e.g. Gonzalez et al., 2006, Borgnia et al., 2010). Based on this work, it is likely that the generalized, opportunistic diet of *Hemiauchenia* allowed for the evolution of the arid adapted *Lama* (guanaco) and *Vicugna* (vicuna).

4.6. Conclusions

This work further clarifies the dietary ecology of extinct Pleistocene Lamini camelids indicating *Palaeolama* was a specialized browser and *Hemiauchenia* was an opportunistic dietary generalist. Additional work is needed to elucidate the proportion of C_4 browse or C_3 grass in the diet of *Camelops*, but it is likely that *Camelops* is not a true generalist and instead is an opportunistic browser. Occurrence data indicates that *Palaeolama* may be restricted to forested environments, much like *Tapirus*, and is found most often with the browsers *Odocoileus* and *Tapirus*. *Camelops* and *Hemiauchenia* both co-occur with a broader range of taxa, suggesting that these taxa could exist in a broader range of habitat types than *Palaeolama*. It is likely that the generalized, opportunistic diet of *Hemiauchenia* may have paved the way for modern Lamini camelids to exist in more extreme environments.

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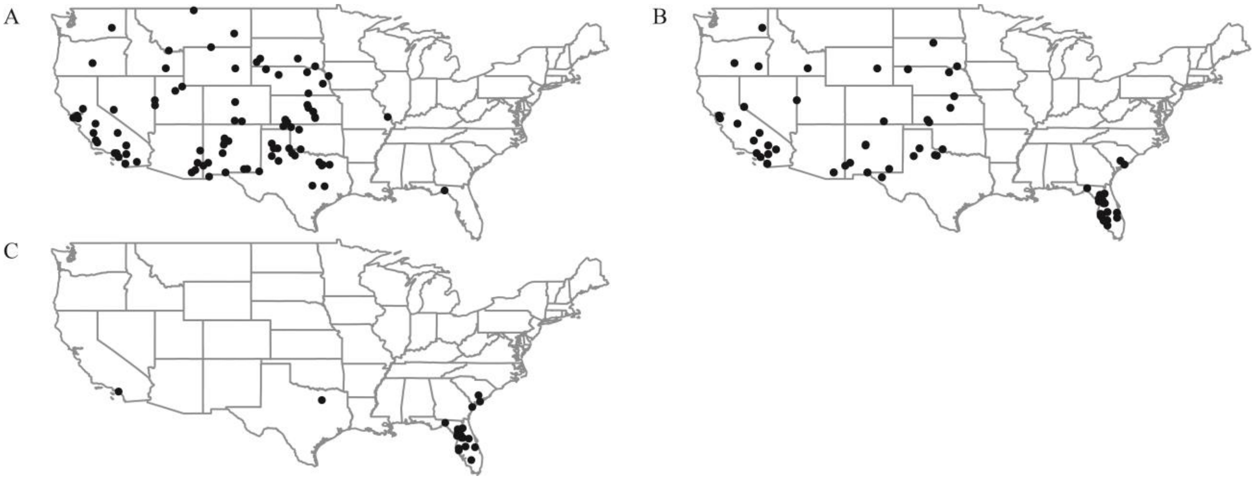

Figure 4.1. Distributions of Pleistocene Lamini camelids. A) *Camelops*, B) *Hemiauchenia*, C) *Palaeolama*.

Figure 4.2. Distributions of Pleistocene sites with two camelids. Solid line=*Palaeolama* and *Hemiauchenia*, dashed line=*Hemiauchenia* and *Camelops*, stars=*Camelops* and *Palaeolama*.

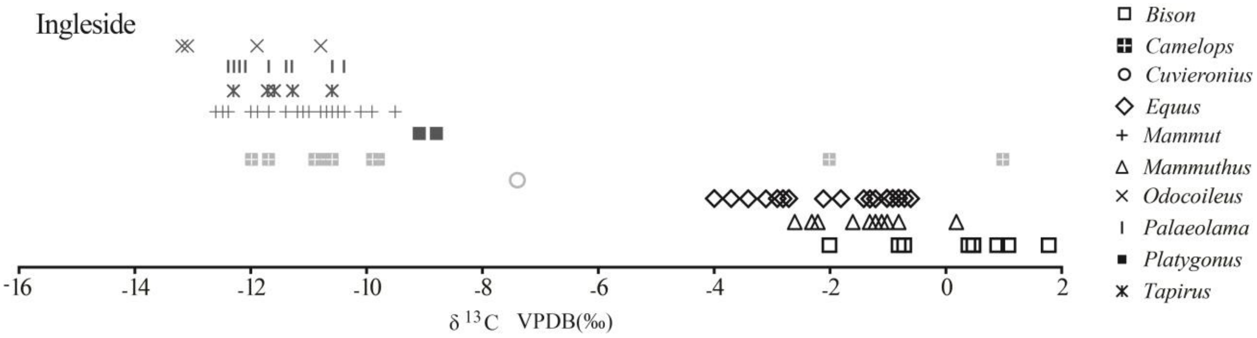

Figure 4.3. δ^{13}C values and dietary niche partitioning of herbivores from Ingleside. Taxa are ordered by increasing mean δ^{13}C values. Dark grey=browsers, taxa with mean values less than -8‰; light grey=mixed feeders, taxa with mean values greater than or equal to -8‰ and less than or equal to -2‰; black=grazers, taxa with mean values greater than -2‰.

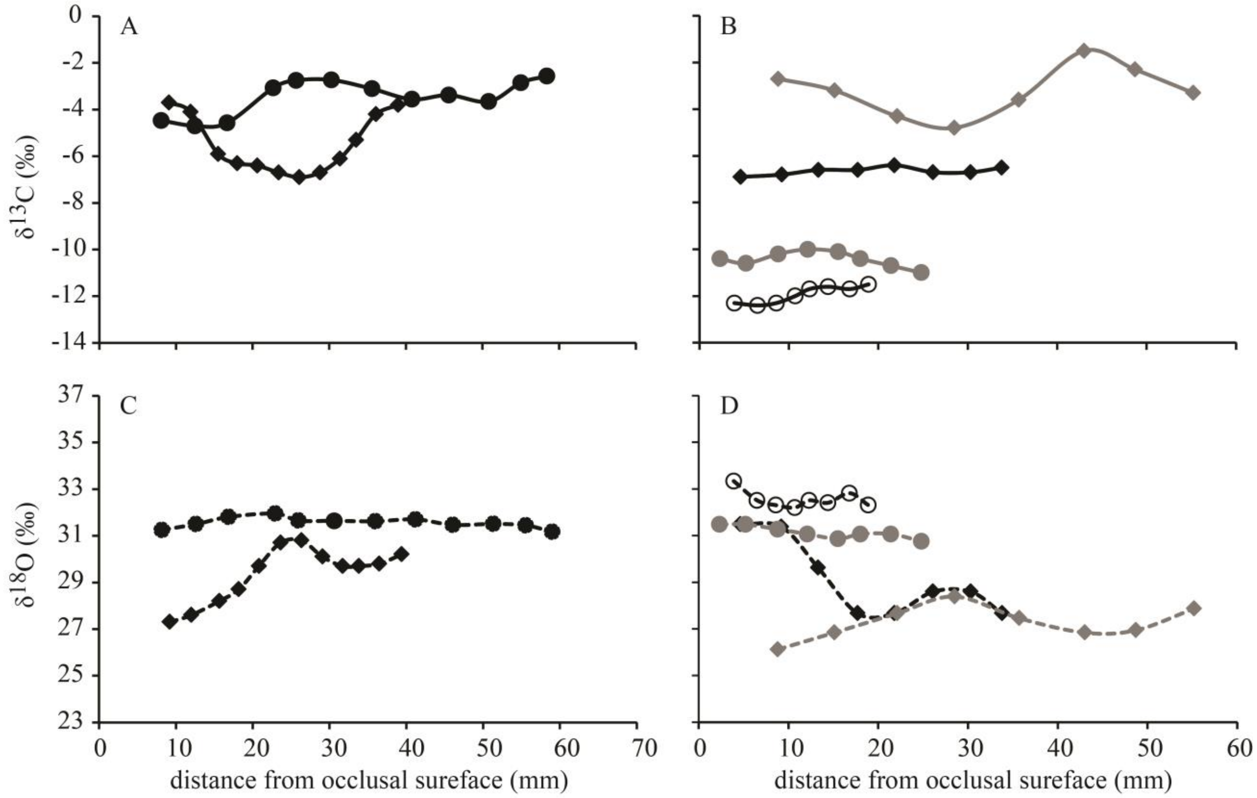

Figure 4.4. δ^{13}C and δ^{18}O serial samples from equids (a and c) and camelids (b and d). Each line represents one tooth. Solid line=carbon, dashed line=oxygen. Circles=Ingleside, diamonds=McKittrick Brea. Black symbols=*Hemiauchenia* and *Equus*, open symbols=*Palaeolama;* gray symbols=*Camelops.*

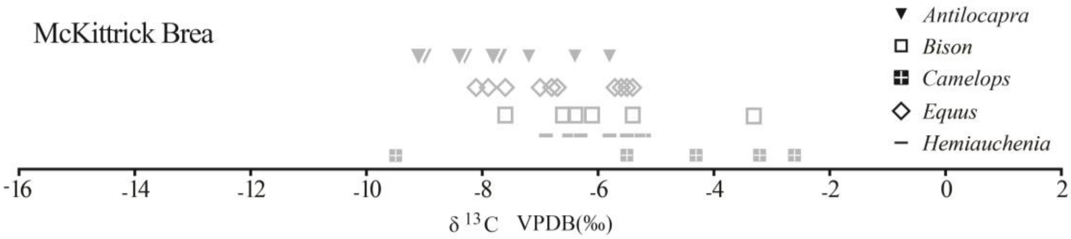

Figure 4.5. δ^{13}C values and dietary niche partitioning of herbivores from McKittrick Brea. Taxa are ordered by increasing mean δ^{13}C values.

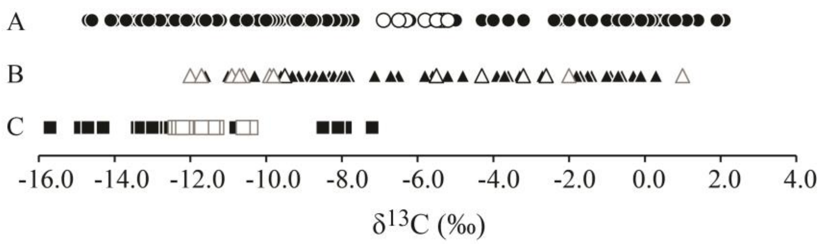

Figure 4.6. Stable carbon isotope values of A)*Hemiauchenia*, B) *Camelops*, and C) *Palaeolama*. Open symbols=this study, solid symbols=previously published values.

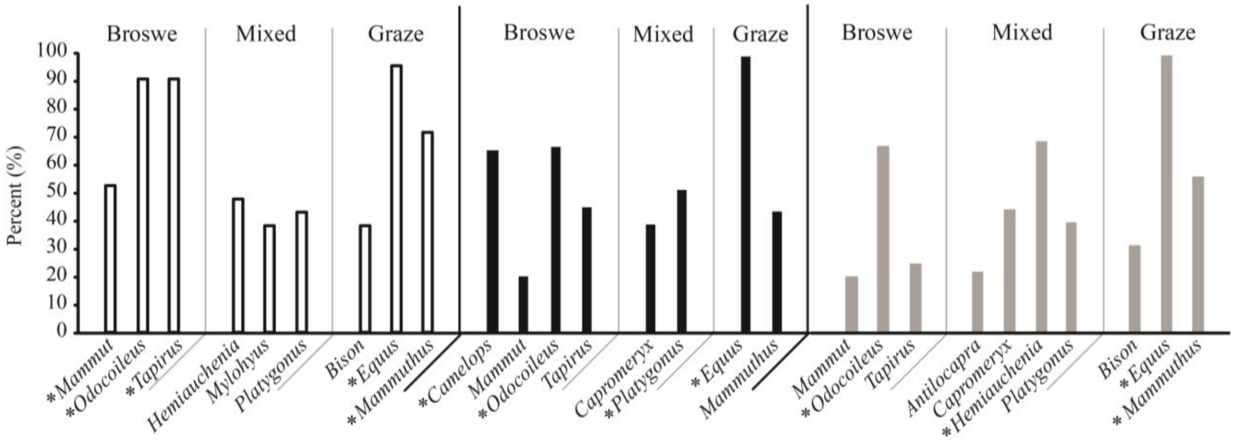

Figure 4.7. Percent of sites where taxa co-occur with each camelid. Open boxes=*Palaeolama*, black boxes=*Hemiauchenia*, grey boxes=*Camelops*. All taxa that co-occurred at less than 20% of all sites were excluded.

Table 4.1. Genus level descriptive statistics for Ingleside and McKittrick Brea.

			Carbon						Oxygen						Offset					
site	taxa	n	mean	min	max	range	SD	SEM	mean	min	max	range	SD	SEM	mean	min	max	range	SD	SEM
Ingleside	*Bison*	9	0.1	-2.0	1.8	3.8	1.2	0.4	31.0	29.4	32.9	3.5	1.2	0.4	0.9	-0.7	2.8	3.5	1.2	0.4
	Camelops	9	-8.5	-12.0	1.0	13.0	4.7	1.6	30.3	29.2	31.3	2.1	0.8	0.3	0.2	-0.9	1.2	2.1	0.8	0.3
	Cuvieronius	1	-7.4	--	--	--	--	--	29.3	--	--	--	--	--	--	--	--	--	--	--
	Equus	24	-2.1	-4.0	-0.6	3.4	1.2	0.2	29.7	26.9	34.3	7.4	1.8	0.4	-0.4	-3.2	4.2	7.4	1.8	0.4
	Mammut	19	-11.1	-12.6	-9.5	3.1	0.9	0.2	30.2	28.5	31.7	3.2	0.9	0.2	--	--	--	--	--	--
	Mammuthus	11	-1.4	-2.6	0.2	2.8	0.8	0.2	30.0	28.0	31.4	3.4	1.0	0.3	--	--	--	--	--	--
	Odocoileus	4	-12.3	-13.2	-10.8	2.4	1.1	0.6	28.7	26.1	31.9	5.8	2.4	1.2	-1.4	-4.0	1.8	5.8	2.4	1.2
	Palaeolama	10	-11.5	-12.4	-10.4	2.0	0.8	0.2	31.1	29.2	32.6	3.4	1.0	0.3	1.0	-0.9	2.5	3.4	1.0	0.3
	Platygonus	2	-9.0	-9.1	-8.8	0.3	0.2	0.1	32.5	32.3	32.6	0.3	0.2	0.2	2.4	2.2	2.5	0.3	0.2	0.2
	Tapirus	5	-11.5	-12.3	-10.6	1.7	0.6	0.3	30.3	29.4	31.3	1.9	0.7	0.3	0.2	-0.7	1.2	1.9	0.7	0.3
McKittrick Brea	*Antilocapra*	10	-7.7	-9.1	-5.8	3.3	1.1	0.3	29.1	27.6	32.0	4.4	1.5	0.5	--	--	--	--	--	--
	Bison	8	-6.1	-7.6	-3.3	4.3	1.3	0.4	25.8	22.1	28.3	6.2	2.2	0.8	--	--	--	--	--	--
	Camelops	5	-5.0	-9.5	-2.6	6.9	2.7	1.2	26.9	23.3	29.9	6.6	2.7	1.2	--	--	--	--	--	--
	Equus	10	-6.6	-8.1	-5.4	2.7	1.0	0.3	28.0	25.7	29.9	4.2	1.4	0.4	--	--	--	--	--	--
	Hemiauchenia	8	-5.9	-6.9	-5.2	1.7	0.6	0.2	28.1	24.7	29.6	4.9	1.7	0.6	--	--	--	--	--	--

n=number of specimens, min=minimum, max=maximum, SD=standard deviation (n-1), SEM=standard error of the mean

Table 4.2. *p*-values for intra-site comparisons of stable carbon isotope values from taxa at Ingleside. Taxa ordered by increasing mean values.

	Mammuthus	*Equus*	*Camelops*	*Mammut*	*Palaeolama*	*Tapirus*
Bison	0.192	**0.047**	**0.0004**	**< 0.0001**	**< 0.0001**	**< 0.0001**
Mammuthus		0.600	**0.015**	**< 0.0001**	**< 0.0001**	**0.001**
Equus			**0.020**	**< 0.0001**	**< 0.0001**	**0.001**
Camelops				0.170	0.103	0.177
Mammut					0.619	0.693
Palaeolama						0.994

Table 4.3. *p*-values for intra-site comparisons of stable carbon isotope values from taxa at McKittrick Brea. Taxa ordered by increasing mean values.

	Hemiauchenia	*Bison*	*Equus*	*Antilocapra*
Camelops	0.740	0.349	0.098	**0.002**
Hemiauchenia		0.491	0.130	**0.002**
Bison			0.432	**0.017**
Equus				0.089

Chapter 5

CONCLUSIONS

Understanding how changing temperatures and changes in aridity affected Pleistocene camelids and their communities can provide clues to future responses and adaptations of modern taxa. Collectively, this work provides a better understanding of the dietary ecology of three Pleistocene Lamini camelids, *Camelops*, *Hemiauchenia*, and *Palaeolama*, through stable isotope analysis of their tooth enamel. Investigations into if and why these camelids modified their dietary niches provide clarity as to the paleoecology of Pleistocene camelids, including potential ancestors of extant South American camelids. Additionally, this work has also allowed for a better understanding of paleoclimates, including documenting changes in aridity in North America - a method with global applications.

In chapter 2, stable oxygen isotope values were used to further develop an aridity index that allows the influences of temperature and precipitation to be separated when assessing paleoclimates. Additionally, results of this work further clarify relative aridity in different regions of North America Camelidae and Antilocapridae were identified as families that are more useful for tracking changing climatic conditions, including aridity, than taxa that have been used in the past (such as Equidae). The identification of camelids as trackers of environmental change allowed for further investigations into differences in relative aridity and into the influences of changing climatic conditions on the dietary niches of Pleistocene taxa. While this method was applied to Pleistocene sites in North America (chapters 2-4), with the identification of evaporation insensitive taxa, this work can be applied to sites through time and across the globe.

In chapter 3, comparisons of four Pleistocene sites in Florida (Tri-Britton, Haile 8A, Leisey 1A, Inglis 1A) indicate that *Hemiauchenia*, *Platygonus*, and *Mylohyus* modified their dietary niches from browser to mixed feeder in response to warming temperatures. This suggests that these three taxa were dietary generalists that took advantage of the abundant vegetation in the environment. *Mammut*, *Palaeolama*, and *Tapirus* maintained a C_3 browsing diet and *Equus* maintained a grazing diet, suggesting these taxa were dietary specialists that did not modify their dietary niche in response to changing environmental conditions. The combination of stable carbon and oxygen isotopes suggests that these four sites had more heterogeneous environments during warmer climates, as Inglis 1A (glacial site) had a fauna dominated by forest browsers while Leisey 1A (interglacial site) and Tri-Britton had multiple forest browsers and open grassland grazers. The presence of more heterogeneous environments also appears to have allowed for the co-occurrence of closely related taxa (i.e., members of the same family) at sites in Florida. This work suggests that changing climates and environments influenced the dietary niches of mammalian herbivores in Florida, while further supporting the idea that dietary niches are not necessarily conserved through time.

In chapter 4, camelids from Ingleside, McKittrick Brea, Tri-Britton, Haile 8A, Leisey 1A, and Inglis 1A were used to further clarify the dietary ecology of extinct Pleistocene Lamini camelids. Stable carbon isotope values indicate that *Hemiauchenia* was a generalist with an opportunistic diet of both C_3 and C_4 vegetation, while *Palaeolama* was a specialist, feeding on C_3 vegetation from fairly dense forests. *Camelops* was likely not a true generalist, but instead an opportunistic browser that consumed C_4 shrubs. Occurrence data indicate that *Palaeolama* was usually found in association with other browsers, like *Tapirus* and *Odocoileus*, indicating that they may have tracked forested environments (like *Tapirus*). The co-occurrence of both *Hemiauchenia* and

Camelops with a broader range of taxa is consistent with the stable carbon values indicating these taxa could live in a broader range of habitats (unlike *Palaeolama*). When *Hemiauchenia* is the only camelid represented in a fossil fauna, it typically had a diet dominated by C_3 browse. When *Palaeolama* and *Hemiauchenia* co-occurred, *Palaeolama* had a C_3 browsing diet, while *Hemiauchenia* consumed more C_4 grass. In the presence of browsing *Camelops*, it appears that *Hemiauchenia* may have again modified its dietary niche to include more grass. When two browsers co-occurred (*Camelops* and *Palaeolama*) *Camelops*'s large body size may have allowed it to take advantage of different browse than the smaller, forest browsing *Palaeolama*. In addition, *Camelops* may have consumed C_4 browse despite the fact that C_4 shrubs are rare or absent in the modern Gulf Coast.

This work further clarifies the dietary ecology of Pleistocene Lamini camelids and suggests that the generalized, opportunistic diet of *Hemiauchenia* allowed for arid adapted *Lama* (guanaco) and *Vicugna* (vicuna) to survive in arid environments of the Andes Mountains. The integration of the Pleistocene fossil record and geochemical tools, such as stable carbon and oxygen isotopes and aridity indices, has allowed for a better understanding of the dietary niches of fossil mammals during different climatic regimes and in different faunal and floral communities. Understanding past dietary and environmental change can also provide insights into current and future biotic responses to climate change.