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Paleoecology of Late Pleistocene megaherbivores: Stable isotope reconstruction of environment, climate, and response

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PALEOECOLOGY OF LATE PLEISTOCENE MEGAHERBIVORES: STABLE ISOTOPE RECONSTRUCTION OF ENVIRONMENT, CLIMATE, AND RESPONSE

By

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ABSTRACT

Paleoecology of Late Pleistocene Megaherbivores: Stable Isotope Reconstruction of Environment, Climate, and Response

by

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Late Pleistocene megaherbivore communities of the Pacific and Mountain West states of California and Nevada are under-analyzed in regard to ecological function (diet, mobility, niche partitioning, and range of ecological tolerance). Stable isotope analysis is a powerful tool that is known to recover primary paleodiet and paleoenvironmental information from biogenic materials, such as enamel and dentin. This dissertation explores the use of carbon and oxygen stable isotopes in Late Pleistocene (40-10 Ka) megaherbivore teeth to gain a better understanding of inter- and intra-specific behavior and reconstruct Late Pleistocene ecosystems of California and Nevada (Chapter 1). Radiocarbon dates exist for most of the assemblages included in this study (Potter Creek Cave, Samwel Cave, Devil Peak Cave, Gilcrease Site, and Tule Springs), allowing for the isotopic data to be integrated into a temporal framework, thereby making the results more meaningful. The exceptions are the Hawver Cave deposits from northern California and Wilkin Quarry deposits from southern Nevada, which were *sans* dates. The first efforts toward constraining the age of the Hawver Cave deposits were made as part of this study; one date, about 22 Ka, was retrieved which records conditions during the Last Glacial Maximum (Chapter 2).

Tooth enamel or dentin from several taxa of megaherbivores (*Odocoileus*, *Euceratherium*, *Equus*, *Bison*, *Mammuthus*, *Ovis*, *Nothrotheriops*, and *Megalonyx*) was analyzed from seven localities in northern California and southern Nevada. Most isotope paleoecology studies of mammals are conducted on enamel, due to its high resistivity properties against post-mortem alterations. However, ground sloths lack enamel, so dentin was examined for the ground sloth genera *Nothrotheriops* and *Megalonyx*. To identify the viability of primary isotopic signatures in dentin and enamel, X-ray diffraction (XRD) and scanning electron microscopy (SEM) was utilized. XRD and SEM results show that carbonate hydroxylapatite in fossil teeth underwent recrystallization, although chemical composition of fossil dentin samples are identical to modern dentin, while enamel samples were nearly identical. XRD and SEM validates the purity of the fossil material and supports the use of carbon and oxygen isotope analysis on dentin and enamel.

This is the first isotopic study on *Nothrotheriops* dentin, and it adds to a very small number of studies on *Megalonyx* dentin. Results show that $\delta^{13}C$ and $\delta^{18}O$ data from ground sloth dentin are primary and allow for an interpretation of diet for each taxon; the data indicate ecological partitioning between co-occurring ground sloth genera (Chapter 3). In addition to the ground sloth results, averaged $\delta^{13}C$ and $\delta^{18}O$ data for all the megaherbivores analyzed show that different species were able to tolerate a wide range of diets and habitats, while serial data show that individual animals exhibit less ecological flexibility. Serial $\delta^{13}C$ data reveal that individuals consumed a similar type of vegetation throughout the year, and serial $\delta^{18}O$ data suggest that individuals had limited mobility or occupied similar habitats seasonally. Paleoclimate models show that environmental conditions of northern California and southern Nevada during the Last Glacial Maximum were 5.5 to 7.5 ^{O}C cooler than modern temperatures and received up to 30% more precipitation. The models reveal that Late Pleistocene precipitation was distributed more

abundantly through the year (i.e., less winter/summer extremes), which provides support for the serial isotopic results (Chapter 4). Isotopic data acquired in this study were compared to two prior isotopic analyses of megaherbivore teeth from Nevada and California, in order to gain a larger-scale, regional interpretation of Late Pleistocene environments of the western United States. Northern California and northern Nevada had environments which hosted predominantly browsing species, while many of the same species in southern Nevada occupied an array of herbivorous niches (browsing, mixed feeding, and grazing). These data reveal a wide range of ecological plasticity for Late Pleistocene megaherbivore species. Fitting the isotopic information into the radiocarbon dates, for the assemblages, reveals that environments were becoming warmer and more arid toward the close of the Late Pleistocene. Data from *Equus*, *Mammuthus*, *Bison*, *Camelops*, and *Nothrotheriops* reveal that these taxa did not respond to this warming trend by increasing C_4 consumption; rather, individuals expanded their dietary breadth to include increased browsing and increased grazing. This expansion in diet resulted in niche conservatism at the generic, if not at the specific, level for taxa through the Late Pleistocene (Chapter 5).

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CHAPTER ONE

DISSERTATION OVERVIEW AND FOUNDATION

Introduction

The purpose of this research is to reconstruct the ecological and environmental history of Late Pleistocene (40-10 Ka) large-mammal, herbivore communities in southern Nevada and northern California (Figure 1). The primary means of accomplishing this task is the use of stable isotopic analysis of megaherbivore teeth (Table 1). Stable carbon and oxygen isotope values are used to interpret environmental conditions (climate, precipitation, seasonality) and ecological information (diet, water source, niche partitioning, mobility patterns) (Koch, 1998).

Isotopic analyses of fossils have become increasingly common in recent years, and many studies have been conducted to unveil dietary or paleoclimatic information. What sets this research apart from many other studies is the comprehensive nature of the assemblages that are addressed (temporally and spatially). In addition, I analyze many taxa of megaherbivores, some of which have never before been examined using stable isotope analysis, and ask new questions about the paleoecology of Late Pleistocene herbivores. I am interested in more than just how an individual behaved within its environment but also how entire communities of megaherbivores functioned. Data from taxonomically similar assemblages that have large geographic ranges can reveal complex ecological interactions within communities and help determine the range of environmental parameters that individuals were able to tolerate, especially with respect to diet. Tracking this information through the last forty thousand years of the Pleistocene has allowed me to make inferences about the evolutionary paleoecology of extinct species. This is of particular interest in light of major climatic shifts that occurred during

the Late Pleistocene and the resulting influences these shifts may have had on large mammal behavior.

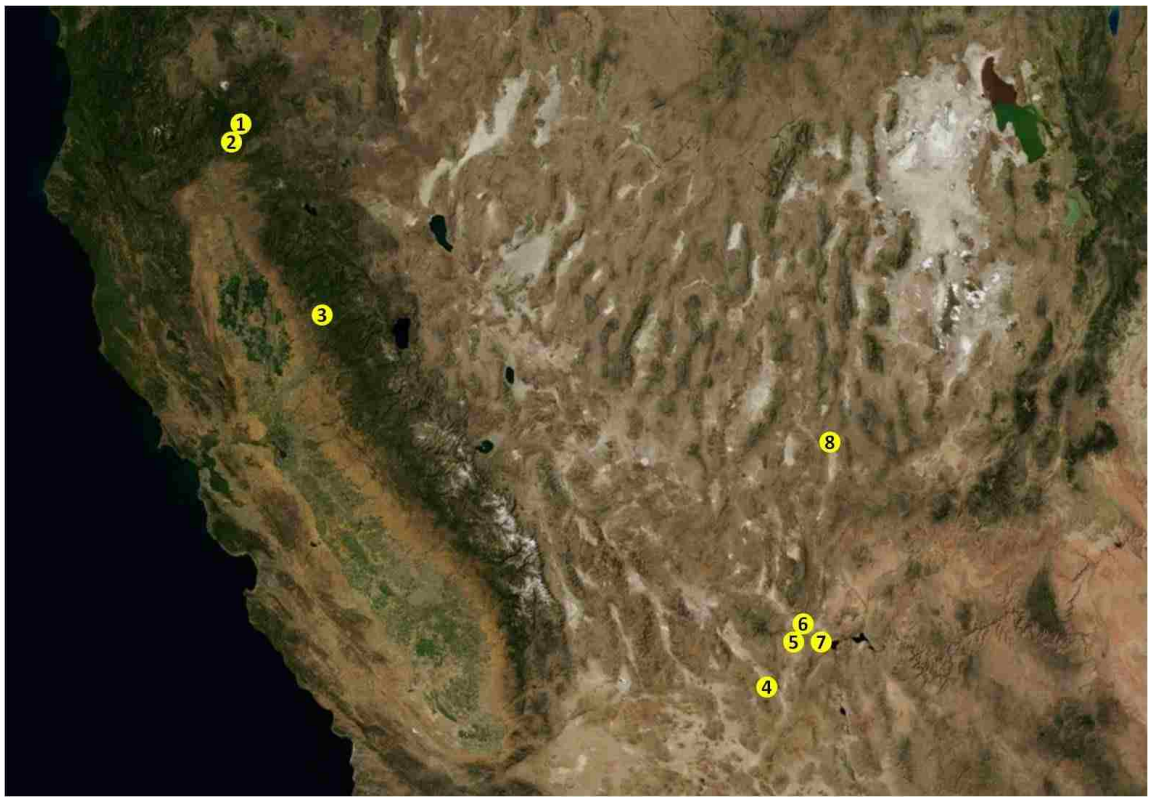


Figure 1. Locality map of all assemblages analyzed from California and Nevada: (1) Samwel Cave, CA, (2) Potter Creek Cave, CA, (3) Hawver Cave, CA, (4) Devil Peak Cave, NV, (5) Gilcrease Site, NV, (6) Tule Springs, NV, (7) Gypsum Cave, NV (fossils are unanalyzed), (8) Wilkin Quarry, NV.

The Late Pleistocene marks the very last phase in a long sequence of glacial-interglacial cycles over the past 2 million years, followed by the transition into the Holocene interglacial period. This frame of time records a high degree of variability in paleoclimatic and environmental conditions and includes the Last Glacial Maximum (LGM) episode. The LGM (26.5 to 19 ka) refers to the most recent, maximum extent of continental ice sheets and montane glaciers before warming and rapid glacial retreat during the end of the Pleistocene. This had a strong influence over environmental conditions and likely caused considerable strain on floral and faunal composition and biogeography. In addition to this large-scale, global

cooling-to-warming phase, there were smaller, dramatic swings in climate occurring over multidecadal to millennial time scales. Organisms occupying North America during this period of time had to cope with rapid climatic fluctuations. This research investigates how large-bodied, herbivorous mammals responded to environmental changes. This is an important research question in light of the remarkable decline of the North American megafauna through the Late Pleistocene, when approximately two-thirds of all megafaunal species went extinct (Barnosky *et al*., 2004), including many of the species analyzed in this study.

In addition to revealing ecological information about megaherbivores during the Late Pleistocene, I close with comments about how this research may have applications concerning modern, large-mammal ecosystem functionality under the stress of global climate change. Identifying the range of environmental flexibility of megaherbivores under changing climates in the recent past could assist in the management of modern analogues. Determining the range of tolerance that modern, large-bodied herbivores can withstand will result in a better understanding of anticipated large-mammal adaptations to projected climatic changes.

Table 1. List of assemblages and all taxa analyzed in this study.

Location/Taxon	Element	Collection	Specimen #	County	State	# samples
Devil Peak Cave						
Nothrotheriops shastensis	M3	NSM-LV	200728	Clark	NV	14
Gypsum Cave						
Nothrotheriops shastensis	hair	UCMP	76920	Clark	NV	TBA[1]
Tule Springs						
Nothrotheriops shastensis	M3	UCMP	64232	Clark	NV	1
Gilcrease Site						
Mammuthus columbi	M5	Private	3	Clark	NV	6
Mammuthus columbi	M5	Private	4	Clark	NV	6
Wilkin Quarry						
Bison latifrons	M3	Private	n/a	Lincoln	NV	10
Potter Creek Cave						
Euceratherium collinum	M3	UCMP	8730	Shasta	CA	13
Euceratherium collinum	M3	UCMP	8385	Shasta	CA	11
Equus occidentalis	M3	UCMP	8616	Shasta	CA	7
Odocoileus sp.	M3	UCMP	4181	Shasta	CA	5
Odocoileus sp.	M3	UCMP	4174	Shasta	CA	4
Ovis sp.	M2	UCMP	8451	Shasta	CA	6
Nothrotheriops shastensis	M3	UCMP	8141	Shasta	CA	9
Nothrotheriops shastensis	M3	UCMP	8715	Shasta	CA	5
Megalonyx jeffersonii	M3	UCMP	8498	Shasta	CA	1
Samwel Cave						
Euceratherium collinum	M3	UCMP	35742	Shasta	CA	5
Euceratherium collinum	M3	UCMP	9488	Shasta	CA	6
Equus sp.	M3	UCMP	8853	Shasta	CA	7
Equus sp.	M3	UCMP	8867	Shasta	CA	7
Odocoileus sp.	M3	UCMP	23082	Shasta	CA	4
Odocoileus sp.	M3	UCMP	35714	Shasta	CA	4
Nothrotheriops shastensis	M3	UCMP	9664	Shasta	CA	4
Nothrotheriops shastensis	M3	UCMP	9663	Shasta	CA	2
Megalonyx jeffersonii	M2	UCMP	9668	Shasta	CA	2
Megalonyx jeffersonii	M3	UCMP	9666	Shasta	CA	1
Hawver Cave						
Euceratherium collinum	M2	UCMP	114876	El Dorado	CA	6
Odocoileus hemionus	P4	UCMP	11016	El Dorado	CA	2
Bison sp.	M3	UCMP	11006B	El Dorado	CA	4
Nothrotheriops shastensis	M3	UCMP	21473	El Dorado	CA	1

[1]TBA = To be analyzed.

Hypotheses

1. *Isotope paleoecology of ground sloths*

Ground sloths have traditionally not been included in isotopic studies because their teeth do not contain enamel, the desired medium to study. Their teeth are composed exclusively of dentin, which is slightly less dense than enamel and has raised concerns about diagenetic alteration. For this reason there is a paucity of isotopic data on all species of ground sloths.

In Chapter 3, I explore the hypothesis that isotopic analysis of ground sloth dentin can yield meaningful paleoecologic results. Using chemical treatments and methods routinely used on enamel, I test whether the data will reveal variations in $\delta^{13}C$ and $\delta^{18}O$ values reflective of diet and water source, respectively. If successful, the isotopic approach will be especially useful for ground sloths from localities that have never been analyzed, thereby filling a paleoecologic gap for a unique group of mammals and a large region of the Pacific and Mountain West. I will use isotopic analysis to support, or falsify, previous paleoecologic studies of ground sloths, including *Nothrotheriops* and *Megalonyx*, which are suggested to have had differences in diet and habitation. These earlier studies were based on morphology (Naples, 1987; Naples, 1990), geographic distribution (McDonald, 1996; Schubert *et al*., 2004; McDonald, 2005; Hoganson and McDonald, 2007; McDonald and Jefferson, 2008; McDonald and Morgan, 2011), microwear (Green, 2009), and preserved dung (Harrington, 1933; Martin *et al*., 1961; Hansen, 1978; Thompson *et al*., 1980; Poinar *et al*., 1998; Hofreiter *et al*., 2000). In particular, McDonald and Morgan (2011) investigated the occurrence of *Nothrotheriops* and *Megalonyx* in Pliocene/Pleistocene deposits of New Mexico. They found that the two genera did not overlap temporally; *Megalonyx* occurred during the Pliocene and Early Pleistocene while *Nothrotheriops* occurred during the Late Pleistocene. Therefore, these two species do not occur together in

fossil deposits of New Mexico. McDonald and Morgan (2011) hypothesized that the lack of overlap between *Nothrotheriops* and *Megalonyx* was due to a difference in their preferred habitat and environmental conditions; *Megalonyx* was a browser in gallery forests/riparian habitats, and *Nothrotheriops* was a browser in arid, desert habitats (McDonald, 1996). McDonald and Morgan (2011) suggested that the changing environmental conditions in New Mexico through the Pleistocene led to the exclusion of *Megalonyx* and the appearance of *Nothrotheriops* by the Late Pleistocene. In contrast, these two genera of ground sloths have been found to co-occur in the Late Pleistocene deposits in this study, providing an excellent opportunity to directly compare their diets. I will use stable isotope analyses to test the McDonald-Morgan hypothesis that these two genera preferred different food resources and habitats, leading to an understanding of how they were able to co-exist at the Late Pleistocene localities in this study.

2. *Autecology of megaherbivores from different regions*

Several of the same taxa of large Pleistocene herbivores occurred in northern California and southern Nevada, regions with markedly different environments today as well as during the Late Pleistocene. I compare the diets of these species at different locations and investigate the range of ecological variation between these taxa.

In Chapter 4, I test the hypothesis that herbivores living in different geographic regions consumed different percentages of C_3 and C_4 plants. I anticipate that organisms from the northern California localities consumed a higher percentage of C_3-type vegetation than individuals of the same species from the southern Nevada localities. Further, I expect that this difference will reflect cooler climates and wetter conditions in the northern localities.

This hypothesis can most easily be tested by comparing bulk values of $\delta^{13}C$ and $\delta^{18}O$. If my hypothesis is correct, then when all values are compared there will be a significant

difference between the assemblages, with the northern taxa having more negative $\delta^{13}C$ and $\delta^{18}O$ values.

3. *Seasonal variation within individual megaherbivores*

Sequential sampling of a single tooth provides several months to several years of isotopic information that record environmental changes occurring during the biomineralization of the tooth, including seasonality. What is not well documented is whether seasonality is more distinct in some Late Pleistocene taxa than in others, revealing migratory patterns or changes in diet throughout the year. I explore this question in Chapters 3 and 4.

I hypothesize that serial sampling of individual teeth will show variation in $\delta^{13}C$ values, indicating that herbivore diets fluctuated through the year as a response to the availability of dominant plant species. I hypothesize that $\delta^{18}O$ values will also vary, recording fluctuations in temperature and precipitation. Bulk values and serial values can independently support interpretations concerning diet and environmental conditions, although coupling the information makes a much stronger case. I anticipate that $\delta^{13}C$ and $\delta^{18}O$ variations will track seasonal temperatures, where low $\delta^{13}C$ and $\delta^{18}O$ values will correlate to increased precipitation and plant availability during the winter, and high $\delta^{13}C$ and $\delta^{18}O$ values will correlate to decreased precipitation and plant availability during the summer.

Serial samples that show little to no variation in $\delta^{18}O$ and $\delta^{13}C$ values indicate that there was little seasonal variability during the period of tooth biomineralization. This would suggest that winter temperatures may have been warmer or summers cooler, so that a large swing in temperatures was not evident during the growth of the tooth. This would indicate that seasonal migration was not necessary because the animal's preferred food sources were available throughout the year.

4. *Utilization of isotopic data from multiple studies*

This project will combine new isotopic data, collected in this study, with data from previous studies (Connin *et al*., 1998; Vetter, 2007) to create a more complete reconstruction of ecosystem functionality in Nevada and California during the Late Pleistocene (40-10 Ka). This can be done if the isotopic data from this study are complementary with data from previous studies, the analyses of which were performed in different labs. I explore this question in Chapter 5.

I hypothesize that isotopic data acquired in this study will complement data attained by previous researchers. There will likely be a small discrepancy in isotopic values as a result of samples being processed in various laboratories or with different methodologies, however even if there is a 1-2‰ difference, the overall trends will still be apparent and meaningful. I anticipate that the compiled data will show that there is a gradient in $\delta^{13}C$ and $\delta^{18}O$ values from southern Nevada and southern California to northern Nevada and northern California. I anticipate that results will reflect more arid conditions (increased $\delta^{13}C$ and $\delta^{18}O$ values) in the southern localities, transitioning to cooler climates in northern Nevada (decreased $\delta^{18}O$ values), transitioning to wetter and even cooler climates in California (decreased $\delta^{13}C$ and $\delta^{18}O$ values).

5. *Response of megaherbivores to Late Pleistocene climate change*

Late Pleistocene climate shifts had profound impacts on ecosystem composition and functionality. I investigate how large herbivores within the study region responded to environmental changes during this period of time and at what taxonomic level (i.e., specific, generic) were the changes most impactful. Research has shown that stable isotopes can record mammalian evolutionary ecology over long intervals of time, millions of years. For example, MacFadden (2000) used isotopic analyses to track environmental changes in Florida during the Late Miocene, recording the transition from a C_3-dominated to a C_4-dominated landscape, with

the evolution of grasses. In Chapter 5, I explore the question of whether this sort of change can be recorded on a much smaller time scale, over several thousands to tens of thousands of years.

I hypothesize that climate through the Late Pleistocene was influencing megaherbivore diet and behavior and that changes can be observed over thousands of years; revealing subtle changes in the ecological niche of a species. Because $\delta^{18}O$ values reflect water source and climate, I expect that $\delta^{18}O$ values of enamel or dentin will correlate with documented climatic changes through the last 30 Ka of the Late Pleistocene. Further, I hypothesize that $\delta^{13}C$ values will fluctuate through the Late Pleistocene, with more positive values recording warmer intervals (~35-23 Ka and ~13-11 Ka) and more negative values recording cooler periods (~23-13 Ka). Observing these sorts of changes in species through time can show how communities were functioning and changing toward the close of the Pleistocene. This research may lead to paleobiological inferences about megaherbivore function and how these animals may be affected by climatic stress, a prominent topic within the modern climate change research community.

Isotopes as Paleoecological Indicators

Stable isotopes recorded in minerals and proteins of fossil remains yield environmental information concerning climate, water availability, vegetation, migration, and niche partitioning throughout an organism's lifetime (Koch, 1998; Kohn and Cerling, 2002). Isotopic analyses can be used to distinguish among the three main feeding types of herbivorous mammals: (1) grazers, which feed on grasses and other monocots, (2) browsers, which feed on dicot trees and shrubs, and (3) mixed feeders, which feed on both (Janis, 2008; Ungar, 2010). This powerful tool allows paleoecologists to examine such things as vegetation and water utilization, and inter- and

intra-specific actions in extinct species. The use of stable isotope analysis in this project allows for an understanding of the roles that herbivorous, large-bodied mammals played in Pleistocene communities. This creates a broader understanding of their environment, biogeography, and niche within Late Pleistocene landscapes of western North American.

I analyzed carbon and oxygen isotopes sequestered in the structural carbonate of hydroxylapatite in fossil tooth enamel and dentin. Enamel is the preferred material for isotopic research because it is formed in a chronological fashion and is resistant to resorption by the body. Dentin also forms in this manner, but it is slightly less structurally dense (Fricke and O'Neil, 1996; Koch *et al*., 1997; Balasse, 2002). Bone is the least suitable material because during an animal's lifetime it continuously mineralizes and remodels carbon and oxygen stable isotopes, thereby losing its chronologic record (Koch *et al.*, 1997; Koch, 1998). For this reason, analyses of stable isotopes in fossil bone can lead to an inaccurate record of physiological processes (i.e., incremental growth of the animal) and seasonality. In contrast, these variables remain intact in enamel and dentin. Further, the structural carbonate in the hydroxylapatite of enamel and dentin is more resistant than bone to diagenetic alterations, making it the most dependable material. The exception to this is very young bone, which can be analyzed for collagen when enamel is not available; collagen has been found to retain useful isotopic information (Clementz *et al*., 2009).

The issue of time-averaging of the isotopic signals has been the topic of studies by Passey and Cerling (2002), Zazzo *et al*. (2005), and Zazzo *et al*. (2006). They determined time-averaging to occur during amelogenesis, or enamel formation, although on a very fine scale. The degree of time-averaging can be reduced by careful microsampling downtooth which records isotopic signatures through a time series. Unfortunately, stable isotopic sampling

results in irreparable damage to the fossil, although advances in sample treatment methods and mass spectrometry have allowed for smaller sample sizes, thereby limiting damage to the fossil. During sampling, I removed the least possible amount of material needed for processing in order to minimize damage to the fossil teeth.

Other stable isotopes (e.g., nitrogen and strontium) and sampling methods (e.g., laser ablation) exist, but are not included in this study. $\delta^{15}N$ values are retrieved from organic material; the fossils included in this study have very little, to no, organic material remaining. This was determined through personal communication with Paul Koch, University of California Santa Cruz, (February 2009) and Bob Feranec, New York State Museum, Albany, New York (December 2010), and in futile attempts to obtain radiocarbon dates (Chapter 2). Strontium ratios are used as an indicator of migration. The $^{87}Sr/^{86}Sr$ ratios of herbivores are equivalent with that of ingested plants, which is a measure of the Sr levels in soil. Soils are derived from bedrock, therefore environmental $^{87}Sr/^{86}Sr$ ratios are characteristic of geography. Relating Sr ratios of an herbivore tooth to environmental ratios, can track the movement of animals (Hoppe *et al*., 1999). $^{87}Sr/^{86}Sr$ ratios are produced via thermal ionization mass spectrometer, the Las Vegas Isotope Science lab is not outfitted with this machinery as it analyzes stable isotopes, not radiogenic isotopes, thus, was not included in this study. Laser ablation techniques (Cerling and Sharp, 1996; Kohn *et al*., 1996; Sharp and Cerling, 1998) were not feasible for this study. This technique permits very fine-scale sampling, although it is not a preferable method when analyzing carbonate in enamel, as the oxygen molecules in phosphate of the enamel become analyzed simultaneously (Pellegrini *et al*., 2011), causing a conflict in the data since oxygen values retrieved from phosphate and carbonate vary by several ‰.

Carbon and oxygen isotopes are reported as delta notation (δ), which is a comparison of the sample to a known standard and expressed in parts per thousand (‰) (Koch *et al*., 1997), as shown below. The standard for oxygen is V-SMOW, while there are two standards for carbon: V-PDB and V-SMOW (Koch *et al*., 1997). In this study, both carbon and oxygen values are reported using V-PDB, unless noted.

$$\delta = [(R_{sample}/R_{standard}) - 1] \text{ X } 1000$$

where

$$R = {}^{13}C/{}^{12}C \text{ yielding } \delta^{13}C_{V\text{-}PDB}$$

or

$$R = {}^{18}O/{}^{16}O \text{ yielding } \delta^{18}O_{V\text{-}PDB}$$

For oxygen values, V-PDB can be translated to V-SMOW, as follows:

$$\delta^{18}O_{V\text{-}SMOW} = (\delta^{18}O_{V\text{-}PDB} + 29.98)/0.97002$$

Carbon Isotopes in Bioapatite

In herbivores, each feeding strategy produces a distinctive carbon isotope value ($\delta^{13}C$) which is a reflection of the vegetation the animal consumed (Vogel, 1978). Vegetation using C_3-type photosynthesis includes trees, shrubs, herbs, cool-climate and high-latitude/elevation grasses. These plants result in $\delta\,{}^{13}C_{plant}$ values of approximately -27 ± 3‰. A thick-forest feeder would be even more negative due to recycling of carbon in a thick-canopy setting. Vegetation using C_4-type photosynthesis includes warm-climate and lower-latitude/elevation grasses and sedges which yield $\delta\,{}^{13}C_{plant}$ values of approximately -13 ±2‰ (O'Leary, 1988; Farquhar *et al*., 1989; Tieszen and Boutton, 1989). Crassulacean Acid Metabolism (CAM) type vegetation (e.g., cacti and yucca) yield $\delta\,{}^{13}C_{plant}$ values that fall in between C_3 and C_4 values (Ehleringer, 1989).

Due to a consistent fractionation of +14‰, carbon isotopes mineralizing through body tissue result in an enrichment with enamel $\delta^{13}C$ averaging about -13‰ for strict C_3 feeders (browsers) and +1‰ for strict C_4 feeders (grazers) (Cerling *et al*., 1997; Cerling and Harris, 1999; Passey *et al*., 2005) (Figure 2). Studies show that fractionation in dentin occurs very similarly to that of enamel and is considered to have the same fractionation factor (Ruez, 2005).

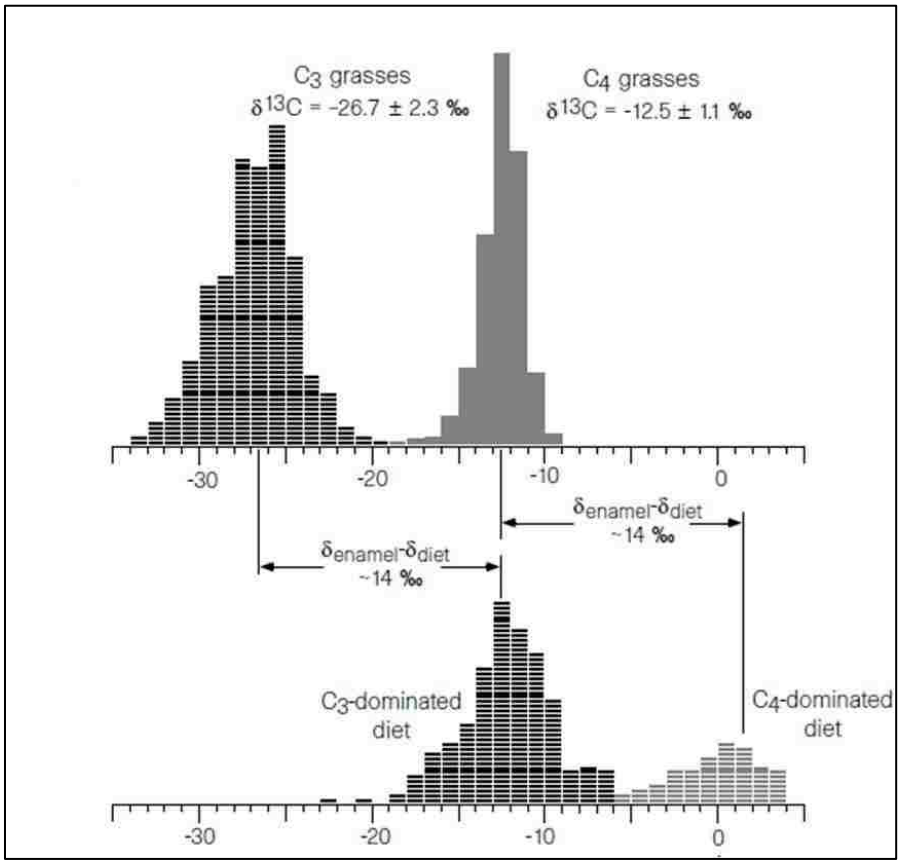


Figure 2. Fractionation of $\delta^{13}C$ values in plants and enamel. The $\delta^{13}C_{plant}$ values for C_3 average -27 ± 3‰ and C_4 average -13 ± 2‰. The fractionation factor for enamel results in an enrichment of +14‰. Average $\delta^{13}C_{enamel}$ is about -13‰ for C_3 and +1‰ for C_4 (Cerling *et al*., 1997).

Taking into account the precision and range of values that C_3 and C_4 plants can produce in enamel and dentin, herbivores consuming dominantly C_3 vegetation have $\delta^{13}C_{enamel}$ values of about -8‰ or lower, while herbivores with a diet consisting of dominantly C_4 vegetation have $\delta^{13}C_{enamel}$ values of about 0‰ or higher (Cerling *et al*., 1997; Koch, 1998; Passey *et al*., 2005;

DeSantis *et al*., 2009). Values falling in between are considered to represent herbivores that utilize CAM or mixed vegetation, so it can be inferred that an animal consuming 50% C_3 and 50% C_4 vegetation, results in $\delta^{13}C_{enamel}$ values of about -4‰ (Feranec *et al*., 2009) or represents a diet consisting of primarily succulents.

The spatial distribution of C_3 and C_4 vegetation may be highly variable, with a more abundant, yet patchy distribution of C_3 grasses compared to C_4 grasses. This variability is reflected in the diets of browsers and grazers in a given ecosystem (Gordon, 2003). If, as an example, camels, ground sloths, and deer in the same community are all browsers but were consuming different types, or amounts, of C_3 vegetation, this will be reflected in the $\delta^{13}C$ values recorded in their teeth. Further, the ground sloth *Nothrotheriops shastensis* is interpreted to have consumed large amounts of yucca (evidence from preserved dung), which is not attributed to the diets of deer or camel. Yucca utilizes a CAM-type photosynthetic pathway, so *N. shastensis* should show more positive $\delta^{13}C$ values, closer to that of CAM vegetation, which would not be expected for the other, more strict C_3 browsers. That said, if results do not show much variation in $\delta^{13}C$ values, a possible interpretation is that plant resources were not partitioned between species, indicating competition for the same food resources (France *et al*., 2007). Serial data, revealing seasonality, can be used to interpret such results in greater detail, with respect to the availability of food throughout the year. Serial stable isotope results will show variations within inter- and intra-specific diets of megaherbivores on a seasonal basis.

Previous researchers have constructed several equations, listed below, using $\delta^{13}C$ of *Bison* enamel to calculate environmental parameters, including percentage of C_4 vegetation in the ecosystem (Hoppe *et al*., 2006) (1) and percentage of C_4 vegetation in an animal's diet (Hoppe *et al*., 2006) (2). Another equation was formed, using the $\delta^{13}C$ of exclusively browsing

megaherbivores (-8.8‰, or less) to calculate Mean Annual Precipitation (MAP). This equation can be used for localities with known elevation and latitude parameters (Kohn and McKay, 2012) (3).

$$\%C_4 \text{ (environment)} = [9.16(\pm 0.94) \text{ X mean } \delta^{13}C_{enamel}] + 112.80(\pm 0.80) \quad (1)$$

$$\text{Mean } \%C_4 \text{ (diet)} = [0.72(\pm 0.07) \text{ X measured } \%C_4] + 3.02(\pm 3.85) \quad (2)$$

$$MAP = 10\text{^}[(\delta^{13}C+10.29-0.000194*\text{elevation}+0.0124*\text{latitude})/-5.61] - 300 \quad (3)$$

Oxygen Isotopes in Bioapatite

Oxygen isotopes in enamel are not as easily interpreted as are carbon isotopes. $\delta^{13}C$ yields information about an animal's diet, whereas $\delta^{18}O$ yields information about environmental conditions which can be influenced by a number of parameters. Primarily, oxygen isotopes in enamel correlate to surface, or environmental waters (vis-à-vis meteoric precipitation) because mammalian teeth mineralize at a constant temperature (~37 ^{O}C) in equilibrium with body water (Luz *et al*., 1984; Bryant and Froelich, 1995; Hoppe, 2006). Large mammals that are dependent on a local water source (and not on water from food) display $\delta^{18}O$ values which closely correlate to local precipitation, although there may be slight variations among taxa (D'Angela and Longinelli, 1990; Ayliffe *et al*., 1992; Delgado Huertas *et al*., 1995). This allows the $\delta^{18}O$ values of teeth to be used as proxies for paleoprecipitation (Longinelli, 1984; Luz *et al*., 1984; Ayliffe *et al*., 1992; Kohn *et al*., 1996; Fricke *et al*., 1998; Sharp and Cerling, 1998) and paleoclimate, via local average surface temperatures (Dansgaard, 1964; Bryant and Froelich, 1995; Koch, 1998) (Figure 3). Although, caution must be taken as oxygen isotopes from surficial sources (e.g., rivers, ponds, springs) can vary from $\delta^{18}O$ of precipitation to that source. For example, surface water reservoirs in humid regions may have values very similar to the precipitation which feeds it,

although surface waters in arid regions may be enriched in ^{18}O compared to precipitation due to high evaporation levels, where ^{16}O is readily removed from the water source as vapor (Fricke *et al*., 2008). Another type of oxygen isotope modification to be aware of is the potential for "mixing" of various hydrological sources, such as groundwaters feeding springs or input of meteoric waters to long river systems (Fricke *et al*., 2008).

Prior analyses of oxygen isotopes in fossil materials show that $\delta^{18}O$ values are more positive during periods of time when climate is warmer and more arid, and at warm, dry geographic locations. Enriched $\delta^{18}O$ values may also indicate open habitats, dry seasons, or summer seasonality. Conversely, $\delta^{18}O$ values are more negative during periods of time that are cooler and wetter, and at cool, moist geographic locations. Depleted $\delta^{18}O$ values may also indicate more forested environments, wet seasons, or winter seasonality (Longinelli, 1984; Kohn *et al*., 1996; Feranec, 2004; Higgins and MacFadden, 2004; Hoppe, 2006; Levin *et al*., 2006; DeSantis *et al*., 2009; Feranec *et al*., 2010a; Feranec *et al*., 2010b; Nunez *et al*., 2010).

The large-bodied, herbivorous mammals included in this study are obligate drinkers, thus their tooth enamel records ingested $\delta^{18}O$ values of meteoric water. Because of this, there is no concern that $\delta^{18}O$ values might have been distorted by biotic (i.e., plant water) or physiologic processes; these values will therefore reflect environmental factors (Feranec *et al*., 2009). Serial sampling will show changes in $\delta^{18}O$ values for one or more years of an animal's life, thereby tracking regional temperatures and precipitation, seasonally, at the time the animal lived. If serial values do not show oscillating patterns, as would be expected from environmental changes throughout the year, this could indicate that the climate was less seasonal at that point in time (DeSantis *et al*., 2009).

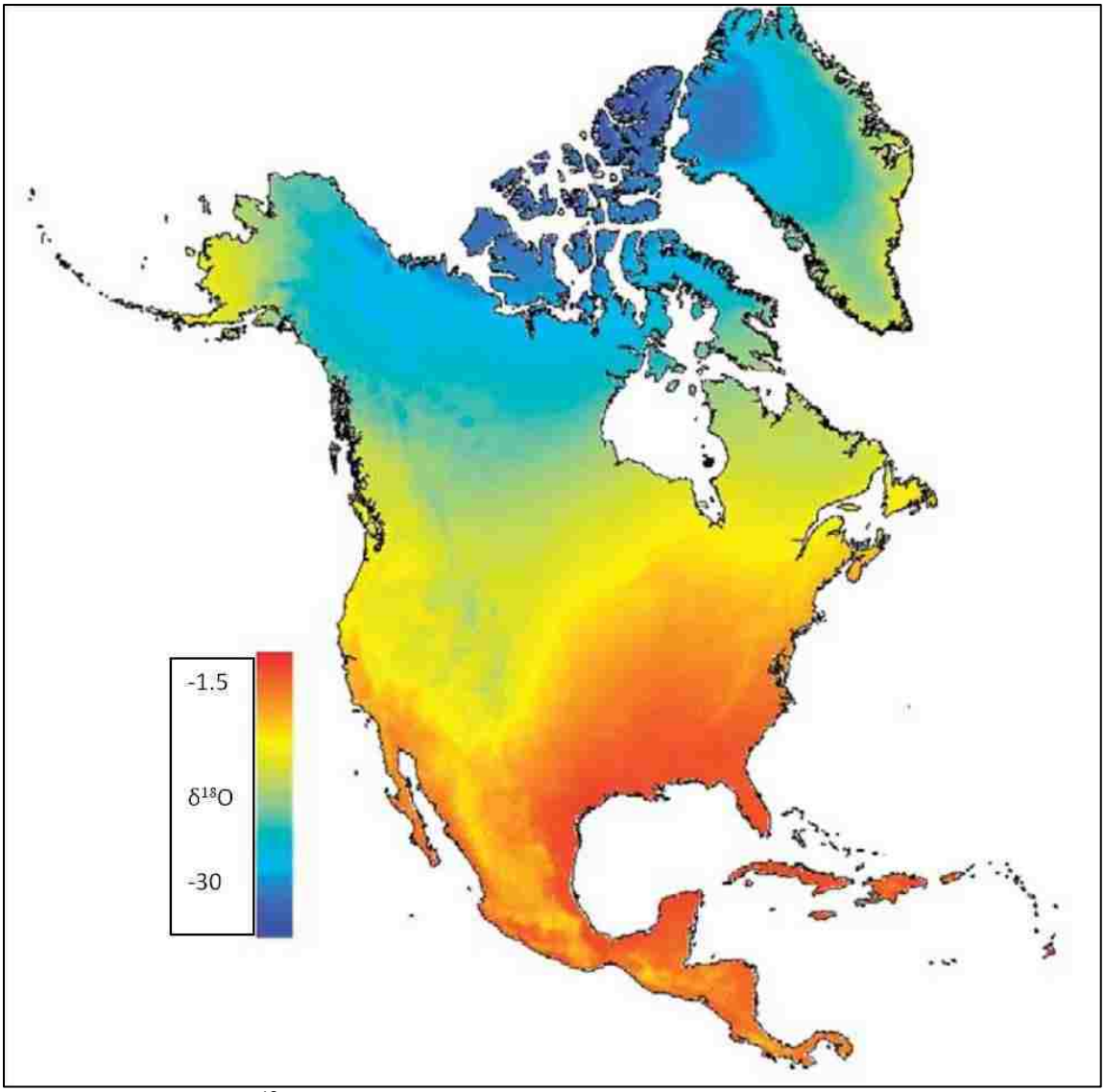


Figure 3. Variation in $\delta^{18}O$ of modern precipitation across North and Central America. This can be compared to $\delta^{18}O$ values in fossil teeth which record Late Pleistocene precipitation (West *et al*., 2006).

Oxygen isotopes may also serve as an indicator of migrational tendencies. $\delta^{18}O$ values of meteoric water decrease with distance from source (i.e., ocean water), as well as with higher elevations and lower temperatures, as demonstrated by Yurtsever and Gat (1981). Therefore, oxygen isotopes in water are characteristic of varying ecological environments, where $\delta^{18}O$ varies with geography and local meteoric precipitation. Ehleringer *et al*. (2008) were able to demonstrate that human hair was indicative of geographic location and found that it was

possible to track movement patterns of people across the United States by measuring $\delta^{18}O$ values in their hair. Hair forms sequentially, similar to enamel and dentin, so the principles of Ehleringer *et al*. (2008) can be applied to data from this study. Because $\delta^{18}O$ values in an animal's teeth track the $\delta^{18}O$ signature of water the animal consumes through its lifetime, the oxygen values in teeth can reflect the physical environment of ingested waters, leading to interpretations concerning mobility patterns (Schwarcz *et al*., 1991; White *et al*., 1998; Dupras, 2001). Migration may be apparent, and distinguishable from seasonality, if the range of $\delta^{18}O$ values recorded in the teeth exceeds the annual range of $\delta^{18}O$ values of environmental waters. For example, modern precipitation for the localities in this study experience a fluctuation in $\delta^{18}O$ values of about 4-6‰ seasonally. I would suspect that megaherbivores are exhibiting a history of migration if their serial $\delta^{18}O$ values exceed these seasonal variations, indicating that they were ingesting water from multiple sources. Oxygen isotope values of Late Pleistocene and modern precipitation, for each locality, are discussed further in Chapter 4.

$\delta^{18}O$ values of *Bison* enamel have been used to calculate the relationship between carbonate and local water (Hoppe, 2006) (4). As previously mentioned, the $\delta^{18}O$ values of carbonate in mammalian teeth mineralize in equilibrium with surface waters. Because global $\delta^{18}O$ values in meteoric water are strongly correlated to Mean Annual Temperature, MAT can be calculated from $\delta^{18}O_{water}$ (Grafenstein *et al*., 1996) (5).

$$\delta^{18}O_{water} = (\delta^{18}O_{carbonate}\text{-}30.06) / 0.7 \qquad (4)$$

$$MAT = (\delta^{18}O_{water} + 14.48) / 0.58 \qquad (5)$$

Mammal Tooth Formation and Structure

This section provides an abbreviated explanation of tooth growth in the orders of mammals that are involved in this study (Table 2). In cases where the Pleistocene species is extinct, a modern relative is used in which tooth formation is known.

Knowledge of tooth biomineralization is integral to this study to support the use of intra-tooth, serial isotopic sampling at appropriate tooth intervals and with consideration for the timing of growth and direction. The permanent molariform tooth, m3, was chosen for sampling as this is typically the last tooth to mineralize. Diphyodonts, organisms with two successive sets of teeth, typically begin to mineralize molars after the animal is weened, thereby reflecting the true diet of the animal without the influence of mother's milk. Sloths and elephantids are an exception to this type of tooth formation; sloths are born with a permanent set of evergrowing teeth and elephantids produce new teeth in succession (with a maximum of six per quadrant) throughout their lives, so these animals do not follow the aforementioned strategy. For diphyodonts, deciduous molars are found to be depleted in $\delta^{13}C$ by about 2.5‰ compared to m3 molars, due to a milk signature (Forbes *et al*., 2010). Information on the timing of eruption of the m3 allows for a more precise interpretation of seasonality for each taxon. For the mammals involved in this study, enamel – or dentin, in the case of sloths – mineralizes incrementally, with each increment taking a few weeks up to three months. Mineralization begins at the crown of the tooth and proceeds toward the root (Balasse, 2002; Passey and Cerling, 2002; Higgins and MacFadden, 2004; Zazzo *et al*., 2005) (Figure 4). This growth pattern results in a small amount of time-averaging of each increment, all the while retaining the original isotopic signal (Passey and Cerling, 2002). Therefore the oldest enamel/dentin, representing the earliest stage of mineralization, is recorded at the crown. The youngest

enamel/dentin, representing later stages of mineralization, is recorded at the root (Figure 5). Continual wear on the occlusal surface of the tooth is acknowledged, although this rate of wear has not been quantified in the literature and therefore is considered minimal. When interpreting seasonal information, I take into account the fact that a small amount of the oldest enamel may have worn away on some teeth.

Table 2. Taxonomy of analyzed specimens. Orders are discussed in text as to tooth formation.

Taxonomic Level	**Group**	**Genus/Species**	**Source**
Order	Artiodactyla		
Family	Bovidae	*Bison* sp.	this study; Connin *et al*., 1998; Vetter, 2007
		Bison latifrons	
Subfamily	Caprinae	*Euceratherium collinum*	this study
		Ovis sp.	this study
Family	Cervidae	*Odocoileus* sp.	this study
		Odocoileus hemionus	
Family	Antilocapridae	*Tetrameryx* sp.	Connin *et al*., 1998
Family	Camelidae	*Camelops hesternus*	Connin *et al*., 1998; Vetter, 2007
Order	Perissodactyla		
Family	Equidae	*Equus* sp.	this study; Connin *et al*., 1998; Vetter, 2007
		Equus occidentalis	
Order	Proboscidea		
Family	Elephantidae	*Mammuthus columbi*	this study; Connin *et al*., 1998; Vetter, 2007
Order	Xenarthra		
Family	Nothrotheridae	*Nothrotheriops shastensis*	this study
Family	Megalonychidae	*Megalonyx jeffersonii*	this study

The primary mineral in enamel and dentin is inorganic carbonate hydroxylapatite, $Ca_{10}(PO_4)_6(OH)_2$, where the incorporation of carbonate $(CO_3)^{2-}$ is able to substitute in the apatite lattice at either the $(OH)^-$ or $(PO_4)^{3-}$ sites (Sponheimer and Lee-Thorp, 1999; LeGeros, *et al*., 2009). Biogenic apatites are often impure and can contain trace amounts of other elements such as fluorine, magnesium, chorine, sulfur, sodium, silica, iron, and aluminum, which can

substitute into the Ca, P, and OH sites (Michel *et al*., 1995; Kohn *et al*., 1999; Jacques *et al*., 2008; Metcalfe *et al*., 2009; Hinz and Kohn, 2010; Vaseenon, 2011; Kohn *et al*., 2013).

Structural carbonate within the hydroxylapatite of enamel and dentin was analyzed from teeth in this study. Enamel contains about 97% hydroxylapatite, while dentin contains about 72% hydroxylapatite, the rest being organic collagen and water (Hillson, 2005). It is for this reason that enamel is the preferred medium in stable isotope paleontology; the higher content of hydroxylapatite makes enamel more impervious to diagenetic alteration.

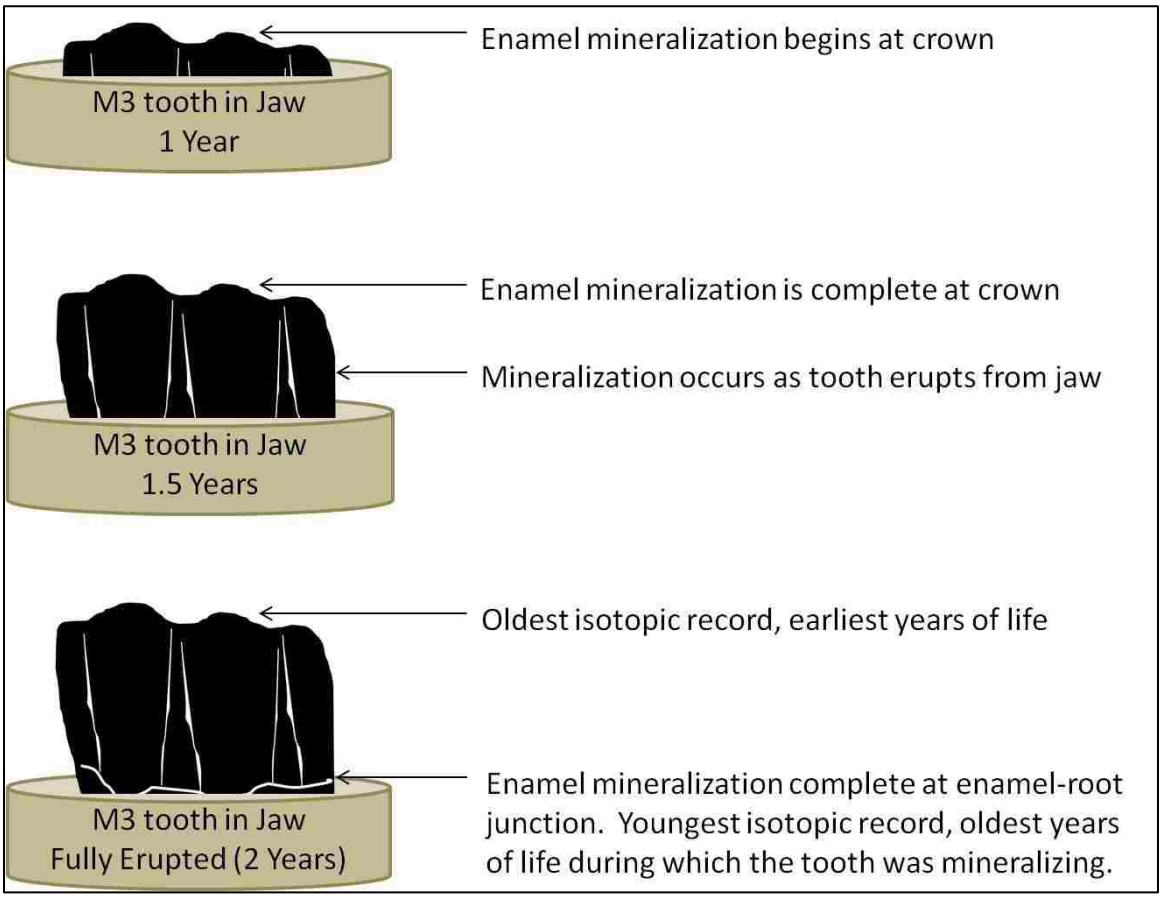


Figure 4. Enamel mineralization in ungulate teeth. Illustration depicts formation of the m3 as it erupts from the jaw. Enamel mineralizes from the crown downward toward the root.

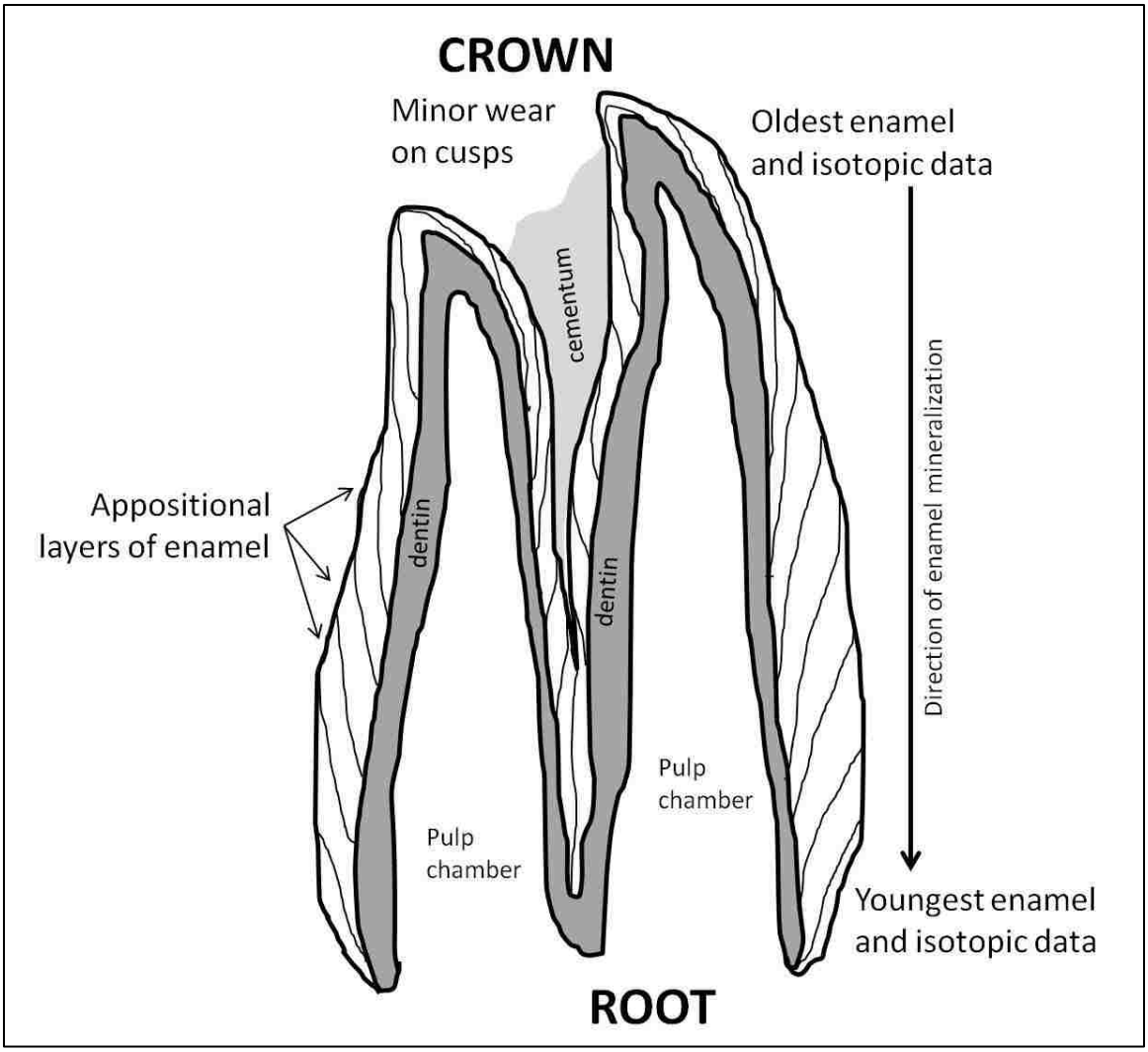


Figure 5. Model of enamel apposition and corresponding isotopic record. Earliest record of life is at the crown and older is toward the root. Sampling is performed from the crown to the root on appositional layers of enamel to capture a chronologic signature. Modified from Hillson (2006).

Order Artiodactyla

Hypsodont cheek teeth are typical of the artiodactyls included in this study except for the cervids, although to varying degrees. During formation, premolars and molars experience wear while erupting and throughout development of the root, all the while continually mineralizing enamel (Hillson, 2005). The degree of wear is dependent on crown morphology, tooth attrition, and diet, and is very difficult to quantify, even within a species (Hillson, 2005). The premolars in juveniles are deciduous and are replaced by a second set of permanent

premolars, while molars grow in permanently. The m1 and m2 form during the first year, while the animal is still nursing and then weaned. The m3 begins to form at the end of the first year or later, after the animal has been weaned. Therefore, it was important to use only teeth which would yield a diet signature, without interference from a milk signal, so that all the teeth in this study recorded information from the vegetation consumed. Research shows that enamel from the m1 and m2 have decreased $\delta^{13}C$ and $\delta^{18}O$ values by 2-3‰ relative to the m3, as a result of the influence of the milk they were consuming while the teeth were forming (Gadbury *et al*., 2000). This discrepancy would distort environmental interpretations, especially when considering varying taxa and geographic localities, as in this study. All teeth sampled in this study are m3, with the exception of one p4 tooth from a deer (*Odocoileus*). In deer, the permanent p4 erupts post weening (Severinghaus, 1949; Patricia Holroyd, UCMP, pers. comm., May 2011), so in this instance I used a p4 when an m3 was unavailable. Research has shown that m3 record data equally, or with weak variation, regardless of where the tooth is positioned in the mouth (upper or lower jaw, left or right side) (Gadbury *et al*., 2000; Higgins and MacFadden, 2004). Therefore it makes no significant difference which m3 is used for analysis.

Additionally, constraining teeth to the m3 allows for seasonality to be factored into interpretations. For example, in modern *Ovis* and *Bos*, m3 eruption occurs when the animal is no older than two years (Fricke and O'Neil, 1996). Within these genera, as well as in *Bison*, calves are born in the spring. *Bison* m3 teeth erupt between nine and fifteen months of age (Fricke and O'Neil, 1996; Gadbury *et al*., 2000), and they record environmental data for about eighteen months until the tooth is completely formed (Higgins and MacFadden, 2004). This means that the tooth begins recording environmental information in the winter, spring, or summer when the calf is about one year old and then continues up to the third year when tooth

mineralization is complete. This assumes that *Bison* during the Late Pleistocene had gestation periods and birthing seasons similar to those of modern *Bison*.

Order Perissodactyla

Perissodactyls in this study, represented by *Equus*, have similar tooth formation as artiodactyls. *Equus* has hypsodont cheek teeth which are selenodont (Hillson, 2005). Incisors and premolars are deciduous, being replaced by a permanent set. Molars, which are permanent, erupt between two and five years of age (Hoppe *et al*., 2004; Hillson, 2005), with individual molars recording between one and a half and three years of environmental data (Higgins and MacFadden, 2004; Hoppe *et al*., 2004).

Order Proboscidea

Proboscideans are represented in this study by *Mammuthus columbi*. Mammoths have a total of twenty-four loxodont teeth throughout their lifetime, six from each quadrant of the mouth. The six teeth from each quadrant are commonly called m1 through m6, with "m" referring to premolars (m1-m3) as well as molars (m4-m6). Each tooth is successively shed with only one to two teeth in wear in each quadrant at a single time (Hillson, 2005). The teeth are continually moving through the jaw in a sequence or "conveyer-belt motion" from the back to the front of the mouth, where the worn m1 through m5 teeth are eventually shed. *Mammuthus* molariform teeth consist of enamel plates surrounding a dentin core, held together by cementum. The teeth have a semi-smooth, concave (mandibular) or convex (maxillary) occlusal surface from constant grinding. For isotopic analyses, the m5 molar is preferable to sample because it represents the animal's later years of life; it erupts at about fourteen years of age and is in wear in the mouth until about age forty (Hillson, 2005).

Order Xenarthra

Xenarthrans are represented in this study by two ground sloth species, *Megalonyx jeffersonii* and *Nothrotheriops shastensis*. A distinctive feature of this group is the total lack of enamel in the teeth (Naples, 1990; Vizcaíno *et al*., 2008). In lieu of enamel, ground sloth teeth have a rigid outer layer of dentin, called orthodentin, which is structurally distinct from the softer inner layer (Naples, 1990; Hillson, 2005; Kalthoff, 2011). Dentition in *M. jeffersonii* and *N. shastensis* is similar in composition but not in number. *M. jeffersonii* has one additional tooth in each quadrant of the mouth that is functionally equivalent to a canine and is called a caniniform. In both species, all molariform teeth are completely erupted during infancy as is the caniniform in *Megalonyx*. Infant and juvenile sloths can be distinguished from adult sloths by the size of the teeth and wear of the occlusal surface; infants and juveniles have conical teeth from limited wear (Naples, 1990). Unlike hypsodont ungulate teeth, which form continuously over several years until root formation is complete at which time they start to become worn down (Gadbury *et al.*, 2000), sloth teeth are non-deciduous and ever-growing, forming high-crowned cusp structures on the occlusal surface (Naples, 1990). Therefore, while enamel in ungulates records the earlier years of life, dentin in ground sloths records the latest years of life. Because dentin is inherently softer than enamel it wears more easily, causing the earliest years to have worn away. Sloth teeth cannot be used to estimate the animal's age since it is undeterminable how much of the dentin has worn, however a seasonal signal is still recorded, showing seasonality in the years before death.

Material and Methods

Sampling

The following procedure was used on all fossils analyzed in this study. Enamel/dentin powder samples were obtained at the Las Vegas Isotope Science lab (LVIS), on the University of Nevada Las Vegas campus, and at the University of California Museum of Paleontology collections (UCMP), Berkeley, California. Before beginning any destructive sampling, I photographed the teeth including collections tags. This photodocumentation was continued throughout the sampling process, recording fossil condition from pre- to post-sampling. At their request, UCMP was supplied with a copy of all photos taken on specimens in their collections, as was the Nevada State Museum in Las Vegas. As discussed above, m3 teeth in artiodactyls and perissodactyls, molariform teeth in sloths, and m5 teeth in mammoths were chosen to sample. Most teeth were sampled sequentially, from crown to root; on extremely delicate specimens, I chose to spare the tooth from serial sampling and took only one or two samples. The teeth were cleaned before sampling. If a tooth was coated in a consolidant (e.g., glyptol or shellac) the consolidant was removed prior to drilling, even though Stephan (2000) showed that consolidants have no measurable impact on oxygen isotopes. As an added precaution, I carefully scraped the consolidant from the tooth surface using a dental pick and scalpel, exposing a fresh surface of enamel or dentin. I sampled each tooth in increments of a few millimeters. The increments, which were dependent on tooth length, ranged from two to four millimeters. Samples were collected using a Dremel hand-held rotary tool, with a foot pedal for controlled speed, and outfitted with a 0.5 mm diamond-encrusted carbide drill bit. Approximately 2-4 mg of powdered enamel or dentin was drilled from each tooth increment. Drilling was conducted under a microscope to monitor the depth of each sample and to ensure

that the enamel/dentin junction, in ungulates, or the outer/inner layer of dentin, in ground sloths, was not perforated. After each sample was collected, the tooth was brushed and cleaned to prevent contamination of the next sample. Each enamel or dentin powder sample was then weighed, recorded, and placed into a 1 mL plastic centrifuge vial where it was stored in preparation for the treatment process.

Treatment

The following methods for sample preparation were learned at the University of California, Santa Cruz in the Koch Lab. I was invited to visit the lab in February 2009 to learn the chemical treatment methods which currently remain the principle methods in use for isotopic paleoecology sample preparation (Koch *et al*., 1997). The fossils in this study have little, or no, organic matter remaining; therefore it was not worth pursuing analysis of nitrogen isotopes. Only carbon and oxygen isotopes retained in the structural carbonate of hydroxylapatite have been analyzed. The treatment process for this method follows.

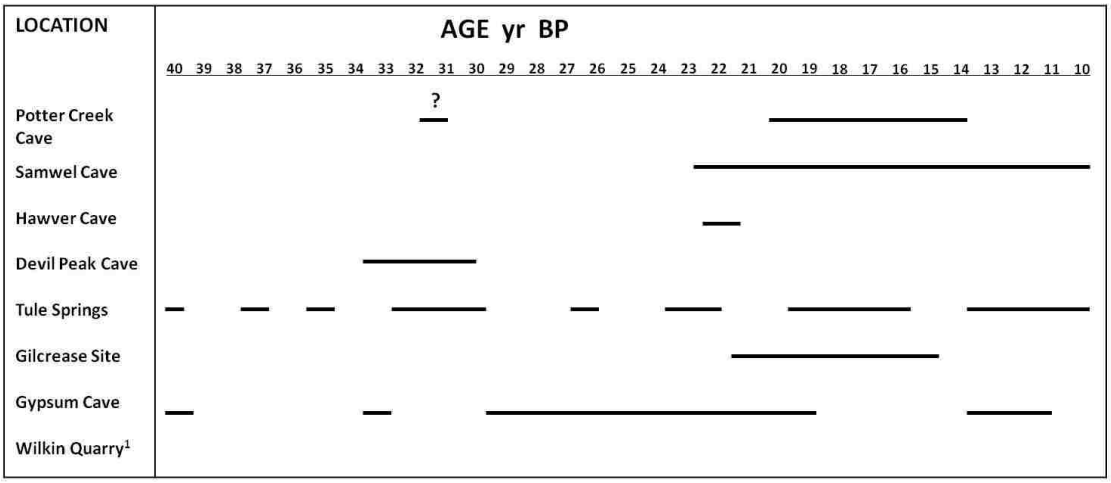
Some of the sample is lost during the treatment process. Each pre-treated powdered sample weighed 2-4 mg, leaving at least 1-1.5 mg of powder post-treatment. I calculated that on average 0.9-1.4 mg of powder was lost during the treatment process, with the amount of powder lost directly proportional to the initial weight (i.e., large samples lost more powder than small samples). Treatment began with a 30% hydrogen peroxide (H_2O_2) soak, pipetted into sample vials. The amount of H_2O_2 is proportional to the amount of powder, 1 mL of solution per 1 mg of sample, or 10% volume H_2O_2 to weight of powder. After H_2O_2 was added, samples were agitated for about ten seconds using a vortex genie. Samples were then refrigerated for twenty-four hours with loosened lids for offgassing. Samples were agitated three times during the twenty-four hour period. After twenty-four hours, samples were removed from the refrigerator,

agitated, and loaded into a microcentrifuge. Samples were centrifuged at 11,000 rpm for ten minutes. H_2O_2 was then aspirated off with a pipettor or pipette vacuum, followed by a cleansing process. To cleanse, 1 mL of MilliQ water was added to each sample, agitated for ten seconds, and centrifuged for ten minutes more. The water was aspirated from each sample, and the entire cleansing process was repeated four times. After cleansing, each sample was then treated with a calcium buffered acetic acid solution (Ca-acetic acid), buffered to a pH of 5. The process for adding Ca-acetic acid followed the same procedure described above for H_2O_2, with the exception that only half the amount of Ca-acetic acid solution was used as H_2O_2 per sample. Once the samples were soaking in Ca-acetic acid, they were agitated and placed in the refrigerator for exactly twenty-four hours, and agitated three times within this period. After twenty-four hours, I repeated, exactly, the cleansing process used for H_2O_2, although, on the fourth rinse with MilliQ water, the water was aspirated off and the vial was covered with a cap of tinfoil. Samples were then frozen and then freeze-dried. Finally, I roasted the samples for at least one hour at 60 ^{O}C in a heating oven, to extract any remaining liquid, before loading for analysis. Caution should be taken to not roast higher then 60 ^{O}C as vial plastic may turn volatile with higher temperatures. Samples, along with vials of standard (USC-1), were then loaded into the Kiel IV device. An automated process introduced each purified sample to phosphoric acid and then passed the resulting gas through to the ThermoElectron Delta V Plus Stable Isotope Ratio Mass Spectrometer. The $\delta^{13}C$ and $\delta^{18}O$ values are reported using a standard deviation of one per mil (‰) value to the nationally recognized standard of V-PDB.

Background of Assemblages

Radiocarbon Dates

I chose the fossil assemblages used in this study on the basis of taxonomic similarity and also previously determined radiocarbon dates. Assemblages range from 40-10 Ka (Figure 6). In order to understand paleoecologic and environmental change through time, it is necessary to place information gained from isotopic analyses into a solid temporal framework. Because most of the radiocarbon dates used in this study are compiled from previous studies, I was able to focus on biological and environmental questions using isotopic analyses.



[1]Radiocarbon dates attempted, lack of collagen has presented complications in acquiring a date.

Figure 6. Radiocarbon dates of localities in this study. Dates are for Potter Creek Cave (Feranec *et al*., 2007; Feranec, 2009), Samwel Cave (Feranec *et al*., 2007; Feranec, 2009; Blois *et al*., 2010), Hawver Cave (this study), Devil Peak Cave (Gromny, 2003), Tule Springs (Haynes, 1967; Quade, 1986; Springer *et al*., 2010), Gilcrease Site (Vetter, 2007), Gypsum Cave (Poinar *et al*., 1998; Hofreiter *et al*., 2000; Glowiak, 2007; Cole *et al*., 2011).

To underscore the significance of the Late Pleistocene, Figure 7 displays $\delta^{18}O$ and deuterium (dD) values for the past 200,000 years. The box encloses the 40-10 Ka interval, which is the focus period in this study. Of particular importance during this period is the relatively

slow cooling toward the Last Glacial Maximum (LGM) from 40-18 Ka, followed by rapid deglaciation to the current interglacial period. Included in this figure are speleothem data from Devils Hole, which show that fluctuations in the regional climate of the western United States were tracking global changes. Other speleothem studies supports that southern Nevada was wetter and colder at 18.6 Ka (Lachniet *et al*., 2011), followed by a marked increase in drier, drought conditions in the Southwest by 16.5 ka. (Oster, 2010; Polyak *et al*., 2012). Therefore, the biotas in Nevada and California would have been influenced by these fluctuations, especially by the rapid climatic excursions such as the Bølling-Allerød (B-A) warming and Younger-Dryas (Y-D) cooling. These were millennial-scale climate shifts occurring after the LGM. Radiocarbon dates (Figure 6) show that most of the assemblages in this study were in existence through these excursions. The significance of this 40-10 Ka interval is that organisms would have had to mold their behaviors and community structure around the dramatically changing landscapes and paleoclimates during the close of the Pleistocene. This time frame affords an excellent opportunity to understand how large, herbivorous mammals were responding to abrupt changes in climate in the past.

This project is the first of its kind to isotopically sample megaherbivore fossils from cave deposits from northern California. Fossils from the Rancho La Brea deposits of southern California have been the subject of isotopic work (Coltrain *et al*., 2004; Feranec *et al*., 2009), however there is a noticeable lack of paleoecologic studies on deposits from northern California. This study fills that gap by analyzing fossils from Potter Creek Cave, Samwel Cave, and Hawver Cave (Figure 1). Potter Creek Cave and Samwel Cave have received limited study (mostly on small mammals) in recent years (Feranec *et al*., 2007; Feranec, 2009; Blois *et al*., 2010), while Hawver Cave is essentially unstudied since the original description of the fauna.

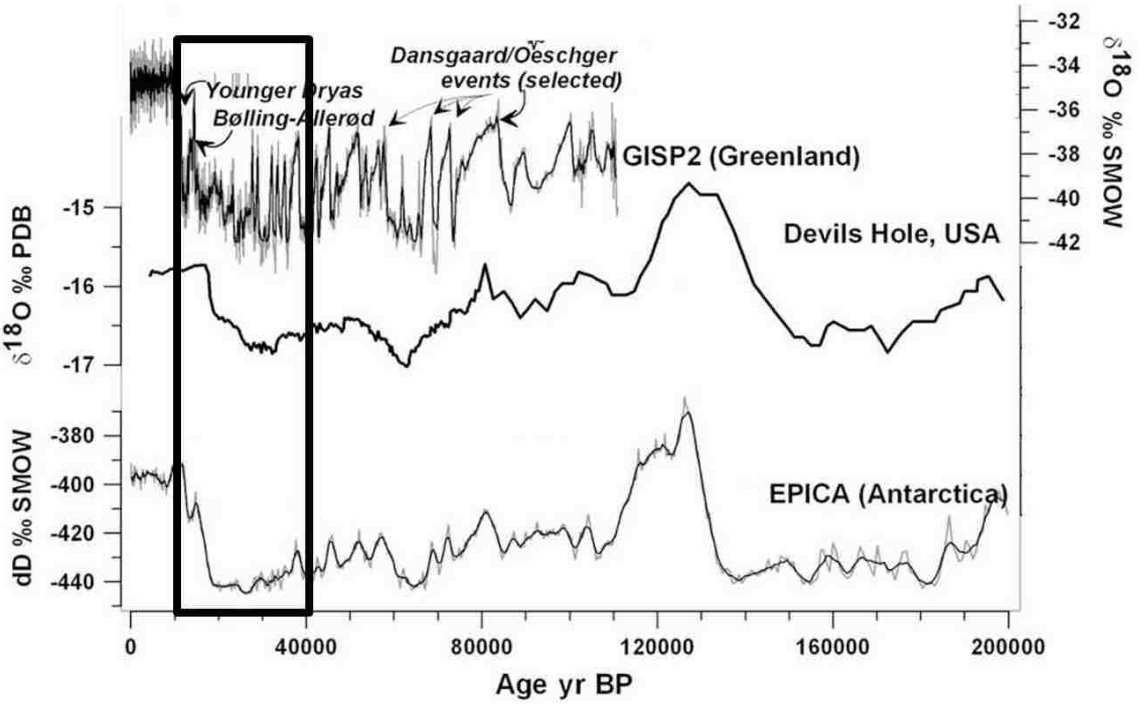


Figure 7. Global and regional paleoclimate of the Pleistocene. Records are from speleothems (Devils Hole) and ice cores (GISP 2 and EPICA) and reveals their connectivity to Pleistocene global climate. The box outlines the age interval examined in this study. Of particular interest is the noticeable change in global climate during this time frame and its regional signal in the North American Southwest (Devils Hole, USA). Modified from Lachniet (2009).

Study Localities

When Potter Creek Cave, Samwel Cave, and Hawver Cave were excavated in the early twentieth century, the primary goal was to discover interactions between Pleistocene humans and animals, as was the case in many European caves. But none of these northern California cave deposits recorded such interactions (Merriam, 1906; Payen and Taylor, 1976). There is a record of Native American bones and artifacts in Samwel Cave (Furlong, 1906), and splintered bone that is thought to be human was found in Potter Creek Cave (Sinclair, 1904). But these human bones and artifacts postdate the extinction of the Pleistocene megafauna. Human bones, objects, and projectile points have also been reported from Hawver Cave, and thought to be a burial site (Wallace and Lathrap, 1952) with a crude age estimate of about four thousand

years old (Heizer and Cook, 1949; Wallace and Lathrap, 1952). This is analogous to the history of Gypsum Cave and Tule Springs in southern Nevada in that the goal was to document the contemporaneity of humans and the Pleistocene megafauna, and yet the deposits failed to provide the requisite evidence (Shutler, 1967; Glowiak, 2007). Because the purpose of many of the original studies of the localities examined in this study was human-megafaunal interactions, the faunas themselves have been largely neglected. These understudied localities can provide a new perspective on the paleoecology of California and Nevada at the end of the Pleistocene. Comparing the same taxa between regions can improve our understanding of Late Pleistocene large herbivore behavior and paleoecology and, on the whole, expand the knowledge of the evolution of ecological landscapes of California and Nevada.

The following section discusses the historical records for each deposit. Knowing the history, geology, stratigraphy, and chronology for each site is imperative to aid in the interpretations of reconstructing the environments of the Late Pleistocene.

Potter Creek Cave

Located in Shasta County, California, Potter Creek Cave is at an elevation of 454 meters above sea level and 243 meters above the McCloud River, in the foothills of the Cascade range (Merriam, 1906) (Figure 8). It formed in the Carboniferous McCloud Limestone by water percolating along fissures trending northwest-southeast, parallel to the strike of the formation. A terrace located just above the cave opening indicates that the McCloud River ran at much higher levels at some point in the past (Merriam, 1906; Sinclair, 1904). The presence of speleothems indicates that this is a wet cave system.

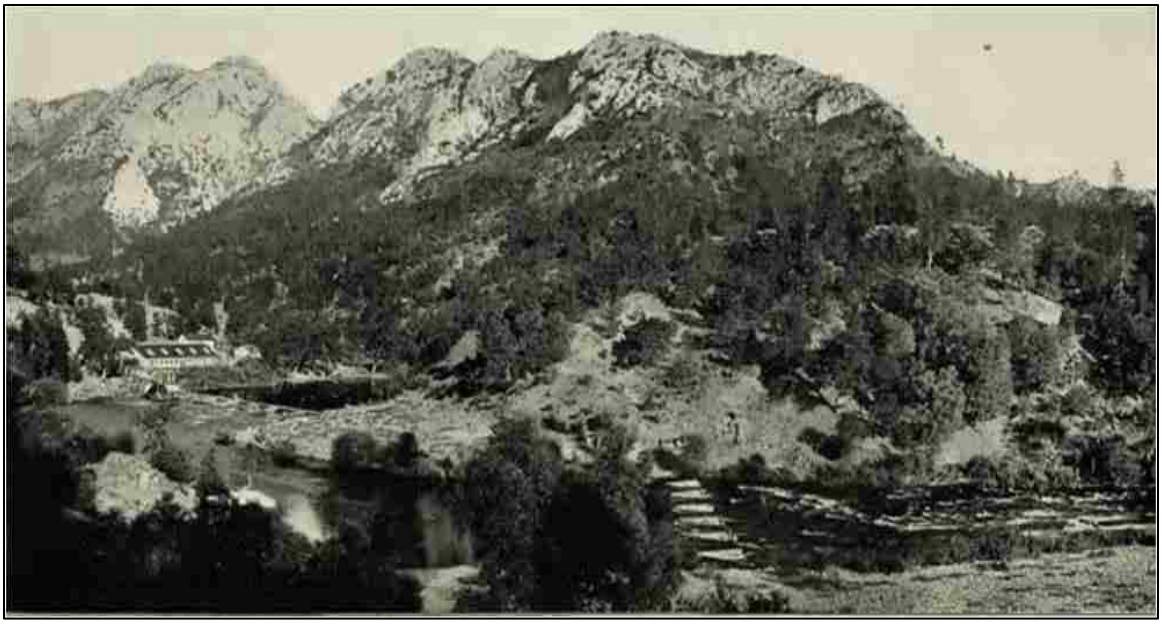


Figure 8. Image of Potter Creek Cave entrance. The cave entrance is on the saddle on the right side of the photo. Note the display of modern vegetation and McCloud River in foreground. From Sinclair (1903).

Cave deposits consist of stratified pebbly clay, cave breccias, stalagmite talus, and volcanic ash (Sinclair, 1903 and 1904). Fossils were reported and excavated from deposits in the lower chamber of the cave; the excavations were to a depth of 25 feet. Merriam (1906) stated that all specimens were labeled with reference to their position within the cave deposits. If this was the case then it would be possible to estimate dates based upon stratigraphy. However, not all specimens from Potter Creek Cave have accession notes associated with them, and of the ones that do, only some contain grid and depth information. However, there is no record of mapping information, thus rendering the grid and depth information useless. The fossil-bearing units of the lower chamber were designated by Sinclair (1904), who considered them to be one stratigraphic unit. When this cave was originally excavated, fossils obtained from throughout this "layer" were collected without any sort of micro-stratigraphic records. Several fossils from this interval have subsequently been dated. Feranec (2009) dated four mammalian fossils from

Potter Creek Cave, three of which fell between the ages of 20.5-14.1 Ka, the fourth being an unconfident outlier.

The specimens cannot be related to recorded stratigraphy as all original field notes have been lost (Patricia Holroyd, UCMP, pers. comm., May 2011). Therefore, it is impossible to place the fossils into a stratigraphic framework or even make correlations to the dated layer of Feranec (2009). As a result, the fossils can only be constrained to the known age ranges acquired for the deposit. I investigated obtaining more dates, directly on the teeth in this study, to better constrain their age, however analytical techniques would have required the destruction of entire teeth and so this was not a viable option. As an aside, a younger Holocene date (8.2 Ka) from one *Euceratherium* bone was reported from the entrance chamber of the cave (Payen and Taylor, 1976). However this date is considered unreliable, possibly due to contamination or improper sampling, since no other *Euceratherium* remains have ever been dated younger than 10 Ka (Feranec, 2009).

Fifty-two species were originally reported in the Potter Creek Cave fossil assemblage (Sinclair, 1904). This number has since been re-evaluated to be thirty-nine species (Feranec, 2009), small mammals being the most abundant. Kurtén and Anderson (1980) briefly discussed the inferred ecology based upon the presence of certain species. The presence of California ground squirrel (*Otospermophilus beecheyi*), Douglas tree squirrel (*Tamiasciurus douglasii*), and northern flying squirrel (*Glaucomys sabrinus*) indicates that the area must have been dominated by a coniferous to mixed forest during their inhabitance. The presence of mountain beaver (*Aplodontia rufa*) suggests that the forest was humid in the past, as this species is currently limited to the Pacific Northwest. The presence of mountain goat (*Oreamnos americanus*) and shrub ox (*Euceratherium collinum*) indicates that there was ecological diversity surrounding the

cave since mountain goats are mixed feeders and prefer rocky slopes down to sheltered valleys or lower hills, the latter also being the preferred habitat for the specialized grazer *Euceratherium collinum* (Kurtén and Anderson, 1980). Stable isotope analyses of the teeth of the large, herbivorous mammals permits me to test Kurtén and Anderson's (1980) interpretations, as well as my own hypotheses, about the paleoecology of the area around Potter Creek Cave. This includes proportions of C_3/C_4 vegetation in the landscape, climatic information, and ecological preference and interactions for megaherbivores.

Samwel Cave

Samwel Cave is located in Shasta County, California, at an elevation of 455 meters above sea level and 106 meters above the east bank of the McCloud River, just below a river terrace (Merriam, 1906). Samwel Cave is situated in the foothills of the Cascade Range. It is very close to Potter Creek Cave, approximately five kilometers to the northeast (Feranec, 2009). Its origin is similar to Potter Creek Cave in that it, too, formed in the Carboniferous McCloud Limestone by gradual dissolution and subterranean water flow when the water table and crest of the McCloud River were higher (Furlong, 1906). Upon lowered water levels of the McCloud River, the cave provided two main chambers that were accessible to animals. Both chambers amassed bones, many of which were found lying on the surface when the cave was discovered, although the bones continued down to the lowest depths. The majority of the bones were recovered from the first, deeper chamber, closest to the cave entrance (Furlong, 1906).

Cave stratigraphy is similar in chambers one and two, consisting of limestone bedrock overlain by cave breccia, flowstone, more cave breccia, gravel, and capped by another layer of flowstone and fine red clay; the total thickness of the deposits measures about 1.5 m (Furlong, 1906). Fossils were reportedly recovered from 0.25 m intervals within 2 foot by 2 foot (0.60 m

by 0.60 m) square grids (Furlong, 1906), although original notes are not detailed and most specimens do not have associated provenance data indicating from which layer they were exhumed. Very few specimens studied in this project have recorded stratigraphic information that assists in narrowly constraining the age of individual intervals, using previous researchers' radiocarbon dates.

Feranec *et al*. (2007) dated small mammal fossils from Samwel Cave and were able to acquire five radiocarbon dates, with a range of 23.6-17.1 Ka. Later, Feranec (2009) dated three additional rodent fossils resulting in a younger range extension from 22.0-14.7 Ka. These dates place the Samwel Cave assemblage as being nearly contemporaneous with the Potter Creek Cave assemblage. Feranec *et al*. (2007) warn that caution must be taken concerning these dates as they found one older sample positioned stratigraphically above a younger sample, thereby indicating that the layers are unstratified. In a later publication, Blois *et al*. (2010) excavated cave sediments to a depth of 110 cm [although in a different location in the cave than the excavations of Feranec *et al*. (2007) and Feranec (2009)], and they found the ages of the samples to be in stratigraphic order, suggesting minimal bioturbation. This supports the use of known radiocarbon dates for Samwel Cave and aids in constraining the age ranges of taxa in this study to 23.6-14.7 Ka.

Forty-five vertebrate fossil species have been recovered from Samwel Cave (Feranec *et al*., 2007), most of which also occur in Potter Creek Cave. This is as one might expect, due to the proximity of these two caves to one another, and the similar elevations. The close correlation of the faunal lists between the two caves indicates nearly identical environmental conditions, as interpreted by Kurtén and Anderson (1980). The presence of California ground squirrel and Douglas tree squirrel (*Otospermophilus beecheyi* and *Tamiasciurus douglasii*, respectively),

together with the northern flying squirrel (*Glaucomys sabrinus*) indicate a coniferous to mixed forest around the cave. The presence of mountain goat (*Oreamnos americanus*) indicates the proximity to high elevation, rocky slopes, while the presence of shrub ox (*Euceratherium collinum*) indicates a closeness to low elevation, grassy areas (Kurtén and Anderson, 1980).

Hawver Cave

Hawver Cave is located in El Dorado County, California, in the foothills of the Sierra Nevada Range, at an elevation of 393 m. This cave is situated about 250 km to the southeast of Potter Creek Cave and Samwel Cave, and records many of the same taxa. Hawver Cave formed in the Carboniferous Calaveras Limestone in a tributary to the middle fork of the American River (Furlong, 1907). Like Potter Creek Cave and Samwel Cave, Hawver Cave is a wet cave system having experienced intermittent periods of water flow, evident by a brecciated layer. Most of the fossils were recovered from this brecciated horizon, which is composed of angular limestone, broken stalactite fragments, and reddish-brown clay from the outside surface (Stock, 1918). Stock (1918) described most of the bones as fragmentary, however upon examination of the collection at the University of California Museum of Paleontology, I found that the majority of bones are whole, or nearly complete, but without association. The vertebrate collection is significantly smaller than that of Potter Creek Cave and Samwel Cave, both in diversity of species recovered and in numbers of specimens. This could indicate that the cave was not in existence, or not accessible, for as long a period as the other two. However, Dick Hilton of Sierra College, Rocklin, California, (pers. comm., December 2011) suggested to me that there are more fossils yet to be recovered from Hawver Cave, implying that the relatively small, lower diversity assemblage (compared to Potter Creek Cave and Samwel Cave) may be due to collection bias.

Radiocarbon dating of Hawver Cave specimens has not been attempted until this study. Chapter 2 addresses the dating of Hawver Cave fossils. A single date was retrieved, placing the cave deposits at approximately 22 Ka. This is slightly older than Potter Creek Cave and contemporaneous with the oldest dates from Samwel Cave. There is essentially no stratigraphic work recorded for Hawver Cave, so it is impossible to know how this date fits into the full age range of the cave deposits.

Stock (1918) reported twenty-six vertebrate species from Hawver cave. Many of these species are also known from Potter Creek Cave and Samwel Cave, and the presence of certain species, such as California ground squirrel and Douglas tree squirrel (*Otospermophilus beecheyi* and *Tamiasciurus douglasii*, respectively), mountain beaver (*Aplodontia rufa*), and shrub ox (*Euceratherium collinum*) indicates similar environmental conditions (Kurtén and Anderson, 1980). However, the addition of some small mammal taxa (brush mouse, *Peromyscus boylii*, and dusky-footed woodrat, *Neotoma fuscipes*) indicates that Hawver Cave had the added component of a chaparral environment in the vicinity of the cave (Kurtén and Anderson, 1980). This supports Stock's (1918) claim that Hawver Cave contains fewer forest-dwelling taxa, and that this assemblage reflects a lower elevational grassland environment. Stock drew this conclusion based upon the presence of three species of ground sloth. An abundance of Shasta ground sloth (*Nothrotheriops shastensis*) and Harlan's ground sloth (*Paramylodon harlani*) remains indicate the environment was chaparral/grassland/woodland, while the less abundant Jefferson's ground sloth (*Megalonyx jeffersonii*) suggest a montane/woodland ecosystem (Stock, 1918).

In the past, faunal composition has been the primary method for interpreting the paleoenvironment in the vicinity of each of the three northern California caves. However, as

previously mentioned, collection bias may have distorted ecological interpretations. Stable isotopic analysis of fossils from each assemblage provides an additional test of paleoenvironments. This approach will provide new, and more detailed, information about the ecological characteristics and interactions of the animals and the environments in which they lived.

Potter Creek Cave, Samwel Cave, and Hawver Cave are all in an area that is physiographically distinct from the caves/locations in Nevada. Below are descriptions of the southern Nevada localities examined in this study.

Devil Peak Cave

Devil Peak Cave is located in Clark County, Nevada, at an elevation of 1097 meters. Unlike the California caves, Devil Peak Cave is a dry cave that formed as a vertical chimney in Mississippian Limestone of the Monte Cristo Formation (Gromny, 2003). Fossils have been recovered from the lowest 4 m of cave fill (total depth of fill is 10 m) and collected from the interstitial sands and silts overlain by coarse fill (Reynolds *et al*., 1991). A total of twenty vertebrate species have been reported from the cave, most of which are small mammals (Reynolds *et al*., 1991). The single large mammal is a nearly complete skeleton of a Shasta ground sloth (*Nothrotheriops shastensis*). Gromny (2003) attempted to radiocarbon date a sloth bone from Devil Peak Cave, but a lack of collagen prevented dating. He was able to determine the sloth skeleton to be approximately 32 Ka by dating avian egg shell above and below the sloth. Aside from radiocarbon dating, studies of the cave deposits and fossils extend as far as morphometric analysis of the sloth (Gromny, 2003). Ecological information has not been attained for the Devil Peak Cave sloth, nor has an environmental reconstruction of the cave and surrounding area during the Late Pleistocene.

Tule Springs

Tule Springs deposits are located in the Upper Las Vegas Wash in Clark County, Nevada, at an elevation of about 700 m. A large amount of literature exists concerning Tule Springs, based upon geological, paleohydrological, and paleoenvironmental investigations (Quade, 1986; Quade *et al*., 2003; Springer *et al*., 2011; Springer *et al*., 2012), stratigraphy and sedimentology of the Las Vegas Formation (Longwell *et al*., 1965; Haynes, 1967; Quade *et al*., 1995; Quade *et al*., 2003), archaeological (Harrington and Simpson, 1961; Shutler, 1967; Shutler, 1968), and paleontological (Mehringer, 1965; Mawby, 1967; Springer *et al*., 2005; Springer and Manker, 2010; Springer *et al*., 2010; Springer *et al*., 2012). The fossil-rich Las Vegas Formation in the Tule Springs area is the result of a predominantly fluvial system with periods of marshy conditions, correlating to moister periods of the Late Pleistocene (30-15 Ka) (Quade, 1986; Quade *et al*., 1995), as indicated by the presence of tufa deposits (Springer and Manker, 2010; Springer *et al*., 2012). The groundwater discharge deposits that are recorded in the region formed from the damming of Pleistocene groundwater against the local faults (Quade *et al*., 1995).

Numerous fossils have been recovered from throughout the Las Vegas Formation which is sub-divided into units A-G and date back to 250 Ka (Springer *et al*., 2010), thereby providing an excellent record of multiple glacial-interglacial cycles through the Late Pleistocene. In addition to paleontological studies, pollen analyses have also been conducted (Mehringer, 1967). The pollen record indicates that pluvial periods (40-34 & 23-10 Ka) were cooler and wetter with piñyon-juniper woodland, thereby showing a depression of vegetation zones about 1200 m downslope from what is present in the area today (Mehringer, 1967). Prior bulk isotopic studies have been conducted on Tule Springs (Connin *et al*., 1998). Because of the information gained from Connin *et al*. (1998), I analyzed only *Nothrotheriops shastensis* from Tule Springs,

which was not included in Connin *et al*.'s (1998) study and has never before been isotopically analyzed.

Gilcrease Site

The Gilcrease Site is also within the Las Vegas Formation in the Tule Springs area, but I will discuss it separately. It is located on private land owned by Bill Gilcrease, adjacent to the Gilcrease Nature Sanctuary. Fossils occur within the remnants of one cauldron spring. Fossils date the spring to approximately 22-16 Ka (Vetter, 2007). This site has been the subject of several studies including taphonomic (Bonde *et al*., 2008), hydrologic (De Narvaez, 1995), and paleoecologic (Vetter, 2007). Due to the isotopic analyses previously conducted on the Gilcrease fossils (Vetter, 2007), this site provided a baseline for testing isotopic analyses on vertebrate fossils in the Las Vegas Isotope Science Lab (LVIS). LVIS had not processed vertebrate samples prior to this study, and the Gilcrease fossils permitted verification that isotopic data retrieved correlated with the data previously obtained from the site (Vetter, 2007). Vetter (2007) had analyzed her samples at the University of California, Davis. The data from both labs were found to be compatible, which seemingly validated the isotope data produced in the LVIS lab. Analyzed fossils from Gilcrease Site are included in discussions in this study.

Wilkin Quarry

The Wilkin Quarry is located near Panaca, in east-central Nevada, on private property owned by Jim Wilkin. One partial skull of *Bison latifrons* has been recovered, along with tusk material (presumably from *Mammuthus columbi*). The deposits are certainly Rancholabrean in age, although a radiocarbon date for *B. latifrons* has not been obtained due to a lack of collagen and prohibiting differentiation between its existence in the Sangamonian interglacial or Wisconsin glaciation. Because of limited studies on this site, paleoecologic information is

lacking. A sedimentological analysis was performed, determining that the deposits are fluvial in origin and from ephemeral discharge (Vetter *et al*., 2007). Isotopic analysis on a *B. latifrons* m3 provides a record of paleoecology and seasonality for this region of Nevada (Bonde and Rowland, 2011). These findings are coupled with isotopic data from other sites to create a larger paleoenvironmental reconstruction for California and Nevada.

Gypsum Cave

Gypsum Cave is located in Clark County, Nevada, approximately 30 km east of Las Vegas, at an elevation of 454 m. Gypsum Cave formed in Paleozoic limestone by differential solution; it is named after large, well-formed selenite crystals found within the cave system (Stock, 1931). Excavation of the cave, in 1930, showed that the bottom layer of cave sediments is fragmented limestone overlain by a gypsiferous layer, and covered by a layer of sloth dung approximately 66 cm thick (Harrington, 1933; Kurtén and Anderson, 1980). Gypsum Cave records over fourteen different species, the most abundant fossils are of *Nothrotheriops shastensis*, represented by dung, bones, and hair (Kurtén and Anderson, 1980; Glowiak, 2007). Permission was not granted to sample Gypsum Cave sloth teeth for isotopic analyses, although it was granted to study sloth hair. Hair requires a different analytical method than tooth enamel/dentin and, as of yet, is unanalyzed. So no isotopic data from Gypsum Cave are available at this time. However, previous work on dung (Laudermilk and Munz, 1934; Poinar *et al*., 1998; Hofreiter *et al*., 2000; Gill *et al*., 2009) and radiocarbon dating (Poinar *et al*., 1998; Hofreiter *et al*., 2000; Glowiak, 2007) can provide comparisons for paleoecological interpretations for southern Nevada, to isotopic results from this study.

Radiocarbon ages for Gypsum Cave deposits range from about 40-11 Ka. Analysis of *N. shastensis* dung suggests that, through this time interval, the region experienced a cooler

climate than at present, and with higher humidity levels. This was determined from the presence of plant species within the dung that currently can be found only at higher elevations or higher latitudes (e.g., *Yucca brevifolia*, the primary constituent of the dung) (Hofreiter *et al*., 2000). Pollen in the dung is direct evidence of Late Pleistocene floral composition and diet of the Shasta ground sloth. Previous research on these parameters will be helpful as a base for comparing the isotopic values retrieved from dentin for *N. shastensis* in this study. This research can contribute to the paleoecology of *N. shastensis* by adding seasonal data directly to the specimens. Dung provides a snapshot of what sloths ate, but it is also time-averaged and cannot be put into a precise chronological context, as can data retrieved from serial stable isotope analysis.

CHAPTER TWO

RADIOCARBON AGE OF THE VERTEBRATE FOSSIL ASSEMBLAGE OF HAWVER CAVE, EL DORADO COUNTY, CALIFORNIA, USA

Abstract

Hawver Cave contains a diverse Late Pleistocene assemblage of vertebrate fossils including bones and teeth of megaherbivores. The deposits have long been considered to be Late Pleistocene based upon the presence of certain taxa, however they have remained undated. This report is the first to assign an age to the deposits, placing the timing of deposition during the Last Glacial Maximum. This date corroborates prior thought and establishes that at least a portion of the assemblage is coeval with the older fossils of Samwel Cave, CA, and slightly older than the oldest dated fossils from Potter Creek Cave, CA.

Introduction

Hawver Cave is one of two localities within this study for which radiocarbon dates were lacking (the other undated locality is Wilkin Quarry, NV). It was prudent to acquire dates for the Hawver Cave fossils for two main reasons: (1) to clarify the age of the assemblage, which was previously assumed to be Late Pleistocene based upon the taxa present (Furlong, 1906; Stock, 1918), and (2) to constrain the timing of existence of the organisms recovered from the cave, thereby permitting a more temporally-specific interpretation of the stable isotope results obtained in this study.

Hawver Cave fossils are housed in the University of California Museum of Paleontology (UCMP) collections in Berkeley, California. A large number of fossils have been excavated from Hawver Cave, although there is no accompanying stratigraphic information. Discussions with UCMP vertebrate collections manager Patricia Holroyd (pers. comm., December 2011), determined that the museum does not have documentation of original field notes and stratigraphic information, including mapping information for excavated fossils. Such data have never been published for the cave. Therefore, choosing specimens proved to be extremely difficult, and with limited funding, I chose three specimens to date. One of the objectives of dating Hawver Cave fossils was to constrain the age of the deposits, although the lack of recorded field notes prevented me from using stratigraphic information in the selection of specimens to date. I selected fossils that are well preserved, not associated with other fossils, and non-diagnostic. The three bones I chose were a fragmentary, unidentifiable mammalian bone, an incomplete femur of *Lepus*, and a fragmentary metacarpal of *Nothrotheriops shastensis* (Figure 9). I conducted an isotopic analysis of a *Nothrotheriops shastensis* tooth from Hawver Cave in this study, so dating the *N. shastensis* metacarpal was a desired choice. Stock (1918) stated that, based on skeletal material, only two individuals of *N. shastensis* were thought to have been recovered from Hawver Cave. Therefore, the potential existed that the metacarpal might be an associated element of the *N. shastensis* that was isotopically sampled. Radiocarbon dating is a destructive process, and to date a tooth that had been isotopically sampled (although ideal) would have destroyed the entire tooth. It was not an option to destroy such an important paleontological specimen, so I chose the metacarpal fragment.

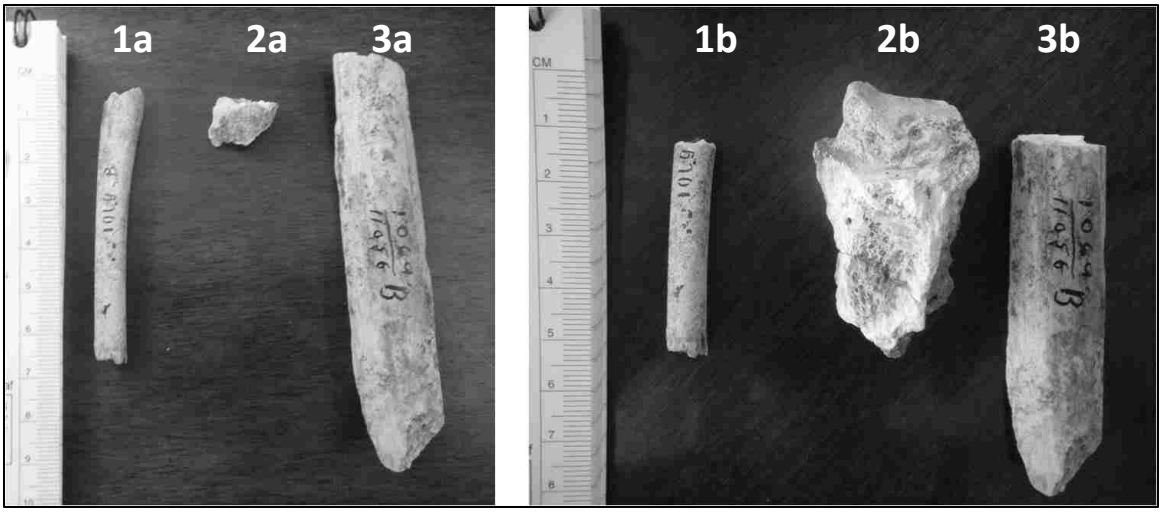


Figure 9. Hawver Cave fossils analyzed for radiocarbon dates. Photographs of fossils before (a) and after (b) sampling: (1) *Lepus* femur (specimen # 195577), (2) *Nothrotheriops shastensis* metacarpal (2a was dated which was a loose piece of 2b) (specimen # 19872), (3) unidentifiable mammal bone (specimen # 11056).

Results

Samples were sent to Beta Analytic Inc. for examination and pretreatment, collagen extraction, and standard Accelerated Mass Spectrometer (AMS) dating. INTCAL09 was used by Beta Analytic Inc. to determine a calibrated date. Of the three samples, only one sample (specimen # 195577, the *Lepus* femur) provided enough collagen to be dated. The *Lepus* femur provided a date of 18,420±70 ^{14}C years, or 22,230-21,770 ka.

Table 3. Radiocarbon dates acquired for Hawver Cave.

BETA#	UCMP#	Identifiable taxon	Element	^{14}C Age	^{13}C/^{12}C Ratio	2-σ age range (cal BP)
-	19872	*Nothrotheriops shastensis*	Metacarpal	no date	-	-
314206	195577	*Lepus* sp.	Femur	18420±70 BP	-20.1‰	22230-21770
-	11056	Mammalia	Limb fragment	no date	-	-

Discussion

Figure 10 shows the range of dates for the three northern California caves (Potter Creek Cave, Samwel Cave, and Hawver Cave). Based on the date found for the *Lepus* femur, approximately 22 Ka, at least a portion of the Hawver Cave assemblage is slightly older than the Potter Creek Cave assemblage, or at least records the onset of deposition prior to the earliest known date for Potter Creek Cave. The Hawver Cave date is contemporaneous with the older dates from Samwel Cave. There is essentially no stratigraphic information for Hawver Cave, so it is impossible to know how this date fits into the full age range of the cave deposits. Based upon the fossil assemblages and the percentage of extinct organisms present in each of the caves, it was previously thought that the Hawver Cave assemblage was older than the Samwel Cave fossils but younger than those from Potter Creek Cave (Furlong, 1906; Stock, 1918). A date of 22 Ka for Hawver Cave implies the opposite to be the case; Samwel Cave records the oldest date with the longest record of the Late Pleistocene, and Potter Creek Cave has a younger date than Hawver Cave (Figure 10). Further dating would almost certainly show a more complex age relationship among these three caves.

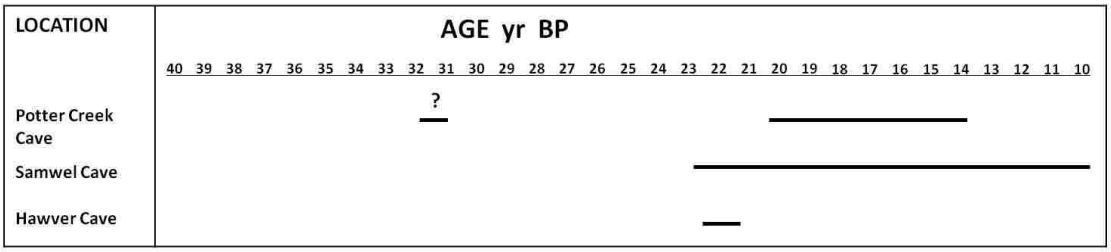


Figure 10. Calibrated radiocarbon dates for northern California localities. Sites include Hawver Cave (this study), Potter Creek Cave (Feranec *et al*., 2007; Feranec, 2009), and Samwel Cave (Feranec *et al*., 2007; Feranec, 2009; Blois *et al*., 2010). The oldest date for Potter Creek Cave (~31.5 Ka) is deemed an unreliable outlier (Blois *et al*., 2010) and is not considered in this study.

This date does not cover the entire range of the assemblage, but at least identifies a starting point for dating the Hawver Cave fossils. The date for Hawver Cave contributes toward

a better understanding of the paleoecology of northern California during the Late Pleistocene and can be considered roughly age-equivalent to Potter Creek Cave and Samwel Cave.

Hawver Cave formed by dissolution and subterranean water flow where the lower rooms in Hawver Cave were submerged by heightened river levels, or at least experienced active water flow, evident by a brecciated layer of angular limestone and broken stalactite fragments (Furlong, 1907; Stock, 1918). By the Last Glacial Maximum, Hawver Cave was vacant of water (allowing for animal occupancy) indicating that water levels associated with the American River were lower at 22 Ka than at earlier times. Hawver Cave had formed prior to – and was exposed during – the LGM, recording this period of fossil accumulation. This leads to the interpretation that during the LGM, northern California was drier than at previous times, as water levels were not at maximum heights when the bones accumulated. Stable isotope data from large herbivore teeth can add to paleoenvironmental interpretations and create a more complete paleoecological reconstruction within the region of Hawver Cave.

Conclusion

One date, ~22 Ka, was retrieved for Hawver Cave, placing the timing of fossil deposition during the Last Glacial Maximum. This agrees with previous estimates and is correlative with the other two well-known Late Pleistocene caves from northern California, Potter Creek Cave and Samwel Cave.

Additional dates should be obtained for Hawver Cave; the single date does not permit satisfactory age constraint for this fossil assemblage. However, this date does provide a platform for connecting paleoecological studies, using stable isotope analysis, to a specific time in the Late Pleistocene.

CHAPTER THREE

NICHE PARTITIONING AND PALEOECOLOGY OF LATE PLEISTOCENE GROUND SLOTHS USING STABLE ISOTOPE ANALYSIS

Abstract

Stable isotope analyses in paleoecological studies typically examine carbon and oxygen isotopes in tooth enamel. In the past, this had precluded the inclusion of ground sloths (Order Xenarthra), an important group of mammals in Late Pleistocene communities. Xenarthran teeth lack the densely crystalline enamel coating that is present in other orders of mammals. The teeth of ground sloths, and other fossil and extant xenarthrans, are composed of several types of dentin and cementum, making them more susceptible to post-mortem chemical alteration. For this reason, very few studies have used stable isotopes to examine the paleoecology of ground sloths.

Ground sloths deserve a closer examination in order to better understand their unique behaviors and paleoecological significance. To begin filling this gap, I analyzed carbon and oxygen stable isotopes from a total of ten Late Pleistocene ground sloth teeth, from two species, *Nothrotheriops shastensis* and *Megalonyx jeffersonii*, from five localities in Nevada and California. As a test for diagenetic alteration, I also examined a subset of the Late Pleistocene ground sloth dentin, together with samples of Late Pleistocene enamel, alongside modern dentin from a 9-banded armadillo (*Dasypus novemcinctus*) using X-ray diffraction (XRD) and scanning electron microscopy (SEM). Mineral identification from diffraction patterns, crystallite integrity, and chemical composition of modern and fossil dentin were nearly identical (O, C, Ca, P, and Na). Trace amounts of other elements were also identified in fossil enamel (Mg, Al, and Si), that were not identified in the fossil and modern dentin, although all are known constituents

of hydroxylapaptite. XRD patterns show clear evidence of recrystallization in the fossil dentin and enamel, which is a common phenonmenon in fossil biogenic apatites. XRD and SEM results support the use of stable isotopic analyses on ground sloth dentin.

Isotopic results show variations in carbon and oxygen isotopes between species and localities, occurring within anticipated ranges. $\delta^{13}C$ data reveal that *N. shastensis* and *M. jeffersonii* utilized a range of dietary strategies, from browsing to mixed-feeding, dependent upon location. When co-occurring, *N. shastensis* and *M. jeffersonii* yielded $\delta^{13}C$ values that varied by up to 2‰, indicating a preference for different types of vegetation and a partitioning of resources. Further, when co-occurring, $\delta^{18}O$ data reveal that *M. jeffersonii* values are consistently lower than those of *N. shastensis*, indicating a tendency for *Megalonyx* to consume vegetation from humid areas that did not experience high amounts of evapotranspiration. Isotope data support prior suggestions that *M. jeffersonii* and *N. shastensis* utilized different habitats within an ecosystem.

Serial sampling of *N. shastensis* teeth reveals multi-year cycles with inter-annual seasonal fluctuations. In three of the four *N. shastensis* teeth sampled, $\delta^{13}C$ values were found to increase through the last few years of life, while $\delta^{18}O$ values did not. Results of this study show that with the effective use of XRD and SEM diagenetic testing, conventional isotopic methods and serial sampling of ground sloth dentin measure primary isotopic signatures, yielding a chronological record through life and providing useful ecological information. Therefore, this unique group of mammals should not be overlooked in stable isotope analyses and can contribute toward a better understanding of Late Pleistocene ecosystem composure and functionality.

Introduction

The first pulse of ground sloth immigration into North America came from South America in the Late Miocene, followed by another pulse in the Pliocene, the latter occurring across the Isthmus of Panama as part of the Great American Biotic Interchange (Marshall *et al*., 1982; Marshall, 1988; McDonald, 2005). By the Late Pleistocene, ground sloths were a common component of megafaunal communities in North America and are represented by four genera: *Megalonyx*, *Nothrotheriops*, *Paramylodon*, and *Eremotherium*. To understand the structure of Pleistocene communities it is necessary to gain a better understanding of how ground sloths functioned as large-bodied herbivores. A powerful tool for addressing paleoecological questions among vertebrates involves isotopic analyses of teeth. However, sloths present a challenge in isotopic analyses because their teeth are composed entirely of dentin, lacking the enamel coating that is present, and usually examined, in most other mammals. It has been suggested that, as an evolutionary response to the lack of enamel, ground sloths evolved hypselodont teeth with several layers of dentin (orthodentin, osteodentin, vasodentin) and cementum (Ferigolo, 1985; Vizcaíno, 2009; Kalthoff, 2011). Orthodentin is the surficial and most resistant layer of dentin, considered to be the functional analog of enamel, although orthodentin is softer (H = 3.8) than enamel (H = 5.7), on Moh's Hardness Scale (H) (MacFadden *et al*., 2010).

Pleistocene ground sloths have been underrepresented in previous studies of stable isotope paleoecology due to the uncertainty of diagenetic alterations to all layers of dentin, especially orthodentin, the layer used in isotopic examinations. Not only are ground sloth teeth difficult to sample due to the extreme frailty of the outer surface of orthodentin, but also they inherently hold less carbonate in the apatite structure of the dentin, than is present in enamel.

Problematically, the lower inorganic, apatite content (~70%) and higher organic/water content (~30%) (Hillson, 2005) leads to uncertainties when considering post-mortem alteration, and also produces excess water during analysis. Excess water production can result in mechanical issues and/or skewing of oxygen values. These challenges have contributed toward an inclination for researchers to avoid using ground sloths in isotope paleoecology studies. In this study, I demonstrate that when working cautiously with geologically young, well-preserved ground sloth dentin, viable isotopic data can be obtained and are useful for paleoecological and paleoenvironmental reconstructions.

In stable isotope analysis, the primary mineral examined in enamel, dentin, and bone is inorganic carbonate hydroxylapatite, $Ca_{10}(PO_4)_6(OH)_2$, where the incorporation of carbonate $(CO_3)^{2-}$ is able to substitute in the apatite lattice at either the $(OH)^-$ or $(PO_4)^{3-}$ sites (Sponheimer and Lee-Thorp, 1999; LeGeros, *et al*., 2009). Flourine (F^-) is also present as a substitution phase for the $(OH)^-$ group of apatite, resulting in a molecular formula of fluoroapatite as $Ca_{10}(PO_4)_6(F)_2$ (Elliott *et al*., 2002; LeGeros, *et al*., 2009). Biogenic apatites are often impure and can contain trace amounts of other elements such as magnesium, chlorine, sulfur, sodium, silica, iron, and aluminum, which are able to substitute into the Ca, P, and OH sites (Michel *et al*., 1995; Kohn *et al*., 1999; Jacques *et al*., 2008; Metcalfe *et al*., 2009; Hinz and Kohn, 2010; Vaseenon, 2011; Kohn *et al*., 2013).

Although the teeth in this study come from geologically young, Late Pleistocene deposits, chemical changes begin immediately post-mortem (Tuross *et al*., 1989). In terms of diagenetic vulnerability, dentin is more prone to chemical alterations than enamel due to a higher organic constitutent and less dense internal crystalline structure (LeGeros, 1981; Krueger, 1991; Lee-Thorp and van der Merwe, 1991; Ayliffe *et al*., 1994; Bryant *et al*., 1994; Koch *et al*., 1994; Wang and Cerling, 1994; Michel *et al*., 1995; Koch *et al*., 1997; Kohn *et al*., 1999;

Sponheimer and Lee-Thorp, 1999; Kohn and Cerling, 2002; Tütken *et al*., 2008), although it is more highly crystalline than bone (MacFadden *et al*., 2010). Of primary concern for the specimens isotopically analyzed in this study is that teeth from northern California were recovered from deposits within wet caves, making them likely subjects of elemental exchanges with ground or meteoric waters (Tuross *et al*., 1989; Wang and Cerling, 1994; Iacumin *et al*., 1996; *Kohn et al*., 1999). It is important in this study to characterize alterations affecting the purity, and physical and crystallographic nature of the apatite in ground sloth dentin.

A significant body of research exists for the analysis of the effects and extent of diagenesis on fossil material and several mechanisms can been used to test the chemical composition and crystallinity of bone, enamel, and dentin for diagenesis. These include infrared spectroscopy (IR) (Hassan *et al*., 1977; Lee-Thorp and van der Merwe, 1991; Michel *et al*., 1995; Sponheimer and Lee-Thorp, 1999; Reiche *et al*., 2002; Lee-Thorp and Sponheimer, 2003; Metcalfe *et al*., 2009; MacFadden *et al*., 2010), rare earth element analysis (REE) using inductively coupled plasma mass spectrometry (ICP-MS) (Sponheimer and Lee-Thorp, 2006; Tütken *et al*., 2008; Hinz and Kohn, 2010; MacFadden *et al*., 2010; Kohn *et al*., 2013), X-ray fluorescence (Piga *et al*., 2009; Kuczumow *et al*., 2010), ion microprobe (Kohn *et al*., 1999), cathodoluminescence (Schoeninger *et al*., 2003), X-ray diffraction (XRD) (Tal *et al*., 1976; Hassan *et al*., 1977; Michel *et al*., 1995; Person *et al*., 1995; Koch *et al*., 1997; Reiche *et al*., 2002; Tütken *et al*., 2008; Metcalfe *et al*., 2009; Piga *et al*., 2009; Kuczumow *et al*., 2010), transmission electron microscopy (TEM) (Kohn *et al*., 1999; Reiche *et al*., 2002), nitrogen content (Tütken *et al*., 2008) and scanning electron microscopy (SEM) (Tal *et al*., 1976; Kohn *et al*., 1999; Jacques *et al*., 2008). The most current method for detecting diagenetic alteration in xenarthran teeth was developed by MacFadden *et al*. (2010). They used uptake of rare earth elements (REE) in teeth to quantify the degree of diagenesis, using ICP-MS analysis. MacFadden *et al*., (2010)

discovered that ground sloth teeth dating back to the Miocene, along with other types of xenarthran teeth, can result in REE values that fall within acceptable limits, similar to unaltered modern xenarthran dentin. They concluded that providing this test of diagenesis leads to the recovery of primary isotopic signatures in ground sloth teeth and meaningful interpretations for paleodietary and paleoenvironmental information. I communicated with Bruce MacFadden (pers. comm., April 2013) about the feasibility of this test with my dataset, and he determined that my data would not yield the minimum number of statistical comparisons to be significant. In addition to ruling out this method, the other tests for diagenesis were also ruled out based upon too large of sample size needed to conduct the analysis (most sample material was already sacrificed to stable isotope analysis), destruction of dentin architecture during sampling, or availability of machinery. MacFadden (pers. comm., April, 2013) then supported the use of XRD to assess diagenetic alteration of ground sloth dentin. Therefore, I have chosen to use a multi-proxy approach of X-ray diffraction (XRD) and scanning electron microscopy (SEM) in an attempt to quantify the degree of diagenesis that dentin has undergone. This characterization is of utmost importance to the utility of primary carbon and oxygen isotope data in teeth and is essential when making paleodietary and paleoenvironmental interpretations.

In this study, I examined carbon and oxygen isotopes in ground sloth dentin. Stable carbon isotopes capture information about an animal's diet (Vogel, 1978). Browsing herbivores consume dominantly C_3-type vegetation and have $\delta^{13}C$ values of -8‰ or lower, while grazing herbivores consume predominantly C_4-type vegetation with $\delta^{13}C$ values of 0‰ or higher (Cerling *et al*., 1997; Koch, 1998; Passey *et al*., 2005; DeSantis *et al*., 2009). Mixed feeders have $\delta^{13}C$ values ranging between -8 and 0‰, so it can be inferred that herbivores with a diet of 50% C_3 and 50% C_4 vegetation will display $\delta^{13}C$ values of about -4‰ (Feranec *et al*., 2009). Comparing

stable carbon isotope data for a community of herbivores in a given assemblage can lead to interpretations about inter-specific competition and niche partitioning (DeSantis *et al*., 2009).

Stable oxygen isotopes in teeth record the isotopic value of the water an animal ingests, which reflects environmental conditions, including surface/meteoric precipitation, climate, and seasonality. Oxygen isotopes can also record an animal's migratory behavior. The herbivores examined in this study were obligate drinkers (as opposed to herbivores that get their water from the plants they eat) and, therefore, the $\delta^{18}O$ values in teeth directly record the values in the surface water of a region. In turn, the $\delta^{18}O$ of surface water is directly correlated to the $\delta^{18}O$ of meteoric precipitation and regional climate. Cool climate regions and areas which experience high humidity levels are represented by low $\delta^{18}O$ values, while warm climates and more arid regions have higher $\delta^{18}O$ values (D'Angela and Longinelli, 1990; Ayliffe *et al*., 1992; Delgado Huertas *et al*., 1995). When examining serial data, low $\delta^{18}O$ values indicate winter seasonality and high $\delta^{18}O$ values correspond to summer seasonality (Higgins and MacFadden, 2004; Feranec *et al*., 2009; Nunez *et al*., 2010). Because oxygen values reflect the physical environment of ingested waters which are characteristic of varying ecological environments (Schwarcz *et al*., 1991; White *et al*., 1998; Dupras, 2001), migratory behaviors may be identified. This type of behavior may result in $\delta^{18}O$ values that vary in ways which are not indicative of seasonal fluctuations in temperature and humidity.

Previous Isotopic Studies on Ground Sloths

With the appropriate precautions and analytical measures, there is no reason that original isotopic signatures cannot be obtained from ground sloth dentin. Many studies have successfully analyzed dentin from modern and fossil proboscidean tusks (Koch *et al*., 1989; Vogel *et al*., 1990; Fisher *et al*., 2003; Rountrey *et al*., 2007; Uno, 2009; Smith, 2010), while

fewer studies have analyzed ground sloth dentin (Kohn, *et al*., 2005; Ruez, 2005; Kalthoff and Tütken, 2007a). Kohn *et al*. (2005) analyzed carbon and oxygen isotopes in the dentin of *Megalonyx jeffersonii*, while Ruez (2005) examined only carbon isotopes in the dentin of *Paramylodon harlani*. Kohn *et al*. (2005) were uncertain about the validity of the dentin values they obtained, while Ruez (2005) stated that the dentin produced useful data. Kalthoff and Tütken (2007a and 2007b) focused on the dentin structure of modern and fossil sloths and analyzed for carbon, nitrogen, and oxygen isotopic compositions. They found that the good preservation of dentin in fossil material allows dentin to be suitable for use in biogeochemical studies. Given these very few studies, two of the three researchers concluded that they were confident that they obtained reliable ecologic information, with values that fell within anticipated ranges.

In order to effectively analyze ground sloth teeth using serial analyses, and to understand the chronological importance of the results, it is necessary to understand how ground sloth teeth form. Unlike ungulate teeth, which form continuously over several years until root formation is complete (Gadbury *et al.*, 2000), sloth teeth are non-deciduous and ever-growing. High-crowned cusp structures on the occlusal surface are formed by wear on the dentin as it is continually being produced and worn away (Naples, 1990). Therefore, while enamel in ungulates records the early years of life, dentin in ground sloths records the latest years of life. Sloth teeth cannot be used to estimate the animal's age since it is undeterminable how much of the dentin has worn, however seasonal signals may still be obtained, showing seasonality in the years before death. Rate of dentin growth in ground sloth teeth is unknown. Based upon serial analyses in this study, I have made estimates of growth rate.

Hypotheses

The few prior isotope studies of ground sloths involved just one species of ground sloth per study, sometimes within a diverse megafunal assemblage (Kohn *et al*., 2005; Ruez, 2005). Questions remain as to the dietary niches of ground sloths and how two or more species partitioned resources when occurring together in an ecosystem. To address these questions, I have analyzed two species of ground sloths: *Nothrotheriops shastensis* (Shasta ground sloth), which has never before been analyzed using isotopic methods, and *Megalonyx jeffersonii* (Jefferson's ground sloth) (Table 4). I test two main hypotheses. First, I hypothesize that isotopic analysis of ground sloth dentin will yield primary carbon and oxygen signatures. Primary signatures will be recognizable as consistent, or anticipated, differences between ecologically distinct taxa. I anticipate that the data will produce variations in $\delta^{13}C$ and $\delta^{18}O$ values reflective of diet and surface water, respectively. This will result in meaningful paleoecological interpretations for these two species of ground sloths from the Late Pleistocene of western North America. Second, I hypothesize that $\delta^{13}C$ and $\delta^{18}O$ values in *N. shastensis* will be different than those in *M. jeffersonii*, reflecting differences in diet and habitat. On the basis of biogeography and temporal occurrence, McDonald and Morgan (2011) suggested that both *N. shastensis* and *M. jeffersonii* were browsers, but that *M. jeffersonii* browsed mostly in moist, riparian environments while *N. shastensis* browsed in arid and semi-arid environments. I use stable isotope analysis to test the McDonald-Morgan hypothesis. If this hypothesis is correct, $\delta^{13}C$ values in *N. shastensis* should be elevated compared to those in *M. jeffersonii*, when the two species co-occur, due to the consumption of more arid-adapted, C_4 vegetation by *N. shastensis*. The McDonald-Morgan hypothesis also predicts that *N. shastensis* will have consistently higher $\delta^{18}O$ values than *M. jeffersonii*, verifying that the former inhabited arid environments compared to the moist, riparian habitats utilized by *M. jeffersonii*.

Table 4. Ground sloths analyzed in this study. Specimens are from the University of California Museum of Paleontology (UCMP), Berkeley, CA and Nevada State Museum (NSM-LV), Las Vegas, NV. The locations of the fossil assemblages are shown in Figure 11.

Location/Taxon	Element	Collection	Specimen #	County	State	# samples
Potter Creek Cave						
Nothrotheriops shastensis	M3	UCMP	8141	Shasta	CA	9
Nothrotheriops shastensis	M3	UCMP	8715	Shasta	CA	5
Megalonyx jeffersonii	M3[1]	UCMP	8498	Shasta	CA	1
Samwel Cave						
Nothrotheriops shastensis	M3	UCMP	9664	Shasta	CA	4
Nothrotheriops shastensis	M3	UCMP	9663	Shasta	CA	2
Megalonyx jeffersonii	M2	UCMP	9668	Shasta	CA	2
Megalonyx jeffersonii	M3	UCMP	9666	Shasta	CA	1
Hawver Cave						
Nothrotheriops shastensis[2]	M3	UCMP	21473	El Dorado	CA	1
Tule Springs						
Nothrotheriops shastensis	M3	UCMP	64232	Clark	NV	1
Devil Peak Cave						
Nothrotheriops shastensis	M3	NSM-LV	200728	Clark	NV	14

[1]Tag was unspecific, although size and morphology indicate m3.
[2]*Nothrotheriops shastensis* from Hawver Cave was reported as a new subspecies, *Nothrotherium shastense hawveri* (Stock 1918). Communication with Greg McDonald (November, 2011) indicates his disagreement with this subspecies designation.

Commonly, megafaunal assemblages contain only one species of ground sloth. This lack of diversity is typically attributed to the occupation by ground sloths of fairly specialized niches (McDonald, 1996; McDonald and Morgan, 2011). Where possible, I chose fossil assemblages in which different species co-occur; *N. shastensis* and *M. jeffersonii* were found together in four of the five fossil assemblages chosen for this study (Figure 11). Unfortunately, however, in two of these cases (Hawver Cave and Tule Springs) *M. jeffersonii* teeth could not be analyzed. In Hawver Cave, no *M. jeffersonii* teeth were preserved, only bone, and at Tule Springs, one *M. jeffersonii* caniniform tooth was preserved, but I deemed it untrustworthy due to human restorative actions. In these situations, even though *M. jeffersonii* was present in the

assemblage it was not included in the analyses. A third species of ground sloth, *Paramylodon harlani*, was present in western North America during the Late Pleistocene, and it overlaps with the other two species at several localities in California, including Hawver Cave. However, at Hawver Cave *P. harlani* is represented by only one tooth (figured in Stock, 1918), and this specimen is too scientifically important to destructively sample.

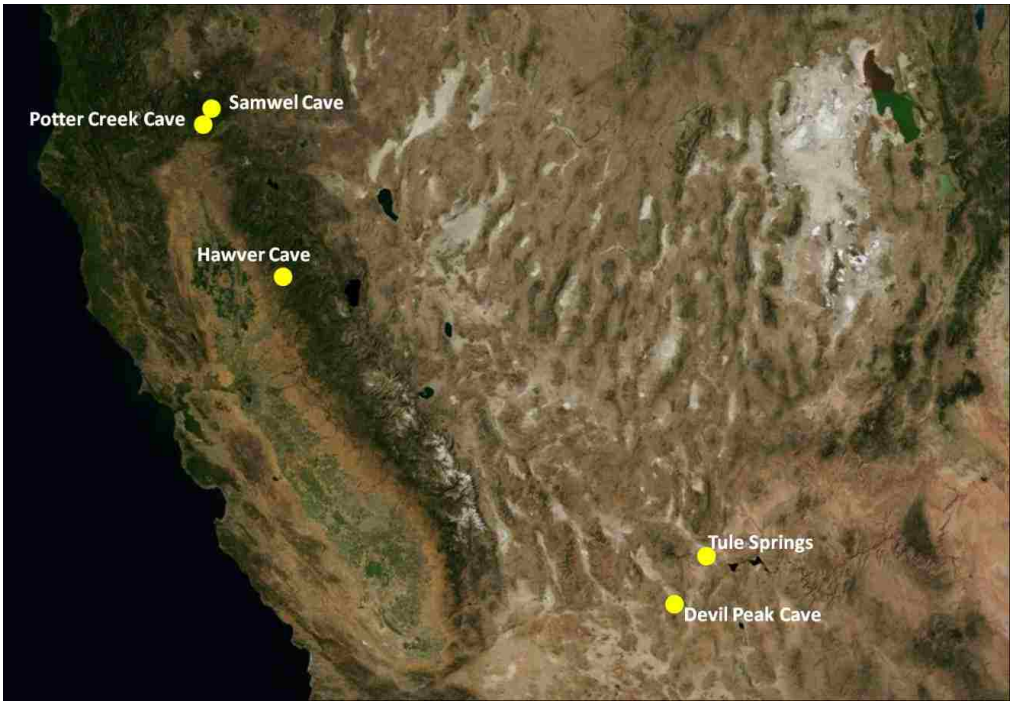


Figure 11. Locality map of assemblages in this study containing ground sloths. California localities include Potter Creek Cave, Samwel Cave, and Hawver Cave. Nevada localities include Tule Springs and Devil Peak Cave.

McDonald (1996, 2003, and 2005) and McDonald *et al*. (2012) hypothesized that the little biogeographic overlap of ground sloths and the absence of *P. harlani* within many megafaunal assemblages from the interior of the western United States was due to its preferred habitat. Based on geographic occurrence, he determined that *P. harlani* inhabited very different ecosystems than the other two species (*Megalonyx jeffersonii* and *Nothrotheriops shastensis*)

found in western North America. He suggested that *P. harlani* was a coastal dwelling species that preferred grazing in chaparral environments. Other interpretations suggest that *P. harlani* was a mixed feeder, based on morphology (Naples, 1989) and isotopic analysis (Ruez, 2005). In this study, I am unable to contribute new insights on the preferred habitat and diet of this species.

Figure 12 shows the ages of the five fossil assemblages. Direct radiocarbon dates on sloth elements do not exist; the dates apply to the fossil assemblages in which sloths were present at least some of the time recorded.

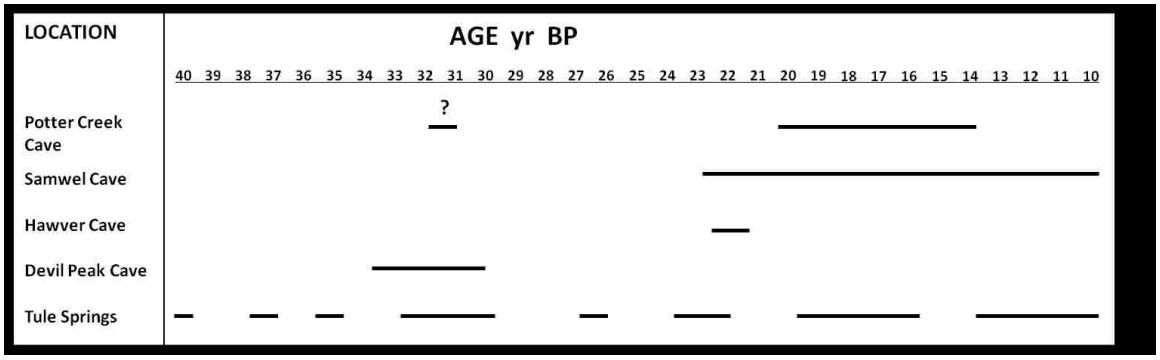


Figure 12. Radiocarbon dates for the assemblages containing ground sloths. Dates are for Potter Creek Cave (Feranec *et al*., 2007; Feranec, 2009), Samwel Cave (Feranec *et al*., 2007; Feranec, 2009; Blois *et al*., 2010), Hawver Cave (this study), Devil Peak Cave (Gromny, 2003), and Tule Springs (Haynes, 1967; Quade, 1986; Springer *et al*., 2010). The oldest date for Potter Creek Cave (~31.5 Ka) was considered by Blois *et al*. (2010) to be an unreliable outlier and is not considered in this study.

Methods

X-ray Diffraction

XRD is a non-destructive technique that analyzes inorganic samples for mineralogic and crystallographic information (Reiche *et al*., 2002). X-rays are transmitted through a crystalline material and the diffraction pattern scattered by the crystals is measured; each crystal results in a unique pattern with a measurable crystalline index which can determine the crystal structure

and composition of a material. I employed XRD to evaluate crystalline changes or exogenous mineral incorporation into the tooth hydroxylapatite.

A subset of the northern California Late Pleistocene ground sloth teeth are the focus of XRD analysis because of their association with wet caves and the concern for enhanced diagenesis. For comparison, I analyzed a sample of modern dentin, as well as fossil enamel from *Euceratherium collinum* from the same localities as the ground sloth dentin. In total, five dentin and enamel samples were analyzed. Ground sloth orthodentin includes Potter Creek Cave specimen PC-8498 (*Megalonyx jeffersoni*) and Hawver Cave specimen HC-21473 (*Nothrotheriops shastesis*). Enamel was analyzed from Potter Creek Cave specimen PC-8730 and Hawver Cave specimen HC-114876, both of which belong to the species *Euceratherium collinum*. One sample of modern dentin (A-1) was analyzed as a reference for unaltered dentin; this sample came from a nine-banded armadillo, *Dasypus novemcinctus* (Table 5). Armadillo teeth are comprised of orthodentin (Kalthoff, 2011), and so are comparable to the dentin samples from the ground sloths.

Approximately 0.8-1 mg of finely powdered dentin or enamel was analyzed from each specimen. To concentrate the small sample size, powders were inserted into a 500 nm deep slit in an aluminum sample plate. Diffraction patterns were measured on a PANalytical X'Pert Pro diffraction spectrometer with a copper X-ray tube, in the XRD/XRF lab at University of Nevada Las Vegas. Samples were scanned with Cu Kα-radiation between the angles of 5^{O} to 65^{O} 2θ with a step size of 0.008 2θ and 51 s per step. The acceleration voltage was 40 kV and 20 mA.

Scanning Electron Microscopy

The five samples analyzed using XRD (A-1, HC-21473, HC-114876, PC-8498, and PC-8730) were also analyzed using SEM. In addition, three samples of ground sloth dentin were analyzed which were not subjected to any chemical treatment. These included two samples of dentin from *Nothrotheriops shastensis* (SC-9663 and TS-64232) and one sample of dentin from *Megalonyx jeffersonii* (SC-9668) (Table 5).

Samples were analyzed in the Electron Microanalysis & Imaging Laboratory (EMiL) at the University of Nevada Las Vegas. Powdered dentin and enamel samples were carbon coated and analyzed using a JEOL JSM-5610 scanning electron microscope (SEM) equipped with a backscattered electron detector and Oxford ISIS electron dispersive spectrometer (EDS). One sample was also analyzed on the JEOL field-emmission SEM, model JSM-6700F. SEM was used to observe grain structure and integrity, and to detect chemical spectra. The latter is a semi-quantitative method to quantify chemical concentrations in a sample using spot or spectrum analysis.

Stable Isotope Analysis

Sampling and analytical methods are described in Chapter 1, including a chemical treatment protocol to remove diagenetic carbonate (following Koch *et al*., 1997). My research strategy was to serially sample teeth of *N. shastensis* and *M. jeffersonii* to gain a chronological series of isotopic data that can be used to differentiate between diet preference, water usage, seasonality, and ecological interactions. Due to the frailty of the dentin, only four of the ten ground sloth teeth in this study could be serially sampled (all of which are *N. shastensis*). The other six teeth were sampled at just one or two locations on the tooth.

It is important to discuss taxonomic sample size (*n*) for this project. Studies have been conducted to determine the optimal number of samples of species from a single deposit, to obtain statistically meaningful, reproducible results. Different authors have reached different conclusions, with sample size varying between taxa. For example, Clementz and Koch (2001) determined *n* = 5 for *Bison*, while Coltrain *et al*. (2004) determined *n* = 9 for *Equus*. These studies involved either modern taxa or fossil assemblages in which many individual animals were available, such as the fossiliferous deposits of Rancho La Brea. In this study, there simply were not enough specimens available to sample a large population of individuals at each locality, and some teeth available are too scientifically important to permit destructive sampling. Because of this, my sample sizes are very small: *N. shastensis n* = 2 for Potter Creek Cave and Samwel Cave, and *n* = 1 for Hawver Cave, Tule Springs, and Devil Peak Cave; *M. jeffersonii n* = 1 for Potter Creek Cave, and *n* = 2 for Samwel Cave. It is worth noting that when *n* = 2, the data group very closely, thereby lending some confidence to the data. In this field of research, where an abundance of specimens is not available, it is better to have one confident data point (or dataset) then none at all, "confident"meaning that the analysis produced irrefutably viable data.

Many isotope paleoecology studies perform statistical tests on data when they are analyzing $\delta^{13}C$ and $\delta^{18}O$ data from a population of individuals from a single assemblage (Coltrain *et al*., 2004; Kohn *et al*., 2005; Vetter, 2007; Feranec *et al*., 2009; Feranec *et al*., 2010a; Forbes *et al*., 2010; Nunez *et al*., 2010; Maung-Thein *et al*., 2011). In those studies, numerous individuals of each species were sampled ($n \leq 21$). The bulk values were then used to perform various statistical tests to compare significant differences in $\delta^{13}C$ and $\delta^{18}O$ values between taxa. The important difference between these prior studies and this study is that the prior studies analyzed many different individuals from just one assemblage, while in this study I analyze one or two individuals from many different assemblages. Therefore, the statistical tests done in

prior studies to test the significance of differences between taxa are not applicable to the data in this study; however, Chapter 5 combines data in this study to data from prior studies, creating a larger dataset and allowing for statistical functions to be incorporated. In light of this, the statistical functions that I have calculated for Chapters 3 and 4 include averaged values of a species and region (calculated from serial data), and covariance and Pearson product moment correlation coefficient (*r*), to measure the association of $\delta^{13}C$ and $\delta^{18}O$ from serial data. Covariation is a measure of how two series of bivariate data vary together, positive covariance of $\delta^{13}C$ and $\delta^{18}O$ identifies that the series varies together and negative covariance means that they vary inversely, where the higher the value the stronger the relationship. The correlation coefficient (*r*) measures the strength of the linear relationship between $\delta^{13}C$ and $\delta^{18}O$ in a sample, where 1 is a perfect positive correlation, -1 is a perfect negative correlation, and 0 is no correlation between the series.

Samples were processed and analyzed in the Las Vegas Isotope Science (LVIS) lab at the University of Nevada, Las Vegas; data reflect a precision of ± 0.2‰ for $\delta^{13}C$ and ± 0.15‰ for $\delta^{18}O$. As mentioned above, analyzing the dentin samples resulted in excess water production, as a result of dentin having a higher component of intercrystalline water content (10%) compared to enamel (1%) (Hillson, 2005). To counteract this problem, smaller sample sizes were used (~0.6-0.8 mg), in order to reduce water production yet produce a high enough amount of CO_2 gas for analysis.

Results

X-Ray Diffraction

X-ray diffractions patterns are shown in Figures 13 and 14. Primary apatite peaks show reflections at 26^{O}, 32^{O}, 40^{O}, and 51.5^{O} 2θ. As anticipated, the modern dentin formed a hydroxylapatite diffraction pattern (Andreev, 1994), with a single broad peak at 32^{O} 2θ (Figure 13a). The Late Pleistocene dentin and enamel diffractions show a separation of this main peak (Figure 13b-e). Peak sharpening occurs with increased crystalllinity (Kohn and Cerling, 2002; Tütken *et al*., 2008; Metcalfe *et al*., 2009). Counts and peak intensities are relatively low due to small sample size. The prominent peaks at 38.5^{O} and 44.5^{O} 2θ are indicative of aluminum, these appear because of the aluminum sample plate that was used.

Hydroxylapatite was definitively identified. Flouroapatite was also identified, because these two minerals have nearly identical diffraction patterns with peak overlap, especially at lower angles. The fossil dentin also registered carbonate hydroxylapatite peaks at 31^{O} 2θ, as an inconspicuous shoulder from the main apatite peak (Figure 13). No other minerals were identified. A magnified view of the main hydroxylapatite diffraction peaks better illustrates the degree of recrystallization, where separated peaks are labeled with indices (Figure 14).

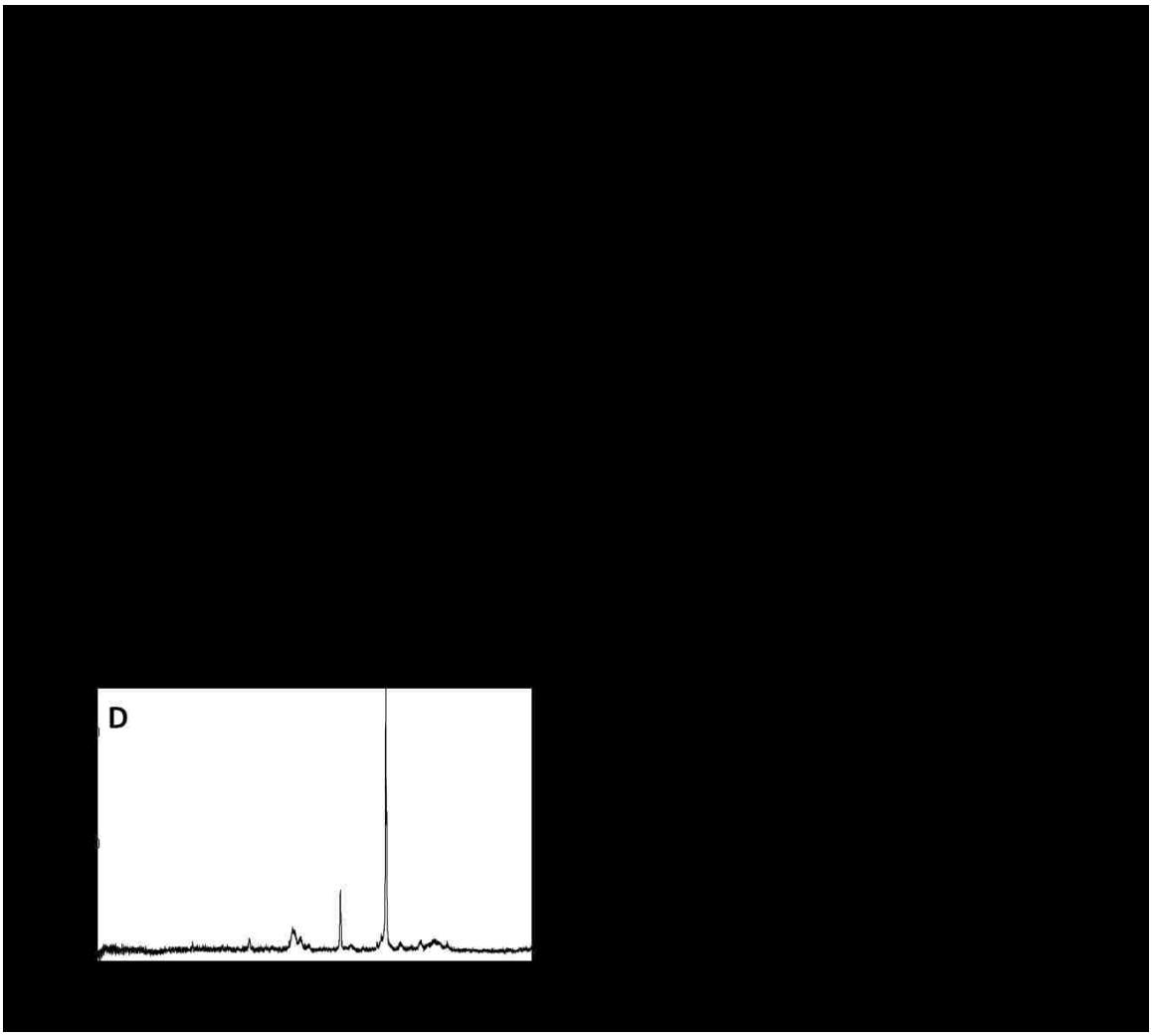


Figure13. Raw XRD patterns of dentin and enamel: (A) modern armadillo dentin, specimen A-1, (B) Late Pleistocene ground sloth dentin from *Nothrotheriops shastensis* (HC-21473) and (D) *Megalonyx jeffersonii* (PC-8498), and Late Pleistocene enamel samples from *Euceratherium collinum* specimens HC-114876 (C) and PC-8730 (E). Primary apatite peaks are apparent at 26^{O}, 32^{O}, 40^{O}, and 51^{O} 2θ. The prominent peaks at 38.5^{O} and 44.5^{O} 2θ are aluminum, and were detected from the aluminum sample plate that was used.

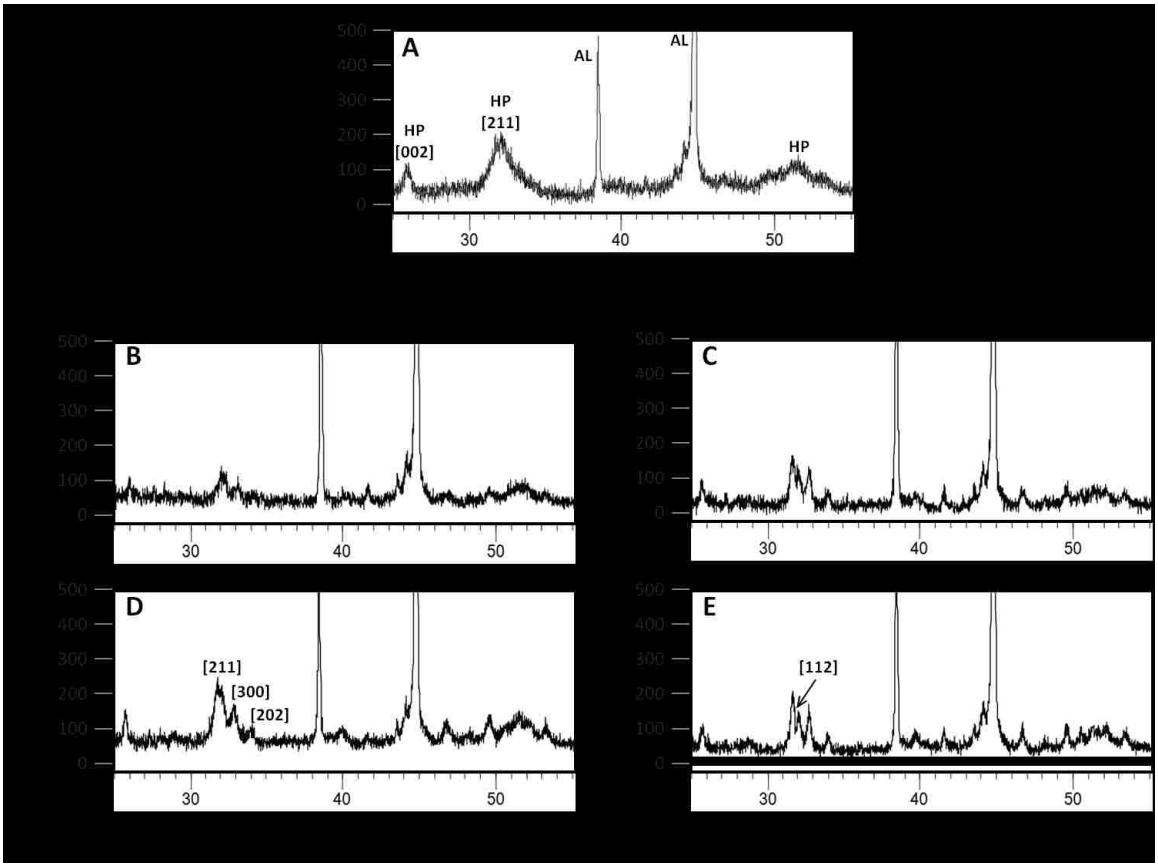


Figure 14. Magnified view of Figure 13 between the angles of 25^{O} to 55^{O} 2θ. Peaks are of modern armadillo dentin (A), and Late Pleistocene ground sloth dentin (B and D) and enamel (C and E). Hydroxylapatite (HP) and aluminum (AL) mineral peaks are identified (A), Late Pleistocene dentin and enamel exhibits a separation of the main peak [211], with indices labeled (D and E).

Scanning Electron Microscopy

All SEM images, chemical spectra, and elemental weight % compositions can be found in Appendix 1. SEM spot and spectrum analysis reveals that elemental compositions of teeth are quite similar, and all elements identified are natural consitutents of hydroxylapatite, either as major or trace amounts. Elements identified with higher weight %'s include oxygen, carbon, calcium, and phosphorus, while elements with trace amounts include sodium, magnesium, aluminum, and silicon (Table 5).

Table 5. Specimens analyzed using XRD and SEM. Elements are listed which were identified in the chemical spectrum. For age, M=modern and LP=Late Pleistocene. For treated/untreated, N=no and Y=yes, referring to whether the sample was chemically treated to remove organic and diagenetic carbonate prior to isotopic analysis.

Sample	Material	Age	Species	Method	Treated/ Untreated	Chemical spectra
A-1	Dentin	M	*D. novemcinctus*	XRD/SEM/ FE-SEM	N	O, C, Ca, P, Na
HC-21473	Dentin	LP	*N. shastensis*	XRD/SEM	Y	O, C, Ca, P
HC-114876	Enamel	LP	*E. collinum*	XRD/SEM	Y	O, C, Ca, P, Na, Mg, Al
PC-8498	Dentin	LP	*M. jeffersonii*	XRD/SEM	Y	O, C, Ca, P, Na
PC-8730	Enamel	LP	*E. collinum*	XRD/SEM	Y	O, C, Ca, P, Na, Al, Si
SC-9668	Dentin	LP	*M.jeffersonii*	SEM	N	O, C, Ca, P, Na, Al, Si
SC-9663	Dentin	LP	*N.shastensis*	SEM	N	O, C, Ca, P, Na
TS-64232	Dentin	LP	*N. shastensis*	SEM	N	O, C, Ca, P, Na

Figure 15 shows a graphical representation of the elements identified by SEM EDS plotted against their corresponding weight %. No clear difference exists between the varying weight %'s in fossil dentin and enamel (n = 14) (see Appendix 1). To unobscure the data, I averaged the Late Pleistocene dentin and enamel samples weight %'s for each element, with high and low values indicated (Figure 15). Averaged fossil dentin and enamel percentages show a depletion in O and Na, compared to modern dentin. While averaged fossil dentin and enamel is enriched in C, Ca, and P, compared to modern dentin. Averaged fossil dentin and enamel samples are very similar to modern human dentin Ca and P weight %'s. SEM EDS did not identify Mg, Al, or Si in the modern armadillo dentin, but these elements were identified in three of the eight fossil samples, two of which are enamel (Table 5 and Figure 15).

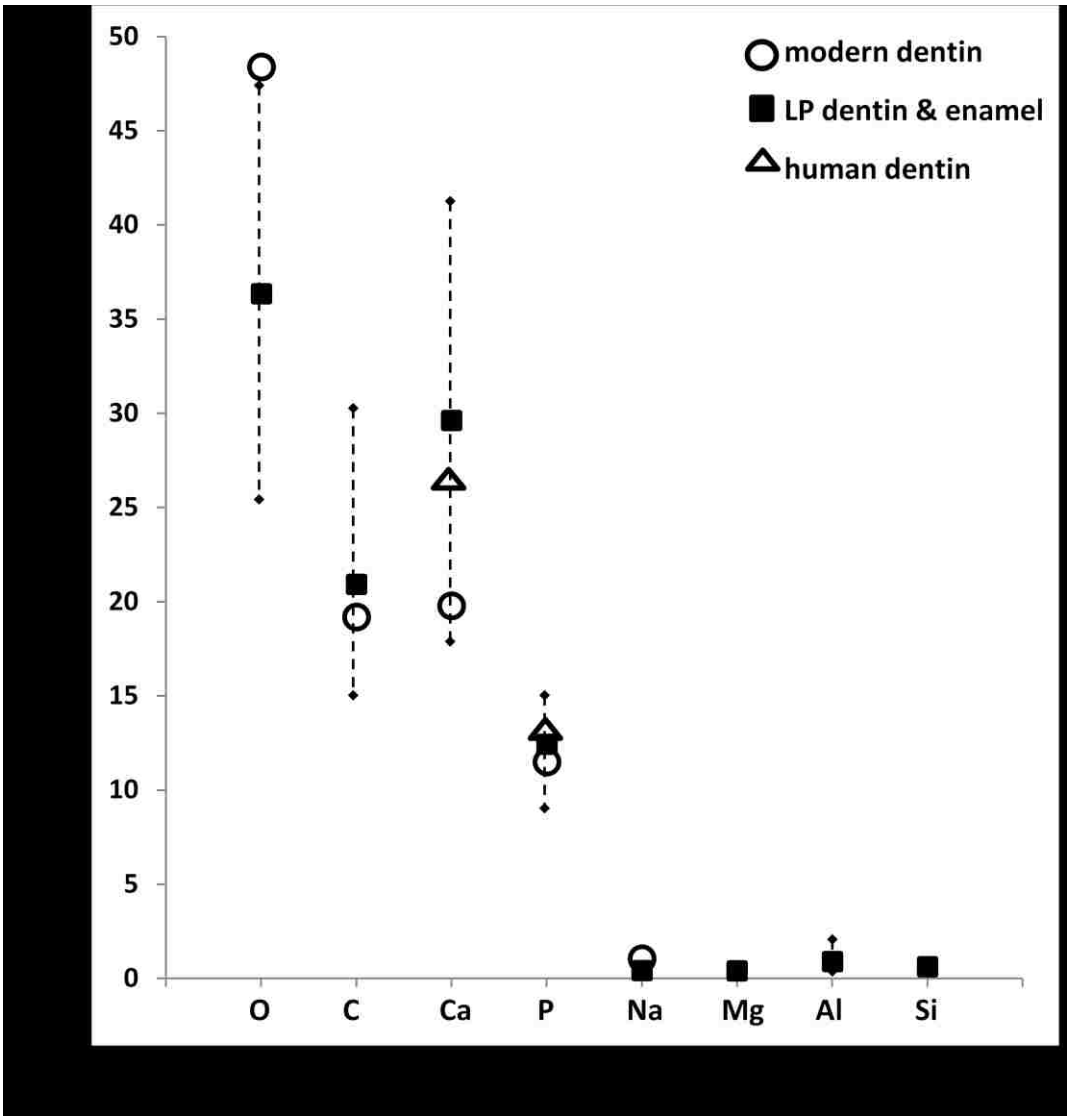


Figure 15. Dentin and enamel elemental composition and weight %. Elements were identified by SEM EDS chemical spectrum. Solid squares indicate average values for all Late Pleistocene (LP) dentin and enamel samples analyzed (*n* = 14, see Appendix 1), dashed lines indicate high and low values. Open circles represent data from modern armadillo dentin. Open triangles represent standard Ca and P weight %'s for human dentin (Driessens and Verbeeck, 1990).

SEM images show magnification between 75-3000X of modern dentin (Figure 16), Late Pleistocene dentin (Figure 17) and Late Pleistocene enamel (Figure 18). Because samples were powdered, tooth structures, such as dentin tubules, are visible when grains were positioned at

certain angles. Tubule aperatures measured up to 1 micron in modern dentin, and up to 4 microns in fossil dentin (Figures 16 and 17), similar to that found by Kalthoff (2011) for modern sloths. Comparison of the surfaces of modern dentin, fossil dentin, and fossil enamel reveals that modern dentin and fossil dentin grains are similar in appearance, indicating that fossil dentin is outwardly well-preserved (Figures 16 and 17). By contrast, fossil enamel shows major recrystallization of surfaces (Figure 18a and c). Finer structural features of dentin tubules and enamel rods are not visible in the 3000X magnification SEM images here, and are only visible using an order higher of magnification (Vaseenon, 2011).

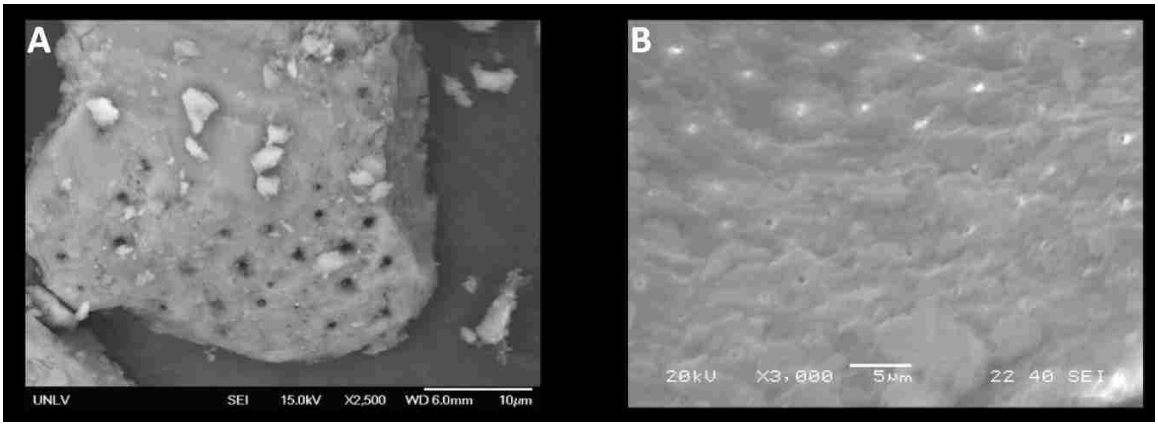


Figure 16. SEM images of modern dentin. Both are of specimen A-1, modern armadillo dentin (*Dasypus novemcinctus*) on a FE-SEM (A) and SEM (B). Tubule structures are apparent as black spots; illuminated spots are tubule aperatures that appear to be "glowing" because of a concentration of electrons where carbon coating did not reach.

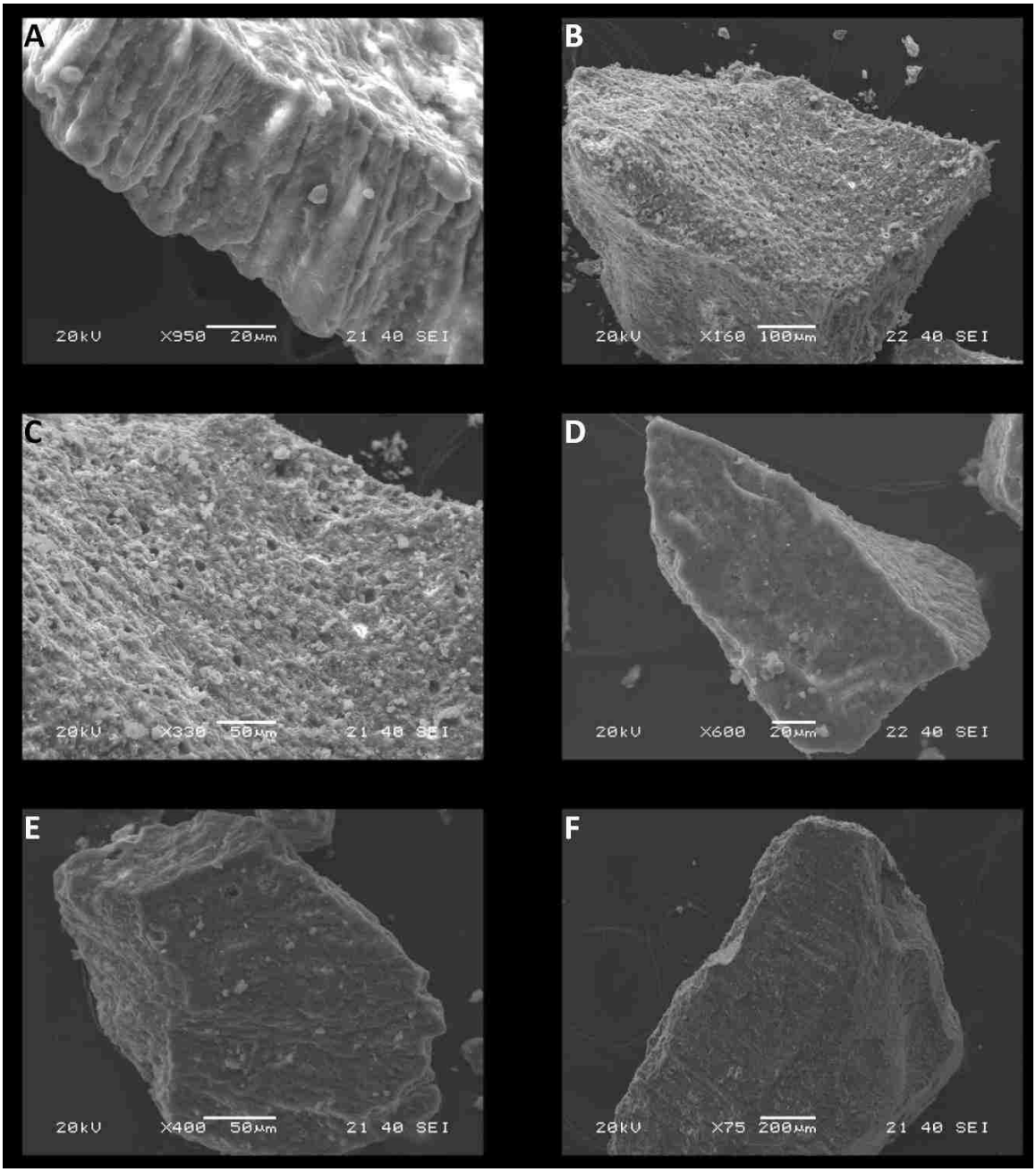


Figure 17. SEM images of fossil dentin. Dentin is from Late Pleistocene ground sloths. Treated dentin includes *Nothrotheriops shastensis* (HC-21473) (A) and *Megalonyx jeffersonii* (PC-8498) (B and C). Untreated dentin includes *Megalonyx jeffersonii* (PC-9668) (D) and *Nothrotheriops shastensis* (SC-9663 and TS-64232, E and F, respectively). Dentin tubules are also present and appear as black spots (see C).

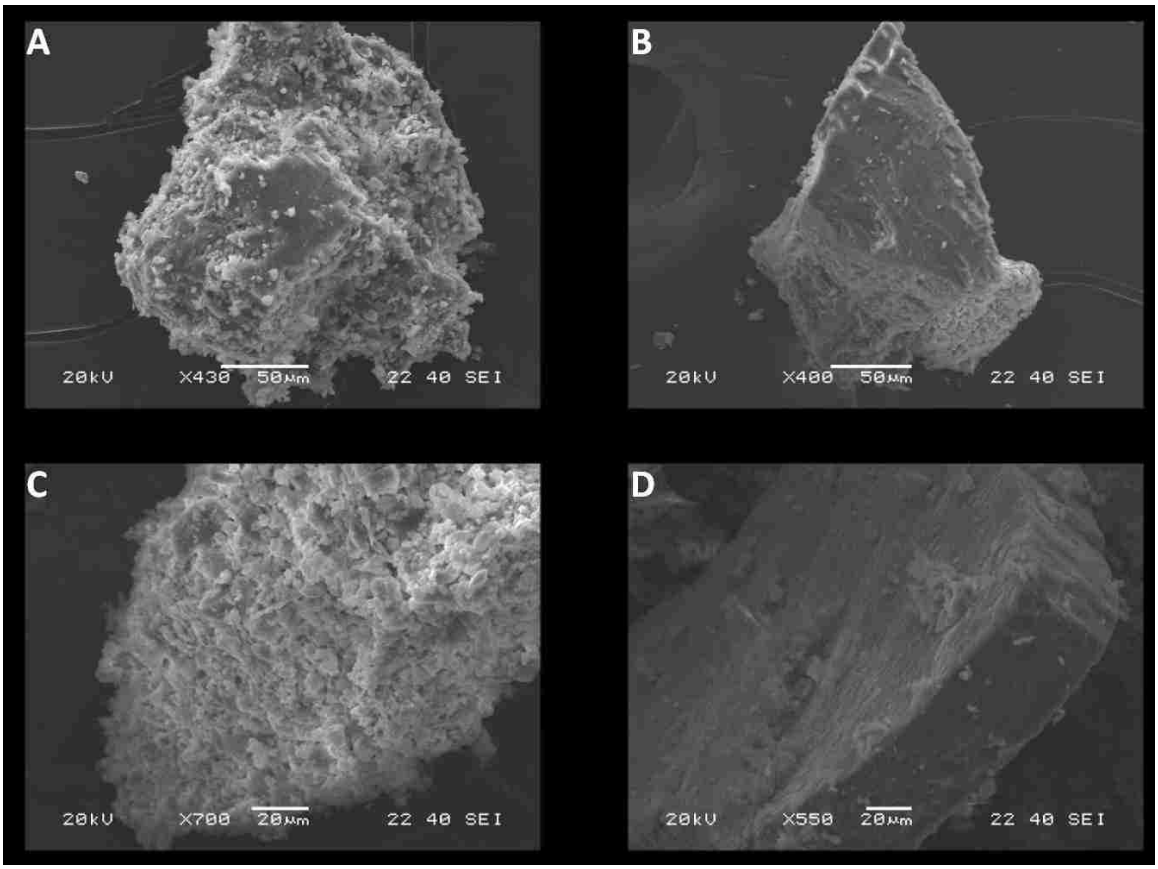


Figure 18. SEM images of fossil enamel. Late Pleistocene enamel is from *Euceratherium collinum*. Samples are from Hawver Cave (HC-114876) (A and B) and Potter Creek Cave (PC-8730) (C and D). Enamel grains appear to have undergone extensive recrystallization on surfaces.

Stable Isotope Averaged Serial Values

Isotopic results for ground sloth specimens analyzed in this study are listed in Appendix 2. Table 6 lists averaged carbon and oxygen stable isotope values for *N. shastensis* and *M. jeffersonii* by region, calculated from averaged serial values of all teeth for each species. These data are graphed in Figure 19. The averaged isotope data show a grouping of *N. shastensis* from northern California (Potter Creek Cave, Samwel Cave, and Hawver Cave) compared to those from southern Nevada (Tule Springs and Devil Peak). The specimens of *N. shastensis* from

southern Nevada have higher $\delta^{13}C$ values (-4.4‰) compared to the specimens from northern California (-9.0‰). The averaged $\delta^{18}O$ value of all specimens of *N. shastensis* from southern Nevada (-6.5‰) are depleted in comparison to the averaged $\delta^{18}O$ value of all *N. shastensis* from northern California (-4.8‰).

M. jeffersonii data, only from northern California, do not show an obvious grouping. The three specimens of *M. jeffersonii* from northern California have an averaged $\delta^{13}C$ value of -7.9‰ (Table 6). The specimens of *M. jeffersonii* from northern California yield an average $\delta^{18}O$ value (-6.5‰) that is the same as the average value for *N. shastensis* from southern Nevada.

Table 6. Averaged $\delta^{13}C$ and $\delta^{18}O$ values of ground sloths, by region. Averaged values for northern California specimens include *Nothrotheriops shastensis* from Potter Creek Cave, Samwel Cave, and Hawver Cave, and *Megalonyx jeffersonii* from Potter Creek Cave and Samwel Cave. Averaged values for southern Nevada specimens include *Nothrotheriops shastensis* from Tule Springs and Devil Peak Cave.

Taxon	$\delta^{13}C_{V\text{-}PDB}$ (‰)	$\delta^{18}O_{V\text{-}PDB}$ (‰)
Nothrotheriops shastensis: Northern California specimens	-9.0	-4.8
Megalonyx jeffersonii: Northern California specimens	-7.9	-6.5
Nothrotheriops shastensis: Southern Nevada specimens	-4.4	-6.5
Nothrotheriops shastensis: Combined CA and NV specimens	-7.7	-5.2

Averaged $\delta^{13}C$ and $\delta^{18}O$ values plotted together exhibit variation between locations (Figure 19). Values for the averaged serial data, by individual, are listed in Table 7. Individuals of *N. shastensis* have a wide range of averaged $\delta^{13}C$ values, ranging from -11.4‰ to -4.1‰, with the most negative value at Hawver Cave. *N. shastensis* from Potter Creek Cave and Samwel Cave yielded very similar $\delta^{13}C$ values, ranging between -8.9 to -8.0‰. *N. shastensis* from Tule

Springs and Devil Peak Cave have the least negative $\delta^{13}C$ values of all the ground sloths analyzed (-4.7‰ and -4.1‰, respectively). Averaged $\delta^{13}C$ values for individuals of *M. jeffersonii* range from -10.6‰ to -6.3‰; the specimen from Potter Creek Cave is more negative (-10.6‰) than the specimens of *M. jeffersonii* from Samwel Cave (-6.8 and -6.3‰). In the two cases where the two species co-occur, Potter Creek Cave and Samwel Cave, averaged $\delta^{13}C$ values do not overlap. At Potter Creek Cave *M. jeffersonii* is more negative (-10.6‰) than *N. shastensis* (-8.6‰ and -8.4‰), while at Samwel Cave *M. jeffersonii* is more positive (-6.8‰ and -6.3‰) than *N. shastensis* (-8.9‰ and -8.0‰) (Table 7 and Figure 19).

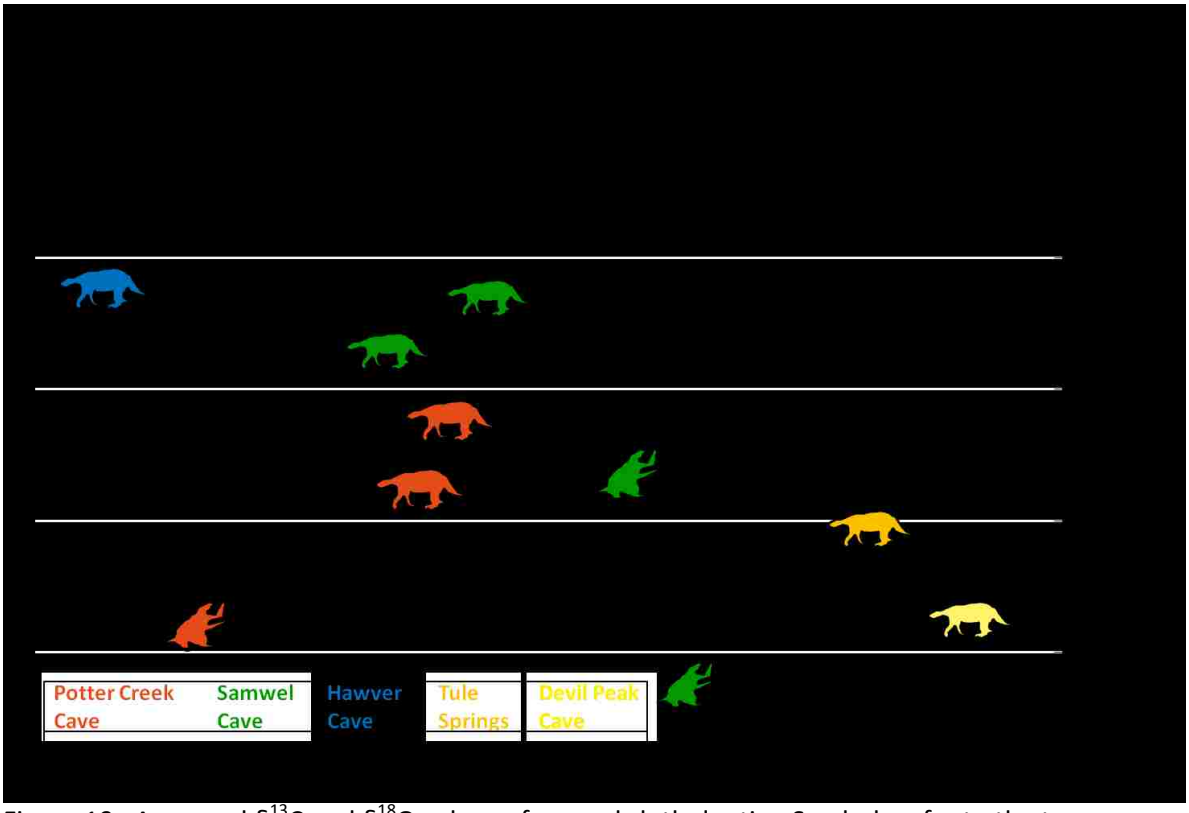


Figure 19. Averaged $\delta^{13}C$ and $\delta^{18}O$ values of ground sloth dentin. Symbols refer to the two species of ground sloths analyzed, *Nothrotheriops shastensis* and *Megalonyx jeffersonii*. Colors refer to locations: red represents Potter Creek Cave, CA; green represents Samwel Cave, CA; blue represents Hawver Cave, CA; orange represents Tule Springs, NV; yellow represents Devil Peak Cave, NV.

Averaged $\delta^{18}O$ values for individuals of *N. shastensis* reveal a gradual increase in values from southern Nevada to northern California (Figure 19). The specimen from Devil Peak Cave has the most negative $\delta^{18}O$ value (-6.9‰), while the specimen from Hawver Cave has the most positive $\delta^{18}O$ value (-4.2‰). Averaged $\delta^{18}O$ values for individuals of *M. jeffersonii* range from -7.3 to -5.6‰, with -7.3‰ being the most negative of all ground sloth $\delta^{18}O$ values in this study. For the two localities where the two species co-occur, *M. jeffersonii* is consistently more negative than *N. shastensis*. At Potter Creek Cave *M. jeffersonii* displays a low $\delta^{18}O$ value (-6.8‰) compared to *N. shastensis* (-5.7 and -5.2‰), and at Samwel Cave *M. jeffersonii* also has lower $\delta^{18}O$ values (-7.3 and -5.6‰) than *N. shastensis* (-4.7 and -4.3‰) (Figure 19 and Table 7).

Table 7. Averaged $\delta^{13}C$ and $\delta^{18}O$ values of all ground sloths. Ground sloths are listed by location: northern California assemblages (Potter Creek Cave, Samwel Cave, and Hawver Cave) and southern Nevada (Devil Peak Cave and Tule Springs).

Location	Taxon	$\delta^{13}C_{V\text{-}PDB}$ (‰)	$\delta^{18}O_{V\text{-}PDB}$ (‰)
Potter Creek Cave	*Nothrotheriops shastensis*	-8.6	-5.7
	Nothrotheriops shastensis	-8.4	-5.2
	Megalonyx jeffersonii	-10.6	-6.8
Samwel Cave	*Nothrotheriops shastensis*	-8.9	-4.7
	Nothrotheriops shastensis	-8.0	-4.3
	Megalonyx jeffersonii	-6.3	-7.3
	Megalonyx jeffersonii	-6.8	-5.6
Hawver Cave	*Nothrotheriops shastensis*	-11.4	-4.2
Devil Peak Cave	*Nothrotheriops shastensis*	-4.1	-6.9
Tule Springs	*Nothrotheriops shastensis*	-4.7	-6.1

Stable Isotope Serial Values for *Nothrotheriops*

Ground sloth teeth that yielded four or more samples are discussed in this section; this is the smallest number of samples I considered necessary to represent a meaningful trend in the data. Four of the ten ground sloth teeth met this criterion, all of which are *N. shastensis*; two teeth are from Potter Creek Cave, one tooth is from Samwel Cave, and one tooth is from Devil Peak Cave (Figure 20). These data are graphed in Figure 21. Specimens of *M. jeffersonii* were not able to be serial sampled due to the fragility of the dentin. Because teeth were sampled from the occlusal surface (oldest part of the ever-growing tooth) toward the root (newest part of the ever-growing tooth), incrementally, the earliest record of the sloth's life is plotted on the left, with progressively older years toward the right (Figure 21). Serial samples were often difficult to obtain, due to the fragile nature of the surface of the outer layer of orthodentin. Numerous micro-fractures exist on the teeth, which resulted in chipping of the dentin during sampling. Because of this, the integrity of the dentin dictated where samples could be taken, sometimes resulting in a somewhat erratic pattern of sampling. Sampling increments ranged from 1-10 mm, but averaged about 4 mm (Figure 21). Tooth DP-200728, from Devil Peak Cave, yielded the highest number of serial samples, with thirteen viable values; fourteen samples were taken, but the last one resulted in a questionable value due to low CO_2 gas volume, which was probably a result of small sample size. For this reason, this value has been rejected (Figure 21d).

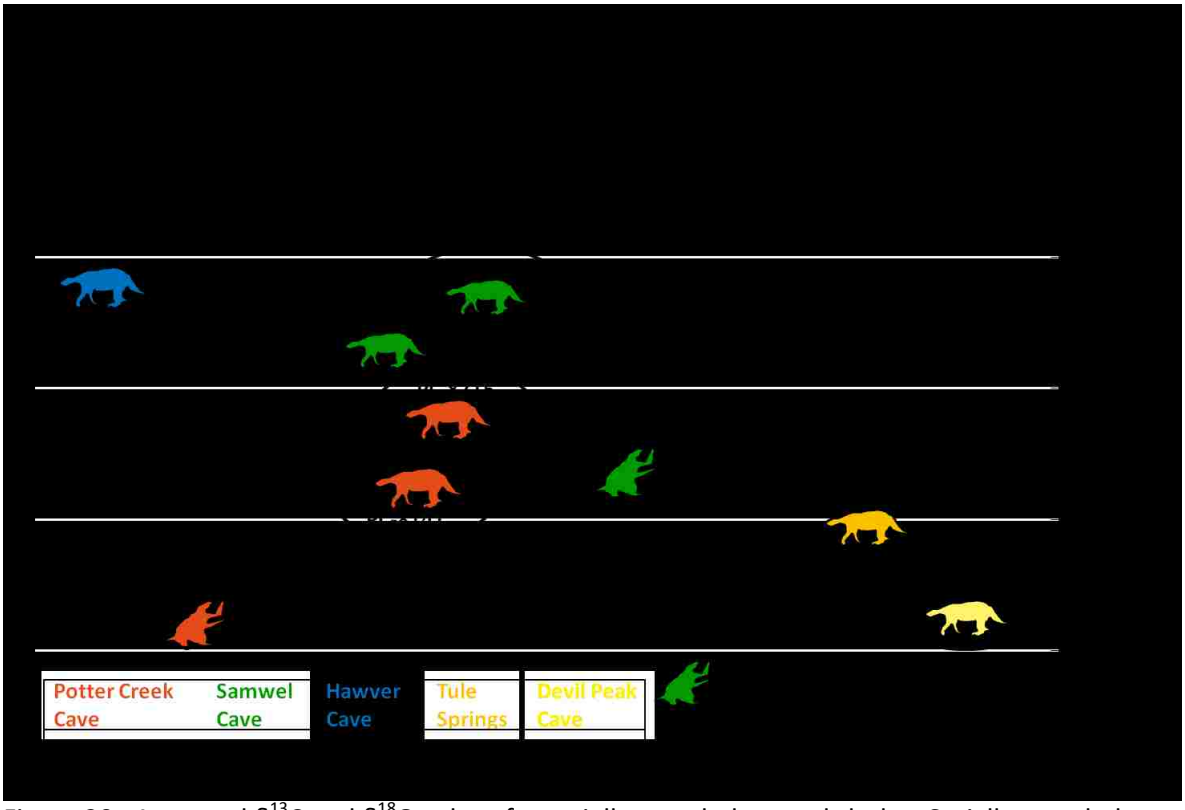


Figure 20. Averaged $\delta^{13}C$ and $\delta^{18}O$ values for serially sampled ground sloths. Serially sampled specimens are circled with specimen numbers indicated.

As hypothesized, serial data show fluctuations in $\delta^{13}C$ and $\delta^{18}O$ through life (Figure 21a-d). The $\delta^{13}C$ values in the three northern California *N. shastensis* teeth exhibit an unanticipated trend, with low values in the earlier years and higher values in the later years. This $\delta^{13}C$ increase is fairly steady and continuous, ranging from about 1‰ in the Samwel Cave tooth SC-9664 and Potter Creek Cave tooth PC-8715, to 2.7‰ in Potter Creek Cave specimen PC-8141. In the Devil Peak Cave tooth, DP-200728, $\delta^{13}C$ values are much more erratic, although they display an increase of 4.5‰ from the earliest to the latest record. The fluctuations in the serial data show that $\delta^{13}C$ values for the northern California *N. shastensis* (PC-8141, PC-8715, and SC-9664) fluctuate by 1-3‰ through life, while $\delta^{13}C$ values for the one southern Nevada specimen (DP-200728) fluctuate by up to 10‰ through life (Figure 21).

The $\delta^{18}O$ values show different patterns in different teeth (Figure 21a-d). In the Potter Creek Cave samples, $\delta^{18}O$ values for PC-8141 range from -6.1 to -5.4‰, while PC-8715 has a range that is more than twice as great, from -6.0 to -3.3‰. In the Samwel Cave tooth, SC-9664, $\delta^{18}O$ values covary with $\delta^{13}C$ values steadily increasing through the latest years of life, with $\delta^{18}O$ values ranging from -5.0 to -3.9‰. In the Devil Peak Cave tooth, DP-200728, $\delta^{18}O$ values range from -10.1 to -6.2‰; the $\delta^{18}O$ values closely co-vary with $\delta^{13}C$ values, with three exceptions (at 10, 19, and 23 mm). Serial data for *N. shastensis* from northern California (PC-8141, PC-8715, and SC-9664) have $\delta^{18}O$ records that fluctuate by 1-3‰, while the southern Nevada specimen (DP-200728) has $\delta^{18}O$ values that fluctuate by up to 4‰ through time (Figure 21).

Examining $\delta^{18}O$ and $\delta^{13}C$ trends together reveal that the two values covary differently between the ground sloth samples. In PC-8141, $\delta^{18}O$ and $\delta^{13}C$ covaries the weakest of all the *N. shastensis* serially sampled (0.07), with divergences at 2 mm and 32 mm; these have a weak, positive correlation (r = 0.38) (Figure 21a). Specimen PC-8715 shows that $\delta^{18}O$ and $\delta^{13}C$ values covary (-0.12), although $\delta^{18}O$ exhibits larger fluctuations than $\delta^{13}C$ and in the opposite direction, causing this specimen to have weak, negative correlation (r = -0.26) (Figure 21b). In sample SC-9664, $\delta^{18}O$ and $\delta^{13}C$ covary (0.20) throughout the record and have very strong, positive correlation (r = 0.99) (Figure 21c). In specimen DP-200728, $\delta^{18}O$ and $\delta^{13}C$ values exhibit the strongest covariance (1.50) of all the *N. shastensis* teeth that were serially sampled; throughout most of the tooth, with conspicuous divergences at three points, and has strong, positive correlation (r = 0.60) (Figure 21d).

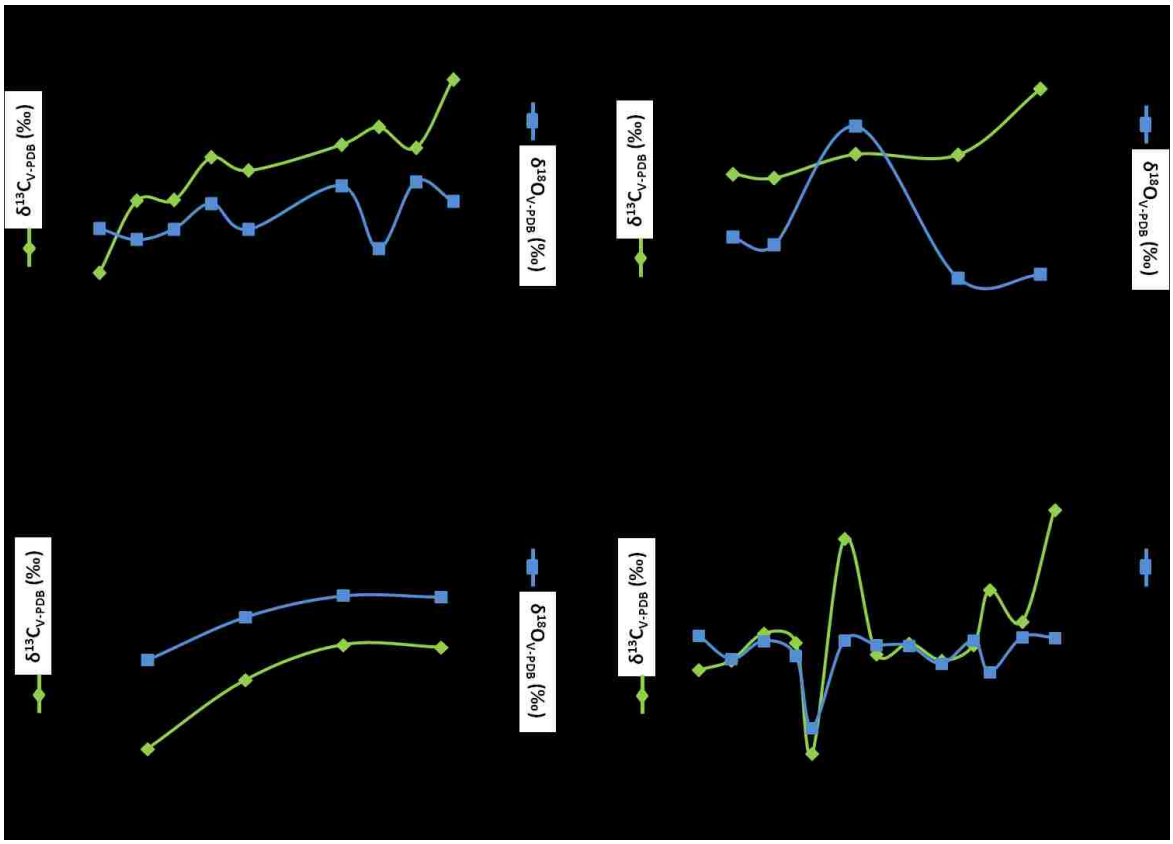


Figure 21. Serial $\delta^{13}C$ and $\delta^{18}O$ values of ground sloth dentin. Isotopic data is from *Nothrotheriops shastensis* from: (A) Potter Creek Cave, CA, specimen PC-8141, (B) Potter Creek Cave, CA, specimen PC-8715, (C) Samwel Cave, CA, specimen SC-9664, and (D) Devil Peak Cave, NV, specimen DP-200728. Sampling increments are listed in millimeters along the x-axis; samples are inconsistent due to micro-fracturing of the dentin. For example, Graph A shows a wide gap between 18 mm and 28 mm; this tooth had a large fracture preventing sampling near the break. Graph C has a short record with poor resolution due to extensive micro-fracturing along the sampling surface.

Discussion

XRD and SEM

If dentin from a fossil assemblage has been deemed unaltered, it stands to reason that the more resistant enamel from the same assemblage is also unaltered. Following this logic, if the ground sloth dentin fom Potter Creek Cave and Hawver Cave, which are contemporaneous

wet cave deposits, is found to be primary, then it, too, stands to reason that ground sloth teeth from drier, nearly contemporaneous settings, such as southern Nevada, are also unaltered.

Modern armadillo dentin was used as a baseline for pure, unaltered dentin. X-ray diffraction resulted in a broad reflection of the main apatite peak, due to small crystallite size, compared to fossil apatite, or because the crystal structure is intrinsically less well ordered. The Late Pleistocene ground sloth dentin from Potter Creek Cave and Hawver Cave was found to have undergone recrystallization, apparent by the separation of the main hydroxylapatite peak (Figure 22b and d), while enamel samples from the same sites were also found to be recrystallized, although to greater degree (Figure 22c and e) (Kohn and Cerling, 2002; Tütken *et al*., 2008; Metcalfe *et al*., 2009). Bioapatite crystallite size increases with fossilization, resulting in peak sharpening in XRD reflections (Tal *et al*., 1976; Hassan *et al*., 1977; Sillen and Sealy, 1995; Suvorova and Buffat, 2001; Reiche *et al*., 2002). Therefore, fossil dentin and enamel are more highly crystalline than modern dentin.

Biogenic apatite can recrystallize quite quickly and has been found to do so almost immediately post-mortem, resulting in increased crystallinity (Person *et al*., 1995). To exemplify the rate at which recrystallization can occur, experimental and chemical treatments (Tal *et al*., 1976; Sillen and Sealy, 1995), including those used to isolate the carbonate in the teeth, are capable of recrystallizing pristine hydroxylapatite in just days (Lee-Thorp and van der Merwe, 1991; Rountrey, 2009). It is difficult to identify the effects of chemical treatment on the crystallinity of hydroxylapatite; this creates an extra complication in determining the degree of crystallographic change caused by natural diagenesis compared to those caused by chemical treatment. In certain demonstrations, the severe recrystallization recorded from chemical treatment processes has been found to override the effects of natural diagenesis in Late

Pleistocene fossil apatite (Sillen and LeGeros, 1991; Sillen and Sealy, 1995; Koch *et al*., 1997). I attempted to address this issue by analyzing both chemically treated and untreated fossil dentin grains using SEM. The preservation of the dentin between treated and untreated samples is invariable, suggesting that chemical treatment had no enhanced effect on recrystallizing the dentin (Figures 16 and 17). I am unable to determine if the extensive recrystallization of apatite observed in enamel, as seen in SEM images, is natural or artificial (Figure 22 c and e). Whichever the case may be, recrystallization (i.e., increased crystallinity) is not an indication of carbonate isotopic alteration in hydroxylapatite (Lee-Thorp and Sponheimer, 2003). Therefore, the recrystallization of carbonate hydroxylapatite may not have any ill effect on the carbon and oxygen isotopic signatures in teeth, as endogenous carbonate ions are still present and unaltered; they are merely reorganized into different sites in the crystal lattice (Sponheimer and Lee-Thorp, 1999; Lee-Thorp and Sponheimer, 2003). It is essential, therefore, to determine the purity of the carbonate hydroxylapatite and nullify the potential of exogenous carbonate incorporation into fossil teeth, discussed below.

Late Pleistocene dentin and enamel XRD resulted in identical mineral identification as modern dentin, hydroxylapatite and flouroapatite. Fluorine can be found in the apatite lattice of carbonate hydroxylapatite with time (Weiner, 2010), and has been considered a diagenetic indicator (Koch *et al*., 1997). Flourine incorporation at higher weight percents (e.g., >1.5 %) indicates contamination of hydroxylapatite and recrystallization into a more stable form of apatite, fluoropapatite (Hassan *et al*., 1977; Sillen, 1989; Person *et al*., 1995; Koch *et al*., 1997; Kohn *et al*., 1999; Jacques *et al*., 2008; Kuczumow *et al*., 2010). XRD diffraction identified flouroapatite, although peaks could not be readily distinguished from hydroxylapatite, the difference in d-spacing is about 0.006, especially at lower angles. The primary indicator that the hydroxylapatite XRD pattern is real, and the flouropapatite pattern is not, is that SEM EDS

chemical analysis did not identify the presence of flourine in any of the teeth (Table 5 and Figure 15), indicating that the recrystallization of hydroxylapatite was not progressive enough to recrystallize to flouroapatite.

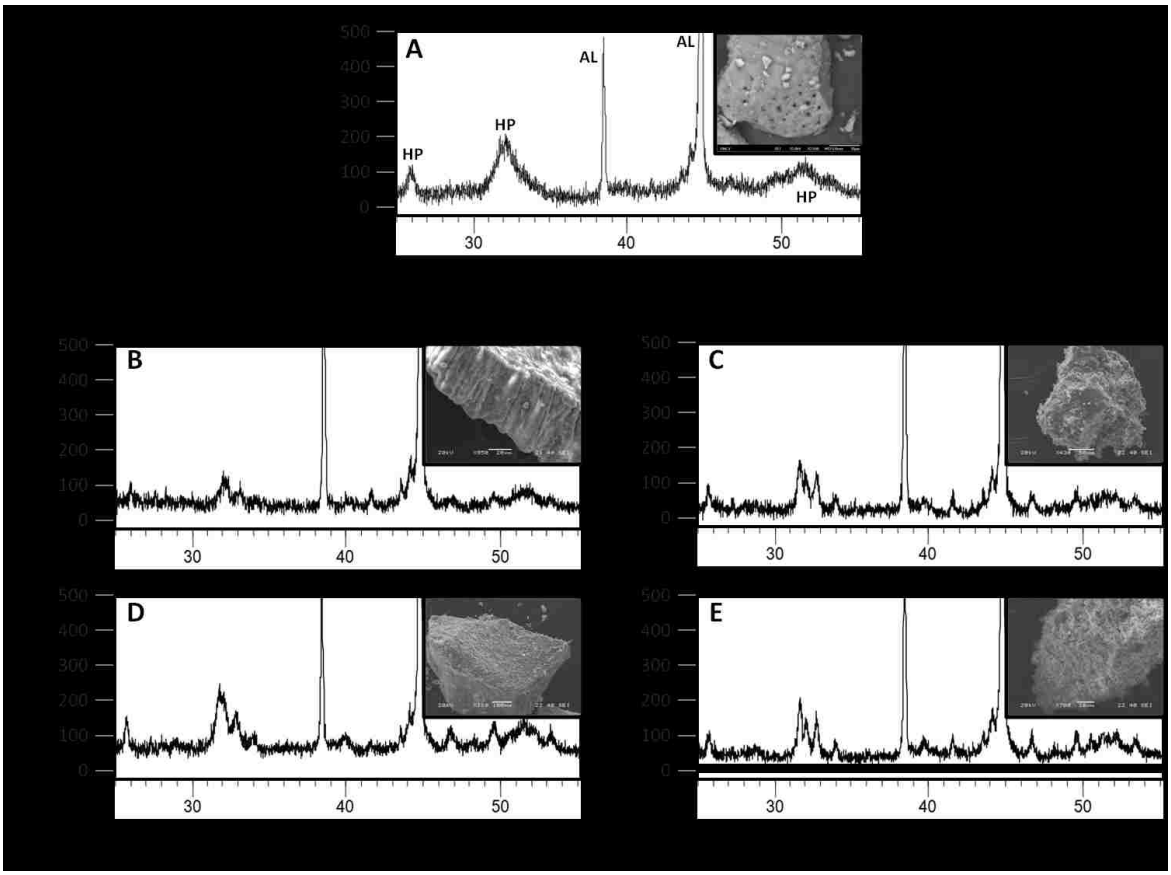


Figure 22. Combined XRD patterns with SEM images inset. Specimens include modern armadillo dentin, A-1 (A), dentin from Late Pleistocene ground sloths *Megalonyx jeffersonii*, HC-21473 (B), and *Nothrotheriops shastensis*, PC-8498 (D), and enamel from Late Pleistocene *Euceratherium collinum*, HC-114876 (C) and PC-8730 (E).

The presence of authigenic cave minerals, such as clay, silica, calcite, or aragonite, was not detected by XRD. Nor were other biogenic forms of hydroxylapatite, such as brushite or whitlockite (Lee-Thorpe and van der Merwe, 1991; Sillen and Sealy, 1995; Koch *et al*., 1997; Weiner, 2010). SEM EDS analysis did not identify any exogenous minerals in the fossil dentin or

enamel. The main constituents (O, C, Ca, P, Na) and trace consitutents (Al, Mg, Si) were variable although not outside normal ranges (Figure 15).

It is likely that carbonate hydroxylapatite in dentin and enamel would be the most sensitive to diagenetic exchange with authigenic cave calcium carbonate. This would occur via preferential dissolution of the hydroxylapatite at the carbonate and phosphate sites, and reprecipitation of carbonate in those lattices (Sponheimer and Lee-Thorp, 1999) (Figure 23). To identify whether carbonate in hydroxylapatite is genuine and has not exchanged with cave carbonate, there should be an equal representation of Ca, P, O, and/or C weight %'s between modern and fossil dentin/enamel hydroxylapatite. SEM EDS chemical spectrum results show that the averaged P weight % of fossil teeth is nearly identical to that of modern armadillo and human dentin, indicating no, or undetectable, amounts of alteration to Late Pleistocene tooth apatite. Averaged Ca weight % in hydroxylapatite is slightly higher in fossil dentin and enamel than in modern dentin, although to varying degrees, with the range of fossil material occurring well within modern values (Figure 15). Further, if the interaction with cave fluids were to replace O ions in the hydroxylapatite carbonate or hydroxide sites, a conspicuous increase in O weight % would be apparent due to the inclusion of exogeneous oxygen ions (Hassan *et al*., 1977), while C would remain unaffected (Wang and Cerling, 1994). The results of this study show that the average O composition of Late Pleistocene dentin and enamel is lower than the value in modern dentin (Figure 15). This indicates that ionic exchanges between hydroxylapatite and ambient fluids might have occurred, although to a limited and undetectable extent. Late Pleistocene averaged C weight % in dentin and enamel is nearly identical to modern C weight %, indicating yet another example of unaltered fossil dentin and enamel compared to modern dentin.

Figure 23. Elemental exchange between carbonate ions. Simplified, unbalanced exchange of carbonate in hydroxylapatite and calcium carbonate from cave deposits, HP = hydroxylapatite.

The field of isotope paleoecology has evolved to the point that vertebrate fossils as far back as the Mesozoic have been found to retain primary isotopic signatures (Lee-Thorp and Sponheimer, 2003; Schoeninger *et al*., 2003; Fricke *et al*., 2008; Jacques *et al*., 2008; Fricke *et al*., 2011). At the same time, some geologically "young" fossils (i.e., from the Holocene) have been found to be altered (Koch *et al*., 1997). Therefore, diagenetic alteration is more dependent on the environment of deposition than on the age of the fossil (Person *et al*., 1995; Sponheimer and Lee-Thorp, 1999; Schoeninger *et al*., 2003; Jacques *et al*., 2008; MacFadden *et al*., 2010). Koch *et al*. (1997) characterized the likelihood of diagenetic alteration as follows: "The extent of alteration may vary with depositional environment, depending on the isotope composition of

reservoirs that might exchange with the fossil and locally controlled variations in the rate of alteration." For this reason it is essential to provide a test of the degree of alteration that fossils have experienced, before assuming isotopic data is primary. XRD and SEM studies can provide that test. The results of XRD and SEM in this study reveal that modern and Late Pleistocene dentin are structurally and chemically similar. Therefore carbon and oxygen isotopes in ground sloth dentin, from the sites in this study, can provide primary and meaningful paleodietary and paleoenvironmental information.

Averaged $\delta^{13}C$ Values

Averaged carbon isotope values (Table 6) reveal that the diet of *N. shastensis* ranged from exclusive C_3 browse (averaged northern California specimens; $\delta^{13}C$ = -9.0‰) to mixed browse and/or increased CAM (averaged southern Nevada specimens; $\delta^{13}C$ = -4.4‰). The diet of *M. jeffersonii* was also quite varied (C_3 browse to mixed browse), considering all specimens came from northern California. The absence of *M. jeffersonii* data from southern Nevada prevents me from determing whether the diet of *N. shastensis* was more diverse than that of *M. jeffersonii*. Where they co-occur, *N. shastensis* and *M. jeffersonii* do not have overlapping $\delta^{13}C$ values (Figure 19), possibly recording a partitioning of resources. My data are compatible with the McDonald-Morgan hypothesis that *N. shastensis* and *M. jeffersonii* were both primarily browsers to mixed-feeders, although they utilized different feeding strategies. In the case of Potter Creek Cave, *M. jeffersonii* has a more negative $\delta^{13}C$ value than does co-occurring *N. shastensis*, but at Samwel Cave this relationship is reversed, with *M. jeffersonii* having more positive values than *N. shastensis*. Therefore, if these two species partitioned food resources, they did not do so in a predictable way.

Ground sloths from northern California have consistently lower $\delta^{13}C$ values than compared to those from southern Nevada, suggesting that the environment around Potter Creek Cave, Samwel Cave, and Hawver Cave was comprised of a much higher content of C_3-type vegetation, compared to southern Nevada. This supports my hypothesis of significant environmental differences (e.g., vegetation, climate, and moisture) between the regions which would manifest itself in the isotopic signature recorded in ground sloth dentin. *N. shastensis* at Hawver Cave is the most depleted in averaged $\delta^{13}C$ (-11.4‰), indicating this area was likely a thick, forested environment where the sloths must have fed exclusively on C_3 vegetation. Values of $\delta^{13}C$ are highly depleted in such environments due to a closed-canopy and recycling of leaf litter into the soil (van der Merwe *et al*., 1988). *N. shastensis* and *M. jeffersonii* at Potter Creek Cave and Samwel Cave also fall within the $\delta^{13}C$ range of a C_3-dominated ecosystem, although the more positive averaged $\delta^{13}C$ values indicate that the forest canopy was more open than at Hawver Cave. Hawver Cave is not as high in elevation as Potter Creek Cave and Samwel Cave, however it is on the western margin of the Sierra Nevada Range and under the influence of an orographic rain-out effect. This would have resulted in higher amounts of precipitation, and meteoric runoff at Hawver Cave, thereby supporting a high abundance of C_3-type vegetation. Potter Creek Cave and Samwel Cave are located at the southern extent of the Cascade Range, proximal to California's Great Valley, which may have been an available source of C_4-type grasses. The $\delta^{13}C$ data suggest that *N. shastensis* and *M. jeffersonii* from Potter Creek Cave and Samwel Cave mostly consumed C_3 vegetation found in the high elevations around the caves, but these sloths may have also taken advantage of C_4 grasses in the open-habitat or grasses found at lower elevations. Comparatively, *N. shastensis* from southern Nevada consumed a higher proportion of CAM or C_4-type vegetation, as more positive averaged $\delta^{13}C$ values (-4.4‰) indicate they were mixed feeders (Figure 19). Assuming that these species were

not highly selective feeders with a preference for CAM or C_4 vegetation, dentin from Tule Springs and Devil Peak Cave reveal that southern Nevada had a greater abundance of CAM and/or C_4 plants than did northern California.

Preserved dung provides an independent dataset on plant material consumed by *N. shastensis* in southern Nevada during the Late Pleistocene (Poinar *et al*., 1998; Hofreiter *et al*., 2000). The dung affords the excellent opportunity to compare carbon isotope results of an extinct organism directly with its known diet. *N. shastensis* from Gypsum Cave in southern Nevada was found to have primarily consumed *Ephedra nevadensis* (C_3), *Sphaeralcea ambigua* (C_3), *Yucca brevifolia* (CAM), and *Atriplex* spp. (C_4), although 13 other families of trees, shrubs, herbs, and grasses were identified within the dung in smaller proportions (Harrington, 1933; MacMahon, 1999; Hofreiter *et al*., 2000). Dung analysis clearly shows that *N. shastensis* was a mixed feeder, thereby corroborating the isotopic data produced in this study. This further supports the validity of using ground sloth dentin in paleoecological studies.

Individuals of *N. shastensis* display a wide range in averaged $\delta^{13}C$ values – of more than 7‰ – indicating that their dietary requirements were very plastic. They were able to opportunistically utilize a wide variety of food resources. The wide dietary range for *N. shastensis* suggests that, rather than being restricted to a certain habitat, this species was able to adjust its diet to consume local vegetation as it dispersed. These data indicate that *N. shastensis* was not an obligate specialist of arid and semi-arid environments (McDonald, 1996; McDonald and Jefferson, 2008).

The presence of *N. shastensis* at Potter Creek Cave, Samwel Cave, and Hawver Cave are the northernmost occurrences of this species in North America, while *M. jeffersonii* dispersed much more widely across the continent and extended as far north as Alaska and the Yukon

(McDonald *et al*., 2000; Graham and Lundelius, 2010). *Megalonyx* has a longer history in North America, having arrived on the continent at about 9 Ma, affording it the opportunity to become more widely dispersed than *Nothrotheriops*, which arrived in North America at about 3 Ma (Marshall *et al*., 1982; Marshall, 1988; Rowland and Needham, 2000; McDonald, 2005). The occurrence of *N. shastensis* in northern California with a C_3 browsing diet was likely the result of slow dietary adaptation to cooler environments as it dispersed northward.

The isotopic data supports the McDonald-Morgan hypothesis in that *N. shastensis* and *M. jeffersonii* utilized different feeding strategies, although the prediction that *N. shastensis* was an arid-adapted browser ($\delta^{13}C$ values in *N. shastensis* will be consistently higher than those in *M. jeffersonii* due to the consumption of more C_4 vegetation by *N. shastensis*) is not supported by the carbon data. The predicted pattern does occur between *N. shastensis* and *M. jeffersonii* at Potter Creek Cave, but the opposite pattern occurs between these two species at Samwel Cave. Furthermore, the sample with the lowest $\delta^{13}C$ value of all of the teeth in this study is from *N. shastensis* (from Hawver Cave) (Figure 19). It appears from the $\delta^{13}C$ data that *N. shastensis* was an extraordinarily adaptive species in terms of its diet.

Averaged $\delta^{18}O$ Values

Averaged oxygen isotope values of dentin, revealing the values in ingested water, were found to vary, although not in a manner I anticipated. I expected to find low $\delta^{18}O$ values for northern California sloths, indicating a cool, moist environment. However, the averaged *N. shastensis* values from higher latitudes (Potter Creek Cave, Samwel Cave, and Hawver Cave) are enriched in ^{18}O ($\delta^{18}O$ = -4.8‰) compared to the lower $\delta^{18}O$ values from lower latitudes at Tule Springs and Devil Peak Cave ($\delta^{18}O$ = -6.5‰) (Table 6). The possible explanations for these results are: (1) southern Nevada was cooler and more forested than northern California in the

Late Pleistocene, (2) southern Nevada *N. shastensis* lived during a colder interval of the Late Pleistocene than did the northern California sloths, or (3) precipitation source and distance from the coast exerted a strong influence on the $\delta^{18}O$ values between the two regions. The first option is not supported by the $\delta^{13}C$ data which show that *N. shastensis* from northern California existed in an open to thick- forested area. Therefore, it is not reasonable that the environment would have been more arid than southern Nevada. The second explanation also does not seem plausible as the ground sloths of different age from the same regions have similar $\delta^{18}O$ values. *N. shastensis* from southern Nevada are known to have lived at different times; the Devil Peak Cave sloth is at least 10 Ka older than the *N. shastensis* specimen from Tule Springs, although these two animals have a difference in averaged $\delta^{18}O$ of less than 1‰. The differences in $\delta^{18}O$ values between southern Nevada and northern California most likely reflect a precipitation source under the influence of the continental effect; this is a depletion of $\delta^{18}O$ values farther inland due to rain-out of the isotopically heavy isotope, ^{18}O, as air masses move inland (Dansgaard, 1964). Therefore, ground sloths ingesting waters from southern Nevada would be consuming isotopically light waters compared to those from northern California, resulting in depleted ^{18}O values in the dentin of southern Nevada ground sloths. Because northern California and southern Nevada do not experience the same atmospheric conditions and meteoric precipitation, these locales cannot be directly compared in terms of $\delta^{18}O$.

The $\delta^{18}O$ values from the ground sloths from northern California can be directly compared with one another since they all were affected by similar precipitation vectors. Where the two species co-occur, $\delta^{18}O$ values of *M. jeffersonii* are always more negative than those of *N. shastensis* (by about 1 to 3‰). McDonald and Morgan (2011) suggested that *M. jeffersonii* inhabited riparian systems while *N. shastensis* inhabited arid environments. If this is so, the plants consumed by *N. shastensis* would have experienced higher rates of evapotranspiration,

resulting in higher levels of $\delta^{18}O$ than would occur in the moist vegetation consumed by *M. jeffersonii*. Evapotranspiration causes plant leaves to be enriched in ^{18}O relative to ground water, because ^{16}O is preferentially lost during transpiration (Koch *et al*., 1994; Dupras, 2001). Thus, the McDonald-Morgan hypothesis predicts that when *N. shastensis* and *M. jeffersonii* occur in the same locality/region, *N. shastensis* will have higher $\delta^{18}O$ values than *M. jeffersonii*, and that is exactly what my data demonstrate. This is direct evidence of how ground sloths avoided interspecific competition. Thus, the oxygen isotope data show a predictable difference between these two genera of sloth and how they partitioned resources, even though the carbon isotope data do not show such a predictable difference.

$\delta^{13}C$ and $\delta^{18}O$ Serial Values

In all of the serially sampled *N. shastensis* teeth, $\delta^{13}C$ values increase toward later years of life (Figure 21a-d). The isotopic patterns in the three northern California sloths record a relatively smooth transition from a dominant C_3 diet in early years of life, toward a mixed diet of C_4 and/or CAM plants before death. The southern Nevada specimen, DP-200728, also records a positive shift in $\delta^{13}C$ values near the end of its life and transitions from a mixed feeder early in life to a dominant C_4 consumer by its time of death (Figure 21d). However, the $\delta^{13}C$ record for DP-200728 is much more erratic in its younger years than is the case with the northern California sloths. This individual of *N. shastensis* appears to have had a much less predictable source of food from one year to the next.

In this study, I find distinct seasonal signals within $\delta^{13}C$ and $\delta^{18}O$ serial data of three of the four *N. shastensis* teeth, revealing that, during the Late Pleistocene, winter and summer temperatures varied enough to be manifest in sloth dentin. One of the serially sampled teeth, Potter Creek Cave sample PC-8141, displays a very cyclic pattern of both $\delta^{13}C$ values and $\delta^{18}O$

values, with five apparent cycles (Figure 24a). Peaks in the $\delta^{18}O$ values are interpreted to record summer high-temperature intervals, while valleys record winter cool intervals. Two of the other three *N. shastensis* teeth for which I was able to collect serial data (PC-8715 and DP-200728) display enough cyclicity to permit inferences regarding yearly cycles (Figure 24b and d, respectively). The Samwel Cave tooth (SC-9664) has only four data points for $\delta^{13}C$ and $\delta^{18}O$, and with no apparent cyclicity.

The serial data show that $\delta^{13}C$ fluctuated throughout the year, with higher C_3 consumption usually occurring during wet seasons (presumably winter/spring) and increased mixed/C_4 consumption during arid periods (presumably summer/fall). A small number of the seasonal cycles show an inverse relationship which could be caused by a dry winter in which the sloths were consuming more C_4 vegetation than normal. Examples of this are Potter Creek Cave specimen PC-8141 at the 32 mm interval (Figure 24a), and Devil Peak Cave specimen DP-200728 at the 19 mm interval (Figure 24d).

Potter Creek Cave teeth PC-8141 and PC-8715 and Samwel Cave tooth SC-9664 show variations in $\delta^{18}O$ values of between 1 and 2‰, seasonally (Figure 24a, b, and c, respectively). These sloths lived near large, well-established rivers, which existed in the Late Pleistocene and still exist today. *N. shastensis* from these regions had an available water source throughout the year, which explains the small variation in $\delta^{18}O$ values. *N. shastensis* from Devil Peak Cave (DP-200728) shows a slighty larger variability in $\delta^{18}O$, about 4‰, seasonally (Figure 24d). Devil Peak Cave is far from a reliable water source, causing that sloth to experience more stress in the availability of water seasonally, and from one year to the next. Highly variable $\delta^{18}O$ values are anticipated in this animal as a consequence of the reliance on meteoric precipitation in an arid region. Meteoric water will have relatively low $\delta^{18}O$ values due to the long distance air masses

travel from the Pacific Ocean, but evaporation from bodies of water will cause ^{18}O to become more concentrated, thereby, increasing the $\delta^{18}O$ value in comparison to meteoric water.

Fluctuating diets in conjunction with available water sources indicate that migration might not have been a factor in *N. shastensis* behavior. Serial stable isotope data are compatible with the interpretation that the sloths remained near a reliable water source and consumed vegetation available in that environment through the year. If *N. shastensis* were migratory, I would expect to see larger-scale fluctuations in $\delta^{18}O$ values, as a product of the animals traveling long distances and utilizing different bodies of water. This is not apparent in the $\delta^{18}O$ data. A discussion by McDonald and Pelikan (2006) supports a non-migratory interpretation for ground sloths. They infer that modern and extinct sloths share a similar digestive physiology, and that nutrients gained from plant material are maximized due to a slow transit time through the digestive tract, supported by morphology of preserved *N. shastensis* and *Mylodon darwinii* dung. This characteristic, combined with a slow metabolism led McDonald and Pelikan (2006) to suggest that ground sloths did not experience the need to migrate seasonally and that they probably occupied a small home range. Contrary to this, Hansen (1978) inferred, based on the composition of vegetation in *N. shastensis* dung from Rampart Cave in the western Grand Canyon, that it was nomadic and occupied a large home range, eating specific foods or seasonally abundant species instead of consuming all browse available locally. The $\delta^{13}C$ data in this study are compatible with Hansen's interpretations regarding diet, although do not support *N. shastensis* as a nomad, using $\delta^{18}O$ data.

Ground Sloth Dentin Growth Rate

Mineralization rates of dentin growth in ground sloths, as well as in extant tree sloths, are unknown, and no direct measurements exist for interpreting yearly patterns based upon

tooth growth rates in sloths. Dentin mineralization rates in other mammals have been measured, however. Dean and Scandrett (1996) found dentin apposition in human teeth to vary from 1 to 6 µm/day, depending upon where measurements were taken; cusps have higher growth rates than do cervical areas. However, unlike sloths, human teeth are not ever-growing, and dentin formation is limited to early years of life. Because of this, I investigated other mammals with ever-growing teeth and dentin. In rats, incisor dentin forms at a rate of up to 15 µm/day (Fatani and Raja, 1977), while voles form incisor dentin at a rate of 12-24 µm/day (Klevezal, 1996). These small mammals have a much higher rate of metabolism than sloths (Aiello, 1985), so their dentin growth may be much faster. Elephantids, including mammoths, grow tusk dentin continuously through their lives. Adult mammoth tusks have been found to have mineralized dentin at a rate of 4-8 mm/year, equivalent to 11-22 µm/day (Koch *et al*., 1989; Fisher *et al*., 2003). As it turns out, the rate of dentin mineralization in mammoth tusks does not differ significantly from that of small mammals. I considered these rates of growth when analyzing isotopic information from ground sloth dentin for yearly and seasonal patterns.

For consistency, I interpreted yearly cycles beginning with the first data point retrieved from each sloth. In two of the teeth for which I was able to collect serial samples, I found yearly patterns to be apparent in the data (Figure 24a and d), with a range of 5-8 mm of recorded dentin growth per year (~14-22 µm/day). Based upon interpreted cyclicity within the data the *N. shastensis* tooth from northern California shows a faster rate of dentin growth than the *N. shastensis* tooth from southern Nevada; PC-8141 averages 7-8 mm/year (Figure 24a) and DP-200728 averages 5 mm/year (Figure 24d). I am unable to measure the growth rate in the teeth of specimens PC-8715 and SC-9664. Sample PC-8715 has fluctuations in the serial carbon and oxygen values indicative of seasonal variations although a poor sampling resolution does not

allow me to identifiy exact cycles, while sample SC-9664 has no seasonal cyclicity so I am unable to assign a rate of growth to these teeth (Figure 24b and c, respectively).

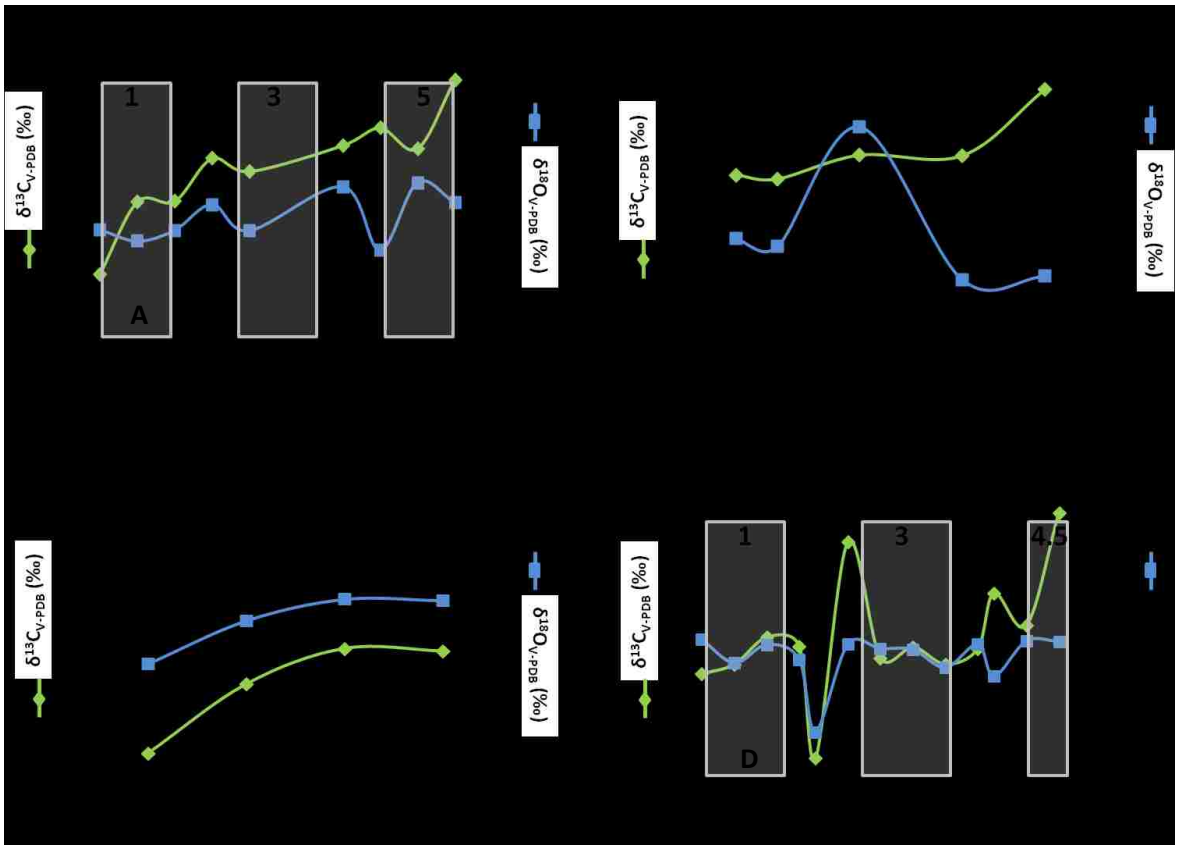


Figure 24. Yearly patterns apparent in serial $\delta^{13}C$ and $\delta^{18}O$ isotope data. *Nothrotheriops shastensis* from: (A) Potter Creek Cave, CA, specimen PC-8141, (B) Potter Creek Cave, CA, specimen PC-8715, (C) Samwel Cave, CA, specimen SC-9664, and (D) Devil Peak Cave, NV, specimen DP-200728. Numbers in bold (top) and boxes indicate years of tooth mineralization. Seasonal cycles in A and D allow for an estimate, while B has poorer resolution and cycles are not evident in C. Summers correspond to high $\delta^{18}O$ values while winters are low $\delta^{18}O$ values.

This analysis shows that an *N. shastensis* tooth can record up to five years of life. It is highly unlikely that the teeth record only 1-2 years of growth, as is the case in other large mammalian herbivore teeth (e.g., bison and horse), because that would mean dentin production in *N. shastensis* would have been a great deal faster than in other mammals. For example, PC-8141 tooth measures 40 mm in total length. If it were to record only two years of life, the tooth

would have had to mineralize at a rate of 20 mm/year (about 55 μm/day). This would be an astronomically high rate compared to dentin mineralization in other mammals. These calculations support the conclusion that my serial data record up to five years of life.

I conclude that the *N. shastensis* teeth in this study record up to five years of life, corresponding to the years before death. If ground sloths had life spans similar to those of extant tree sloths, they were able to live about 30 years (Britton, 1941). Therefore a record of the early years of life of an adult sloth is not available, only the few years immediately preceding death. In the two *N. shastensis* teeth where growth rates are estimated, the record begins in a warm period followed by decreasing $\delta^{18}O$ values, representing a cool interval, and then increasing $\delta^{18}O$ values back to a warm period, thus completing a one year cycle. This is exemplified by the first year of life in specimens PC-8141 and DP-200728 (Figure 24a and d, respectively). These cycles continue, more or less, distinctly up until the animal's death. The absence of observable yearly cycles in the Potter Creek Cave (PC-8715) and Samwel Cave (SC-9664) teeth can be explained by the poor sampling resolution, which is more widely spaced at up to 10 mm increments. I recommend sampling ground sloth teeth at 3-4 mm increments, where possible, in order to capture seasonality. As previously mentioned, in this study the fragility of the dentin dictated sampling intervals.

Conclusions

In isotope paleoecology studies, ground sloths have largely been avoided due to the absence of enamel in their teeth, resulting in a depauperate dataset for the group. The strongest evidence for the retention of primary isotopic signatures is the occurrence, within a single deposit, of expected differences among ecologically distinct taxa (Koch, 1998). The

results of this study display such differences, yet tests for diagenesis were conducted to determine the degree of alteration to teeth. In the absence of performing other, more quantitatively definitive, diagenetic tests, which can detect rare earth element content in hydroxylapatite at the ppm or ppb range, XRD and SEM results can show mineralogic, crystallographic, structural, and chemical changes to dentin and enamel. Therefore these tests should be considered as an accessible and low-cost method to testing the validity of primary carbon and oxygen signatures for isotopic analyses on fossil teeth. XRD results in this study show that carbonate hydroxylapatite in fossil dentin and enamel underwent recrystallization, compared to modern dentin, apparent by peak sharpening of diffraction patterns in fossil material. Chemical spectra, using SEM EDS, reveals that although recrystallization occurred, chemical composition of teeth are nearly identical between modern and fossil dentin and fossil enamel. Trace elements (Al, Mg, Si) were detected in three of the eight teeth analyzed, although all are natural constituents of hydroxylapatite and therefore do not represent elemental incorporation from alteration.

This research shows that biogeochemical analyses of ground sloth dentin yield paleoecologically meaningful data, and should be used on these taxa to obtain ecological and environmental information for the Late Pleistocene. The results of this study support my hypothesis that ground sloth dentin can result in primary carbon and oxygen isotopic signatures. A caveat to this statement is that geological age and depositional setting must be considered, and that diagenetic alteration is always a concern (as it is with all isotopic studies). As far as this study is concerned, the Late Pleistocene ground sloth teeth analyzed resulted in primary isotopic signatures.

Averaged $\delta^{13}C$ data reveal that in northern California, *Nothrotheriops shastensis* was dominantly a C_3 browser living in open to thickly-forested environments. In southern Nevada,

N. shastensis had a much higher component of C_4 and/or CAM vegetation in its diet, resulting in mixed feeding strategies in open, arid environments. *Megalonyx jeffersonii* occupied a browsing and mixed feeding niche in northern California. My data support the hypothesis that *N. shastensis* and *M. jeffersonii* utilized different feeding strategies. When co-occurring, averaged $\delta^{13}C$ data show partitioning between the species, indicating that they were not in competition for the same resources. However, the nature of this partitioning of food resources is not consistent. In the case of Potter Creek Cave, *M. jeffersonii* was consuming more C_3 browse than was *N. shastesis*, while in the case of Samwel Cave this situation is reversed. Averaged $\delta^{18}O$ data reveal that, when co-occuring, *M. jeffersonii* has consistently lower values than does *N. shastensis*; I interpret this to reflect the tendency for *N. shastensis* to consume a higher percentage of plants with relatively high rates of evapo-transpiration from their leaves. These data support the McDonald-Morgan hypothesis that *M. jeffersonii* inhabited mesic habitats and *N. shastensis* inhabited open, drier areas, and was able to contribute to this hypothesis by showing that *N. shastensis* was an extraordinarily versatile species in terms of its diet and was also capable of inhabiting forested areas.

Serial sampling of *N. shastensis* teeth resulted in a multi-year record of seasonality. Teeth sampled in this project record up to five years of life, and show that dentin mineralization in ground sloths occurred at a rate of 5-8 mm/year.

A surprise that emerged from the serial data is that $\delta^{13}C$ values increased through life, fairly steadily in the northern California sloths and more erratically in the Devil Peak Sloth. I interpret this multi-year increase in $\delta^{13}C$ data to record changes in diet from predominantly browsing to a mixed diet in the northern California sloths, and a mixed diet with an increase in C_4 and/or CAM in the case of the Devil Peak Sloth in southern Nevada. Serial $\delta^{18}O$ values

generally record low-amplitude seasonal fluctuations, suggesting that the ground sloths were not, for the most part, water-stressed during dry seasons.

Future work should include analyzing ground sloths from different regions, as well as including the other two species of North American, Late Pleistocene ground sloths (*Paramylodon harlani* and *Eremotherium laurillardi*). The most useful ecological information can be gained when working with multiple species of ground sloths from the same fossil assemblage.

CHAPTER FOUR

STABLE ISOTOPE PALEOECOLOGY OF LATE PLEISTOCENE MEGAHERBIVORES FROM WESTERN NORTH AMERICA

Abstract

Large-bodied herbivores from seven Late Pleistocene assemblages in California and Nevada were examined. The enamel or dentin of their teeth was serially sampled and analyzed for stable carbon and oxygen isotopes. The carbon data reveal diet and vegetation type, and how megaherbivores behaved in differing environments. $\delta^{13}C$ data record the presence of dominantly browsing communities of megaherbivores in northern California. This indicates an abundance of C_3-type vegetation in the region, leading to an interpretation that the environment was a thick forest to open-woodland. Northern California taxa exhibiting averaged $\delta^{13}C$ values that align with exclusive C_3 browsing diets include *Odocoileus* (-12.4 to -11.0‰), *Equus* (-10.8 to -9.4‰), and *Bison* (-10.4‰). Taxa which incorporated various amounts of C_4-type shrubs and grasses have averaged $\delta^{13}C$ values indicative of a range of herbivorous niches, browsing to mixed feeding. These include *Nothrotheriops* (-11.4 to -8.0‰), *Euceratherium* (-11.2 to -8.4‰), *Ovis* (-8.2‰) and *Megalonyx* (-10.6 to -6.3‰). $\delta^{13}C$ data reveal that southern Nevada environments were open-woodland to mixed grassland and provided a wide range of niches that supported a diversity of herbivores. Taxa from southern Nevada exhibit diets that include C_3 browsing and mixed feeding on arid-adapted foliage. Browsing *Mammuthus* yield averaged $\delta^{13}C$ values of -10.3 and -8.8‰, while mixed feeding *Bison* and *Nothrotheriops* have averaged $\delta^{13}C$ values of -6.6 and -4.1‰, respectively. The $\delta^{13}C$ data indicate that, during the Late Pleistocene, southern Nevada hosted a variety of C_3 plants and C_4 grasses and shrubs.

Further, variability in $\delta^{13}C$ data, reflecting diet, reveals that when co-occurring megaherbivores partitioned food resources in order to avoid competition.

Serial $\delta^{18}O$ isotope data show small amplitude variations suggesting that seasonality was less prominent during the Late Pleistocene than it is today. This resulted in a dampening of seasonally derived diet fluctuations, thereby reducing the need for seasonal mobility of megaherbivores. Paleoclimate modeling of Late Pleistocene localities supports the inference that temperatures were 5.5 to 7.5 ^{O}C cooler than modern with up to 30% more precipitation; the precipitation was distributed more evenly throughout the year, compared to the prominent wet/dry seasonal patterns at the localities today.

Introduction

Biogeochemical studies used for paleoecology and paleoenvironmental reconstructions have become increasingly common in recent years (Kohn *et al*., 2005; France *et al*., 2007; Fox-Dobbs *et al*., 2008; Feranec, *et al*., 2010; Forbes *et al*., 2010; Nunez *et al*., 2010; Fabre *et al*., 2011; Maung-Thein *et al*., 2011). Stable isotopes captured in the hydroxylapatite of teeth reveal an abundance of information about past ecosystems and climate. Carbon isotopes ($\delta^{13}C$) are a measurement of diet, yielding the proportion of C_3/C_4 vegetation consumed (Lee-Thorp and Van der Merwe, 1987), as well as behavior and ecological interactions. Oxygen isotopes ($\delta^{18}O$) record ingested water of an animal, which provides an indirect proxy for identifying climatic conditions while the animal was living, such as precipitation amount and relative temperature (Luz *et al*., 1984; Sponheimer and Lee-Thorp, 1999). Herbivore browsers that eat >90% tree and shrub foliage and <10% grasses, typically have $\delta^{13}C$ values of -8‰ or less. In contrast, grazers that consume >90% grasses and <10% tree and shrub foliage typically have $\delta^{13}C$ values of about

0‰ or higher. Mixed feeders consume between 10-90% grasses, which yield $\delta^{13}C$ values ranging from -8 to 0‰ (Janis and Ehrhardt, 1988; Cerling *et al*., 1997; Koch, 1998; Pérez-Barbería, 2001; Passey *et al*., 2005; DeSantis *et al*., 2009). A more comprehensive overview of the use of stable carbon and oxygen isotopes in biogeochemical analyses is presented in Chapter 1.

Hypotheses

The objective of this study is to analyze Late Pleistocene megaherbivore teeth from California and Nevada, using carbon and oxygen isotopes, to obtain information about paleoecology and paleoenvironment. In this study, I address three main hypotheses. Because megaherbivore species inhabited markedly different environments in western North America, I hypothesize that averaged carbon isotope results will reveal a wide range of ecological variation in their diet and will reflect niche partitioning between species when they co-occur in a fauna. I anticipate that northern California taxa consumed higher amounts of C_3-type vegetation than taxa from southern Nevada, thereby reflecting cooler climates and wetter conditions in the northern localities. Secondly, I hypothesize that averaged oxygen isotopes will reveal that environmental differences between northern California and southern Nevada in the Late Pleistocene were similar to today, except that during the Late Pleistocene these regions were cooler and experienced higher amounts of precipitation than modern levels. Thirdly, I hypothesize that serial sampling of the teeth will identify seasonality and mobility (or lack thereof), where intra-tooth $\delta^{13}C$ and $\delta^{18}O$ variations will track dietary and environmental fluctuations, respectively, on a sub-year to multi-year scale. Combining isotopic information obtained from averaged and serial data, I expect to characterize the range of ecological and environmental variability under which megaherbivore species (averaged results) and individuals (serial results) were capable of existing.

To test these hypotheses, I analyzed eight species of Late Pleistocene megaherbivores from seven localities in California and Nevada (Figure 25). I focused this study on regions of the Pacific and Mountain West from which there is currently little or no isotopic information. Megaherbivore fossils from northern California have never before been isotopically analyzed. Megaherbivore fossils from southern Nevada have received a small amount of attention in previous isotopic analyses (Connin *et al*., 1998; Vetter, 2007); for these sites, I focused my analyses on specimens which could contribute new information. Therefore, assemblages were chosen to fill in paleogeographic and paleoecologic gaps for these regions. Regions of the West and Southwest which have been the focus of prior isotopic studies on the Late Pleistocene megafauna include southern California (Connin *et al*., 1998; Coltrain *et al*., 2004; Feranec *et al*., 2009), Nevada (Connin *et al*., 1998; Vetter, 2007), Arizona (Connin *et al*., 1998; Higgins and MacFadden, 2004), and New Mexico (Connin *et al*., 1998; Higgins and MacFadden, 2004). This study contributes to a better understanding of megaherbivore behavior in Late Pleistocene communities and environments of the North American West.

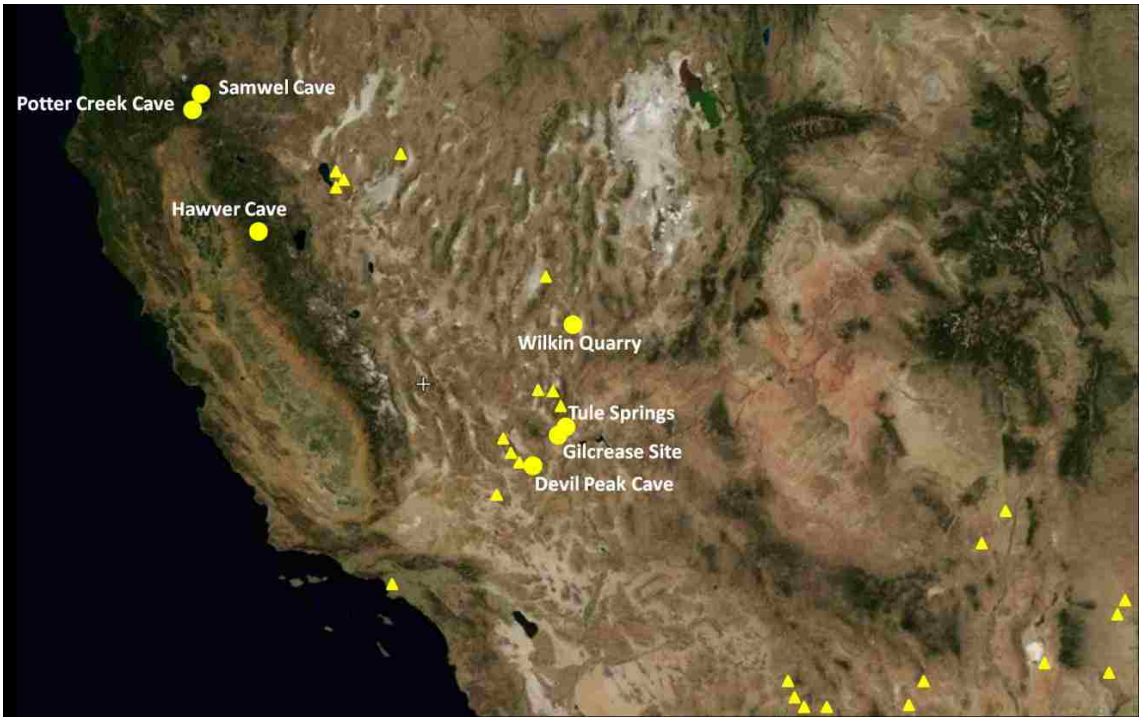


Figure 25. Localities of prior isotopic studies from the West and Southwest. Localities received isotopic analysis on Late Pleistocene megaherbivores in this study (circles) and from previous researchers (triangles) (Connin *et al*., 1998; Coltrain *et al*., 2004; Higgins and MacFadden, 2004; Vetter, 2007; Feranec *et al*., 2009).

Analyzed Taxa

Megaherbivores examined in this study are listed in Table 8. Preference was placed on analyzing taxa that occur in multiple assemblages, thereby allowing for the measurement of interspecific variability across different environments. Megaherbivores from northern California received the most attention due to the lack of isotopic data for that region. Individuals from southern Nevada were examined which would supplement data from previous studies (Connin *et al*., 1998; Vetter, 2007).

Table 8. All megaherbivores analyzed in this study. Specimens are from University of California Museum of Paleontology (UCMP), Berkeley, California, Nevada State Museum (NSM-LV), Las Vegas, Nevada, or had previously been collected, with permission, from privately owned property.

Location/Taxon	Element	Collection	Specimen #	County	State	# samples
Devil Peak Cave						
Nothrotheriops shastensis	M3	NSM-LV	200728	Clark	NV	14
Tule Springs						
Nothrotheriops shastensis	M3	UCMP	64232	Clark	NV	1
Gilcrease Site						
Mammuthus columbi	M5	Private	MT-3	Clark	NV	6
Mammuthus columbi	M5	Private	MT-4	Clark	NV	6
Wilkin Quarry						
Bison latifrons	M3	Private	B-1	Lincoln	NV	10
Potter Creek Cave						
Euceratherium collinum	M3	UCMP	8730	Shasta	CA	13
Euceratherium collinum	M3	UCMP	8385	Shasta	CA	11
Equus occidentalis	M3[1]	UCMP	8616	Shasta	CA	7
Odocoileus sp.	M3	UCMP	4181	Shasta	CA	5
Odocoileus sp.	M3	UCMP	4174	Shasta	CA	4
Ovis sp.	M2	UCMP	8451	Shasta	CA	6
Nothrotheriops shastensis	M3	UCMP	8141	Shasta	CA	9
Nothrotheriops shastensis	M3	UCMP	8715	Shasta	CA	5
Megalonyx jeffersonii	M3[1]	UCMP	8498	Shasta	CA	1
Samwel Cave						
Euceratherium collinum	M3	UCMP	35742	Shasta	CA	5
Euceratherium collinum	M3	UCMP	9488	Shasta	CA	6
Equus sp.	M3[1]	UCMP	8853	Shasta	CA	7
Equus sp.	M3[1]	UCMP	8867	Shasta	CA	7
Odocoileus sp.	M3	UCMP	23082	Shasta	CA	4
Odocoileus sp.	M3	UCMP	35714	Shasta	CA	4
Nothrotheriops shastensis	M3	UCMP	9664	Shasta	CA	4
Nothrotheriops shastensis	M3	UCMP	9663	Shasta	CA	2
Megalonyx jeffersonii	M2	UCMP	9668	Shasta	CA	2
Megalonyx jeffersonii	M3	UCMP	9666	Shasta	CA	1
Hawver Cave						
Euceratherium collinum	M2	UCMP	114876	El Dorado	CA	6
Odocoileus hemionus	P4	UCMP	11016	El Dorado	CA	2
Bison sp.	M3	UCMP	11006B	El Dorado	CA	4
Nothrotheriops shastensis	M3	UCMP	21473	El Dorado	CA	1

[1]Tag was unspecific although size and morphology indicates m3.

Stable isotope studies have been used to examine Pleistocene megafauna communities and animal interactions, such as competition (Coltrain *et al*., 2004; Higgins and MacFadden, 2004; Kohn *et al*., 2005; France *et al*., 2007; Feranec *et al*., 2009). This study is the first to perform isotopic analyses on Late Pleistocene megaherbivore communities that include *Nothrotheriops* and *Euceratherium. Nothrotheriops* has been inferred to have been a browser (McDonald, 1996), while *Euceratherium* has had conflicting interpretations and has been inferred to be both a browser (Kropf *et al*., 2007) and a grazer (Kurtén and Anderson, 1980). Stable isotope analysis can elucidate the diets of these taxa, as well as other megaherbivores with which they occur. Examining communities of megaherbivores can reveal how different species partitioned resources while inhabiting an area. Analysis of multiple individuals of a species will allow averaged carbon isotopes in herbivore teeth to characterize the range of food that each taxon consumed. This can lead to insights about whether a species was acting as a specialist, consuming only certain types of vegetation, or if it was acting opportunistically, consuming vegetation that may have been transiently available in the environment.

The megaherbivore species in this study which have had little, or no, prior isotopic analyses include *Nothrotheriops shastensis* (Shasta ground sloth) and *Euceratherium collinum* (shrub-ox). Relatively little isotopic work has been performed on *Ovis* (bighorn sheep) (Kohn and McKay, 2012), *Odocoileus* (deer) (Kohn *et al*., 2005; Nunez *et al*., 2010; Kohn and McKay, 2012) and *Megalonyx jeffersonii* (Jefferson's ground sloth) (Kohn *et al*., 2005; France *et al*., 2007). For these taxa I will use isotopic analysis to better constrain their diet. Taxa included in this study that have received the most attention in prior isotopic studies include *Mammuthus* (mammoth) (Koch *et al*., 1989; Connin *et al*., 1998; Fisher *et al*., 2003; Vetter, 2007; Nunez *et al*., 2010; Kohn and McKay, 2012), *Equus* (horse) (Connin *et al*., 1998; Hoppe *et al*., 2004; Coltrain *et al*., 2004; Higgins and MacFadden, 2004; Kohn *et al*., 2005; France *et al*., 2007; Vetter, 2007;

Feranec *et al*., 2009; Nunez *et al*., 2010; Kohn and McKay, 2012), and *Bison* (Connin *et al*., 1998; Coltrain *et al*., 2004; Higgins and MacFadden, 2004; Hoppe, 2006; Hoppe *et al*., 2006; France *et al*., 2007; Vetter, 2007; Fox-Dobbs *et al*., 2008; Feranec *et al*., 2009; Nunez *et al*., 2010; Kohn and McKay, 2012). In addition to presenting new data for these taxa which have received extensive previous isotopic analysis, I will compare my results to prior studies. Also, information from this study will expand the isotopic database into geographic regions and for paleoenvironments that have not previously been analyzed.

Methods

The methods and treatments used in this study are described in Chapter One. Samples were processed and analyzed at the University of Nevada, Las Vegas in the Las Vegas Isotope Science Lab (LVIS). For analysis, individual powders ranged from 0.6-0.8 mg for dentin samples, and 0.8-1.0 mg for enamel samples. The issue of taxonomic sampling size is addressed in Chapter Three, as is an explanation of the statistical analyses that have been calculated.

Results

All serial data are listed in the Appendix 2, averaged values are listed in Table 9. $\delta^{13}C$ data reflect a precision of ± 0.20‰ and $\delta^{18}O$ data reflect a precision of ± 0.15‰.

Averaged $\delta^{13}C$ and $\delta^{18}O$ Data

Averaged carbon and oxygen results for all specimens are listed in Table 9 and are graphed in Figure 26. Averaged values for $\delta^{13}C$ and $\delta^{18}O$ were calculated by averaging data from

the serial samples. Taxa from northern California have a range of averaged $\delta^{13}C$ values of -12.4 to -6.3‰, with a collective average of all megaherbivores of -9.9‰. Hawver Cave, with $\delta^{13}C$ values ranging from -11.4 to -10.4‰, has the most negative averaged carbon value (-10.9‰) of all the localities. Potter Creek Cave has $\delta^{13}C$ values that range from -12.4 to -8.2‰, while Samwel Cave has $\delta^{13}C$ values ranging from -11.2 to -6.3‰. Total average carbon values for all megaherbivores from Potter Creek Cave and Samwel Cave are comparable, at -9.8‰ and -9.7‰, respectively. Taxa from southern Nevada also have a wide range of averaged carbon values (-10.3 to -4.1‰), although southern Nevada taxa have a significantly lower collective average of all megaherbivores (-6.6‰). Comparing the three southern Nevada sites, megaherbivores from the Gilcrease Site have the most negative $\delta^{13}C$ values (-10.3‰); Wilkin Quarry averages -6.6‰, while Tule Springs and Devil Peak Cave are enriched in ^{13}C (-4.7‰ and -4.1‰, respectively) (Table 9).

Collectively, northern California specimens have an averaged $\delta^{18}O$ value of -5.1‰, while the southern Nevada collective average is considerably more depleted in ^{18}O, averaging -10.1‰ (Table 9). Northern California megaherbivores have a wide range of averaged $\delta^{18}O$ values, -7.4 to -3.5‰. The averaged $\delta^{18}O$ value of all megaherbivores from Samwel Cave is -5.2‰, with individuals ranging from -7.3 to -3.5‰. Potter Creek Cave has the exact same collective averaged $\delta^{18}O$ value as Samwel Cave (-5.2‰), with individuals ranging from -7.4 to -3.8‰. Averaged $\delta^{18}O$ values for Hawver Cave range from -5.5 to -3.5‰, with the highest collective average $\delta^{18}O$ value of all the sites (-4.4‰). Southern Nevada taxa, with values ranging from -13.4 to -6.1‰, have a much wider range of averaged $\delta^{18}O$ values than do northern California taxa. The Gilcrease Site has the most negative averaged $\delta^{18}O$ values (-13.4 and -13.3‰). The single specimen from Wilkin Quarry has a $\delta^{18}O$ value of -10.5‰. Devil Peak Cave and Tule Springs are enriched in ^{18}O with average values of -6.9‰ and -6.1‰, respectively.

Five specimens of *Odocoileus* were analyzed and form a very tight cluster, with averaged $\delta^{13}C$ values ranging from -12.4 to -11.0‰. Three specimens of *Equus* also yielded very close averaged $\delta^{13}C$ values, ranging from -10.8 to -9.4‰. Five specimens of *Euceratherium* resulted in averaged $\delta^{13}C$ values ranging from -11.2 to -8.4‰. One individual of *Ovis* was analyzed, with an averaged $\delta^{13}C$ value of -8.2‰. Three specimens of *Megalonyx* were analyzed, yielding averaged $\delta^{13}C$ values ranging from -10.6 to -6.3‰; the individual most depleted in ^{13}C, from Potter Creek Cave, was about 4‰ more negative than the other two specimens, which came from Samwel Cave. Seven specimens of *Nothrotheriops* were analyzed, these resulted in averaged $\delta^{13}C$ values of -11.4 to -4.1‰; the most negative individual occurred at Hawver Cave and the most positive individual at Devil Peak Cave. Two specimens of *Bison* were analyzed, yielding averaged $\delta^{13}C$ values of -10.4‰ and -6.6‰, from Hawver Cave (*Bison* sp.) and Wilkin Quarry (*Bison latifrons*), respectively. Two individuals of *Mammuthus* were analyzed from the Gilcrease Site, resulting in $\delta^{13}C$ averages of -10.3‰ and -8.8‰.

Table 9. Averaged $\delta^{13}C$ and $\delta^{18}O$ values in enamel and dentin of megaherbivores. Taxa are listed by location: northern California assemblages (Potter Creek Cave, Samwel Cave, and Hawver Cave) and southern Nevada (Devil Peak Cave, Tule Springs, Gilcrease Site, and Wilkin Quarry).

Location	Taxon	$\delta^{13}C_{V\text{-}PDB}$ (‰)	$\delta^{18}O_{V\text{-}PDB}$ (‰)
Potter Creek Cave	*Euceratherium collinum*	-11.1	-3.8
	Euceratherium collinum	-8.4	-5.9
	Equus occidentalis	-10.7	-5.4
	Odocoileus sp.	-11.5	-4.5
	Odocoileus sp.	-12.4	-4.1
	Ovis sp.	-8.2	-7.4
	Nothrotheriops shastensis	-8.6	-5.7
	Nothrotheriops shastensis	-8.4	-5.2
	Megalonyx jeffersonii	-10.6	-6.8
	AVERAGE	-9.8	-5.2
Samwel Cave	*Euceratherium collinum*	-10.0	-4.8
	Euceratherium collinum	-8.9	-5.7
	Equus sp.	-10.8	-6.3
	Equus sp.	-9.4	-5.2
	Odocoileus sp.	-11.0	-5.5
	Odocoileus sp.	-11.2	-3.5
	Nothrotheriops shastensis	-8.9	-4.7
	Nothrotheriops shastensis	-8.0	-4.3
	Megalonyx jeffersonii	-6.3	-7.3
	Megalonyx jeffersonii	-6.8	-5.6
	AVERAGE	-9.7	-5.2
Hawver Cave	*Euceratherium collinum*	-11.2	-3.5
	Odocoileus hemionus	-11.0	-5.5
	Bison sp.	-10.4	-5.4
	Nothrotheriops shastensis	-11.4	-4.2
	AVERAGE	-10.9	-4.4
Northern California	**TOTAL AVERAGE**	**-9.9**	**-5.1**
Devil Peak Cave	*Nothrotheriops shastensis*	-4.1	-6.9
Tule Springs	*Nothrotheriops shastensis*	-4.7	-6.1
Gilcrease Site	*Mammuthus columbi*	-8.8	-13.3
	Mammuthus columbi	-10.3	-13.4
Wilkin Quarry	*Bison latifrons*	-6.6	-10.5
Southern Nevada	**TOTAL AVERAGE**	**-6.6**	**-10.1**

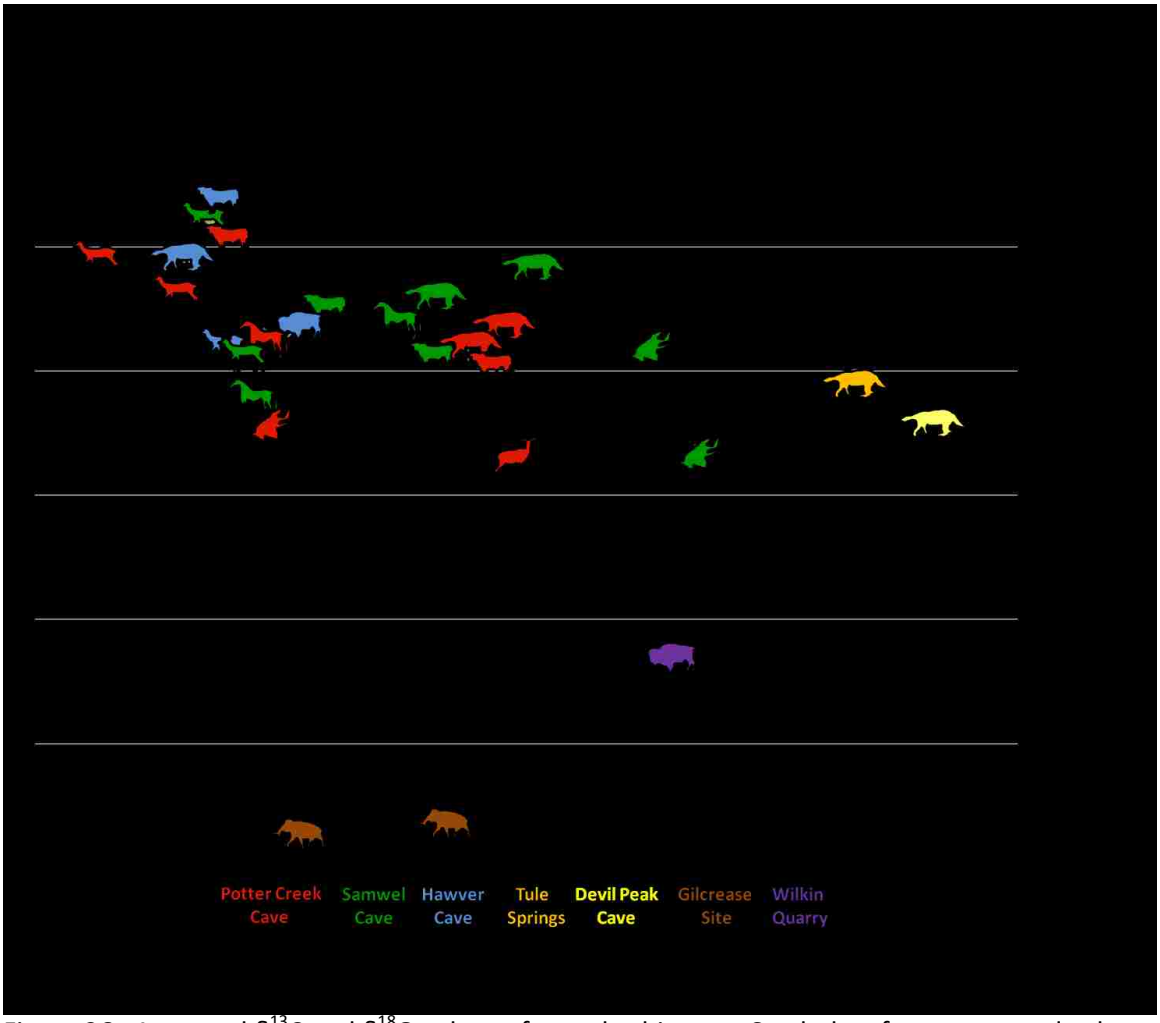


Figure 26. Averaged $\delta^{13}C$ and $\delta^{18}O$ values of megaherbivores. Symbols refer to taxa, and colors refer to locations: red represents Potter Creek Cave, CA; green represents Samwel Cave, CA; blue represents Hawver Cave, CA; orange represents Tule Springs, NV; yellow represents Devil Peak Cave, NV; brown represents Gilcrease Site, NV; and purple represents Wilkin Quarry, NV.

Averaged $\delta^{18}O$ values for specimens of *Odocoileus* range from -5.5 to -3.5‰, where *Odocoileus* from Hawver Cave and one specimen from Samwel Cave are the most depleted in ^{18}O and the second specimen of *Odocoileus* from Samwel Cave is the most enriched in ^{18}O. Averaged $\delta^{18}O$ values for *Equus* range from -6.3 to -5.2‰, which is the range of averaged $\delta^{18}O$ for the two specimens from Samwel Cave, the specimen from Potter Creek Cave has a value that falls within this range. Averaged $\delta^{18}O$ values for *Euceratheruim* range from -5.9 to -3.5‰, the most negative individual is from Potter Creek Cave while the specimen most enriched in ^{18}O is

from Hawver Cave. *Ovis,* from Potter Creek Cave, has an averaged $\delta^{18}O$ value of -7.4‰. *Megalonyx* $\delta^{18}O$ values, from Samwel Cave and Potter Creek Cave, range from -7.3 to -5.6‰. *Nothrotheriops* yielded averaged $\delta^{18}O$ values that range from -6.9‰, the most negative individual (from Devil Peak Cave), to -4.2‰, the most positive individual (from Hawver Cave). The two *Bison* specimens yielded quite different $\delta^{18}O$ values, -10.5‰ at Wilkin Quarry (*B. latifrons*) and -5.4‰ at Hawver Cave (*Bison* sp.). The two *Mammuthus* specimens, both occurring at the Gilcrease Site, yielded a very small $\delta^{18}O$ range of averaged values, -13.4‰ and -13.3‰. These are conspicuously low values compared to all other samples in this study (Figure 26).

Serial $\delta^{13}C$ and $\delta^{18}O$ Data

Of the twenty-eight megaherbivore teeth sampled in this study, I obtained serial samples for twenty of them; sixteen are from northern California and four are from southern Nevada (Figure 27). Serially sampled taxa from northern California include eight individuals from Potter Creek Cave including: *Odocoileus* (PC-4174 and PC-4181), *Euceratherium* (PC-8730 and PC-8385), *Nothrotheriops* (PC-8141 and PC-8715), *Equus* (PC-8616), and *Ovis* (PC-8451). Six individuals are from Samwel Cave including: *Odocoileus* (SC-35714 and SC-23082), *Equus* (SC-8853 and SC-8867), *Euceratherium* (SC-9488), and *Nothrotheriops* (SC-9664). Two individuals are from Hawver Cave including: *Bison* (HC-11006B) and *Euceratherium* (HC-114876). Serially sampled taxa from southern Nevada include: *Nothrotheriops* from Devil Peak Cave (DP-200728), *Bison* from Wilkin Quarry (B-1), and *Mammuthus* from the Gilcrease Site (MT-3 and MT-4) (Figure 27).

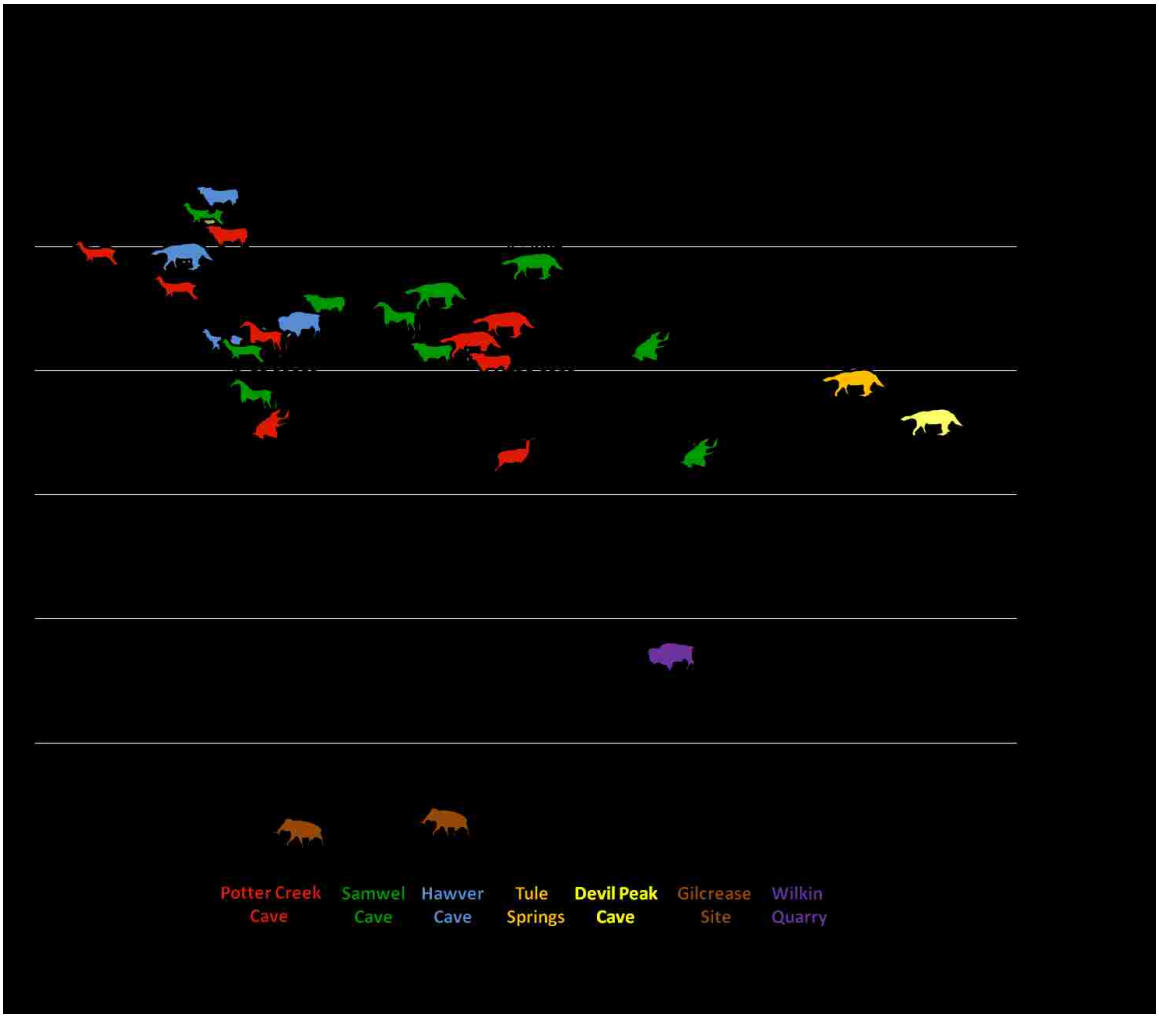


Figure 27. Megaherbivores which received serial sampling. All isotopically analyzed individuals are graphed, those with collection numbers have serial carbon and oxygen data.

Serial data for specimens from Potter Creek Cave are graphed in Figure 28. *Equus* specimen PC-8616 exhibits $\delta^{13}C$ values ranging from -11.4 to -10.2‰ and $\delta^{18}O$ values ranging from -5.7 to -4.9‰, yielding weakly covarying (-0.07), low-amplitude fluctuations with a strong, negative correlation (r = -0.65) (Figure 28a). This negative correlation was also discovered for many other ungulate taxa, where an enrichment in ^{13}C corresponds to a depletion in ^{18}O, and vice versa. Because of the excellent preservation and tooth length, *Euceratherium* teeth (PC-8730 and PC-8385) were sampled with a finer resolution than most other taxa (~4 mm),

resulting in many fluctuations through the record. *Euceratherium* specimen PC-8730 has $\delta^{13}C$ values ranging from -11.6 to -10.1‰ and $\delta^{18}O$ values that have a slightly wider range, from -4.9 to -2.1‰. Specimen PC-8730 has weak covariance (0.01) of $\delta^{13}C$ and $\delta^{18}O$ values and very weak, positive correlation (r = 0.02) (Figure 28b). Comparatively, the other Potter Creek Cave *Euceratherium* specimen, PC-8385, has much larger fluctuations in $\delta^{13}C$ and $\delta^{18}O$ values. PC-8385 has $\delta^{13}C$ values ranging from -11.2 to -4.6‰ and $\delta^{18}O$ values ranging from -7.7 to -3.6‰; these data exhibit very strong covariance (-2.38) and strong, negative correlation (r = -0.74) (Figure 28c). *Odocoileus* (PC-4181 and PC-4174) have short records due to their low-crowned teeth and have very low amplitude $\delta^{13}C$ and $\delta^{18}O$ signals. PC-4181 has $\delta^{13}C$ values ranging from -12.0 to -10.5‰ and $\delta^{18}O$ values that range from -6.4 to -2.9‰ (Figure 28d). The $\delta^{13}C$ and $\delta^{18}O$ values for PC-4181 have a covariance of 0.18 and weak, positive correlation (0.25). PC-4174 has $\delta^{13}C$ values that range from -12.7 to -12.2‰ and $\delta^{18}O$ values that vary from -5.3 to -3.0‰ (Figure 28e); $\delta^{13}C$ and $\delta^{18}O$ values for this specimen covary with a value of -0.13 and have a strong, negative correlation (r = -0.71). *Ovis* specimen PC-8451 has $\delta^{13}C$ values ranging from -9.2 to -6.7‰ and $\delta^{18}O$ values ranging from -9.7 to -5.4‰, revealing fairly high-amplitude fluctuations with weak covariance (-0.02) and very weak, negative correlation (r = -0.02) (Figure 28f). *Nothrotheriops* specimen PC-8141 has $\delta^{13}C$ values that range from -10.1 to -7.4‰ and $\delta^{18}O$ values ranging from -6.1 to -5.4‰ (Figure 28g); the $\delta^{13}C$ and $\delta^{18}O$ values have weak covariance (0.07) and weak, positive correlation (r = 0.38). *Nothrotheriops* specimen PC-8715 has $\delta^{13}C$ values that range from -8.8 to -7.5‰ and $\delta^{18}O$ values ranging from -6.0 to -3.3‰ (Figure 28h). Specimen PC-8715 shows that $\delta^{18}O$ and $\delta^{13}C$ values covary (-0.12), although $\delta^{18}O$ exhibits larger fluctuations than $\delta^{13}C$ and in the opposite direction, causing this specimen to have weak, negative correlation (r = -0.26).

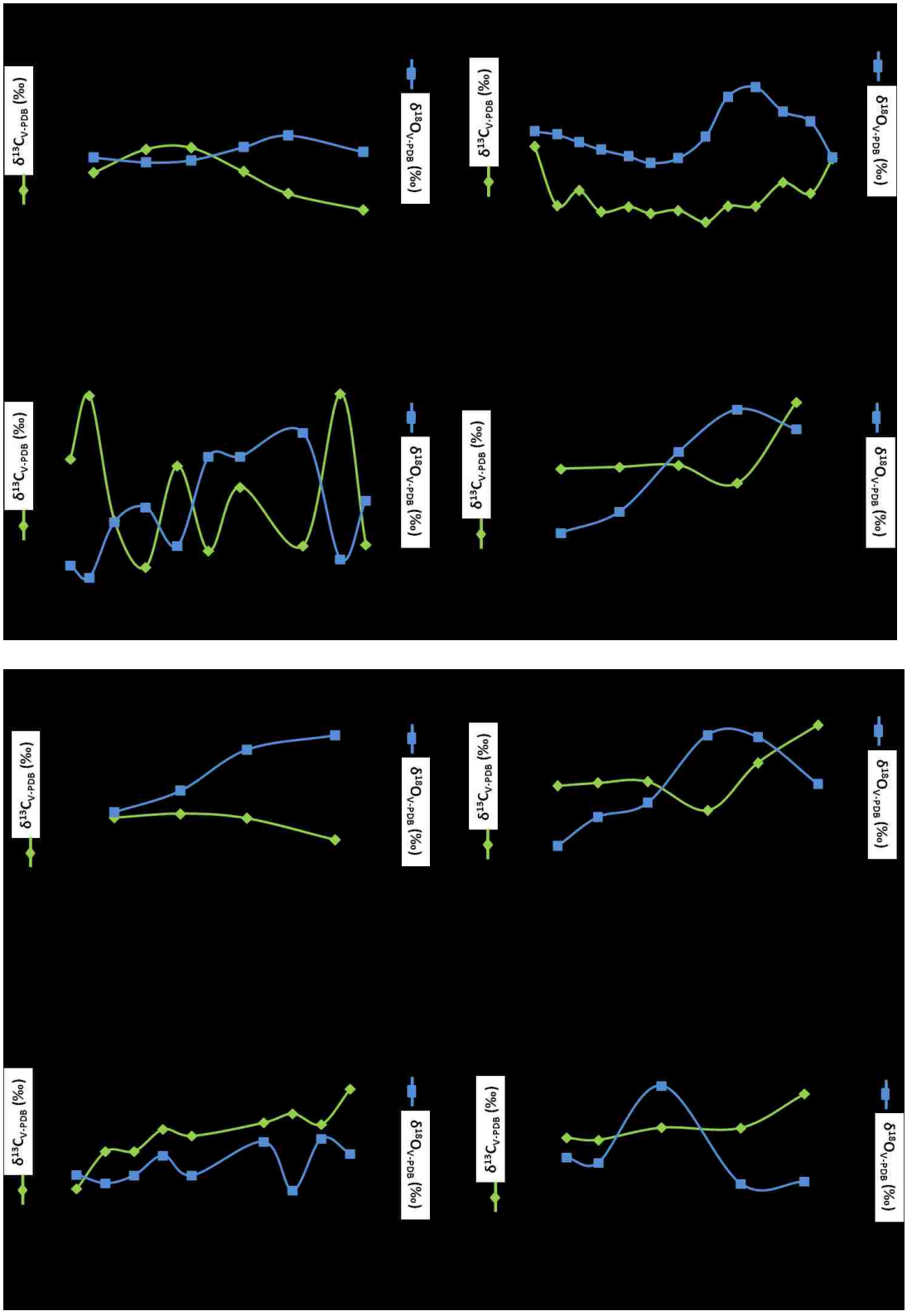


Figure 28. Serial $\delta^{13}C$ and $\delta^{18}O$ values for megaherbivores from Potter Creek Cave. Individuals are identified at the top of each graph by locality, specimen number, and species.

Samwel Cave serial data are graphed in Figure 29. *Equus* specimen SC-8867 has cyclical fluctuations, similar to the isotopic data from the Potter Creek Cave *Equus*. SC-8867 has $\delta^{13}C$ values ranging from -11.2 to -10.3‰, and $\delta^{18}O$ values that range from -7.1 to -5.4‰ (Figure 29a); the $\delta^{13}C$ and $\delta^{18}O$ serial values covary negatively (-0.08) and have a strong, negative correlation (r = -0.54). A second specimen of *Equus* from Samwel Cave, SC-8853, also shows small fluctuations in $\delta^{13}C$ values, ranging from -10.0 to -8.3‰ (Figure 29b), and has serial $\delta^{18}O$ values that range from -5.8 to -4.7‰. $\delta^{13}C$and $\delta^{18}O$ values for SC-8853 have negative covariance (-0.20) and very strong, negative correlation (-0.85). *Euceratherium* specimen SC-9488 has $\delta^{13}C$ values ranging from -10.8 to -8.6‰ and has $\delta^{18}O$ values that range from -6.0 to -3.7‰ (Figure 29c). Serial $\delta^{13}C$ and $\delta^{18}O$ values for SC-9488 result in weak covariance (0.08) and very weak, positive correlation (r = 0.14). Two specimens of *Odocoileus* were sampled from Samwel Cave. *Odocoileus* specimen SC-23082 has a very small range of $\delta^{13}C$ values (-11.2 to -10.7‰) and a slightly larger range of $\delta^{18}O$ values (-6.2 to -5.1‰) (Figure 29d), yielding a weak covariance in serial values (0.02) with weak, positive correlation (r = 0.22). The other Samwel Cave *Odocoileus* specimen, SC-35714, has a nearly identical range of $\delta^{13}C$ values as SC-23082 (-11.6 to -10.5‰) but a wider and more positive range in $\delta^{18}O$ values (-5.1 to -2.4‰). $\delta^{13}C$ and $\delta^{18}O$ serial values for SC-35714 weakly covary (0.11) and correlate positively (r = 0.26) (Figure 29f). *Nothrotheriops* specimen SC-9664 has $\delta^{13}C$ values ranging from -8.7 to -7.6‰ and $\delta^{18}O$ values ranging from -5.0 to -3.9‰; the oxygen and carbon values covary (0.20) and correlate positively, and very strongly (r = 0.99), although without obvious cyclical fluctuations (Figure 29e). Collectively, taxa from Samwel Cave have serial $\delta^{13}C$ values ranging from -11.6 to -6.3‰ (a difference of 5.3‰), which is a smaller range than is seen in the $\delta^{13}C$ data for megaherbivores from Potter Creek Cave; the Potter Creek Cave serial $\delta^{13}C$ values have a range of -12.7 to -4.6‰ (a difference of 8.1‰). Serial $\delta^{18}O$ values for all Samwel Cave megaherbivores range from -7.3 to -2.4‰ (a difference of

4.9‰), while serial $\delta^{18}O$ values for all Potter Creek Cave megaherbivores also has a larger range than those from Samwel Cave, from -9.7 to -2.0‰ (a difference of 7.7‰).

Two specimens from Hawver Cave were serially sampled. *Euceratherium* specimen HC-114876 has $\delta^{13}C$ values that range from -11.5 to -10.8‰; these values graphs as a sinuous curve with small amplitude fluctuations (Figure 29g). This range of values is very similar to $\delta^{13}C$ data for *Euceratherium* from Potter Creek Cave and Samwel Cave. HC-114876 has $\delta^{18}O$ values that range from -4.4 to -2.2‰, together, the serial $\delta^{13}C$ and $\delta^{18}O$ values weakly covary (-0.10) and have strong, negative correlation (r = -0.48). The Hawver Cave *Bison* specimen, HC-11006B, resulted in very small amplitude fluctuations in serial data; the $\delta^{13}C$ values range from -10.5 to -10.2‰ and $\delta^{18}O$ values range from -6.4 to -4.4‰ (Figure 29h). The $\delta^{13}C$ and $\delta^{18}O$ values for HC-11006B covary with a value of 0.11, and have very strong, positive correlation (r = 0.96).

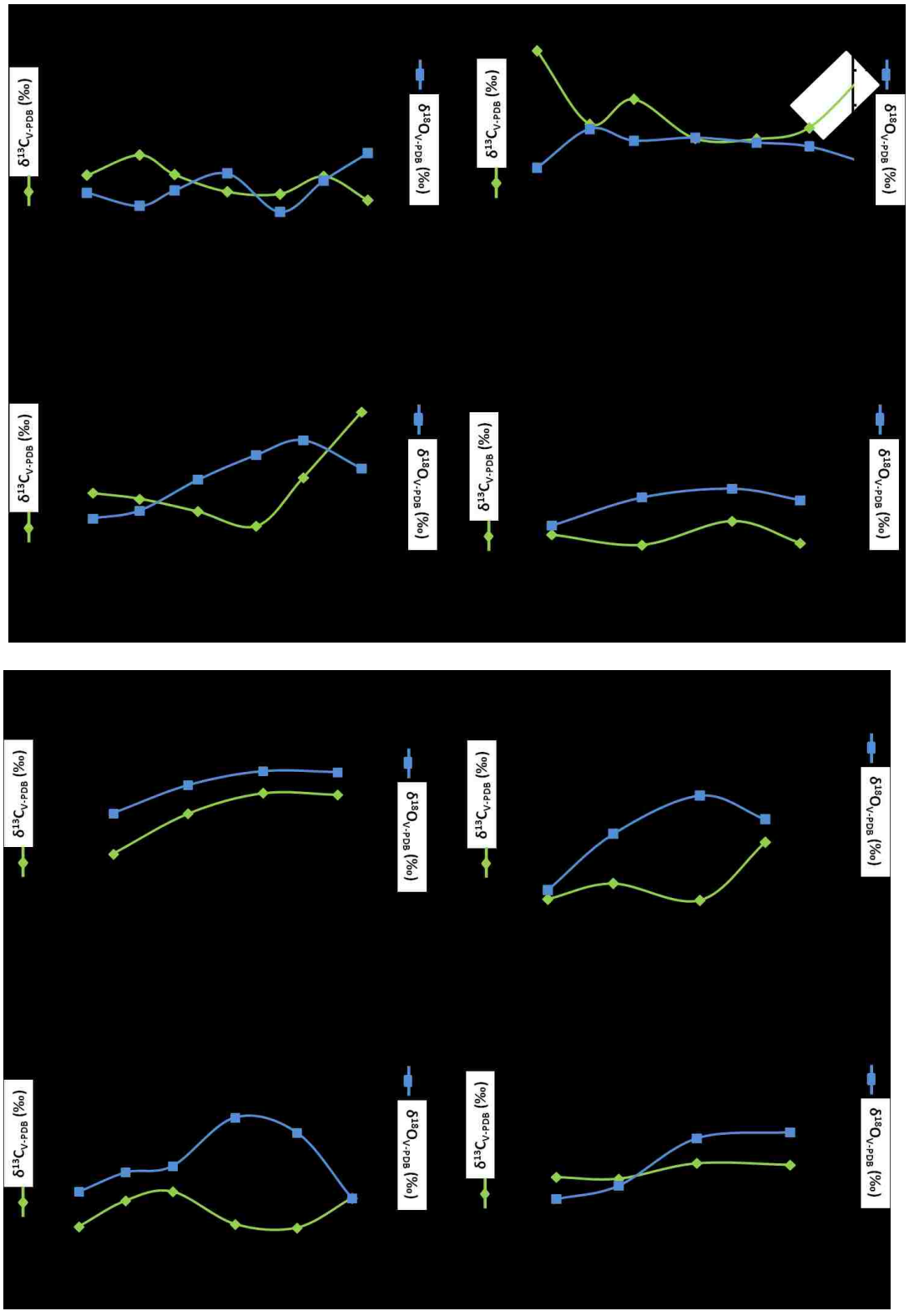


Figure 29. Serial $\delta^{13}C$ and $\delta^{18}O$ values for megaherbivores from Samwel Cave and Hawver Cave. Individuals are identified at the top of each graph by locality, specimen number, and species.

Figure 30 exhibits serial data for Devil Peak Cave, Wilkin Quarry, and the Gilcrease Site. *Nothrotheriops* from Devil Peak Cave, DP-200728, has a wider range of values than *Nothrotheriops* serial data from any of the other localities. DP-200728 has $\delta^{13}C$ values that range from -9.2 to 1.1‰ and $\delta^{18}O$ values that range from -10.1 to -6.2‰. Specimen DP-200728, has $\delta^{18}O$ and $\delta^{13}C$ values that covary strongly (1.50), and has strong, positive correlation (r = 0.60) (Figure 30a).

The Wilkin Quarry *Bison latifrons* specimen, B-1, has $\delta^{13}C$ values ranging from -8.0 to -5.4‰. This is a larger variation in $\delta^{13}C$ values than is seen in the *Bison* sp. from Hawver Cave, and is also considerably more enriched in ^{13}C. $\delta^{18}O$ values for B-1 vary from -11.7 to -9.7‰ (Figure 30b), a range of 2‰. This is the same as the range of $\delta^{18}O$ values in the *Bison* sp. from Hawver Cave, although the Wilkin Quarry *Bison latifrons* $\delta^{18}O$ values are considerabley more negative than the *Bison* sp. values from Hawver Cave. The $\delta^{13}C$ and $\delta^{18}O$ values covary with a value of 0.20 and have strong, positive correlation (r = 0.49).

Mammuthus columbi specimens were analyzed as a pilot test to validate vertebrate isotope analyses in LVIS (a new methodology for the lab). These data correlate well with the original isotope data for the specimens from Vetter (2007), which establishes the reliability of the use of biogeochemical analyses on teeth in the LVIS lab. The samples I retrieved and analyzed were a subset of the serial samples from Vetter (2007). Vetter (2007) analyzed 21 serial samples from the Gilcrease Site *Mammuthus* specimen MT-3 and 19 serial samples from *Mammuthus* specimen MT-4; I analyzed just 6 serial samples from each specimen in order to find if the data correlate (Figure 30c and d). The range of $\delta^{13}C$ values in this study differ from Vetter (2007) by up to 1.5‰ (with the exception of one depleted data point, which I attribute to contamination during sampling), with $\delta^{18}O$ differing by up to 2.0‰. These differences were

anticipated as the samples were run through different labs, and are likely due to slightly different treatment methods, machinery, and standards used between the two labs. Vetter's (2007) samples were analyzed at the University of California, Davis stable isotope lab. Although the serial data between this study and Vetter (2007) are not exact, most importantly, the trends are generally parallel, supporting the compatability of the results between the two labs. For the serial data retrieved in this study, *Mammuthus* specimen MT-3 has $\delta^{13}C$ values that vary from -10.0 to -7.2‰ and $\delta^{18}O$ values ranging from -14.6 to -11.6‰ (Figure 30c), and are very weakly and negatively correlated (r = -0.04). *Mammuthus* specimen MT-4 has $\delta^{13}C$ values that range from -13.5 to -8.8‰ and $\delta^{18}O$ values ranging from -14.5 to -12.7‰ (Figure 30d), which are weakly, positively correlated (r = 0.37).

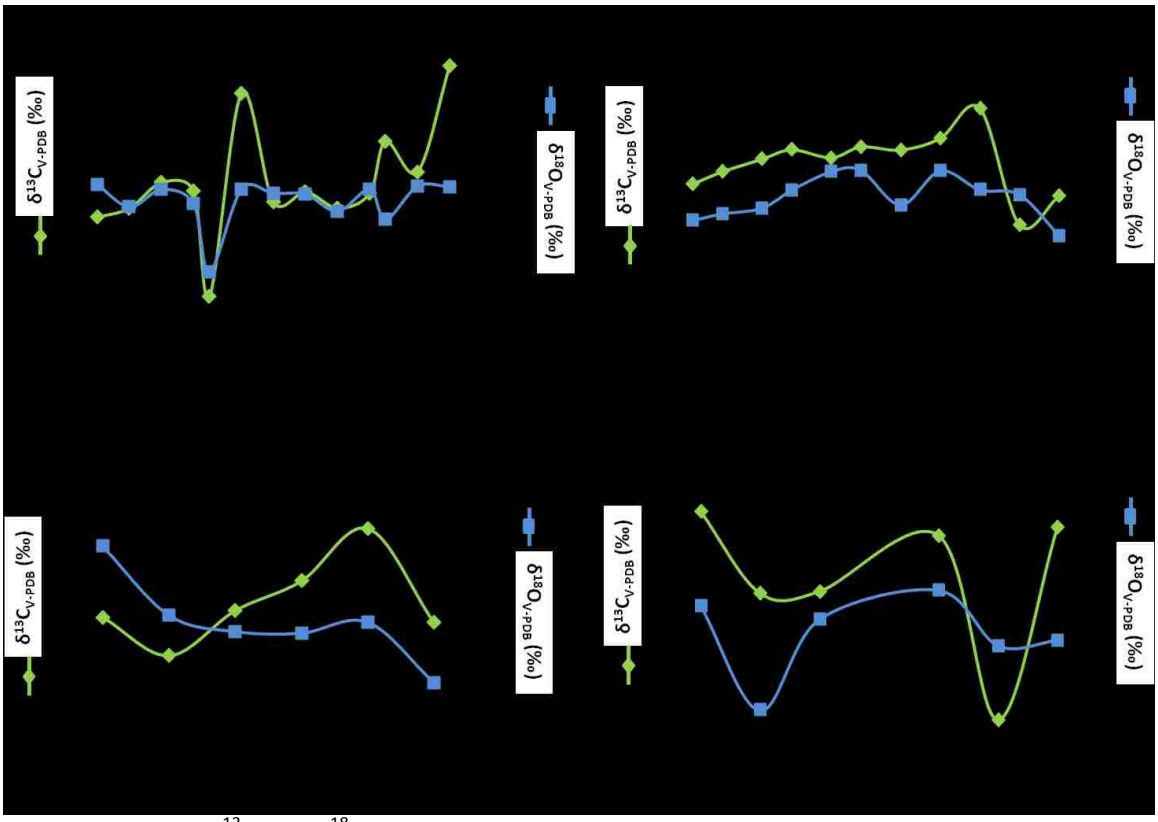


Figure 30. Serial $\delta^{13}C$ and $\delta^{18}O$ values for megaherbivores from Devil Peak Cave, Wilkin Quarry, and Gilcrease Site. Individuals are identified at the top of each graph by locality, specimen number, and species.

Discussion

Averaged $\delta^{13}C$ Results

There is an observable gradient in averaged carbon values between the assemblages, reflecting strong differences in $\delta^{13}C$ values between northern California and southern Nevada. All megaherbivores from Hawver Cave have very negative $\delta^{13}C$ values, which suggests that there was a high concentration of C_3-type vegetation in that area, indicating a dense, closed-canopy forest environment during the Pleistocene (Figure 31). The Potter Creek Cave and Samwel Cave assemblages contain taxa with greater variation in $\delta^{13}C$ values compared to Hawver Cave. Megaherbivores from Potter Creek Cave and Samwel Cave range from strict browsers to mixed feeders, with $\delta^{13}C$ data indicating an increased amount of C_4 grasses or shrubs in the region. This suggests that the area around Potter Creek Cave and Samwel Cave included both closed-forest and open-woodland habitats; some megaherbivores, such as *Odocoileus*, were forest dwellers while others, such as *Nothrotheriops*, foraged more open areas (Figure 31).

The southern Nevada assemblages are interesting in that *Mammuthus* from the Gilcrease Site falls within a browsing range, while the specimen of *Nothrotheriops* from Tule Springs (adjacent to the Gilcrease Site) is clearly a mixed feeder. These results indicate that southern Nevada at lower elevations had a wide range of vegetation available, from forest and open woodland to mixed grassland (Figure 31). The specimen of *Bison latifrons* from Wilkin Quarry has an averaged $\delta^{13}C$ value indicative of a mixed feeding diet, this is quite different from the browsing *Bison* sp. specimen from Hawver Cave, evident by an averaged value depleted in ^{13}C. No megaherbivores in this study displayed $\delta^{13}C$ values indicative of exclusive grazing.

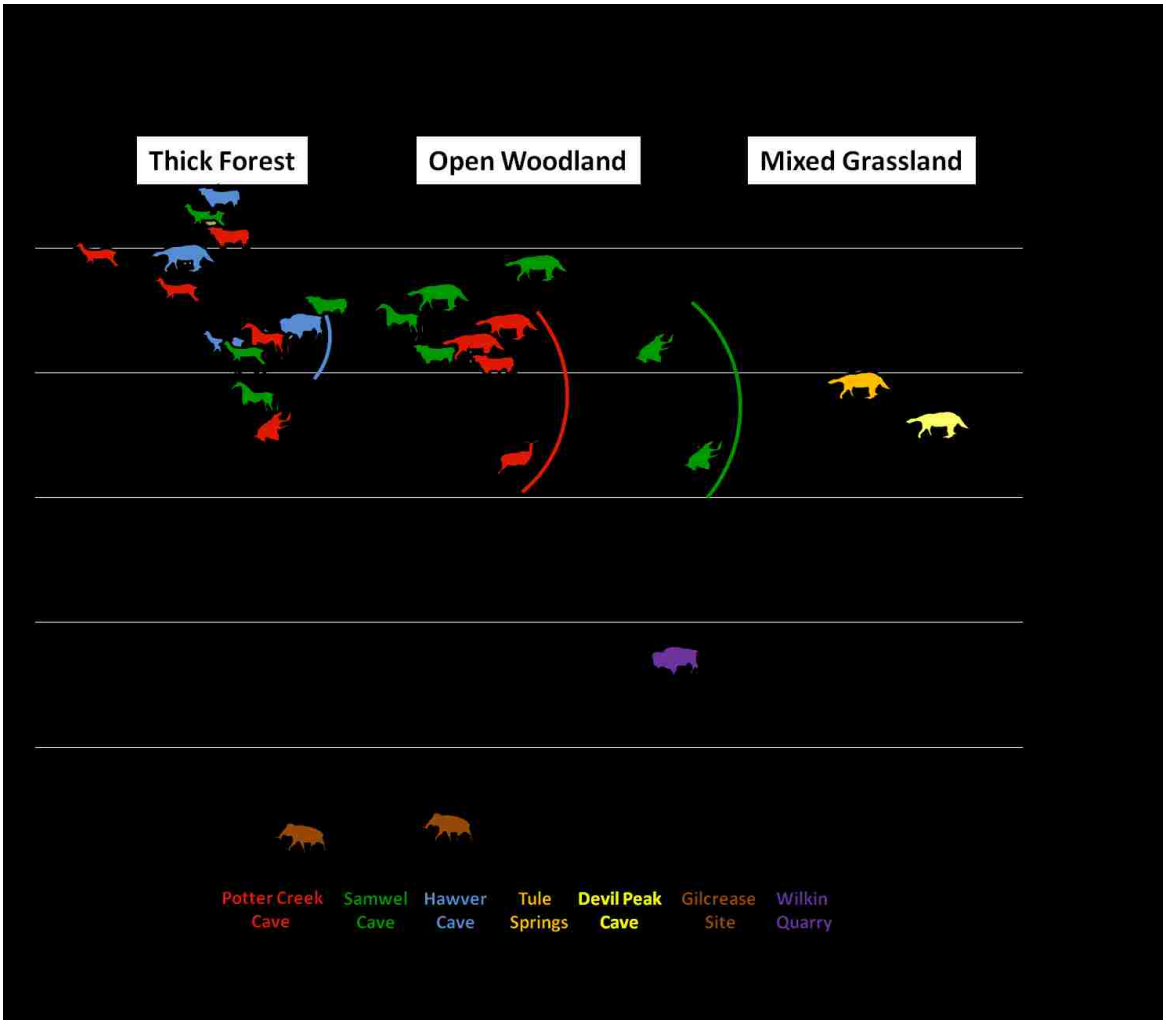


Figure 31. $\delta^{13}C$ and $\delta^{18}O$ data for all megaherbivores in this study. The blue, red, and green arcs show boundaries of $\delta^{13}C$ data for Hawver Cave, Potter Creek Cave, and Samwel Cave, respectively. Carbon isotope and ecosystem equivalents, expressed within stippled arrow, have been modeled after Kohn *et al*. (2005).

Hoppe *et al*. (2006) performed actualistic studies with modern *Bison bison*, comparing the $\delta^{13}C$ values of their teeth to vegetation in their environment. The result was an equation using the $\delta^{13}C$ values in teeth to quantify C_4% in the environment and in diet. Using their calculations (Eq. 1 & 2 – Chapter 1) on *Bison* in this study, the environment around Hawver Cave would have supported about 18% C_4-type grasses and, while *Bison* sp. at the site consumed about 16% of available C_4 vegetation. *Bison latifrons* from Wilkin Quarry consumed about 41%

C_4 grasses, with approximately 52% C_4 grasses comprising the vegetation of the area. According to Hoppe *et al*. (2006), calculations for dietary C_4% may be less by up to 5% in C_3 dominated areas and less by up to 27% in C_4 dominated areas (due to seasonal selectivity in diet). When considering the extremely depleted $\delta^{13}C$ values for Hawver Cave, in this study, these calculations seem generous for dietary C_4%. Therefore, when using these equations the lowest estimates of dietary C_4% abundance are more compatible with the results of this study.

Niche Partitioning of Megaherbivores

Figure 32 depicts the averaged $\delta^{13}C$ values for each megaherbivore taxon, grouped by locality. Averaged $\delta^{13}C$ values for megaherbivores from Potter Creek Cave and Samwel Cave are very similar. This similarity is anticipated since these two caves are very close, geographically, to one another. For these two sites, there is a conspicuous spectrum of $\delta^{13}C$ values, with *Odocoileus* having the most negative $\delta^{13}C$ values, *Equus* having slightly higher values, followed by *Euceratherium*, *Nothrotheriops*, and then *Ovis*, which has the least negative $\delta^{13}C$ values. The one taxon that displays a large difference in $\delta^{13}C$ values between Potter Creek Cave and Samwel Cave is *Megalonyx*. At Potter Creek Cave, *Megalonyx* has similar $\delta^{13}C$ values to *Euceratherium* and *Equus*, while at Samwel Cave, *Megalonyx* has higher $\delta^{13}C$ values than all other taxa.

The $\delta^{13}C$ data indicate that megaherbivores all fall within C_3-browsing to mixed feeding ranges, and reflect slight partitioning of diets. To avoid competition, herbivores have been found to use different food resources, move to different areas, or be more active during certain times of the year (Feranec *et al*., 2009). Data in this study support Feranec *et al*.'s (2009) observation about the utilization of different food resources.

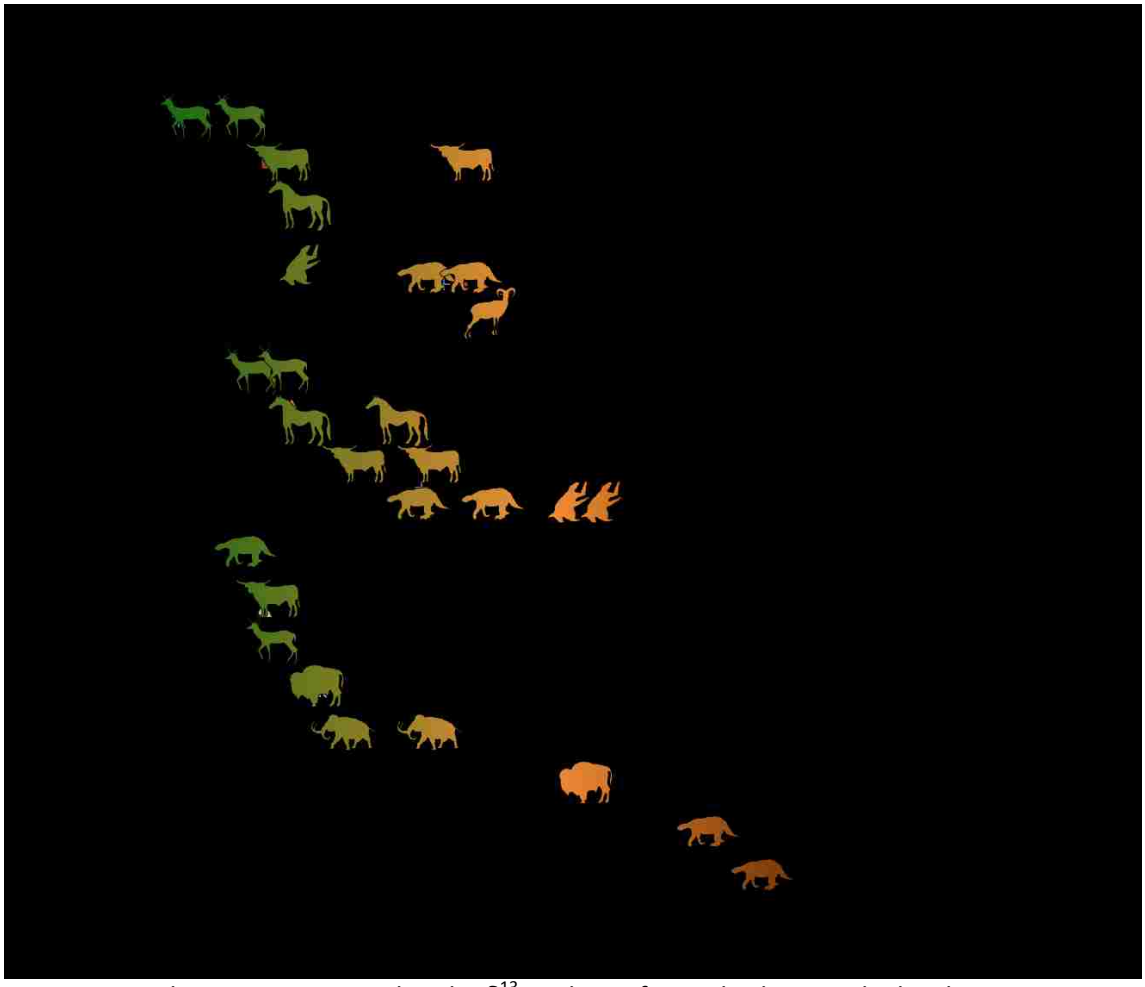


Figure 32. Niche partitioning evident by $\delta^{13}C$ values of megaherbivores, by locality. Taxa are placed along a $\delta^{13}C$ gradient showing C_3 consumers toward the left (green) and mixed to C_4 consumers toward the right (brown). Modeled after DeSantis *et al*., 2009.

The data for Hawver Cave show that all specimens have $\delta^{13}C$ values less than -10‰ and correspond with the $\delta^{13}C$ ranges of the other northern California megaherbivores. The surprising aspect of the Hawver Cave data is the very negative $\delta^{13}C$ values for *Nothrotheriops* and *Bison*. *Nothrotheriops* at Hawver Cave has significantly more negative values than at any other site, especially compared to its southern Nevada counterparts. *Nothrotheriops* displays a wide range in averaged $\delta^{13}C$ values, more than 7‰. This indicates that their dietary requirements were very plastic, allowing them to partition food resources within and between

environments. *Bison* $\delta^{13}C$ values indicate a browsing diet in northern California and a mixed diet in southern Nevada, suggesting that this taxon can also tolerate a vast amount of flexibility in diet, depending on their geographic distribution. This suggests that some taxa of megaherbivores were able to adjust their diet, not only to adapt to the environment in which they occurred, but also as a mechanism to avoid competition with other taxa. It is important to note that the *Bison* from northern California and southern Nevada are probably different species (*B.* sp. and *B. latifrons*, respectively), while *Nothrotheriops* from these localities are the same species (*N. shastensis*). The other two taxa of megaherbivore from Hawver Cave (*Odocoileus* and *Euceratherium*) have $\delta^{13}C$ values that are similar to those acquired from the same genera from Potter Creek Cave and Samwel Cave.

In a study of herbivores from the Late Pleistocene of Virginia, France *et al*. (2007) suggested that a lack of C_4 grasses (as was probably the case at the northern California localities) and reliance on C_3 vegetation may have promoted competition. Competition manifests itself as considerable overlap of $\delta^{13}C$ values between taxa. France *et al*. (2007) found that seven genera of herbivores (*Equus*, *Cervalces*, *Rangifer*, *Megalonyx*, *Mammuthus*, *Mammut*, and *Bootherium*) from a site in Virginia had a collective range in $\delta^{13}C$ values of just 3‰, concluding that this community of megaherbivores may have suffered from extreme competition. In my study, the range of $\delta^{13}C$ values at a given site had a collective range of up to 6‰, which suggests that interspecific competition for food resources was less intense. The co-occurring megaherbivores apparently partitioned themselves into selective niches ranging from strict C_3 browsers to mixed feeders (Figure 32).

The $\delta^{13}C$ data for *Mammuthus* from southern Nevada are very similar to the $\delta^{13}C$ data for *Equus* and *Euceratherium* from northern California. If these taxa had co-occurred, they may

have competed for the same food resources. Fossil material of *Mammuthus*, *Equus*, and *Euceratherium* reveal that these taxa did co-occur at many sites in western North America (Graham and Lundelius, 2010). Although, *Mammuthus* does not co-occur with *Equus* and *Euceratherium* at the localities in this study and, thus, does not allow me to test this hypothesis with isotopic data.

Late Pleistocene Environments

Kurtén and Anderson (1980) used faunal composition of the Potter Creek Cave and Samwel Cave assemblages to infer that the region was humid, coniferous to mixed forest but in proximity to low-elevation grasslands. The range of $\delta^{13}C$ values and interpretation of an open woodland/forest mosaic around Potter Creek Cave and Samwel Cave, in this study, agrees with Kurtén and Anderson's (1980) suggestion about the Late Pleistocene environments of this area. Stock (1918) and Kurtén and Anderson (1980) interpreted that the environment around Hawver Cave was humid, coniferous to mixed forest but with an additional component of chaparral, because of fewer forest dwelling taxa present in the assemblage. My isotopic data do not agree with the inclusion of a chaparral environment suggested by Stock (1918), an interpretation followed by Kurtén and Anderson (1980). The $\delta^{13}C$ data imply that the environment around Hawver Cave was likely a thick forest, as all $\delta^{13}C$ values are -10‰, or less.

Adam and West (1983) analyzed pollen data from west-central California and determined that during the Last Glacial Maximum (LGM) northern California was dominated by juniper and pine woodland at low elevations, which has since been replaced by oak woodland and mixed conifer forest. They suggested that the Mean Annual Temperature (MAT) was 7-8 ^{O}C cooler than present, while precipitation was 3-3.5 times higher. Using the Macrophysical Climate Models of Bryson (2005), I found that temperatures around Samwel Cave and Potter

Creek Cave during the Late Pleistocene were about 6.6 ^{O}C cooler than today (modern MAT is about 14.8 ^{O}C), with approximately 22% more precipitation. The environment around Hawver Cave showed a similar trend; Late Pleistocene temperatures were cooler by about 5.5 ^{O}C (modern MAT is about 14.5 ^{O}C) and precipitation was greater by about 30% (Table 11).

The δ^{13}C values of megaherbivores from southern Nevada suggest that Late Pleistocene environments were open woodland to mixed grassland. Hofreiter *et al*. (2000) analyzed plant material in ground sloth dung from Gypsum Cave, Nevada, (elevation 454 m) and determined that LGM climatic conditions in southern Nevada fluctuated, driving changes in plant communities. They found that *Nothrotheriops* consumed yucca and agave at around 20 Ka, indicating cool, arid conditions for the region. Currently, these plants occur only at higher elevations in southern Nevada (~1000 meters upslope), or at higher latitudes (Cole *et al*., 2011). Packrat midden analysis reveals that LGM vegetation of southern Nevada was dominated by pinyon-juniper woodlands at mid-elevations (550-1525m); these elevations are now occupied by desert scrub (Mehringer, 1967; Van Devender and Spaulding, 1979; Harris, 1985). Bristlecone pine, limber pine, and white fir communities were also depressed downslope into habitats that are now occupied by pinyon-juniper and blackbrush communities (1585-1860 m) (Mehringer, 1967; Van Devender and Spaulding, 1979). The δ^{13}C data in this study corroborate the interpretations from dung and pollen analyses; δ^{13}C data from *Mammuthus* suggest that during the Late Pleistocene a woodland existed where it is desert scrub today, and δ^{13}C data from *Nothrotheriops* support the presence of C_4 and/or CAM (presumably the yucca and agave referred to by Hofreiter *et al*. (2000)).

The Bryson (2005) paleoclimate model used in this study indicates that Tule Springs and Devil Peak Cave, during the Late Pleistocene, experienced a MAT of about 6.5 ^{O}C cooler than

today with 23-29% more precipitation (modern MAT of Tule Springs is about 19.4 ^{O}C and Devil Peak Cave MAT is about 16.7 ^{O}C). Late Pleistocene modeling of the region around Wilkin Quarry indicates that, during the LGM, MAT was 7.6 ^{O}C cooler than today (modern MAT is 10.6 ^{O}C) with 15% more moisture (Table 11). Stable isotope data and paleoclimate models support my hypothesis that southern Nevada and northern California were cooler during the Late Pleistocene and experienced more precipitation. Also, the difference in isotopic data indicates that northern California climates were cooler than southern Nevada, as southern Nevada had an increased component of C_4/CAM vegetation. Therefore, the regional climatic differences between southern Nevada and northern California during the Late Pleistocene were pronounced, as they are today.

Averaged $\delta^{18}O$ Results

Interpreting $\delta^{18}O$ data from megaherbivore teeth is much more complicated than interpreting $\delta^{13}C$ data; $\delta^{13}C$ is a representation of diet, while $\delta^{18}O$ is a representation of moisture and climate, thus it is influenced by many environmental factors. In addition, oxygen isotopes are also susceptible to water induced diagenetic alteration while demonstrations show that carbon isotopes remain unaffected (Wang and Cerling, 1994).

Averaged $\delta^{18}O$ data reveal that there is a very wide range in values between southern Nevada and northern California (up to 9.9‰), reflecting differences in climate and precipitation between the environments. This large variation stems from the much depleted ^{18}O values of *Bison* (Wilkin Quarry) and *Mammuthus* (Gilcrease Site), which are anomalously low compared to the other localities (Figure 31). *Bison* and *Mammuthus* $\delta^{18}O$ data aside, the remaining megaherbivores fall within a smaller range of just 4‰, where mixed feeding taxa are depleted in ^{18}O compared to browsing taxa.

Late Pleistocene surface water $\delta^{18}O_{V\text{-}SMOW}$ values were calculated for each locality, which is a representation of paleoprecipitation levels and relative climate. Typically, low $\delta^{18}O$ values represent cooler climates and/or higher levels of moisture, while increased $\delta^{18}O$ values represent warmer climates and/or lesser amounts of moisture (Luz *et al*., 1984; Sponheimer and Lee-Thorp, 1999). Calculations in this study show that $\delta^{18}O_{V\text{-}SMOW}$ values of Late Pleistocene surface waters (i.e., paleoprecipitation) had a higher degree of variation between the assemblages than what exists today (Table 10). Late Pleistocene surface water/precipitation values were calculated using Hoppe's (2006) least squares regression equation (Eq. 4 – Chapter 1). To form this equation, Hoppe (2006) compared the mean $\delta^{18}O_{V\text{-}SMOW}$ of modern *Bison* carbonate in enamel to $\delta^{18}O_{V\text{-}SMOW}$ of modern precipitation, for many localities across the United States. Using this equation, I calculated $\delta^{18}O_{V\text{-}SMOW}$ values of surface water for the Late Pleistocene assemblages in this study (Table 10). Conforming to Hoppe's (2006) use of *Bison*, I used $\delta^{18}O_{V\text{-}SMOW}$ values from *Bison* at Hawver Cave and Wilkin Quarry. Because not all localities contained *Bison*, I substituted *Equus* $\delta^{18}O_{V\text{-}SMOW}$ for some localities, making the assumption that these two taxa of water-dependant megaherbivores physiologically process water similarly (Table 10).

Modern precipitation $\delta^{18}O$ values were retrieved from the Online Isotopes in Precipitation Calculator (OIPC), using latitude, longitude, and elevation for each site (Bowen, 2012). $\delta^{18}O_{V\text{-}SMOW}$ shows a greater difference between modern and Late Pleistocene precipitation for the northern California localities than for the southern Nevada localities. Modern precipitation at the northern California sites (Samwel Cave/Potter Creek Cave and Hawver Cave) are depleted in $\delta^{18}O_{V\text{-}SMOW}$ by 4.0 to 4.7‰, compared to Late Pleistocene precipitation. Modern precipitation at Devil Peak Cave and Tule Springs, in southern Nevada, are depleted in $\delta^{18}O_{V\text{-}SMOW}$ by 1.7 to 2.1‰, compared to Late Pleistocene values. Wilkin Quarry

$\delta^{18}O_{V\text{-}SMOW}$ of modern precipitation is enriched by 2.1‰ compared to Late Pleistocene precipitation.

The results of the surface water calculations were surprising and contradicted my hypothesis. I had hypothesized that Late Pleistocene conditions were wetter than modern, although the enrichment of Late Pleistocene ^{18}O in precipitation, compared to modern, indicate that conditions were more arid than today. Wilkin Quarry is the only site that shows a depletion in ^{18}O from modern to Late Pleistocene conditions, suggesting that this one locality experienced higher amounts of precipitation than today. This information also contradicts the Bryson (2005) paleoclimate model results for the sites. The model indicates that northern California experienced 30-35% more precipitation than today, while southern Nevada had up to 20% more precipitation than today (Table 11).

Several other studies of Late Pleistocene megafaunal enamel have found this same phenomenon (i.e., depleted levels of ^{18}O in modern precipitation compared to that of the Late Pleistocene) (Kohn *et al*., 1996; Cerling *et al*., 1997; Sponheimer and Lee-Thorp, 1999; Kohn and Cerling, 2002; Hoppe *et al*., 2004; Kohn and McKay, 2012). These researchers suggested the four following possible explanations for this phenomenon:

(*1*) Although it has generally been accepted that ingested meteoric waters mineralize in equilibrium with body water (Luz *et al*., 1984; Byrant and Froelich, 1995), some researchers have suggested that fractionation of oxygen isotopes occurs in body water due to metabolic processing, resulting in an enrichment of ^{18}O. Authors suggest that this could increase $\delta^{18}O$ in teeth by 3-8‰, compared to ingested waters (Kohn and Cerling, 2002; Hoppe *et al*., 2004). Koch *et al*. (2009) state that this complicated interplay is a current topic of study, where $\delta^{18}O$ of biominerals has recently been found to be higher, relative to body water, although the exact

fractionation amount is not yet quantified. If the $\delta^{18}O$ of megaherbivore teeth do experience a positive fractionation from ingested water then the amounts suggested by Kohn and Cerling (2002) and Hoppe *et al*. (2004) could explain the unexpected enrichment of $\delta^{18}O$ values of Late Pleistocene surface waters compared to today.

(*2*) Due to evapotranspiration, leaf water is enriched in ^{18}O compared to ground waters. This would result in browsing taxa being enriched in ^{18}O compared to precipitation because of the high amount of C_3 vegetation that was consumed. This concept explains why browsers and mixed feeders tend to be enriched in ^{18}O compared to grazers (Kohn *et al*., 1996; Cerling *et al*., 1997; Sharp and Cerling, 1998; Sponheimer and Lee-Thorp, 1999). Consequently, the enrichment of ^{18}O in megaherbivore teeth would affect the equations of Hoppe (2006) when calculating Late Pleistocene surface waters.

(*3*) The unexpected enrichment of ^{18}O in Late Pleistocene waters (as calculated from $\delta^{18}O$ values of teeth) may be a result of evaporation levels between the localities. Isotopic compositions of surface waters are sensitive to environmental factors such as Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) (Dansgaard, 1964; Sharp and Cerling, 1998; Sponheimer, 1999). Carbonate in teeth captures the $\delta^{18}O$ of surface water, which may differ when compared to $\delta^{18}O$ of precipitation due to evaporation, especially in arid or semi-arid environments (Hoppe *et al*., 2004). This, too, would result in skewed calculations for $\delta^{18}O$ of Late Pleistocene precipitation.

(*4*) Lastly, I suggest that Hoppe's (2006) equation works well for modern *Bison* when compared directly to modern environments, but that applying the equation to Late Pleistocene *Bison*, or *Equus*, from various geographic areas is inequivalent and yields unreliable results. I found this to be true when using Kohn and McKay's (2012) equation to calculate MAP (Eq. 3 -

Chapter 1) and Grafenstein *et al*.'s (1996) equation to calculate MAT (Eq. 5 – Chapter 1). When applying these equations to the isotopic data in this study, both of these equations yielded incongruous results. I suspect it is because these equations were constructed for particular locations in North America and the parameters of the equations do not translate to the localities in this study. Because of the questionable results obtained using these equations, I turned to paleoclimate modeling, using the Macrophysical Climate Model of Bryson (2005), discussed below.

Using the Hoppe (2006) equation, the calculated $\delta^{18}O$ values of Late Pleistocene precipitation are enriched in ^{18}O compared to modern precipitation (Table 10), suggesting that Late Pleistocene environments were more arid than today. This was very likely the case during certain periods of the Late Pleistocene, although the animals whose remains were analyzed in this study were dated to have lived during the Last Glacial Maximum, an unequivocally wet interval. This also conflicts with many other interpretations that more precipitation occurred during the LGM than today. Paleoclimate models (Bryson, 2005), pollen (Mehringer, 1967; Adam and West, 1983), lake levels (Thompson *et al*., 1993), dung (Poiner *et al*., 1998; Hofreiter *et al*., 2000; Gill *et al*., 2009) and midden data (Van Devender and Spaulding, 1979; Spaulding, 1985) all show that environmental conditions in western North America were wetter during the LGM than today. To exemplify this, Table 11 shows modern and Late Pleistocene Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) for each locality. Late Pleistocene MAT and MAP were derived using the Macrophysical Climate Model (Bryson, 2005). To produce Late Pleistocene data, this modeling program takes into account modern and historical climate data, Milankovitch cycles, atmospheric transparency, position of the jet stream and intertropical convergence zone, among other parameters (Bryson , 2005; Bryson and DeWall, 2007; Bryson *et al*., 2010). In this study, I calibrated the Macrophysical Climate Model with modern climatic data

for each location. Data were retrieved by averaging precipitation and temperature vectors within known radiocarbon age intervals.

Table 10. Average annual $\delta^{18}O_{V\text{-}SMOW}$ of modern and Late Pleistocene precipitation. Modern values were calculated from the Online Isotopes in Precipitation Calculator using latitude, longitude, and elevation (Bowen, 2012). Late Pleistocene values were calculated using Hoppe (2006) where surface waters represent precipitation. Winter (W) and summer (S) values are included to demonstrate variations in seasonality.

Locality	Modern precipitation ($\delta^{18}O_{V\text{-}SMOW}$)	Late Pleistocene (LP) precipitation ($\delta^{18}O_{V\text{-}SMOW}$)	Difference	Taxa used for LP calculation/Source
Samwel Cave/ Potter Creek Cave (lat./long./elev. - Point McCloud, CA)	-11.4‰ (W -11.8/S -7.8)	-6.7‰	4.7‰	*Equus* (Potter Creek Cave, this study)
Hawver Cave (lat./long./elev. - Hawver Cave Trailhead)	-10.7‰ (W -11.2/S -7.0)	-6.7‰	4.0‰	*Bison* (Hawver Cave, this study)
Devil Peak Cave (lat./long./elev. - Goodsprings, NV)	-10.5‰ (W -12.5/S -7.0)	-8.8‰	1.7‰	*Equus* (Kokoweef Cave, Connin *et al*., 1998)
Tule Springs (lat./long./elev. - Tule Springs Ranch, NV)	-10.0‰ (W -12.0/S -6.7)	-7.9‰	2.1‰	*Equus* (Tule Springs, Connin *et al*., 1998)
Wilkin Quarry (lat./long./elev. - Panaca, NV)	-12.2‰ (W -14.8/S -8.6)	-14.3‰	-2.1‰	*Bison* (Wilkin Quarry, this study)

Output from the Macrophysical Climate Model (MCM) supports interpretations from the $\delta^{13}C$ and $\delta^{18}O$ data that the LGM was cooler with higher amounts of precipitation than today. Higher levels of precipitation in the Late Pleistocene should correspond to lower $\delta^{18}O_{V\text{-}SMOW}$ values of surface waters compared to modern conditions, which does not agree with the $\delta^{18}O_{V\text{-}SMOW}$ of surface waters calculated from Hoppe (2006). Therefore, empirical equations that have been constructed for a particular location, or by using data from a particular taxon, are not the best indicator of Late Pleistocene environmental conditions for regions in this study. For this

reason, I employed the MCM, which is independently congruent with the results of my isotopic analysis.

Table 11. Modern and Late Pleistocene Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP). Modern MAT and MAP are from the Western Regional Climate Center (WRCC). Late Pleistocene MAT and MAP average values were obtained using the Macrophysical Climate Model (Bryson, 2005), and were correlated to radiocarbon dates for each site. Winter (W) and summer (S) values are included to demonstrate variation in seasonal values. Late Pleistocene winter values were calculated from December/January/February averages of model outputs, and summer values were calculated from June/July/August averages of model outputs.

Locality	Modern MAT (^{O}C)	Modern MAP (mm)	Late Pleistocene MAT (^{O}C)	Late Pleistocene MAP (mm)
Samwel Cave/ Potter Creek Cave (Lakeshore 2, CA-WRCC)	14.8 (W 6.9/S 23.3)	1742 (W 919/S 56)	8.2 (W -0.6/S 17.6)	2132 (W 385/S 18)
Hawver Cave (Auburn, CA-WRCC)	14.5 (W 7.3/S 22.4)	947 (W 440/S 19)	9.0 (W 2.4/S 16.4)	1237 (W 244/S 6)
Devil Peak Cave (Pahrump, NV-WRCC)	16.7 (W 6.6/S 27.6)	122 (W 50/S 18)	10.2 (W -1.1/S 22.2)	152 (W 28/S 6)
Tule Springs (North Las Vegas-WRCC)	19.4 (W 8.7/S 30.5)	107 (W 47/S 16)	13.1 (W 2.1/S 24.6)	138 (W 15/S 9)
Wilkin Quarry (Pioche – WRCC)	10.6 (W 0.6/S 21.2)	335 (W 109/S 70)	3.0 (W -6.8/S 13.7)	385 (W 54/S 22)

According to the MCM, Late Pleistocene temperatures of California and Nevada were between 5.5 to 7.5 ^{O}C cooler than modern temperatures, with 15 to 30% higher total precipitation levels; northern California experienced up to fifteen times as much precipitation as southern Nevada (which is similar to precipitation differences today). The MCM reveals less winter/summer moisture extremes during the Late Pleistocene, where more moisture occurred year-round resulting in an overall increase of precipitation for all localities (Table 11). Increased precipitation in the West and Southwest during the Late Pleistocene was modulated by position of the intertropical convergence zone, southward displaced westerly atmospheric currents, and

latitudinally lowered jet stream during cool/warm excursions of the Pleistocene, bringing more oceanic moisture inland (Van Devender, 1987; Asmerom *et al*., 2010; Oster, 2010). In contrast to Late Pleistocene precipitation patterns, today California receives most of its precipitation in the winter (January/February), while southern Nevada receives most of its precipitation in the summer (July/August) (Thompson *et al*., 1993). The high levels of summer precipitation in southern Nevada are due to monsoonal storms; the dominant shift from winter to summer precipitation occurred about 12 Ka (Spaulding and Graumlich, 1986). For California, modern controls on precipitation are correlated to westerly flow of precipitation in winter months, whereas Nevada's summer precipitation correlates with southerly monsoonal flow from the Pacific or Gulf of California (Thompson *et al*., 1993). Because of the different sources, precipitation gradients show strong seasonal variations throughout the West and Southwest. Serial $\delta^{18}O$ values of megaherbivore teeth do not show strong variations in Late Pleistocene seasonality, although southern Nevada taxa tend to be depleted in ^{18}O compared to northern California taxa.

$\delta^{13}C$ and $\delta^{18}O$ Serial Data

Examining the covariance between $\delta^{13}C$ and $\delta^{18}O$ of serial data (Figures 28, 29, and 30) reveals that there is not a consistent relationship of these two variables, either within taxa or within localities. Of the fourteen specimens that have $\delta^{13}C$ and $\delta^{18}O$ serial data, six of them covary negatively, while eight specimens covary positively. The negatively covarying specimens include *Equus* (PC-8616), *Euceratherium* (PC-8385), *Odocoileus* (PC-4174), *Ovis* (PC-8451), *Nothrotheriops* (PC-8715), and *Mammuthus* (MT-3). High $\delta^{18}O$ values in many cases correspond to low $\delta^{13}C$ values, which indicate that warm periods correspond to an increase in C_3 vegetation in the diet, and cooler periods correspond to an increase in C_4/CAM vegetation in the diet. This

suggests that warm/wet periods alternated with cool/arid periods. Conversely, serial data from eight specimens covary positively; these include *Euceratherium* (PC-8730), *Nothrotheriops* (PC-8141, SC-9664, and DP-200728), *Odocoileus* (SC-35714), *Bison* (HC-11006B and B-1), and *Mammuthus* (MT-4). These specimens indicate that warm/arid periods alternated with cool/wet periods , where warming trends correspond to increased C_4/CAM plant consumption while cooling trends correspond to increased C_3 plant consumption (Figures 28, 29, and 30).

The inconsistency of covarying serial $\delta^{18}O$ and $\delta^{13}C$ values within taxa and within localities is unexpected, as was the high number of negatively covarying taxa. Negative covariance is best exemplified by *Euceratherium* specimen PC-8385 in Figure 28c, which displays a conspicuous negative covariance between $\delta^{13}C$ and $\delta^{18}O$ values. This inverse relationship has been documented in previous isotopic works on megaherbivore teeth (Feranec *et al*., 2009; Maung-Thein *et al*., 2011; Kohn and McKay, 2012). Kohn and McKay (2012) list a number of potential reasons to explain the negative covariance between $\delta^{18}O$ and $\delta^{13}C$ data. The explanations that seem most plausible and applicable to this study include moisture and diet: 1) Moisture – $\delta^{13}C$ values of plants decrease with increasing moisture availability due to low evapotranspiration rates (Farquhar *et al*., 1989; Kohn, 2010). If summers were relatively wet compared to the other seasons, then this could result in higher $\delta^{18}O$ values in precipitation but lower $\delta^{13}C$ values in plants, 2) Diet – megaherbivores may have utilized different parts of plants in different seasons, such as leaves in the summer and bark or twigs in the winter. Or they may have switched to conifers in winter. Bark, twigs, and conifers are known to be enriched in ^{13}C, compared to leaves, resulting in higher $\delta^{13}C$ values in winter (Kohn and McKay, 2012). I suggest that the negative covariance between $\delta^{13}C$ and $\delta^{18}O$ of megaherbivore teeth in some specimens is a combination of both of Kohn and McKay's (2012) explanations – moisture and diet.

The positive covariance of $\delta^{18}O$ and $\delta^{13}C$ serial values seen in some of the specimens was the type of relationship that was anticipated, reflecting warm/arid summers (higher $\delta^{18}O$ values) corresponding with increased mixed feeding/C_4 consumption (higher $\delta^{13}C$ values), while cool/wet intervals indicate winter seasonality with lower $\delta^{18}O$ values corresponding with increased C_3 consumption (lower $\delta^{13}C$ values).

The MCM (Bryson, 2005) used in this study shows that Late Pleistocene conditions were cooler and wetter than modern conditions, with the increased precipitation levels distributed more evenly throughout the year (Table 11). The model shows that Late Pleistocene winters still received more precipitation than summers, although this model predicts averaged climatic conditions over 100 year intervals. Serial $\delta^{18}O$ and $\delta^{13}C$ data from the taxa in this study can supply more precise environmental data over a multi-year time interval, for the different localities. All of the localities experienced averaged winter temperatures that were close to freezing, and most of the precipitation likely fell as snow. Therefore, in winter the megaherbivores experienced less access to lush vegetation and greater dependence on isotopically heavy plants, or the drier parts of plants, manifesting in teeth as low $\delta^{18}O$ values but high $\delta^{13}C$ values. During the summer months, temperatures were warmer but conditions were still relatively wet and C_3 vegetation could flourish, manifesting itself as higher $\delta^{18}O$ values but low $\delta^{13}C$ values, thus further explaining the negative covariance between $\delta^{18}O$ and $\delta^{13}C$ values.

Migrational tendencies may also be apparent in the carbon and oxygen serial data. The challenge is to decipher the difference between seasonal and migratory fluctuations in $\delta^{18}O$ values of teeth. Migratory behavior is evident when the range of $\delta^{18}O$ values recorded in a tooth exceeds the known seasonal range of $\delta^{18}O$ values in local waters. For example, $\delta^{18}O$ values in modern precipitation in northern California vary by about 4‰ between winter and

summer, while $\delta^{18}O$ values in southern Nevada vary by about 6‰ (Bowen, 2012) (Table 10). If $\delta^{18}O$ values in teeth show isotopic fluctuations that are greater than these seasonal swings, I conclude that the animal was consuming waters from different geographic locations, indicating migratory behavior. The MCM shows that the abundance of seasonal precipitation was less variable in the Late Pleistocene compared to the modern, for each site (Table 11). $\delta^{18}O$ values have not been calculated for Late Pleistocene seasonal precipitation at each site, although if values were less variable than modern values, then migratory patterns should be all the more evident.

Isotopic results from this study show that the range of $\delta^{18}O$ values for serial data is rarely greater than 4‰ (Figures 28, 29, 30). Higher $\delta^{18}O$ values reflect summer seasonality and low $\delta^{18}O$ values reflect winter seasonality. The majority of serial $\delta^{13}C$ values range from 0.5 to 2.5‰. This reflects a small range in diet, indicating that most animals maintained similar diets throughout the year. The $\delta^{18}O$ data indicate that megaherbivores experienced little mobility, as fluctuations in $\delta^{18}O$ of source waters were low (less than 4‰) and did not exceed the seasonal $\delta^{18}O$ range of values for the sites. This information supports the interpretation that environmental conditions were moderated throughout the year, without extreme winter/summer conditions and with abundant vegetation through the seasons. However, two specimens from Potter Creek Cave are not compatible with these interpretations, *Euceratherium* specimen PC-8385 (Figure 28c) and *Ovis* specimen PC-8451 (Figure 28f). These two specimens have serial $\delta^{13}C$ values that fluctuate up to 7‰ and $\delta^{18}O$ values that fluctuate up to about 5‰, thereby indicating that these animals probably migrated seasonally, between differing environments or elevations.

Serial Data by Taxon

Nothrotheriops shastensis and *Megalonyx jeffersonii* – The presence of desert-adapted plants in *N. shastensis* dung from caves in the Southwest have led to the common interpretation that *N. shastensis* was a browser in arid climates. This is supported by isotopic data from Devil Peak Cave (Figure 30a) and Tule Springs, although the depleted $\delta^{13}C$ values from northern California sites indicate that this species had a much more isotopically diverse diet than previously thought (Figure 28g and h, Figure 29e). Serial $\delta^{13}C$ values of some specimens of *N. shastensis* reveal an enrichment in ^{13}C through life, indicating a tendency to consume C_3 or mixed vegetation in earlier years and increasing percentages of C_4 vegetation before death.

Although I have no serial isotopic data for *M. jeffersonii*, averaged carbon isotope data from northern California *M. jeffersonii* specimens reveal that its diet consisted mainly of C_3 vegetation, supporting the idea that it inhabited forested environments (McDonald and Morgan, 2011).

Detailed descriptions of the isotopic results for *N. shastensis* and *Megalonyx* and interpretations of their paleoecology are presented in Chapter 3.

Bison – Some studies have shown extinct *Bison* to have been hypergrazers that consumed greater than 90% grasses (Tieszen, 1994; Nunez *et al*., 2010), while other studies have shown that they had greater dietary diversity (more consistent with mixed feeding) than do modern grass-grazing *Bison*, based on on tooth microwear studies (Rivals *et al*., 2007) and dental bolus analysis (Akersten *et al*., 1988). Rivals *et al*. (2007) concluded that Late Pleistocene *Bison* in North America were more biogeographically diverse than modern *Bison* and occupied a range of habitats, from semi-desert to boreal forest. If this is true, then Late Pleistocene populations would indeed have had a greater dietary variety than modern populations. Hoppe

et al. (2006) analyzed modern *Bison* populations from across central North America and discovered that the $\delta^{13}C$ in diet varies by up to 10‰, showing that the diet of modern *Bison* can vary substantially, even within their contracted geographic range. My data reinforce the conclusions of both Hoppe *et al*. (2006) and Rivals *et al*. (2007). The *Bison* specimens in this study exhibit great variation in diet, with very negative $\delta^{13}C$ values, indicating browsing, at Hawver Cave, to more positive $\delta^{13}C$ values, indicating mixed feeding, at Wilkin Quarry. Serial $\delta^{13}C$ data show an abundance of C_3 vegetation consumed by *Bison* through the year and not just on a seasonal basis. The serial data for *Bison* sp. from Hawver Cave show extremely low-amplitude variations in $\delta^{13}C$ values (0.3‰) (Figure 29h). Serial data for *Bison latifrons* from Wilkin Quarry yielded much more seasonal variation (2.6‰) than *B.* sp. from Hawver Cave, showing a larger variation in diet as a response to environmental conditions (Figure 30b). Although the range of $\delta^{13}C$ values varies between these species of *Bison*, their $\delta^{18}O$ values have the same ranges (2‰), with *B.* sp. from Hawver Cave being depleted in comparison to *B. latifrons* from Wilkin Quarry. Results of this study reinforce the conclusion that, as a genus, Late Pleistocene *Bison* exhibits a wide range in diet. Individuals, however, do not show much variation through life and likely did not migrate seasonally through a wide range of latitudes or elevations.

Equus – Previous studies have concluded that Late Pleistocene *Equus* was a facultative grazer (Tieszen, 1994; Nunez *et al*., 2010). However, my isotopic data, with very negative serial $\delta^{13}C$ values, indicate that *Equus* in northern California had a browsing diet. Vetter (2007) also determined that Late Pleistocene *Equus*, although in southern Nevada (Gilcrease Site), was a browser. The $\delta^{13}C$ values show that *E. occidentalis* at Potter Creek Cave (Figure 28a) and *E*. sp. at Samwel Cave (Figure 29a and b) also consumed C_3 browse, with serial values all lower than -8‰ and averaging less than -10‰. Individuals exhibit very small amplitude fluctuations in $\delta^{13}C$

and $\delta^{18}O$ values inter-annually (less than 1.7‰), suggesting that seasonal variation in their diet and water source was not highly variable, and that C_3 vegetation was available throughout the year. Sharp and Cerling (1998) determined that *Equus* teeth grow at a rate of about 35 mm per year, with sub-annual periodicity. The whole tooth mineralizes in about two years, thereby providing a limited observation of annual changes through life. Based on this growth rate, the *Equus* teeth in this study (which average about 40 mm in length) represent just over one year of recorded growth. The inversely correlated $\delta^{13}C$ and $\delta^{18}O$ serial data exhibit cycles that demonstrate a 1 to 1.5 year growth period (Figures 28a, 29a and b).

Mammuthus columbi – Tieszen (1994) and Nunez *et al*. (2010) determined that Late Pleistocene *Mammuthus* were facultative grazers. Connin *et al*. (1998) used isotopic analysis to conclude that *Mammuthus* from the Southwest fed primarily on grass, with a diet of <20% trees, herbs, and shrubs. These interpretations are supported by the high grass content in *Mammuthus* dung from southern Utah; the dung was found to be comprised of 95 to 99% grasses, sedges, and C_4 shrubs, with only trace amounts of C_3 plants (Hansen, 1980; Mead *et al*., 1986). These discoveries are contradictory to the evidence from my isotopic data, which agrees with Vetter (2007), revealing that Late Pleistocene *M. columbi* in southern Nevada (Gilcrease Site) were browsers, as the serial $\delta^{13}C$ data indicate (Figure 30c and d). $\delta^{18}O$ data show variations in serial data, although *M. columbi* is extremely depleted in ^{18}O compared to all other megaherbivores. The $\delta^{18}O$ values in teeth resemble the $\delta^{18}O$ of local surface waters where they were collected (Table 10), raising suspicions that carbonate oxygen values in teeth may have been affected by ionic exchange with the oxygen in the springs from which they were recovered.

Odocoileus – Of all taxa analyzed, *Odocoileus* has the most negative averaged $\delta^{13}C$ values with a very small range of averaged $\delta^{13}C$ values between assemblages (less than 1.4‰).

Kohn *et al*. (2005) found that fossil *Odocoileus* in South Carolina is very depleted in ^{13}C with values of less than -12‰, which is well within strict C_3-consumer range, and more negative than the $\delta^{13}C$ values in this study. Nunez *et al*. (2010) found a more C_4/CAM signature for *Odocoileus*, in Sonora, Mexico, suggesting that it may have had a more variable diet than strict browsing. This difference in diet can be attributed to two different species of *Odocoileus, O. virginianus* (white-tailed deer) (Kohn *et al*., 2005) versus *O. hemionus* (mule deer) (Nunez *et al*., 2010). *O. virginianus* currently inhabits eastern regions of North America, which has a very different vegetative composition compared to western North America where *O. hemionus* exists, although there was significant overlap in biogeographic range during the Pleistocene (Graham and Lundelius, 2010). Of the five *Odocoileus* teeth analyzed in this study, only one, from Hawver Cave (HC-11016), was identified as *O. hemionus*, and has a bulk value but no serial data. The other four *Odocoileus* teeth have serial data, although collection tags are not specific as to the species and are presumably *O. hemionus*, and are from Potter Creek Cave (Figure 28d and e) and Samwel Cave (Figure 29d and f). All of them are quite depleted in ^{13}C, with very low amplitude fluctuations in $\delta^{13}C$ values through the record, <2‰. Depletion of ^{13}C suggests that *Odocoileus* at Potter Creek Cave and Samwel Cave inhabited a thick forest, consuming exclusively C_3 vegetation through life. $\delta^{18}O$ serial values fluctuate a bit higher than $\delta^{13}C$ values, by up to 3.5‰, but are well within the range of $\delta^{18}O$ seasonal fluctuations for the sites (~4-6‰). This implies that C_3 vegetation was available year-round and that these deer did not migrate large distances or to different environments. *Odocoileus* teeth are low-crowned, providing a very short yearly record. My data indicate that one tooth records about one year of life (e.g., sample SC-23082 in Figure 29d).

Ovis – One specimen of *O.* sp. was analyzed and is from Potter Creek Cave. Serial data show that this animal had a diet of mostly C_3 vegetation when the tooth began to mineralize,

but then it transitioned to being a mixed feeder later in the biomineralization history of the tooth (Figure 28f). If this tooth represents only one year of life, then this is a large amplitude seasonal variation in $\delta^{13}C$ (~3‰) and $\delta^{18}O$ (~4‰). Together, these $\delta^{13}C$ and $\delta^{18}O$ data suggest that *Ovis* may have been a seasonal inhabitant of the region, and that it migrated through a different habitat during part of the year, consuming different vegetation and water from that area.

Euceratherium collinum – Kurtén and Anderson (1980) suggested that *E. collinum* from northern California was a specialized grazer, while Kropf *et al*. (2007) used dung analysis to show that *E. collinum* from the Colorado Plateau had a browsing diet, dominated by over 95% trees and shrubs (*Artemisia, Acacia, Quercus, Chrysothamnus*). *E. collinum* teeth analyzed in this study are all from sites in northern California and, to my knowledge, are the first to be isotopically analyzed. The $\delta^{13}C$ data show that *E. collinum* was able to consume a fairly diverse variety of plant types, although consumed primarily C_3-type vegetation (Figure 28b and c, Figure 29c and g), thereby supporting Kropf *et al*.'s (2007) interpretation that it was predominantly a browser. If the equation of Hoppe *et al*. (2006) for calculating $\%C_4$ in *Bison* diet is applicable to other bovids (Eq. 2 – Chapter 1), then calculations show that the Potter Creek Cave *E. collinum* consumed between 10% to 28% C_4 vegetation.

E. collinum is a high-crowned ungulate, so serial sampling of the teeth provided a multi-year record of seasonality. My data show that *E. collinum* has intra-tooth serial $\delta^{13}C$ variability ranging from just 0.7‰ at Hawver Cave (Figure 29g), up to 6.6‰ at Potter Creek Cave (Figure 28c). Of the four *E. collinum* teeth serial sampled, all yielded averaged $\delta^{13}C$ values less then -8.4‰ (three of which were less than -10‰) with very small fluctuations in serial $\delta^{13}C$ values. $\delta^{18}O$ serial values were dampened compared to $\delta^{13}C$ values, where seasonal fluctuations were

less then 3.6‰. This general pattern supports the conclusions of Kropf *et al*. (2007) that *E. collinum* did not experience much seasonal mobility; their dung analysis indicated that *E. collinum* consumed different types of C_3 browse throughout the year from the same area. However, one of my *E. collinum* specimens, PC-8385 from Potter Creek Cave, does not follow this pattern and exhibits great variation in seasonal diet. PC-8385 shows large, negatively covarying fluctuations in $\delta^{13}C$ and $\delta^{18}O$ (Figure 28c). The $\delta^{13}C$ values for PC-8385 vary by up to 6.6‰, while $\delta^{18}O$ varies by up to 4‰, and indicate a transition from mixed feeder to strict browser on a seasonal basis. This leads to the inference that this individual either migrated seasonally or experienced great environmental changes within its habitat.

Collectively, isotopic data indicate that *E. collinum* was likely not a habitual migrating taxon, although some individuals apparently did move seasonally or else were subjected to significant seasonal environmental changes. It is interesting that *E. collinum* does not occur in southern Nevada fossil assemblages, although it occurs widely in North America (Kropf *et al*., 2007), particularly in the West and Southwest (New Mexico, Arizona, Utah, northern Nevada, and California) (Graham and Lundelius, 2010). There is no obvious reason for the absence of *E. collinum* at the southern Nevada locations; isotopic data suggest that conditions in southern Nevada would have been hospitable. The description of plant species from pollen cores for southern Nevada and northern California, show that these regions hosted similar plant species (Van Devender and Spaulding, 1979; Adam and West, 1983). Further, $\delta^{13}C$ data from *Mammuthus columbi* in southern Nevada are similar to $\delta^{13}C$ values from *Euceratherium collinum* in northern California, between -10 to -8‰ (Figure 30c and d). This leads to the suggestion that, although southern Nevada is known to have a higher abundance of C_4 vegetation than northern California, the open woodland habitat of southern Nevada might have supported *E. collinum*.

Conclusions

$\delta^{13}C$ values of megaherbivore teeth reveal that Late Pleistocene environments of northern California were thick forest to open woodland, supporting predominantly browsing taxa. Late Pleistocene environments of southern Nevada were open woodland to mixed grassland, supporting megaherbivores with elevated $\delta^{13}C$ values, reflecting a greater tendency for C_4/CAM consumption. I hypothesized that environments were different between northern California and southern Nevada and that both reflected cooler, wetter environments than what exists today. Calculated $\delta^{18}O_{V\text{-}SMOW}$ values suggest that Late Pleistocene precipitation was enriched in ^{18}O compared to modern precipitation. These calculations contradict my hypothesis and potential reasons for the enrichment of $\delta^{18}O$ values in teeth may be fractionation of body water from ingested water, consumption from evaporated sources, abundant consumption of C_3 vegetation, (e.g., leaves), or unapplicable empirical equations. On the other hand, the data does support my hypothesis which is in agreement with the Macrophysical Climate Model of Bryson (2005). This model predicts that all sites were 5.5 to 7.5 ^{O}C cooler and experienced up to 30% higher amounts of precipitation than modern, which was distributed more evenly and abundantly throughout the year.

Serial isotopic data support my hypothesis that seasonal variations in diet and climate can be measured by intra-tooth sampling. Teeth were found to contain at least a one-year record of environmental and ecological information. $\delta^{13}C$ data show that most megaherbivores consumed browse to mixed vegetation, with little seasonal variation. Therefore, Late Pleistocene environments supported abundant year-round vegetation, indicating that seasonality was not as extreme as today. This is complimentary to paleoclimate precipitation models, although contrary to what I had predicted, I hypothesized that Late Pleistocene

seasonal patterns would be more pronounced than at present with megaherbivore diets changing more prominently from summer to winter. Serial $\delta^{18}O$ values reveal that the low-amplitude, cool/warm seasonality did not prompt seasonal mobility in most taxa. This supports my hypothesis that migratory behaviors were likely not a factor for most species of megaherbivores included in this study.

The megaherbivore teeth analyzed in this study yielded averaged $\delta^{13}C$ values reflecting niche partitioning of taxa and suggest that competition for food resources was not intense. Each species of megaherbivore apparently occupied a distinct niche within the forested/woodland environments of northern California and woodland/grassland environments of southern Nevada. Isotopic results show that megaherbivores occurring both in northern California and southern Nevada, such as *Bison* and *Nothrotheriops*, had a wide range of diets between the two regions. This suggests that some megaherbivore species were ecologically flexible in the Late Pleistocene; however, individual animals exhibited little variation seasonally, leading to the interpretation that individuals were not as tolerant, or behaviorally plastic, as the species as a whole.

CHAPTER FIVE

MEGAHERBIVORE PALEOECOLOGY AS A RESPONSE TO LATE PLEISTOCENE (40-10 KA) ENVIRONMENTAL CHANGE

Abstract

This project combines new isotopic data from teeth of Late Pleistocene megaherbivores with bulk isotopic results from previous studies. This information improves our understanding of paleoecology and paleoenvironments of western North America during the transition from the Wisconsin glacial to the Holocene interglacial. Stable carbon isotope data suggest that megaherbivores in northern California and northern Nevada were predominantly browsing. Southern Nevada/southeastern California taxa exhibit a very wide range in $\delta^{13}C$ values, reflecting browsing to grazing diets, while a smaller dataset for east-central Nevada reveals the presence of mixed-feeders to grazers. These results, along with $\delta^{18}O$ data, indicate that environments became more arid, during this time interval, with increased abundance of C_4 plants in the lower latitudes of California and Nevada. Grouping all the data together for taxa with good age control (*Equus*, *Mammuthus*, *Bison*, *Camelops*, and *Nothrotheriops*) allows for the documentation of the variation in $\delta^{13}C$ and $\delta^{18}O$ from 40 to 9 Ka. Positive trends in $\delta^{18}O$ data indicate that environments in California and Nevada were becoming progressively warmer by the beginning of the Holocene. Trends in $\delta^{13}C$ data were more consistent through time, despite the apparent increase in temperatures. The biggest changes observed in these genera are expanded dietary ranges, by up to 6‰ in $\delta^{13}C$ values, consuming a wider range of vegetation to reflect increased grazing and increased browsing. Constraining the range of environmental conditions that Late Pleistocene megaherbivores were able to withstand may be useful to conservation biology, in light of current and projected climatic changes. Based upon results of

this study, some modern large herbivore species may be able to respond to ecologic pressures from climate change by expanding their dietary breadth and acting more advantageously in their environments, if the changes occur slowly enough.

Introduction

Isotope paleoecology can provide direct evidence of animal response to climatic changes in the fossil record (Koch *et al*., 2009). Stable carbon and oxygen isotopes in tooth enamel and dentin can reveal how megaherbivores functioned in climatically altered ecosystems of the Late Pleistocene, in particular the last transition from full glacial conditions to the Holocene interglacial period. Understanding animal behavior in the geologic past can assist in the recognition of ecological tolerance for megaherbivore species, lending itself as a tool to prepare for the range of ecological variation extant species of large mammals may experience in a rapidly changing climate. Several Pleistocene taxa examined in this study (*Equus*, *Bison*, *Odocoileus*, and *Ovis*) have extant congeners, thus Late Pleistocene information about these species may be applicable to questions of wildlife management for current and projected climate change.

Previous studies have investigated large to small-scale evolutionary and ecological changes in mammals through the Cenozoic (Graham *et al*., 1996; Cerling *et al*., 1997; Alroy *et al*., 2000; MacFadden, 2000; Fox-Dobbs *et al*., 2008; Blois and Hadley, 2009; Blois *et al*., 2010; Szpak *et al*., 2010). Recently, the concern for mammalian response to modern climatic changes has extended these studies to contribute to the new field of conservation paleobiology – using data from the fossil record to help inform decisions about the management of extant species and

ecosystems (Barnosky *et al*., 2003; Martínez-Meyer *et al*., 2004; DeSantis *et al*., 2009; Hadley and Barnosky, 2009; Koch *et al*., 2009; Kohn and McKay, 2012). This investigation will contribute to these efforts by examining new isotopic data alongside previous works (Connin *et al*., 1998; Vetter, 2007), providing a synthesis of Late Pleistocene megaherbivore isotope paleoecology for California and Nevada. Compiling isotopic data from various localities and environments provides a stronger case for assessing the ecological breadth of a species. In addition, tracking species diets from 40 to 9 Ka can provide information about how species were responding to environmental changes driven by climate. New isotopic data from northern California and southern Nevada are compared to the results of Connin *et al*. (1998) who studied megafaunal herbivores from southern California, southern Nevada, and northern Nevada, and also with the results of Vetter (2007) who analyzed megafaunal herbivores from southern Nevada (Figure 33). This creates a broader environmental and ecological reconstruction of Nevada and California during the Late Pleistocene. In addition, tooth samples for taxa which have good age control have been selected to see how ecological traits of individual species were changing through the last thirty thousand years of the Late Pleistocene. Taxa included in this study are *Equus*, *Mammuthus*, *Bison*, *Camelops*, and *Nothrotheriops*.

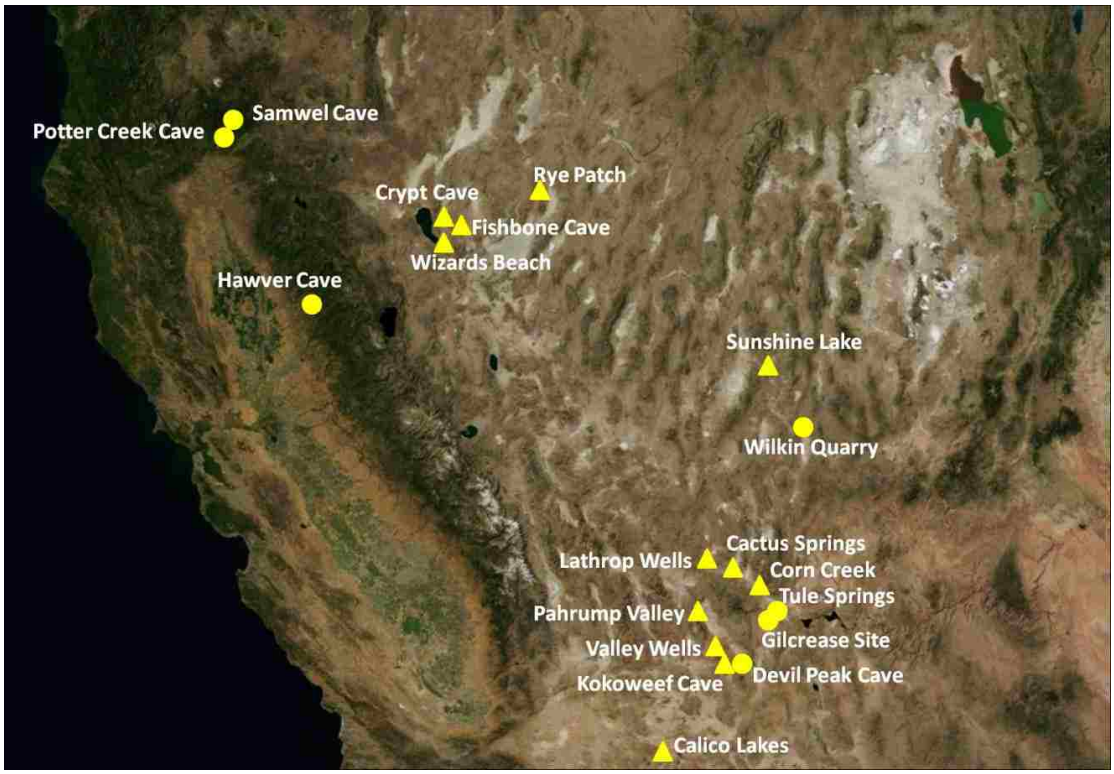


Figure 33. Locality map of comparative isotopic studies on megaherbivores. Circles are data from this study (Samwel Cave, CA; Potter Creek Cave, CA; Hawver Cave, CA; Devil Peak Cave, NV; Gilcrease Site, NV; Tule Springs, NV; Wilkin Quarry, NV). Triangles are from Connin *et al*. (1998) (Sunshine Lake, NV; Rye Patch, NV; Crypt Cave, NV; Fishbone Cave, NV; Wizards Beach, NV; Lathrop Wells, NV; Cactus Springs, NV; Corn Creek, NV; Pahrump Valley, NV; Valley Wells, CA; Kokoweef Cave, CA; Calico Lakes, CA), and Vetter (2007) (Gilcrease Site, NV).

Hypotheses

I hypothesize that isotopic data acquired in this study will complement data obtained by previous researchers, possibly with small differences in isotopic values due to samples being processed in different laboratories or with different methodologies. In this study I analyzed samples in the Las Vegas Isotope Science Lab at University of Nevada, Las Vegas; Vetter (2007) analyzed her samples at the University of California, Davis; and Connin *et al*. (1998) analyzed their samples at the University of Arizona, Tucson. Even if there is a 1-2‰ difference in values, the overall trends will still be apparent and meaningful. I anticipate that the combined data will

show that there is a gradient in $\delta^{13}C$ and $\delta^{18}O$ values from southern Nevada to northern Nevada and northern California, with results reflecting more arid (higher $\delta^{13}C$ values) and warmer (higher $\delta^{18}O$ values) conditions in the southern localities transitioning to cooler climates in northern Nevada (consistent $\delta^{13}C$ and decreasing $\delta^{18}O$ values), and even cooler and wetter climates in California (decreasing $\delta^{13}C$ and $\delta^{18}O$ values).

I also hypothesize that investigating stable carbon and oxygen isotopes from taxa with good age control will reveal information about how species were responding to climatic changes through the last thirty thousand years of the Late Pleistocene. I anticipate that the data will show that significant climatic shifts from glacial to interglacial periods had profound impacts on ecosystem functionality, with strong influences on herbivore diet and behavior. Previous studes have used isotopic analyses to observe changes in the evolutionary ecology of mammals, on a scale of several thousand to several million years (McFadden, 2000; Kohn and McKay, 2012); I anticipate that I will observe such changes over a period of thirty thousand years. I anticipate that $\delta^{13}C$ values will reveal changes in the diet of megaherbivores over this shorter time-frame, while $\delta^{18}O$ will reveal relative environmental conditions (general climate and moisture). I expect to find that $\delta^{18}O$ and $\delta^{13}C$ values fluctuate, with more positive values indicating warm, arid periods (35-30 Ka and 15-9 Ka) and more negative values reflecting cool, wet intervals (22-16 Ka). These results may lead to paleobiological inferences regarding megaherbivore response and tolerance to climatic stress.

Methods

The isotopic methods and treatments used in this study are described in Chapter 1. I will first examine regional patterns of $\delta^{13}C$ and $\delta^{18}O$ values, combining all megaherbivore species within a region together. I will then examine species-specific trends over the last 40 to 9 Ka. Carbon and oxygen values are statistically analyzed, and taxa are compared through time using a parametric test (ANOVA) with a significance level of $\alpha = 0.05$. Data are also graphed and analyzed for linear regression trends with a coefficient of determination (R^2).

Results

Isotopic data from this study are listed in Appendix 2; isotopic data from Connin *et al*. (1998) and Vetter (2007) are listed in Appendix 3. Data show an interesting correlation between regions (Figure 34), which are divided into northern California (*n* = 23), northern Nevada (*n* = 10), southern Nevada/southeastern California (*n* = 55), and east-central Nevada (*n* = 2). Generally speaking, northern California and northern Nevada localities reveal low $\delta^{13}C$ values, reflecting a high percentage of C_3 plants in the diets of the megaherbivores in those regions. Northern California $\delta^{13}C$ values range from about -12.5 to -6‰. The range of northern Nevada $\delta^{13}C$ values are very similar (about -12 to -6‰), with one outlier of -2‰. Southern Nevada and southeastern California are grouped together because of the geographic closeness of the sites (Figure 33). These localities constitute the largest dataset because of the large number of megaherbivores analyzed from the region. Southern Nevada/southeastern California $\delta^{13}C$ values exhibit a wide distribution, ranging from about -12 to -1‰. East-central Nevada has the smallest dataset, with $\delta^{13}C$ values of about -7‰ and -4‰.

In terms of $\delta^{18}O$ values, northern California clumps most tightly, ranging from -7.4 to -3.4‰. Northern Nevada has a much wider range of $\delta^{18}O$ values, from -11.7 to -3.5‰, as does southern Nevada/southeastern California, with a range of -15.5 to -1.4‰. East-central Nevada has $\delta^{18}O$ values of -10.5‰ and -6.9‰.

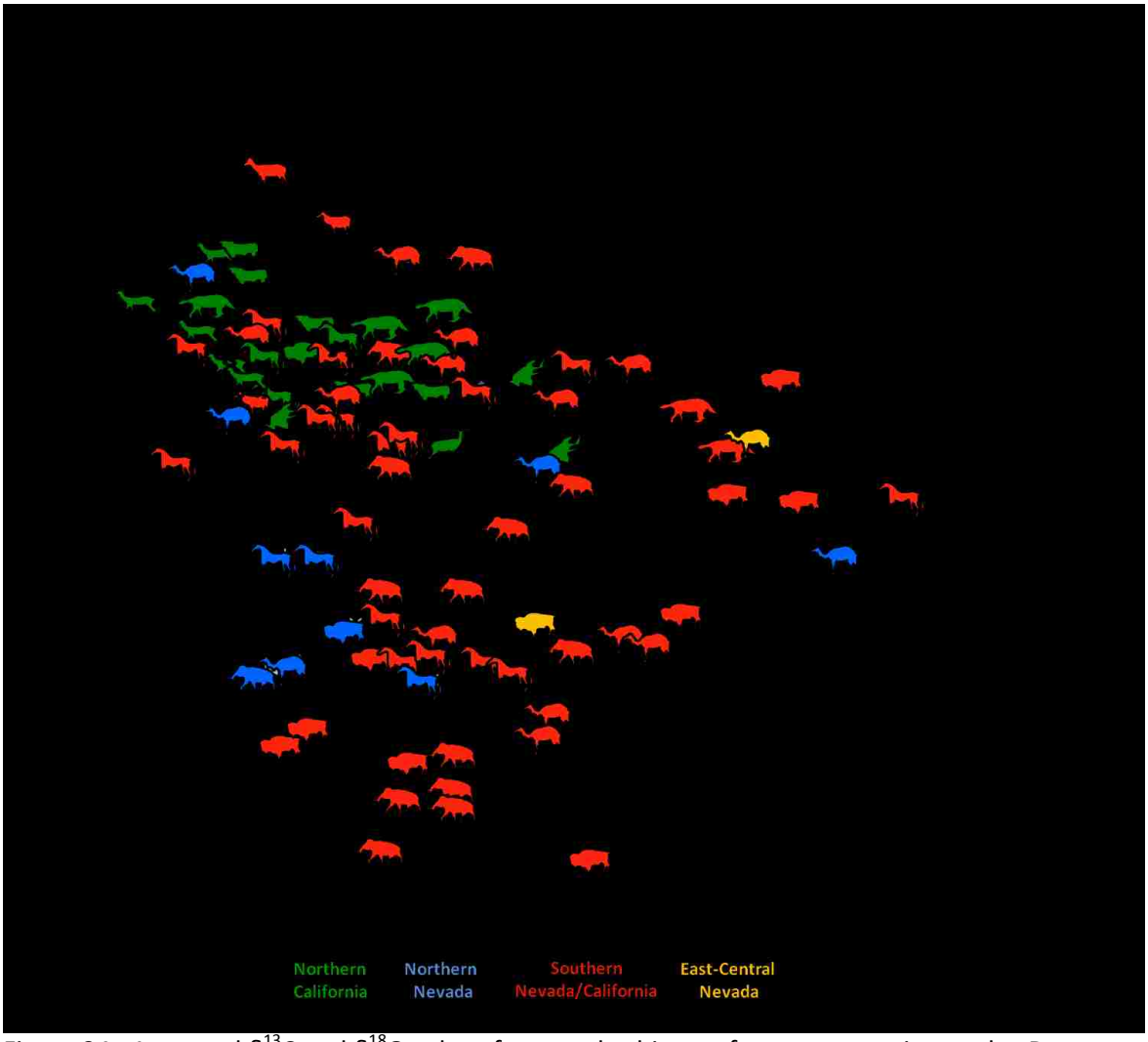


Figure 34. Averaged $\delta^{13}C$ and $\delta^{18}O$ values for megaherbivores from comparative study. Data are from this study, Connin *et al*. (1998), and Vetter (2007). Regions are divided into northern California (green), northern Nevada (blue), southern Nevada/southeastern California (red), and east-central Nevada (orange).

Figure 35 shows averaged $\delta^{13}C$ and $\delta^{18}O$ values of all megaherbivores from each region; circle width indicates one standard deviation from the mean. Northern California contains taxa with an average $\delta^{13}C$ value of -9.9‰ and average $\delta^{18}O$ value of -5.1‰, with the smallest isotopic variance. Northern Nevada has averaged $\delta^{13}C$ and $\delta^{18}O$ values of -8.7‰ and -9.5‰, respectively. Southern Nevada/southeastern California has an average $\delta^{13}C$ value of -8.1‰ and $\delta^{18}O$ value of -8.6‰, with the largest isotopic variance among the four regions. East-central Nevada has an average $\delta^{13}C$ value of -5.3‰ and an average $\delta^{18}O$ value of -8.7‰.

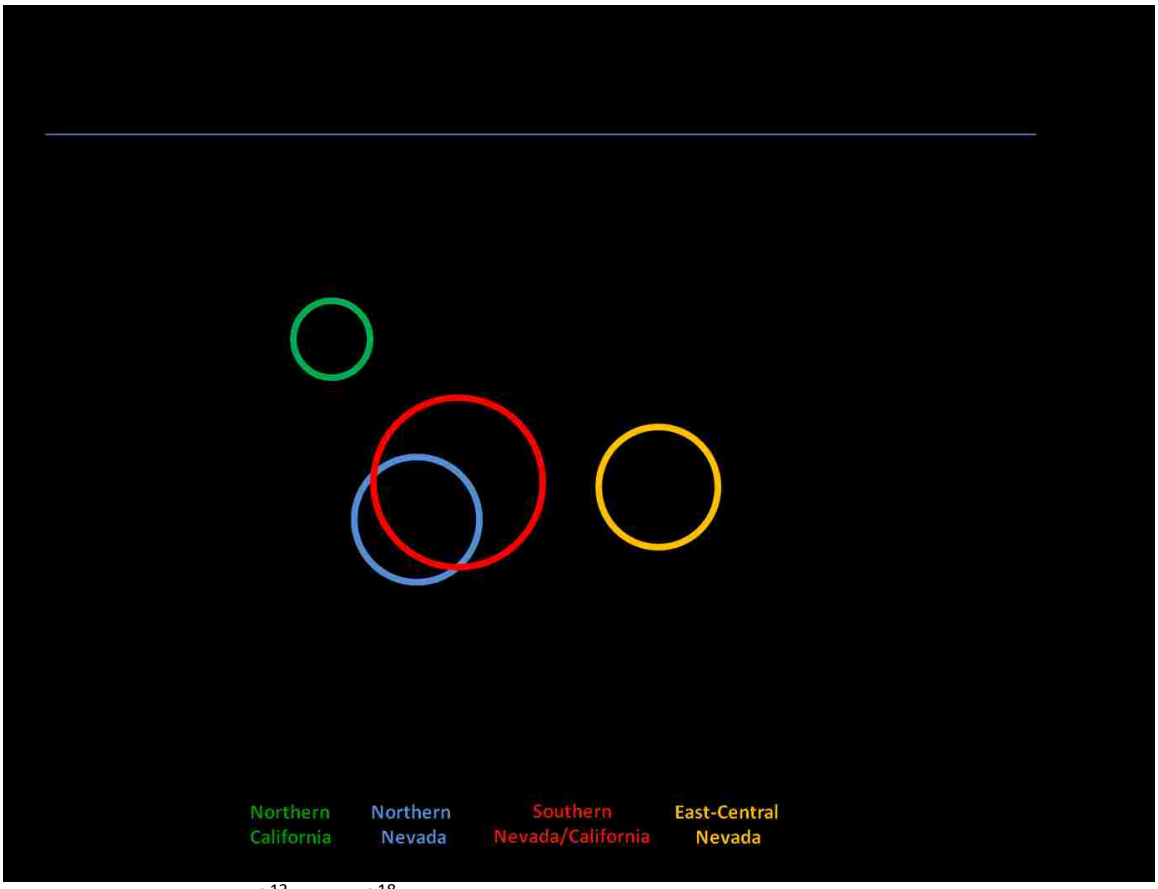


Figure 35. Averaged $\delta^{13}C$ and $\delta^{18}O$ by region. Circles represent one standard deviation.

Good age control allows me to place the isotopic information into a temporal framework, for taxa with abundant isotopic data. Figure 36 shows graphs for *Equus* (*n* = 24), *Mammuthus* (*n* = 14), *Bison* (*n* = 10), *Camelops* (*n* = 18), and *Nothrotheriops* (*n* = 7) in which $\delta^{13}C$ and $\delta^{18}O$ values are plotted against the age of the deposits. Results show that most species had a wide variation in $\delta^{13}C$ and $\delta^{18}O$ values. Trends reveal that $\delta^{18}O$ values increased from 40 to 9 Ka for all genera except *Bison* (R^2 >0.20 and <0.59). Significant differences exist for *Mammuthus*, and *Camelops* through time ($p < 0.03$), while *Equus*, *Bison* and *Nothrotheriops* show no significant differences ($p > 0.06$).

The $\delta^{13}C$ values reveal that trends in *Equus* and *Bison* had observable decreases toward the end of the Pleistocene, while *Mammuthus*, *Camelops*, and *Nothrotheriops* had very little change ($R^2 > 6X10^{-4}$ and <0.55). Significant differences exist for *Equus*, *Mammuthus*, *Bison*, and *Nothrotheriops* through time ($p < 0.04$), while *Camelops* is not significantly different ($p > 0.60$).

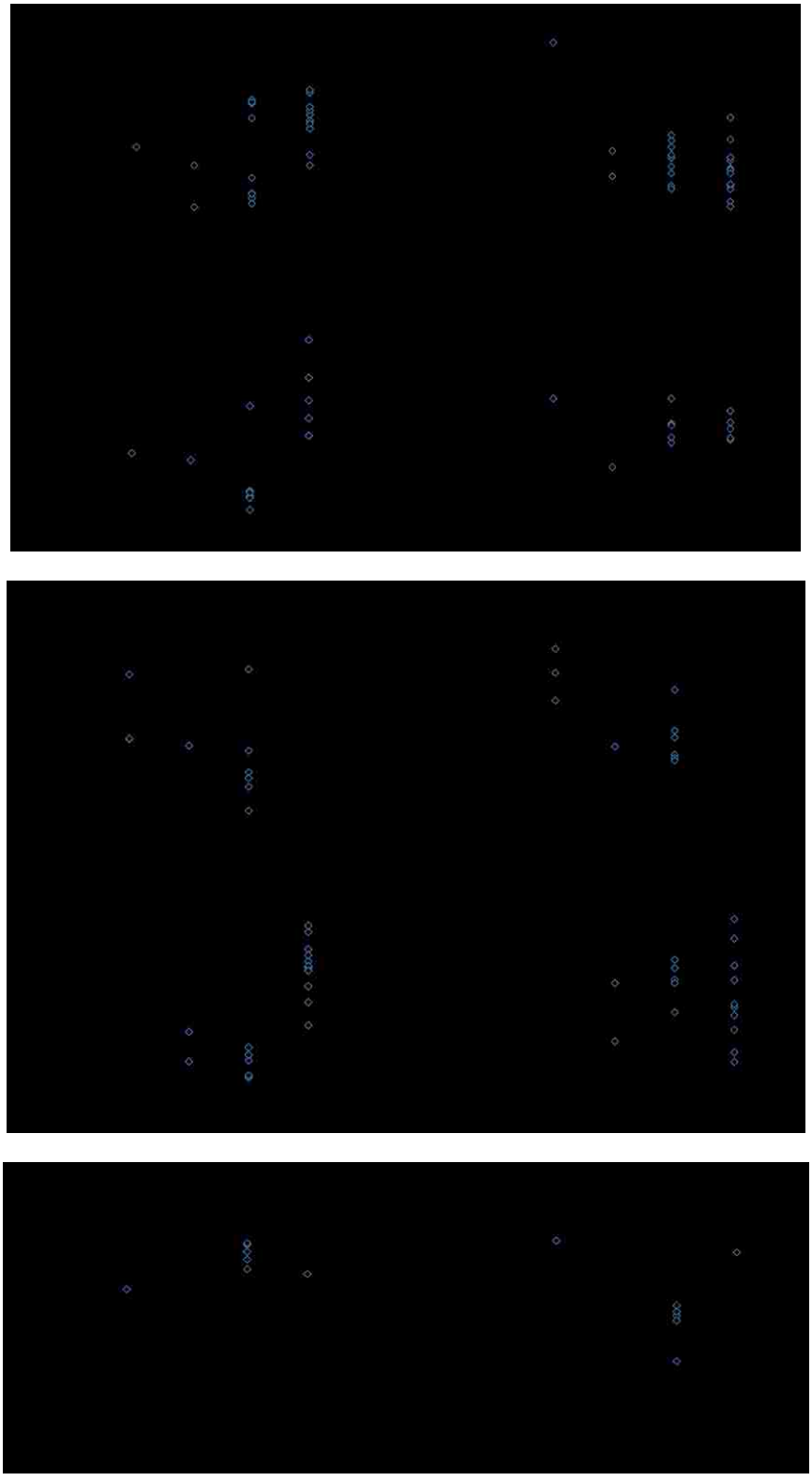


Figure 36. $\delta^{13}C$ and $\delta^{18}O$ of megaherbivores through the Late Pleistocene. Graphs are, from top to bottom, *Equus*, *Mammuthus*, *Bison*, *Camelops*, and *Nothrotheriops*. Data are from this study,

Connin *et al*. (1998), and Vetter (2007). Linear regression trendlines show data trends through time.

Discussion

Combining isotopic results from this study with data from previous studies permits me to maximize regional environmental information and corresponding megaherbivore behavior from 40 to 9 Ka. $\delta^{13}C$ data indicate that northern California and northern Nevada megaherbivores were predominantly browsers, with a large majority of taxa having $\delta^{13}C$ values of -8‰ or less; only four specimens from these regions have values that are higher then -8‰ (two *Camelops* and two *Megalonyx*) (Figure 34). This indicates that the availability of C_3 plants was very similar in northern California and northern Nevada. In contrast, specimens from southern Nevada/southeastern California have a much wider range of $\delta^{13}C$ values (about -12 to -1‰), indicating that these animals filled many herbivorous niches, from exclusively browsing herbivores to mixed-feeders and near strict grazers. East-central Nevada's small dataset reveals mixed-feeding taxa. Figure 37 demonstrates the negative average $\delta^{13}C$ values of taxa from northern California with averages increasing toward lower longitudes in east-central Nevada, indicating a transition in megaherbivores from browsing to mixed feeding toward the east. Similarly, average $\delta^{13}C$ values increase from northern California to lower latitudes in southern Nevada/southeastern California, indicating a transition in megaherbivores from browsing to mixed feeding toward the inter-continental south. In this region of North America, latitude/longitude is inversely correlated to $\delta^{13}C$ values, and, excluding east-central Nevada because of only two taxa, the dietary breadth of megaherbivores increases inter-continentally.

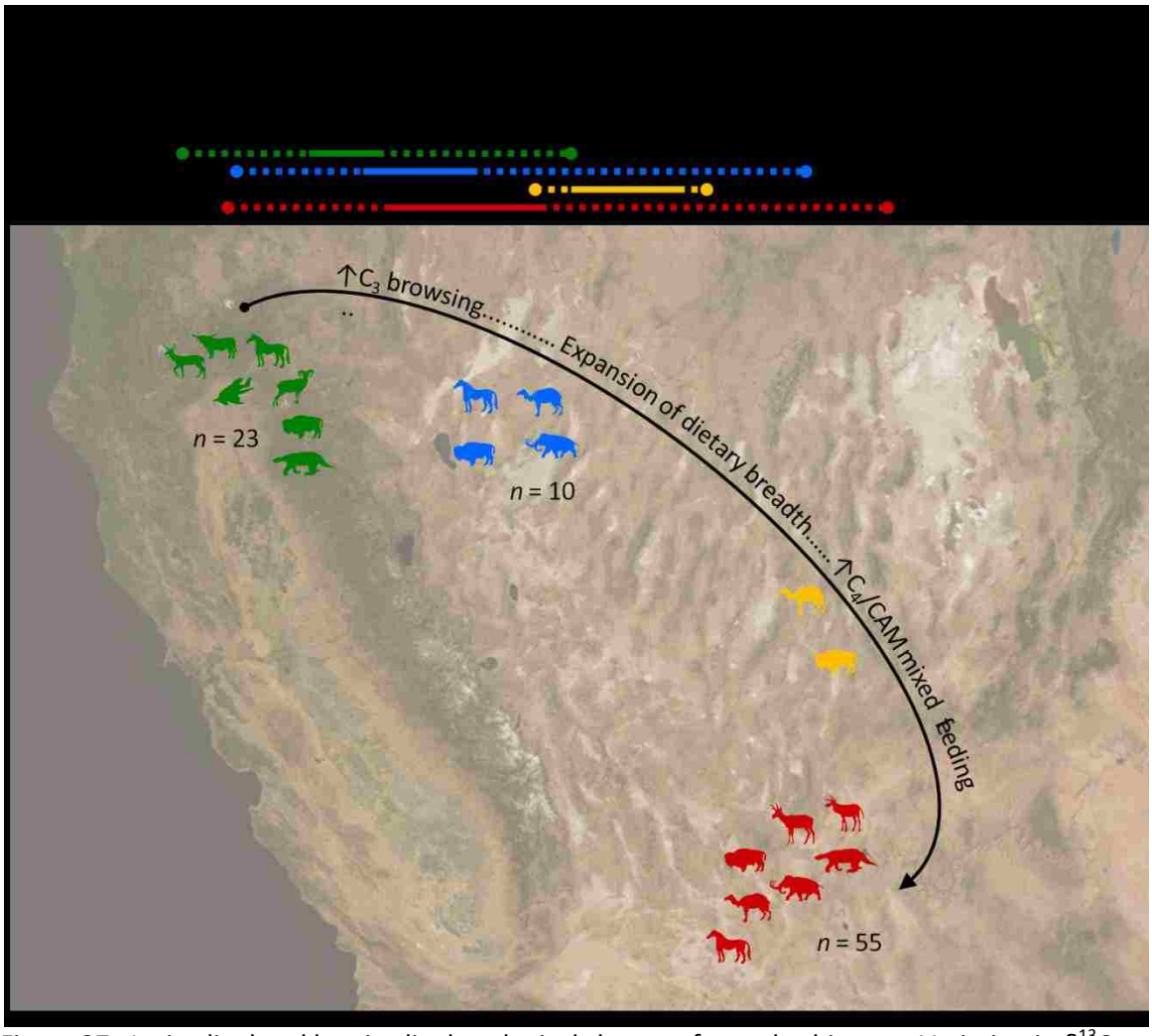


Figure 37. Latitudinal and longitudinal ecological change of megaherbivores. Variation in $\delta^{13}C$ values of megaherbivores between regions of California and Nevada. Icons represent megaherbivores present in each region with number of individuals indicated, see Figure 34 for key to taxonomic icons. Green represents northern California taxa, blue represents northern Nevada, yellow represents east-central Nevada, and red represents southern Nevada/southeastern California. At the top, solid bars indicate averaged $\delta^{13}C$ values with 1 σ, dashed bars represent entire range of values. Underlying image is from google maps and represents modern conditions.

Northern California has the smallest range of $\delta^{18}O$ values (~4‰), indicating that environments were not greatly variable in temperature or moisture. Northern Nevada and east-central Nevada exhibit a wide range in $\delta^{18}O$ values (~ 9‰), although these regions sustained mostly browsing taxa; this indicates that temperatures and moisture were more variable during the Late Pleistocene than in northern California. In southern Nevada/southeastern California

even more variability existed in $\delta^{18}O$ values (~14‰) than in northern Nevada. $\delta^{18}O$ correlates with the $\delta^{13}C$ in that temperatures increased in the southern regions of Nevada and California, accompanied by increasing aridity and a greater abundance of C_4 grasses and high variability in precipitation.

Total averaged $\delta^{13}C$ and $\delta^{18}O$ values by region reveal that northern California specimens have the most depleted $\delta^{13}C$ and most positive $\delta^{18}O$ values (Figure 35). The two Nevada regions have closely associated averages, with overlapping $\delta^{13}C$ and $\delta^{18}O$ fields and wide ranges in values. Total averages show that northern Nevada specimens have more negative $\delta^{13}C$ values than do specimens from southern Nevada/southeastern California or east-central Nevada, which have the most positive $\delta^{13}C$ values. These results agree with the conclusions of Connin *et al*. (1998), who concluded that for the Southwestern region of North America there was increasing abundance of C_4 plants toward the east. Average $\delta^{18}O$ values are less segregated, with southern Nevada/southeastern California and east-central Nevada aligning closely, and northern Nevada being only slightly more depleted, in ^{18}O, comparatively (Figure 35).

The taxon-specific data graphed in Figure 36 for *Equus* (*E. occidentalis*, *E. pacificus*, *E.* sp.), *Bison* (*B. latifrons*, *B.* sp.), *Mammuthus* (*M. columbi*, *M.* sp.), *Camelops* (*C. hesternus*, *C.* sp.), and *Nothrotheriops* (*N. shastensis*) reveal trends over time, from 40 Ka to the beginning of the Holocene. $\delta^{18}O$ values reveal increasing trends corresponding to increasing temperatures through the Late Pleistocene for all taxa, except *Bison*. Trends in $\delta^{13}C$ values decrease over time for *Equus* and *Bison*, while the trend for *Nothrotheriops* decreases slightly less, and trends remain near constant for *Mammuthus* and *Camelops*, revealing niche conservatism at the generic level (Hadley *et al*., 2009); niche conservatism refers to the tendency to retain ecological functions and traits over time (Wiens *et al*., 2010), *sensu* Eltonian niche (Soberón, 2007).

Although these genera generally conserve their dietary preference through the Late Pleistocene, they exhibit a widening in dietary breadth by up to 6‰, this is most observable in the $\delta^{13}C$ values of *Camelops* in Figure 36. Apparently, in response to the ecological changes presented by climatic pressures of the Late Pleistocene, megaherbivores in Nevada and California adjusted their diets to include a broader spectrum of vegetation. The result was a widening of dietary ranges, with taxa adopting broader foraging strategies (increased browsing and increased grazing), resulting in trends staying approximately the same through time. Significant differences support the conclusion that the diets of some taxa were changing through this time interval ($p < 0.04$).

Explanations for the negative $\delta^{13}C$ trend in *Equus* and the negative $\delta^{13}C$ and $\delta^{18}O$ trends in *Bison* (Figure 36) may be found within their data. *Equus* has one anomolously high $\delta^{13}C$ value in the 40-30 Ka time interval which strongly affects the trend of the data. If this point were rejected, the trendline would be more similar to those of *Mammuthus*, *Camelops*, and *Nothrotheriops*. *Bison* has a shorter record than most other taxa, with no data in the 15-9 Ka interval. Thus the data do no permit any conclusions concerning changes in *Bison* niche breadth from post LGM to the beginning of the Holocene for the regions examined.

$\delta^{18}O$ data for *Equus*, *Mammuthus*, and *Camelops* show that the interval of 22-16 Ka recorded some of the lowest $\delta^{18}O$ values (Figure 36). This correlates well with the cool conditions of the Last Glacial Maximum. In contrast, during the intervals of 40-23 Ka and 15-9 Ka most genera reveal comparatively higher $\delta^{18}O$ values, corresponding to the warmer conditions of the time (Thompson *et al*., 1993). The determination coefficient (R^2) provides a measure of how well future outcomes are predicted by a model. In this case, the $\delta^{18}O$ values are weakly correlated with time ($R^2 < 0.31$). The R^2 values are not surprisingly low, considering

the fluctuating climatic conditions preceeding, during, and following the LGM, causing a scattering of the data.

Blois and Hadley (2009) stated that no models exist that are able to link the modes of ecological and evolutionary responses of species to climate change. However, results of this study show that isotopic analysis can be a tool to link dietary behavior and evolutionary ecology of megaherbivores to climate change.

Implications for Future Conservation Efforts

Stable isotope paleoecology can contribute toward conservation paleobiological efforts by identifying the range of ecological conditions in which species have been found to live during periods of fluctuating climate. After the Late Pleistocene megafaunal extinction, surviving mammalian taxa repopulated existing ecosystems, however these species now face the same challenges again: global climate change, habitat loss, fragmented ecosystems, and extinction (Barnosky, 2009). Predicted environmental changes during the next century could have catastrophic effects on mammalian communities (Barnosky *et al*., 2003), where future temperatures are expected to rise beyond a range of temperatures that most mammalian species experience in evolutionary lifetimes (Barnosky, 2009). Models predict that the Southwest will experience rising temperatures in a near linear pattern, by 2.1 ^{O}C to 5.7 ^{O}C, and suffer from decreased precipitation by 3-14%, by the end of this century (Friggens *et al*., 2012). Northward migration of the polar jet stream and reduced moisture delivery to the Southwest due to global warming, compounds the problem of drier conditions in the Southwest (Asmerom *et al*., 2010; Wagner *et al*., 2010). Further, models show that within this same time frame, 55% of current landscapes will contain vegetation that will be incompatible with predicted climates (Friggens *et al*., 2012), causing a trickle down effect on the remaining large herbivores occupying

those regions. Ecological responses to climate changes have already been observed for many groups of organisms, including large mammals (Walther *et al*., 2002).

The obvious response is for vegetation and animals to shift their ranges to the cooler climates that exist at either higher elevations or more northern latitudes in order to cope with warming climates. This is occurring and has been measured to be taking place at a rate of approximately 11 meters/decade, for increases in elevation, and 16.9 km/decade, for shifts to higher latitudes; these rates are 2-3 times faster than previously thought (Chen *et al*., 2011). Late Pleistocene mammals must have also tracked habitable environments during major climatic shifts, exhibiting the niche conservatism revealed by this study, as some still exist today (Martínez-Meyer, 2004). Isotopic data in this study indicate that most taxa of megaherbivores maintained their behavior through the LGM, although some taxa were expanding their range of dietary tolerance by the beginning of the Holocene. $\delta^{13}C$ data through the Late Pleistocene reveal that *Equus*, *Bison*, and *Camelops* expanded their range of $\delta^{13}C$ values by up to 6‰ (Figure 36). *Equus* expanded its $\delta^{13}C$ range from about -8 to -10‰ (browsing) during the LGM to -6 to -12‰ (mixed-feeding to browsing) by the Holocene; *Camelops* also expanded its $\delta^{13}C$ range from about -6 to -10‰ (mixed-feeding to browsing) during the LGM to -2 to -12‰ (grazing to browsing) end of the Pleistocene. However, not all genera experienced such an expansion in dietary behavior; trends show that the diets of *Nothrotheriops* and *Mammuthus* remained nearly constant through the Late Pleistocene. Of course, these interpretations would benefit from a larger dataset, but the data from this study suggest that some species of megaherbivores responded to environmental changes by widening their dietary breadth through the last 30 thousand years of the Late Pleistocene and adapting to other herbivorous niches.

Serial data from individuals, presented in Chapter 4, indicate that megaherbivores did not experience high amounts of seasonal variability in their diet nor were they highly migratory. Megaherbivore taxa that survived the end Pleistocene extinctions will likely suffer significant biodiversity losses as they have not been shown to have a wide range of ecological tolerance, especially considering that in the near future they will experience faster rates of environmental change than did Late Pleistocene populations. The isotopic data in this study suggest that, although losses in numbers are of concern, some megaherbivore taxa are capable of expanding their diets in the face of changing environments if the changes occur slowly enough.

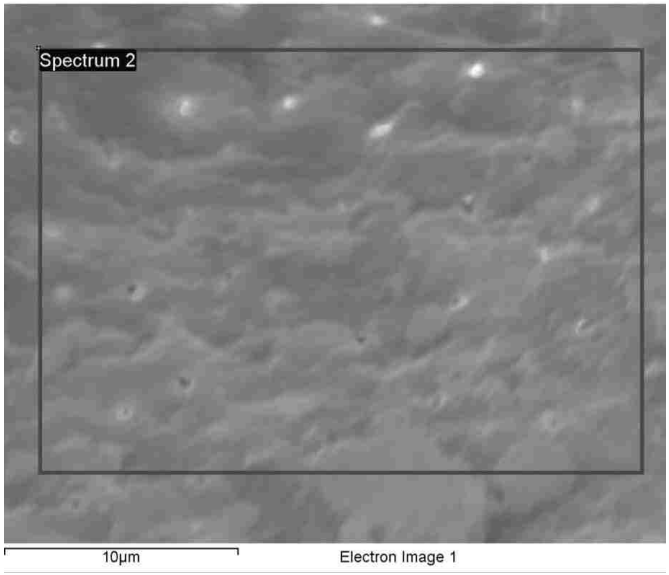
Conclusions

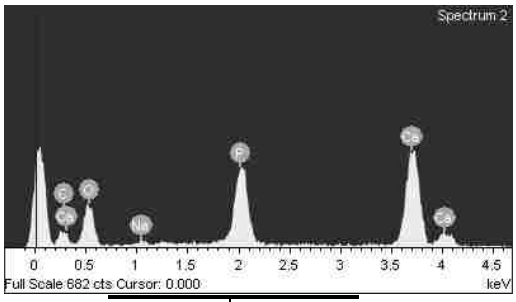
New isotopic data were combined with data from previous studies to construct an extended overview of megaherbivore paleoecology and paleoenvironments in Nevada and California through the Late Pleistocene. The $\delta^{13}C$ and $\delta^{18}O$ data of megaherbivores corroborated the hypothesis of an increased aridity gradient from northern California and northern Nevada to southern Nevada/southeastern California; predominantly browsing taxa in northern localities transitioned to other niches in southern localities (browsing, mixed-feeding, and grazing).

Examining taxa with good age control revealed apparent shifts in $\delta^{18}O$ through the Late Pleistocene, from warm, arid (40-23 Ka) to cool,wet (22-16 Ka), and then warm, arid (15-9 Ka), with the overall trend revealing climates increasing in temperature and becoming drier by the Holocene. I had hypothesized that shifts from stadial to interstadial periods had profound impacts on megaherbivore diet and behavior, however the trends show that most genera

maintained their diets through climatic warming at the end of the Pleistocene. The most significant phenomenon revealed in this study is the LGM to latest Pleistocene expansion of dietary strategies in some taxa (increased browsing or increased grazing). There are many variables involved in the dynamic interplay of an organism and its environment, especially when adding in stress. This study shows that some genera of megaherbivores may respond to modern and future climatic stress by expanding their dietary breadth in order to cope with altered environmental conditions.

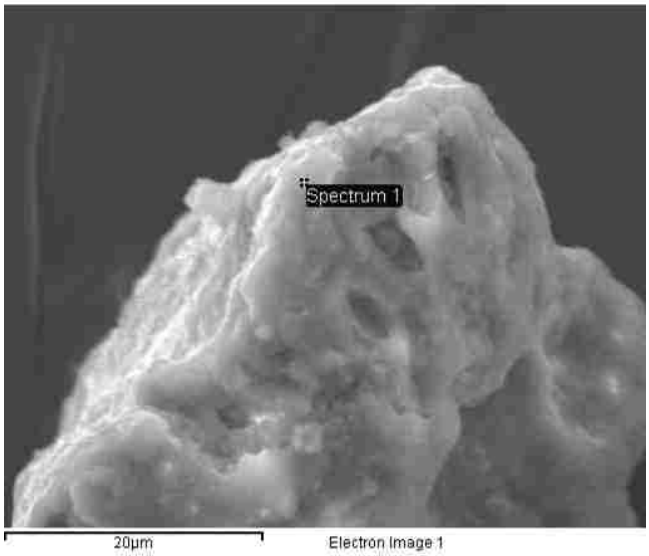
A-1 – *Dasypus novemcinctus* dentin

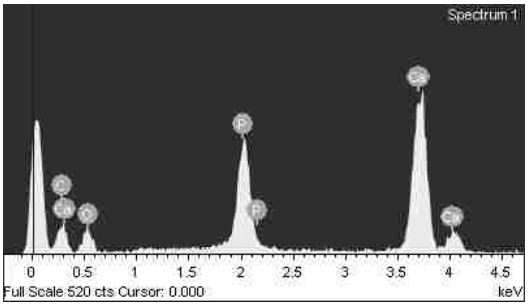




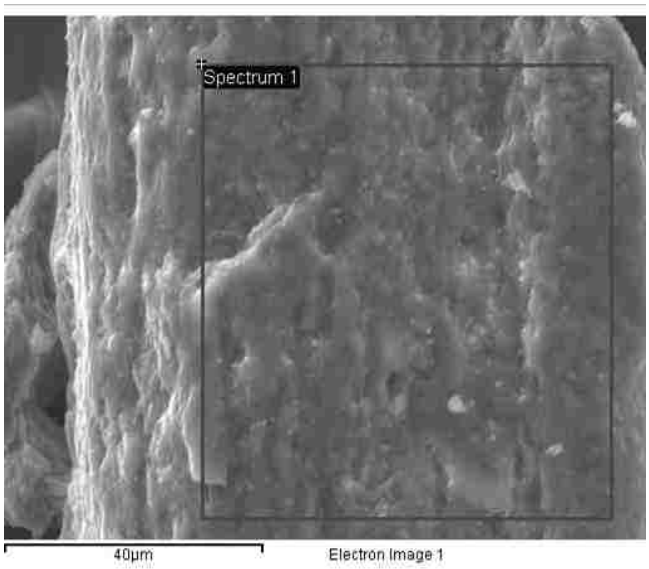
Element	Weight%
C	19.21
O	48.44
Na	1.05
P	11.50
Ca	19.80
Totals	100.00

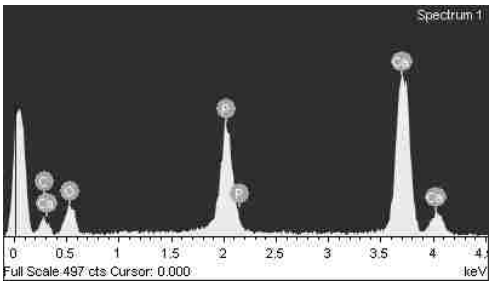
HC-21478 – *Nothrotheriops shastensis* dentin





Element	Weight%
C	30.08
O	30.84
P	12.45
Ca	26.63
Totals	100.00





Element	Weight%
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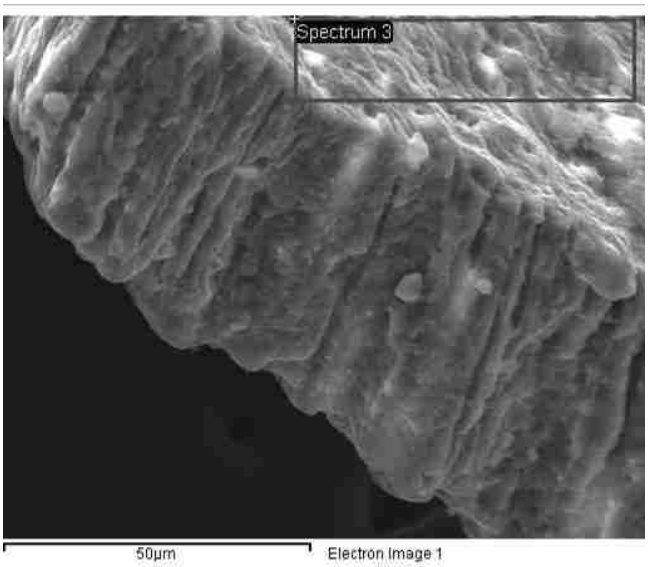
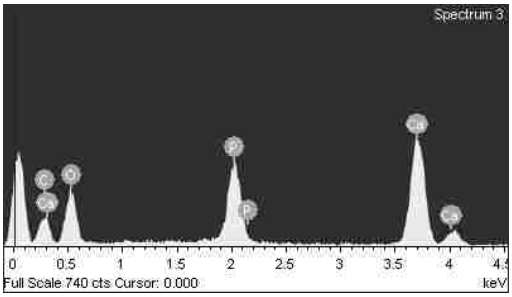
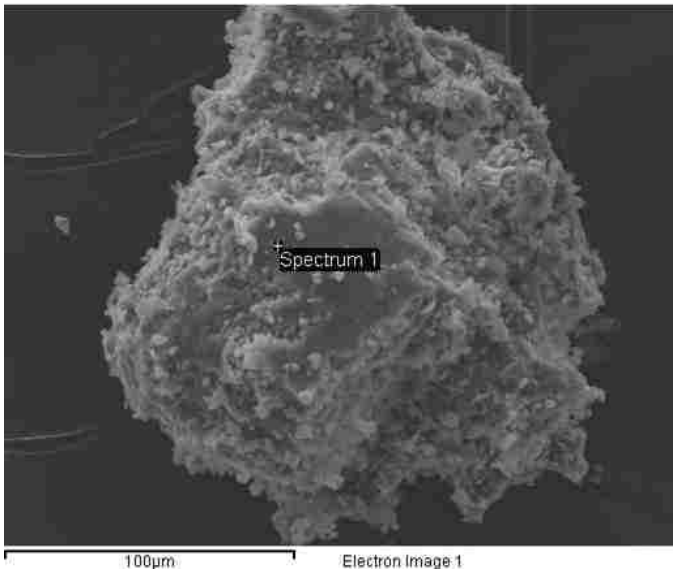
O	38.77
P	12.81
Ca	29.57
Totals	100.00

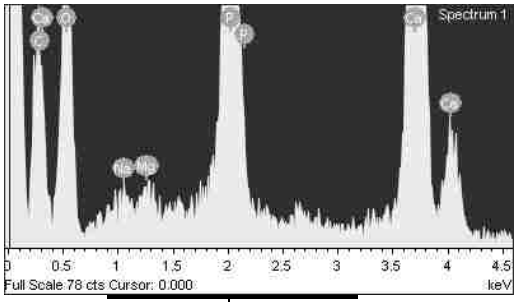




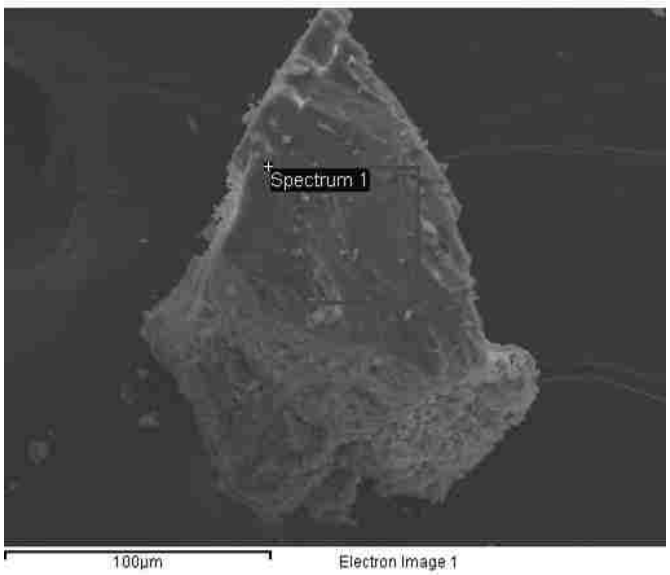
Element	Weight%
C	25.84
O	47.57
P	9.18
Ca	17.41
Totals	100.00

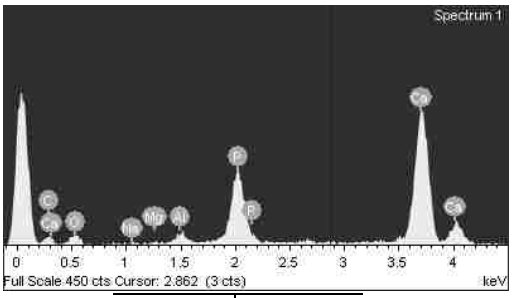
HC-114876 – *Euceratherium collinum* enamel





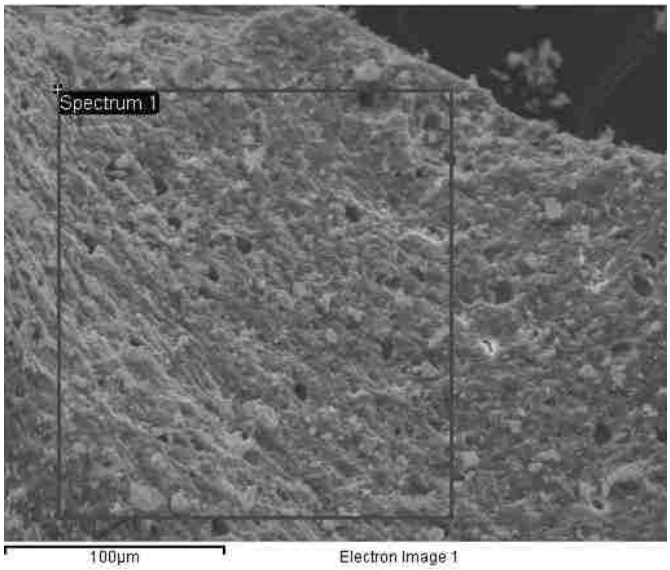
Element	Weight%
C	29.07
O	41.63
Na	0.49
Mg	0.50
P	10.44
Ca	17.88
Totals	100.00

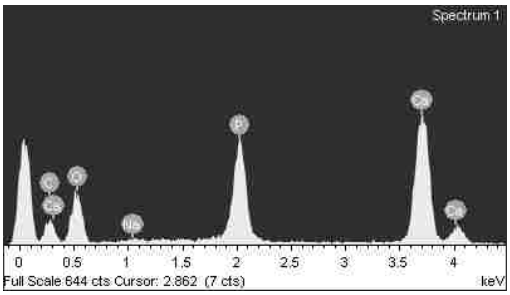




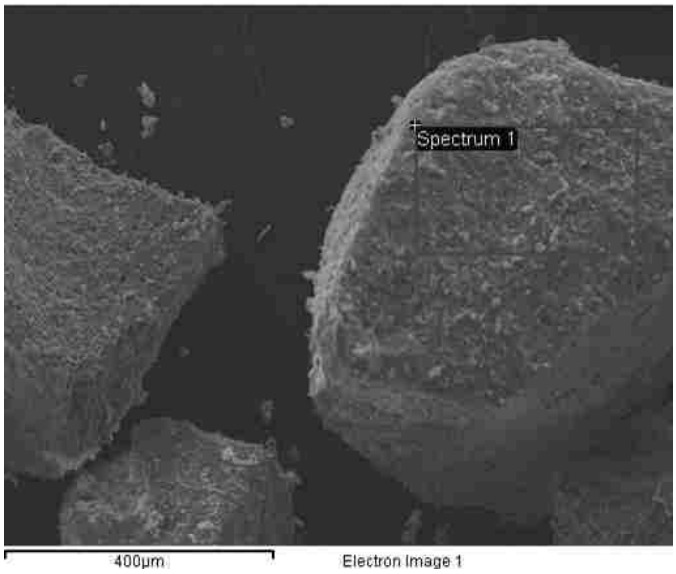
Element	Weight%
C	16.38
O	25.36
Na	0.38
Mg	0.33
Al	1.84
P	14.93
Ca	40.77
Totals	100.00

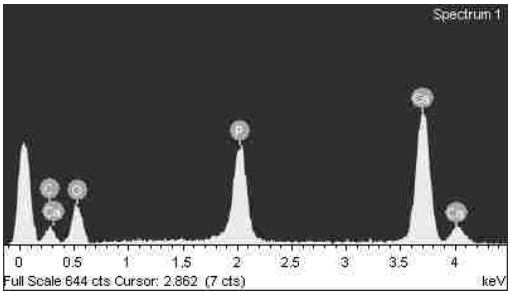
PC-8498 – *Nothrotheriops shastensis* dentin





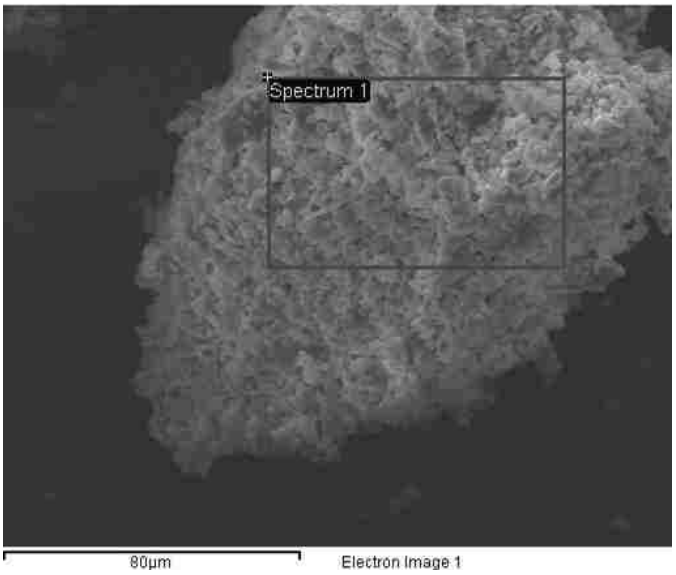
Element	Weight%
C	22.32
O	46.49
Na	0.34
P	10.69
Ca	20.16
Totals	100.00

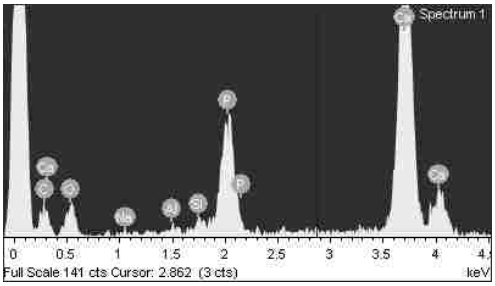




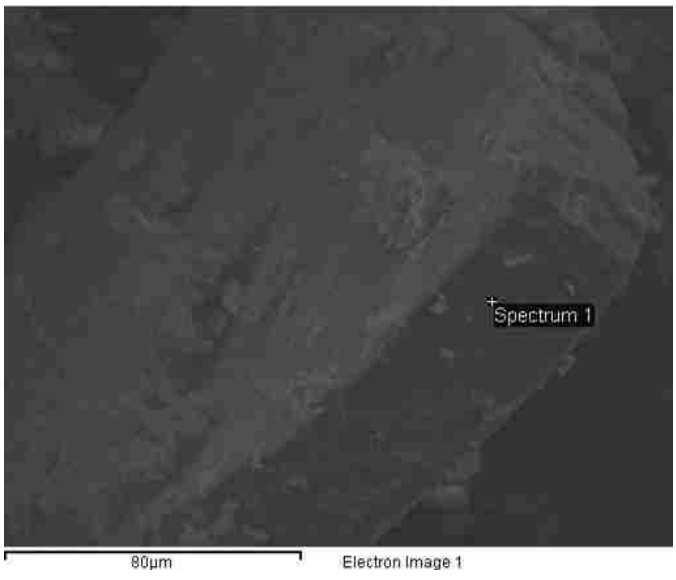
Element	Weight%
C	19.66
O	44.21
P	12.15
Ca	23.98
Totals	100.00

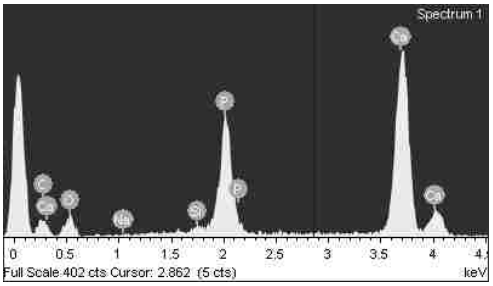
PC-8730 – *Euceratherium collinum* enamel





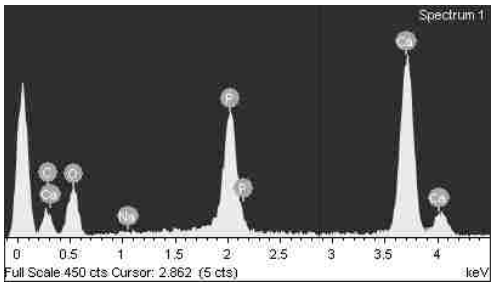
Element	Weight%
C	18.66
O	32.05
Na	0.46
Al	0.47
Si	0.91
P	10.70
Ca	36.75
Totals	100.00



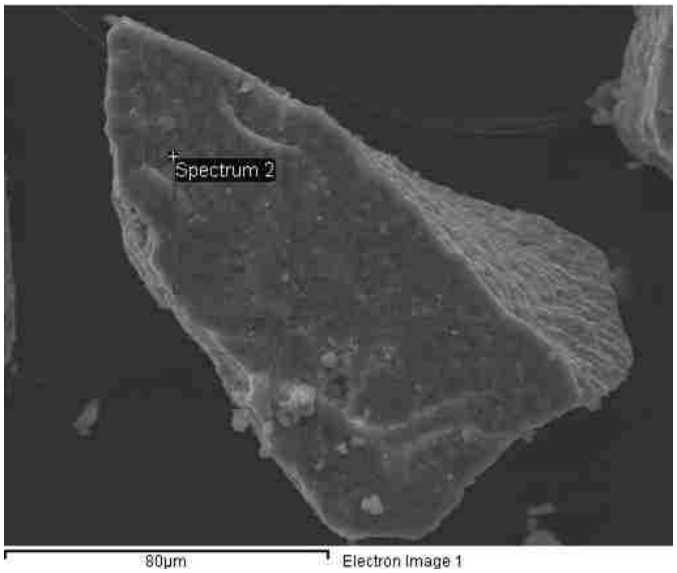


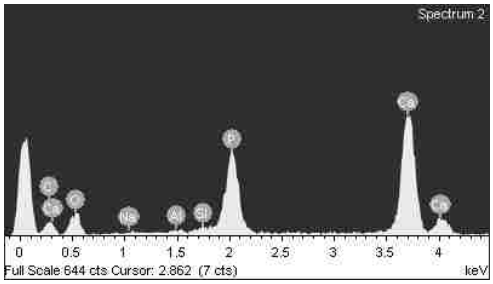
Element	Weight%
C	21.00
O	29.96
Na	0.21
Si	0.57
P	14.08
Ca	34.19
Totals	100.00

SC-9668 – *Megalonyx jeffersonii* dentin (untreated)



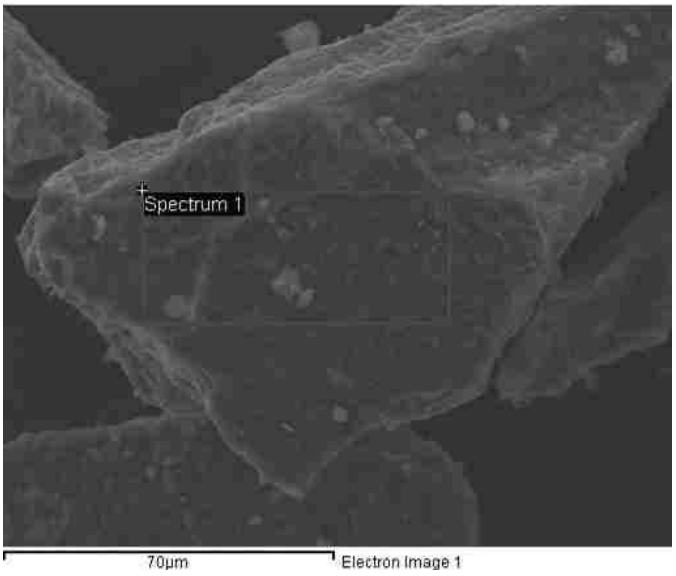
Element	Weight%
C	20.69
O	42.88
Na	0.33
P	11.52
Ca	24.57
Totals	100.00

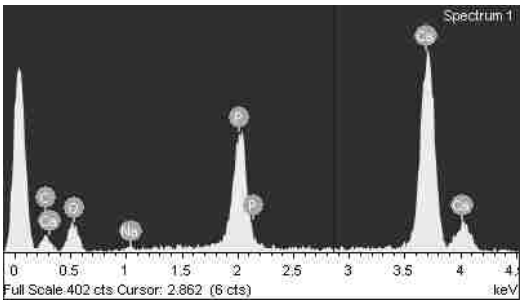




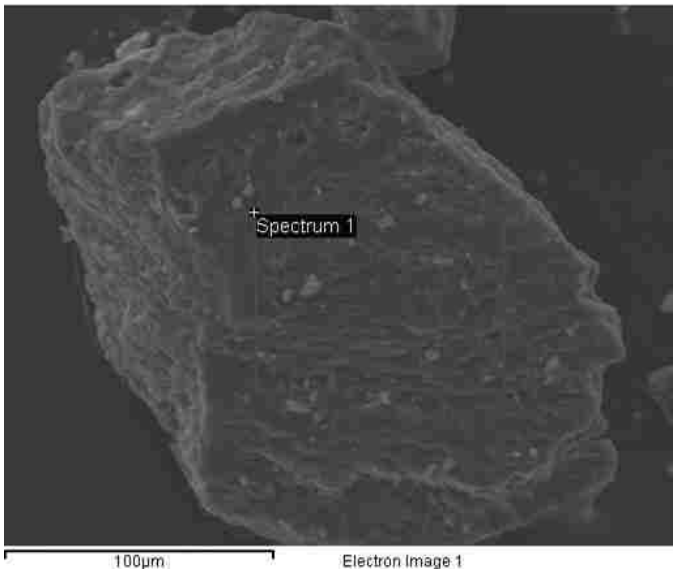
Element	Weight%
C	21.43
O	36.48
Na	0.31
Al	0.39
Si	0.41
P	12.98
Ca	27.99
Totals	100.00

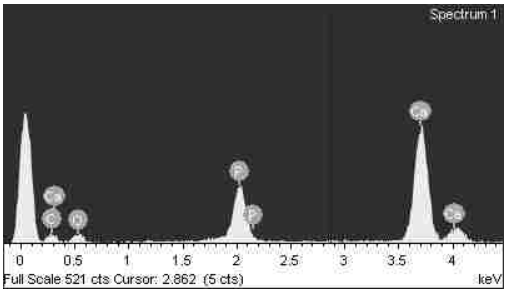
SC-9663 – *Nothrotheriops shastensis* dentin (untreated)





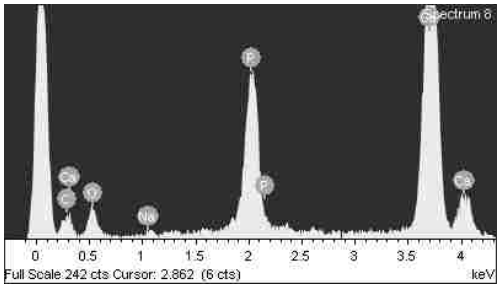
Element	Weight%
C	14.90
O	37.08
Na	0.60
P	13.65
Ca	33.78
Totals	100.00





Element	Weight%
C	17.76
O	27.18
P	13.98
Ca	41.08
Totals	100.00

TS-64232 – *Nothrotheriops shastensis* dentin (untreated)



Element	Weight%
C	16.37
O	28.34
Na	0.66
P	14.62
Ca	40.00
Totals	100.00

APPENDIX 2: ALL ISOTOPIC DATA FROM THIS STUDY

Location	Taxon	Sample ID	$\delta^{13}C_{(V\text{-}PDB)}$ (‰)	$\delta^{18}O_{(V\text{-}PDB)}$ (‰)	$\delta^{18}O_{(V\text{-}SMOW)}$ (‰)
Potter Creek Cave	*Equus occidentalis*	PC-8616-1	-10.65	-5.54	25.20
		PC-8616-2	-10.20	-5.68	25.05
		PC-8616-3	-10.17	-5.62	25.11
		PC-8616-4	-10.63	-5.24	25.50
		PC-8616-5	-11.05	-4.90	25.86
		PC-8616-7	-11.36	-5.38	25.36
	Euceratherium collinum	PC-8730-1	-10.14	-3.71	27.08
		PC-8730-2	-11.28	-3.83	26.96
		PC-8730-3	-10.99	-4.12	26.66
		PC-8730-4	-11.40	-4.41	26.36
		PC-8730-5	-11.30	-4.66	26.10
		PC-8730-6	-11.43	-4.92	25.83
		PC-8730-7	-11.37	-4.74	26.02
		PC-8730-8	-11.60	-3.91	26.88
		PC-8730-9	-11.29	-2.38	28.45
		PC-8730-10	-11.29	-2.01	28.83
		PC-8730-11	-10.84	-2.94	27.88
		PC-8730-12	-11.05	-3.33	27.47
		PC-8730-13	-10.38	-4.70	26.06
	Euceratherium collinum	PC-8385-1	-7.08	-7.38	23.30
		PC-8385-2	-4.65	-7.73	22.94
		PC-8385-3	-9.46	-6.13	24.59
		PC-8385-4	-11.24	-5.71	25.02
		PC-8385-5	-7.36	-6.82	23.88
		PC-8385-6	-10.61	-4.25	26.53
		PC-8385-7	-8.16	-4.25	26.53
		PC-8385-9	-10.42	-3.56	27.24
		PC-8385-10	-4.59	-7.20	23.48
		PC-8385-11	-10.37	-5.51	25.23
	Odocoileus sp.	PC-4181-1	-11.73	-6.44	24.27
		PC-4181-2	-11.70	-5.82	24.90
		PC-4181-3	-11.66	-4.11	26.67
		PC-4181-4	-12.01	-2.89	27.93
		PC-4181-5	-10.45	-3.46	27.34
	Odocoileus sp.	PC-4174-1	-12.30	-5.28	25.46
		PC-4174-2	-12.22	-4.65	26.11
		PC-4174-3	-12.31	-3.45	27.35
		PC-4174-4	-12.73	-3.03	27.78

	Ovis sp.	PC-8451-1	-8.51	-9.69	20.92
		PC-8451-2	-8.43	-8.57	22.07
		PC-8451-3	-8.39	-8.01	22.65
		PC-8451-4	-9.23	-5.37	25.37
		PC-8451-5	-7.84	-5.46	25.28
		PC-8451-6	-6.73	-7.28	23.40
	Nothrotheriops shastensis	PC-8141-1	-10.11	-5.86	24.86
		PC-8141-2	-9.10	-5.98	24.74
		PC-8141-3	-9.09	-5.87	24.85
		PC-8141-4	-8.49	-5.60	25.13
		PC-8141-5	-8.67	-5.87	24.85
		PC-8141-7	-8.31	-5.41	25.32
		PC-8141-8	-8.06	-6.08	24.64
		PC-8141-9	-8.35	-5.37	25.37
		PC-8141-10	-7.39	-5.58	25.15
	Nothrotheriops shastensis	PC-8715-1	-8.72	-5.26	25.48
		PC-8715-2	-8.78	-5.40	25.34
		PC-8715-3	-8.45	-3.30	27.50
		PC-8715-4	-8.45	-5.98	24.74
		PC-8715-5	-7.52	-5.92	24.81
	Megalonyx jeffersonii	PC-8498-1	-10.59	-6.81	23.89
Samwel Cave	*Equus* sp.	SC-8867-1	-10.68	-6.51	24.20
		SC-8867-2	-10.29	-6.89	23.80
		SC-8867-3	-10.66	-6.44	24.26
		SC-8867-4	-10.99	-5.96	24.76
		SC-8867-5	-11.03	-7.07	23.62
		SC-8867-6	-10.70	-6.16	24.56
		SC-8867-7	-11.15	-5.37	25.37
	Equus sp.	SC-8853-1	-8.30	-5.80	24.92
		SC-8853-2	-9.70	-4.69	26.08
		SC-8853-3	-9.22	-5.02	25.73
		SC-8853-4	-9.97	-4.93	25.82
		SC-8853-5	-9.98	-5.08	25.67
		SC-8853-6	-9.77	-5.19	25.56
		SC-8853-7	-8.63	-5.70	25.03
	Euceratherium collinum	SC-9488-1	-10.16	-5.96	24.76
		SC-9488-2	-10.27	-5.74	24.99
		SC-9488-3	-10.51	-4.85	25.90
		SC-9488-4	-10.79	-4.14	26.64
		SC-9488-5	-9.86	-3.72	27.07
		SC-9488-6	-8.61	-4.53	26.23
	Euceratherium collinum	SC-35742-1	-10.28	-5.64	25.10

		SC-35742-2	-9.61	-5.67	25.06
		SC-35742-5	-6.68	-5.90	24.83
	Odocoileus sp.	SC-23082-1	-10.95	-6.17	24.54
		SC-23082-2	-11.15	-5.36	25.38
		SC-23082-3	-10.69	-5.11	25.64
		SC-23082-4	-11.11	-5.44	25.30
	Odocoileus sp.	SC-35714-1	-11.55	-5.07	25.68
		SC-35714-2	-11.26	-3.50	27.30
		SC-35714-3	-11.57	-2.42	28.41
		SC-35714-4	-10.49	-3.09	27.72
	Megalonyx jeffersonii	SC-9666-1	-6.34	-7.27	23.42
	Megalonyx jeffersonii	SC-9668-1	-6.71	-5.02	25.73
		SC-9668-2	-6.91	-6.21	24.51
	Nothrotheriops shastensis	SC-9663-1	-8.67	-4.56	26.20
		SC-9663-2	-9.21	-4.82	25.94
	Nothrotheriops shastensis	SC-9664-1	-8.72	-4.98	25.77
		SC-9664-2	-8.00	-4.24	26.54
		SC-9664-3	-7.63	-3.86	26.92
		SC-9664-4	-7.66	-3.89	26.90
Hawver Cave	*Euceratherium collinum*	HC-114876-1	-11.46	-4.25	26.53
		HC-114876-2	-10.99	-3.72	27.07
		HC-114876-3	-10.82	-3.55	27.25
		HC-114876-4	-11.41	-2.24	28.60
		HC-114876-5	-11.48	-2.65	28.18
		HC-114876-6	-10.94	-4.42	26.35
	Odocoileus hemionus	HC-11016-1	-12.68	-5.34	25.40
		HC-11016-2	-9.39	-5.64	25.09
	Bison sp.	HC-11006B-1	-10.50	-6.38	24.33
		HC-11006B-2	-10.53	-5.99	24.73
		HC-11006B-3	-10.23	-4.62	26.14
		HC-11006B-4	-10.26	-4.44	26.33
	Nothrotheriops shastensis	HC-21473-1	-11.43	-4.16	26.62
Devil Peak Cave	*Nothrotheriops shastensis*	DP-1	-5.68	-6.22	24.50
		DP-2	-5.27	-7.21	23.47
		DP-3	-4.13	-6.44	24.27
		DP-4	-4.51	-7.07	23.62
		DP-5	-9.22	-10.11	20.48
		DP-6	-0.14	-6.42	24.29
		DP-7	-5.01	-6.61	24.09
		DP-8	-4.54	-6.65	24.06
		DP-9	-5.27	-7.41	23.27
		DP-10	-4.62	-6.42	24.29
		DP-11	-2.28	-7.77	22.90

		DP-12	-3.64	-6.28	24.43
		DP-13	1.09	-6.31	24.40
Tule Springs	*Nothrotheriops shastensis*	TS-64232A-1	-4.72	-6.06	24.66
Gilcrease Site	*Mammuthus columbi*	MT-3-1	-9.16	-11.57	18.98
		MT-3-4	-10.01	-13.11	17.39
		MT-3-7	-9.00	-13.47	17.02
		MT-3-10	-8.34	-13.51	16.98
		MT-3-13	-7.17	-13.26	17.23
		MT-3-16	-9.27	-14.62	15.84
	Mammuthus columbi	MT-4-1	-8.79	-12.93	17.58
		MT-4-4	-10.62	-14.49	15.97
		MT-4-7	-10.58	-13.13	17.37
		MT-4-13	-9.33	-12.70	17.81
		MT-4-16	-13.45	-13.53	16.96
		MT-4-19	-9.14	-13.45	17.05
Wilkin Quarry	*Bison latifrons*	B-1	-7.09	-11.21	19.35
		B-2	-6.82	-11.01	19.55
		B-3	-6.54	-10.84	19.73
		B-4	-6.33	-10.31	20.28
		B-5	-6.51	-9.76	20.85
		B-6	-6.26	-9.72	20.89
		B-7	-6.33	-10.75	19.83
		B-8	-6.07	-9.73	20.87
		B-9	-5.40	-10.30	20.29
		B-10	-8.01	-10.44	20.14
		B-11	-7.36	-11.66	18.89

APPENDIX 3: ISOTOPIC DATA FROM CONNIN *ET AL*. (1998) AND VETTER (2007)

Study	Location	Taxon	$\delta^{13}C_{(V\text{-}PDB)}$ (‰)	$\delta^{18}O_{(V\text{-}PDB)}$ (‰)	$\delta^{18}O_{(V\text{-}SMOW)}$ (‰)
Connin *et al*., 1998	Kokoweef Cave	*Equus* sp.	-9.50	-8.64	22.00
		Equus sp.	-11.60	-4.76	26.00
		Equus sp.	-11.90	-6.99	23.70
	Calico Lakes	*Equus* sp.	-10.60	-6.51	24.20
		Equus sp.	-9.60	-6.12	24.60
		Equus sp.	-9.80	-6.12	24.60
		Equus occidentalis	-9.00	-6.99	23.70
		Camelops sp.	-11.00	-4.57	26.20
		Camelops sp.	-5.60	-5.73	25.00
		Camelops sp.	-8.20	-5.34	25.40
		Camelops sp.	-6.50	-5.63	25.10
		Equus occidentalis	-10.80	-4.57	26.20
	Valley Wells	*Mammuthus* sp.	-7.20	-8.74	21.90
	Corn Creek A	*Equus* sp.	-7.70	-5.83	24.90
		Camelops sp.	-8.70	-3.11	27.70
	Pahrump Valley	*Mammuthus* sp.	-8.90	-5.83	24.90
		Mammuthus sp.	-7.90	-3.11	27.70
	Lathrop Wells	*Equus* sp.	-9.80	-5.34	25.40
	Cactus Springs	*Mammuthus* sp.	-8.90	-7.48	23.20
	Tule Springs	*Antilocapridae*	-10.80	-1.36	29.50
		Tetrameryx sp.	-10.90	-6.51	24.20
		Tetrameryx sp.	-9.90	-2.43	28.40
		Equus sp.	-6.30	-5.63	25.10
		Equus sp.	-8.80	-6.70	24.00
		Camelops sp.	-9.60	-5.92	24.80
		Camelops sp.	-8.00	-4.95	25.80
		Mammuthus sp.	-8.30	-10.00	20.60
		Mammuthus sp.	-9.00	-10.00	20.60
		Mammuthus sp.	-6.40	-7.86	22.80
		Bison sp.	-4.90	-10.29	20.30
		Bison sp.	-3.40	-5.73	25.00
		Mammuthus sp.	-6.40	-11.26	19.30
		Equus sp.	-1.60	-8.15	22.50
	Crypt Cave	*Camelops* sp.	-11.60	-3.50	27.30
		Equus sp.	-10.50	-9.32	21.30
	Fishbone Cave	*Camelops* sp.	-6.50	-7.86	22.80
		Camelops sp.	-2.70	-9.32	21.30
	Wizards Beach	*Equus pacificus*	-10.00	-9.32	21.30
		Camelops hesturnus	-6.70	-9.71	20.90

	Rye Patch	*Mammuthus columbi*	-10.70	-11.74	18.80
		Camelops hesturnus	-10.30	-11.55	19.00
		Bison sp.	-9.50	-10.77	19.80
		Equus sp.	-8.40	-11.94	18.60
	Sunshine Lake	*Camelops* sp.	-3.90	-6.89	23.80
Vetter, 2007	Gilcrease Site	*Mammuthus columbi* (1)	-8.00	-13.96	16.52
		Mammuthus columbi (2)	-8.06	-14.32	16.14
		Mammuthus columbi(3)	-8.09	-14.44	16.02
		Mammuthus columbi (4)	-9.18	-15.32	15.11
		Mammuthus columbi (5)	-8.85	-14.08	16.39
		Equus sp. (1)	-7.74	-11.38	19.17
		Equus sp. (2)	-8.15	-11.07	19.49
		Equus sp. (3)	-8.83	-10.08	20.52
		Equus sp. (4)	-7.42	-11.71	18.83
		Equus sp. (5)	-8.64	-11.10	19.46
		Bison sp. (1)	-8.94	-11.13	19.43
		Bison sp. (2)	-9.99	-12.68	17.83
		Bison sp. (3)	-8.50	-13.70	16.78
		Bison sp. (4)	-5.97	-15.42	15.01
		Bison sp. (5)	-10.22	-13.11	17.39
		Camelops sp. (1)	-6.48	-12.54	17.98
		Camelops sp. (2)	-5.23	-11.48	19.07
		Camelops sp. (3)	-6.70	-12.44	18.08
		Camelops sp. (4)	-5.76	-10.67	19.91
		Camelops sp. (5)	-8.49	-11.14	19.42

REFERENCES

Adam, D.P. and West, G.J. (1983) Temperature and precipitation estimates through the last glacial cycle from Clear Lake, California, pollen data. Science, v. 219, p. 168-170.

Aiello, A. (1985) Sloth hair: Unanswered questions *in* Montgomery, G.G. *ed*., The evolution and ecology of armadillos, sloths, and vermilinguas. Smithsonian Institute Press, Washington, p. 213-218.

Akersten, W.A., Foppe, T.M., Jefferson, G.T. (1988) New source of dietary data for extinct herbivores. Quaternary Research, v. 30, p. 92-97.

Alroy, J., Koch, P.L., Zachos, J.C. (2000) Global climate change and North American mammalian evolution. Paleobiology, v. 26, no. 4, p. 259-288.

Andreev, Y.G. (1994) The use of the serial-correlations concept in the figure-of-merit function for powder diffraction profile fitting. Journal of Applied Crystallography, v. 27, no. 3, p. 288-297.

Asmerom, Y., Polyak, V.J., Burns, S.T. (2010) Variable winter moisture in the southwestern United States linked to rapid glacial climate shifts. Nature Geoscience, v. 3, p. 114-117.

Ayliffe, L.K., Lister, A.M., Chivas, A.R. (1992) The preservation of glacial-interglacial climatic signatures in the oxygen isotopes of elephant skeletal phosphate. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 99, p. 179-191.

Ayliffe, L.K., Chivas, A.R., Leakey, M.G. (1994) The retention of primary oxygen isotope composition of fossil elephant skeletal phosphate. Geochimica et Cosmochimica Acta, v. 58, p. 5291-5298.

Balasse, M. (2002) Reconstructing dietary and environmental history from enamel isotopic analysis: Time resolution of intra-tooth sequential sampling. International Journal of Osteoarcheology, v. 12, p. 155-165.

Barnosky, A.D., Hadly, E.A., Bell, C.J. (2003) Mammalian response to global warming on varied temporal scales. Journal of Mammalogy, v. 84, no. 2, p. 354-368.

Barnosky, A.B., Koch, P.L., Feranec, R.S., Wing, S.L., Scheibel, A.B. (2004) Assessing the causes of Late Pleistocene extinctions on the continents. Science, v. 306, p. 70-75.

Barnosky, A.D. (2009) Heatstroke: Nature in an age of global warming. Island Press, p. 1-269.

Blois, J.L. and Hadley, E.A. (2009) Mammalian response to Cenozoic climate change. Annual Review of Earth and Planetary Sciences, v. 37, p. 181-208.

Blois, J.L., McGuire, J.L., Hadley, E.A. (2010) Small mammal diversity loss in response to Late-Pleistocene climatic change. Nature, v. 465, no. 10, p. 771-775.

Bonde, A.M., Rowland, S. (2011) Southern Great Basin Late Pleistocene seasonality and paleoenvironment recorded in *Bison latifrons* tooth enamel. Geological Society of America Abstract with Programs, v. 43, no. 5, p. 262.

Bonde, J.W., Shirk, A.M., Rowland, S. (2008) Taphonomy of the Gilcrease Spring Mound paleontological site, Clark County, Nevada. Geological Society of America Abstracts with Programs, v. 40, no. 1, p. 50.

Bowen, G.J. (2012) The online isotopes in precipitation calculator, version OIPC2.2. http://www.waterisotopes.org.

Britton, S.W. (1941) Form and function in the sloth. The Quarterly Review of Biology, v. 16, no. 1, p. 13-34.

Bryant, J.D., Luz, B., Froelich, P.N. (1994) Oxygen isotopic composition of fossil horse tooth phosphate as a record of continental paleoclimate. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 107, p. 303-316.

Bryant, J.D. and Froelich, P.N. (1995) A model of oxygen isotope fractionation in body water of large mammals. Geochimica et Cosmochimica Acta, v. 59, no. 21, p. 4523-4537.

Bryson, R.A. (2005) Archaeoclimatology *in* Oliver, J.E., *ed*., The Encyclopedia of World Climatology. Springer, Cordrecht, p. 58-63.

Bryson, R.A. and DeWall, K.M. (2007) A paleoclimatology workbook: High resolution, site-specific, macrophysical climate modeling. The Mammoth Site of Hot Springs, South Dakota, p. 1-288.

Bryson, R.A., Agenbroad, L.D., and DeWall, K.E. (2010) Paleoclimate modeling and paleoenvironmental interpretations for three instances of island dwelling mammoths. Quaternary International, v. 217, p. 6-9.

Cerling, T.E. and Sharp, Z.D. (1996) Stable carbon and oxygen isotope analysis of fossil tooth enamel using laser ablation. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 126, p. 173-186.

Cerling, T.E., Harris, J.M., Ambrose, S.H., Leakey, M.G., Solounias, N. (1997) Dietary and environmental reconstruction with stable isotope analyses of herbivore tooth enamel from the Miocene locality of Fort Ternan, Kenya. Journal of Human Evolution, v. 33, p. 635-650.

Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., Ehleringer, J.R. (1997) Global vegetation change through the Miocene/Pliocene boundary. Nature, v. 389, p. 163-168.

Cerling, T.E. and Harris, J.M. (1999) Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia, v. 120, p. 347-363.

Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. Science, v. 333, p. 1024-1026.

Chritz, K.L, Dyke, G.J., Zazzo, A., Lister, A.M., Monaghan, N.T., Sigwart, J.D. (2009) Palaeobiology of an extinct Ice Age mammal: Stable isotope and cementum analysis of giant deer teeth. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 282, p. 133-144.

Clementz, C.T. and Koch, P.L. (2001) Differentiating aquatic mammal habitat and foraging ecology with stable isotopes in tooth enamel. Oecologia, v. 129, p. 461-472.

Clementz, M.T., Fox-Dobbs, K., Wheatley, P.V., Koch, P.L., Doak, D.F. (2009) Revisiting old bones: Coupled carbon isotope analysis of bioapatite and collagen as an ecological and palaeoecological tool. Geological Journal, v. 44, p. 605-620.

COHMAP (1988) Climatic changes of the last 18,000 years – observations and model simulations. Science, v. 241, no. 4869, p. 1043-1052.

Cole, K.L., Ironside, K., Eischeid, J., Garfin, G., Duffy, P.B., Toney, C. (2011) Past and ongoing shifts in Joshua tree distribution support future modeled range contraction. Ecological Applications, v. 21, no. 1, p. 137-149.

Coltrain, J.B., Harris, J.M., Cerling, T.E., Ehleringer, J.R., Dearing, M.D., Ward, J., Allen, J. (2004) Rancho La Brea stable isotope biogeochemistry and its implications for the palaeoecology of Late Pleistocene, coastal southern California. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 205, p. 199-219.

Connin, S.L., Betancourt, J., and Quade, J. (1998) Late Pleistocene C_4 plant dominance and summer rainfall in the southwestern United States from isotopic study of herbivore teeth. Quaternary Research, v. 50, p. 179-193.

D'Angela D., Longinelli, A. (1990) Oxygen isotopes in living mammal's bone phosphate: Further Results. Chemical Geology, v. 86, p. p. 75-82.

Dansgaard, W. (1964) Stable isotopes in precipitation. Tellus, v. 16, p. 436-468.

Dean, M.C., Scandrett, A.E. (1995) Rates of dentine mineralization in permanent human teeth. International Journal of Osteoarcheology, v. 5, no. 4, p. 349.

Delgado Huertas, A., Iacumin, P., Stenni, B., Sanchez Chillon, B., Longinelli, A. (1995) Oxygen isotope variations of phosphate in mammalian bone and tooth enamel. Geochimica et Cosmochimica Acta, v. 59, p. 4299-4305.

De Narvaez, C. (1995) Paleohydrology and paleotopography of a Las Vegas spring. [M.S. Thesis] Northern Arizona University, p. 1-89.

DeSantis, L.R.G, Feranec, R.S., MacFadden, B.J. (2009) Effects of global warming on ancient mammalian communities and their environments. PLoS ONE, v. 4, no. 6, p. 1-7.

Dongmann, G., Nurnberg, H.W., Förstel, H., Wagener, K. (1974) On the enrichment of $H_2{}^{18}O$ in the leaves of transpiring plants. Radiation and Environmental Biophysics, v. 11, p. 41-52.

Driessens, F.C.M. and Verbeeck, R.M.H. (1990) Biominerals. CRC Press, p. 1-403.

Dupras, T.L. (2001) Strangers in a strange land: Stable isotope evidence for human migration in the Dakhleh Oasis, Egypt. Journal of Archaeological Science, v. 28, p. 1199-1208.

Ehleringer, J.R. (1989) Carbon isotope ratios and physiological processes in arid land plants *in* Rundle, P.W., Ehleringer, J.R., Nagy, K.A., *eds*., Stable isotopes in ecological research, ecological studies series. Springer-Verlang, New York, p. 41-54.

Ehleringer, J.R., Bowen, G.J., Chesson, L.A., West, A.G., Podlesak, D.W., Cerling, T.E. (2008) Hydrogen and oxygen isotope ratios in human hair are related to geography. Proceedings of the National Academy of Sciences, v. 105, no. 8, p. 2788-2793.

Elliott, J.C., Wilson, R.M., Dowker, S.P. (2002) Apatite structures. Advances in X-ray Analysis, v. 45, p. 172-181.

Fabre M., Lécuyer, C., Brugal, J.P., Amiot, r., Fourel, F., Martineau, F. (2011) Late Pleistocene climatic change in the French (Jura) recorded in the $\delta^{18}O$ of phosphate from ungulate tooth enamel. Quaternary Research, v. 75, p. 605-613.

Farquhar, G.D., Ehleringer, J.R, Hubick, K.T (1989) Carbon isotope discrimination and photosynthesis. Annual Review of Plant Physiology and Plant Molecular Biology, v. 40., p. 503-537.

Fatani, J.A. and Raja, Z.A. (1977) Rate of growth in lower incisor teeth in the adult white rat. Acta Anatomica, v. 99, no. 1, p. 84-85.

Feranec, R.S. (2004) Geographic variation in the diet of hypsodont herbivores from the Rancholabrean of Florida. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 207, p. 359-369.

Feranec, R.S. (2004) Isotopic evidence of saber-tooth development, growth rate, and diet from the adult canine of *Smilodon fatalis* from Rancho La Brea. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 206, p. 303-310.

Feranec, R.S., Hadly, E.A., Blois, J.L., Barnosky, A.D., and Paytan, A. (2007) Radiocarbon dates from the Pleistocene fossil deposits of Samwel Cave, Shasta County, California, USA. Radiocarbon, v. 49, no. 1, p. 117-121.

Feranec, R.S. (2009) Implications of radiocarbon dates from Potter Creek Cave, Shasta County, California, USA. Radiocarbon, v. 51, no. 3, p. 931-936.

Feranec, R.S., Hadley, E.A., Paytan, A. (2009) Stable isotopes reveal seasonal competition for resources between late Pleistocene bison (*Bison*) and horse (*Equus*) from Rancho La Brea, southern California. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 271, p. 153-160.

Feranec, R.S., García, N., DÍez, J.C., Arsuaga, J.L. (2010) Understanding the ecology of mammalian carnivorans and herbivores from Valdegoba cave (Burgos, northern Spain) through stable isotope analysis. Paleaeogeography, Palaeoclimatology, Palaeoecology, v. 297, p. 263-272.

Feranec, R.S., Hadley, E.A., Paytan, A. (2010) Isotopes reveal limited effects of middle Pleistocene climate change on the ecology of mid-sized mammals. Quaternary International, v. 217, p. 43-52.

Ferigolo, J. (1985) Evolutionary trends of the histological pattern in the teeth of Edentata (Xenarthra). Archives of Oral Biology, v. 30, p. 71-85.

Fisher, D.C., Fox, D.L., Agenbroad, L.D. (2003) Tusk growth rate and season of death of *Mammuthus columbi* from Hot Springs, South Dakota, USA *in* Reumer, J.W.F., De Vos, J., Mol, D., *eds*., Advances in mammoth research. DEINSEA, v. 9, p. 117-133

Forbes, M.S., Kohn, M.J., Bestland, E.A., Wells, R.T. (2010) Late Pleistocene environmental change interpreted from $\delta^{13}C$ and $\delta^{18}O$ of tooth enamel from the Black Creek Swamp Megafauna site, Kangaroo Island, South Australia. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 291, p. 319-327.

Fox-Dobbs, K., Leonard, J.A., Koch, P.L. (2008) Pleistocene megafauna from eastern Beringia: Paleoecological and paleoenvironmental interpretations of stable carbon and nitrogen isotope and radiocarbon records. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 261, p. 30-46.

France, C.A.M., Zelanko, P.M., Kaufman, A.J., Holtz, T.R. (2007) Carbon and nitrogen isotopic analysis of Pleistocene mammals from the Saltville Quarry (Virginia, USA): Implications for trophic relationships. Paleaeogeography, Palaeoclimatology, Palaeoecology, v. 249, no. 3, p. 271-282.

Fricke, H.C., Hencecroth, J., Hoerner, M.E. (2011) Lowland-upland migration of sauropod dinosaurs during the Late Jurassic epoch. Nature, v. 480, p. 513-515.

Fricke, H.C. and O'Neil, J.R. (1996) Inter-and intra-tooth variation in the oxygen isotope composition of mammalian tooth enamel phosphate: Implications for palaeoclimatological and palaeobiological research. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 126, p. 91-99.

Fricke, H.C, Clyde, W.C., O'Neil, J.R. (1998) Intra-tooth variations in $\delta^{18}O$ (PO_4) of mammalian tooth enamel as a record of seasonal variations in continental climate variables. Geochimica et Cosmochimica Acta, v. 62, p. 1839-1859.

Fricke, H.C., Rogers, R.R., Backlund, R., Dwyer, C.N., Echt, S. (2008) Preservation of primary stable isotope signals in dinosaur remains, and environmental gradients of the Late Cretaceous of Montana and Alberta. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 266, p. 13-27.

Friggins, M.M., Warwell, M.V., Chambers, J.C., Kitchen, S.G. (2012) Modeling and predicting vegetation response of western USA grasslands, shrublands, and deserts to climate change *in* Finch, D.M. *ed*., Climate change in grasslands, shrublands, and deserts of the Interior American West: A review and needs assessment. United State Department of Agriculture Forest Serice, General Technical Report (RMRS-GTR-285), p. 1-20.

Furlong, E.L. (1906) The exploration of Samwel Cave. American Journal of Science, v. 22, p. 235-247.

Furlong, E.L. (1907) Reconnoissance of a recently discovered Quaternary cave deposit near Auburn, California. Science, v. 15, no. 636, p. 392-394.

Gadbury, C., Todd, L., Jahren, A.H., Amundson, R. (2000) Spatial and temporal variations in the isotopic composition of bison tooth enamel from the Early Holocene Hudson-Meng Bone Bed, Nebraska. Paleaeogeography, Palaeoclimatology, Palaeoecology, v. 157, p. 79-93.

Gill, F.L., Crump, M.P., Schouten, R., Bull, I.D. (2009) Lipid analysis of a ground sloth coprolite. Quaternary Research, v. 72, p. 284-288.

Glowiak, E.M. (2007) Gypsum Cave revisited: Faunal and taphonomic analysis of a Rancholabrean-to-Holocene fauna in southern Nevada. [M.S. Thesis] University of Nevada, Las Vegas.

Gordon, I.J. (2003) Browsing and grazing ruminants: Are they different beasts? Forest Ecology and Management, v. 181, p. 13-21.

Grafenstein, U.V., Erlenkeuser, H., Muller, J., Trimborn, P., Alefs, J. (1996) A 200 year mid-European air temperature record preserved in lake sediments: An extension of the $\delta^{18}O_{p\text{-}air}$ temperature relation into the past. Geochimica et Cosmochimica Acta, v. 60, p. 4025-4036.

Graham, R.W., Lundelius Jr., E.L., Graham, M.A., Schroeder, E.K., Tommey III, R.S., Anderson, E., Barnosky, A.D., Burns, J.A., Churcher, C.S., Grayson, D.K., Guthrie, R.D., Harington, C.R., Jefferson, G.T., Martin, L.D., McDonald, H.G., Morlan, R.E., Semken Jr., H.A., Webb, S.D., Werdelin, L., Wilson, M.C. (1996) Spatial response of mammals to Late Quaternary environmental fluctuations. Science, v. 272, no. 5268, p. 1601-1606.

Graham, R.W. and Lundelius Jr., E.L. (2010) FAUNMAP II: New data for North America with a temporal extension for the Blancan, Irvingtonian, and early Rancholabrean. FAUNMAP II, version 1.0, http://www.ucmp.berkeley.edu/faunmap/.

Green, J.L. (2009) Intertooth variation of orthodentine microwear in armadillos (Cingulata) and tree sloths (Pilosa). Journal of Mammalogy, v. 90, no. 3, p. 768-778.

Gromny, J.L. (2003) Comparative morphometric analysis of the Devil Peak shasta ground sloth, *Nothrotheriops shastensis*. [M.S. Thesis] University of Nevada, Las Vegas, p. 1-108.

Hadley, E.A. and Barnosky, A.D. (2009) Vertebrate fossils and the future of conservation biology *in* Dietl, G.P. and Fessa, K.W., *eds*., Conservation paleobiology: Using the past to manage for the future. Paleontological Society Papers, v. 15, p. 95-112.

Hadley, E.A., Speath, P.A., Li, C. (2009) Niche conservatism above the species level. Proceedings of the National Academy of Sciences, v. 106, p. 19707-19714.

Hansen, R.M. (1978) Shasta ground sloth food habits, Rampart Cave, Arizona. Paleobiology, v. 4, p. 302-319.

Hansen, R.M. (1980) Late Pleistocene plant fragments in the dung of herbivores at Cowboy Cave *in* Jennings, J.D., *ed*., Cowboy Cave. University of Utah Anthropological Papers, v. 104, p. 179-189.

Harrington, M.R. (1933) Gypsum Cave, Nevada. Southwest Museum Papers, v. 8.

Harrington, M.R. and Simpson, R. D. (1961) Tule Springs, Nevada with other evidences of Pleistocene man in North America. Southwest Museum Papers, no. 18, p. 1-146.

Harris, A.H. (1985) Late Pleistocene vertebrate paleoecology of the West. University of Texas Press, Austin, Texas, p. 1-293.

Hassan, A.A., Termine, J.D., Haynes, C.V. (1977) Mineralogical studies on bone apatite and their implications for radiocarbon dating. Radiocarbon, v. 19, no. 3, p. 364-374.

Haynes, C.V. (1967) Quaternary geology of the Tule Springs area, Clark County, Nevada *in* Wormington, H.M. and Ellis, D., *eds*., Pleistocene studies in southern Nevada. Nevada State Museum Anthropological Papers: Carson City, NV, Nevada State Museum, p. 15-104.

Hillson, S. (2005) Teeth. Cambridge University Press, Second Edition, p. 1-373.

Heizer, R.F. and Cook, S.F. (1949) The archeology of central California: A comparative analysis of human bone from nine sites. University of California Anthropological Records, v. 12, no. 2.

Higgins, P. and MacFadden, B.J. (2004) "Amount Effect" recorded in oxygen isotopes of Late Glacial horse (*Equus*) and bison (*Bison*) teeth from the Sonoran and Chihuahuan deserts, southwestern United States. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 206, p. 337-353.

Hinz, E.A. and Kohn, M.J. (2010) The effect of tissue structure and soil chemistry on trace element uptake in fossils. Geochimica et Cosmochimica Acta, v. 74, p. 3213-3231.

Hofreiter, M., Poinar, H.N., Spaulding, W.G., Bauer, K., Martin, P.S., Possnert, G., and Pääbo, S. (2000) A molecular analysis of ground sloth diet through the last deglaciation. Molecular Ecology, v. 9, p. 1975-1984.

Hoganson, J.W. and McDonald, H.G. (2007) First report of Jefferson's ground sloth (*Megalonyx jeffersonii*) in North Dakota: Paleobiogeographical and paleoecological significance. Journal of Mammalogy, v. 88, no. 1, p. 73-80.

Hoppe, K.A., Koch, P.L., Carlson, R.W., Webb, S.D. (1999) Tracking mammoths and mastodons: Reconstruction of migratory behavior using strontium isotope ratios. Geology, v. 27, no. 5, p. 439-442.

Hoppe, K.A., Amundson, R., Vavra, M., McClaran, M.P., Anderson, D.L. (2004) Isotopic analysis of tooth enamel carbonate from modern North American feral horses: Implications for paleoenvironmental reconstructions. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 203, no. 3-4, p. 299-311.

Hoppe, K.A (2006) Correlation between the oxygen isotope ratio of North American bison teeth and local waters: Implications for paleoclimatic reconstructions. Earth and Planetary Science Letters, v. 244, p. 408-417.

Hoppe, K.A., Paytan, A., Chamberlain, P. (2006) Reconstructing grassland vegetation and paleotemperatures using carbon isotope ratios of bison tooth enamel. Geology, v. 34, no. 8, p. 649-652.

Iacumin, P., Bocherens, H., Mariotti, A., Longinelli, A., (1996) Oxygen isotope analyses of co-existing carbonate and phosphate in biogenic apatite: A way to monitor diagenetic alteration of bone phosphate? Earth and Planetary Science Letters, v. 142, p. 1-6.

Jacques, L., Ogle, N., Moussa, I., Kalin, R., Vignaud, P., Brunet, M., Bocherens, H. (2008) Implications of diagenesis for the isotopic analysis of Upper Miocene large mammalian herbivore tooth enamel from Chad. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 266, p. 200-210.

Janis, C.M. and Ehrhardt, D. (1988) Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. Zoological Journal of the Linnean Society, v. 92, p. 267-284.

Janis, C. (2008) An evolutionary history of browsing and grazing ungulates *in* Gordon, I.J. and Prins, H.H.T *eds*., The ecology of browsing and grazing. Ecological Studies, v. 195, p. 21-45.

Kalthoff, D.C. and Tütken, T. (2007a) Stable isotope and elemental compositions of extant xenarthran teeth and their potential as diet and habitat proxies in fossil xenarthrans (Mammalia). Journal of Morphology, v. 268, no. 12, p. 1091.

Kalthoff, D.C. and Tütken, T. (2007b) Stable isotope compositions of extant xenarthran teeth and their potential for the reconstruction of the diet of fossil xenarthrans (Mammalia). Journal of Vertebrate Paleontology, v. 27, suppl. 3, p. 97A.

Kalthoff, D.C. (2011) Microstructure of dental hard tissues in fossil and recent xenarthrans (Mammalia: Folivora and Cingulata). Journal of Morphology, v. 272, p . 641-661.

Klevezal, G.A. (1996) Recording structures of mammals: Determination of age and reconstruction of life history. A.A. Balkema Publishers, p. 1-271.

Koch, P.L., Fisher, D.C., Dettman, D. (1989) Oxygen isotope variation in the tusks of extinct proboscideans: A measure of season of death and seasonality. Geology, v. 17, p. 515-519.

Koch, P.L., Fogel, M.L., Tuross, N. (1994) Tracing the diets of fossil animals using stable isotopes *in* Lajtha, K., and Michener, B. *eds*., Stable isotopes in ecology and environmental science. Oxford, Blackwell Scientific, p. 63-92.

Koch, P.L., Tuross, N., and Fogel., M.L. (1997) The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. Journal of Archeological Science, v. 24, p. 417-429.

Koch, P.L. (1998) Isotopic reconstruction of past continental environments. Annual Review of Earth and Planetary Sciences, v. 26, p. 573-613.

Koch, P.L., Fox-Dobbs, K., Newsome, S.D. (2009) The isotopic ecology of fossil vertebrates and conservation paleobiology *in* Dietl, G.P. and Fessa, K.W., *eds*., Conservation paleobiology: Using the past to manage for the future. Paleontological Society Papers, v. 15, p. 95-112.

Kohn, M.J. Schoeninger, M.J., Valley, J.W. (1996) Herbivore tooth oxygen isotope compositions: Effects of diet and physiology. Geochimica et Cosmochimica Acta, v. 60, no. 20, p. 3889-3896.

Kohn, M.J., Schoeninger, M.J., Barker, W. (1999) Altered states: Effects of diagenesis on fossil tooth chemistry. Geochimica et Cosmochimica Acta, v. 63, no. 18, p. 2737-2747.

Kohn, M.J. and Cerling, T.E. (2002) Stable isotope compositions of biological apatite. Reviews in Mineralogy and Geochemistry, v. 48, p. 455-488.

Kohn, M.J., McKay, M.P., Knight, J.L. (2005) Dining in the Pleistocene – Who's on the menu? Geology, v. 33, no. 8, p. 649-652.

Kohn, M.J. (2010) Carbon isotope compositions of terrestrial C_3 plants as indicators of (paleo)ecology and (paleo)climate. Proceedings of the National Academy of Sciences, v. 107, p. 19691-19695.

Kohn, M.J. and McKay, M.P. (2012) Paleoecology of Late Pleistocene-Holocene faunas of western and central Wyoming, USA, with implications for LGM climate models. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 326-328, p. 42-53.

Kohn, M.J., Morris, J., Olin, P. (2013) Trace element concentrations in teeth – a modern Idaho baseline with implications for archeometry, forensics, and palaeontology. Journal of Archaeological Science, v. 40, p. 1689-1699.

Kropf, M., Mead, J.I., Anderson, R.S. (2007) Dung, diet, and the paleoenvironment of the extinct shrub-ox (*Euceratherium collinum*) on the Colorado Plateau, USA. Quaternary Research, v. 67, no. 1, p. 143-151.

Krueger, H.W. (1991) Exchange of carbon with biological apatite. Journal of Archaeological Science, v. 18, p. 355-361.

Kuczumow, A., Cukrowska, E., Stachniuk, A., Gaweda, R., Mroczka, R., Paszkowicz, W., Skrzypiec, K., Falkenberg, R., Backwell, L. (2010) Investigation of chemical changes in bone material from South African fossil hominid deposits. Journal of Archaeological Science, v. 37, p. 107-115.

Kurtén, B., and Anderson, E. (1980) Pleistocene mammals of North America. Columbia University Press, p. 1-443.

Lachniet M.S. (2009) Climatic and environmental controls on speleothem oxygen isotope values. Quaternary Science Reviews, v. 28, p. 412-432.

Lachniet, M.S., Asmerom, Y., Polyak, V. (2011) Deglacial paleoclimate in the southwestern United States: An abrupt 18.6 ka cold event and evidence for a North Atlantic forcing of Termination I. Quaternary Science Reviews, v. 30, p. 3803-3811.

Laudermilk, J.D, and Munz, P.A. (1934) Plants in the dung of *Nothrotherium* from Gypsum Cave, Nevada. The Carnegie Institution of Washington Publications, v. 453, p. 29-37.

Lee-Thorp, J., and Van der Merwe, N.J. (1987) Carbon isotope analysis of fossil bone apatite. South African Journal of Science, v. 83, p. 712-715.

Lee-Thorp, J.A. and Sponheimer, M. (2003) Three case studies used to reassess the reliability of fossil bone and enamel isotope signals for paleodietary studies. Journal of Anthropological Archaeology, v. 22, p. 208-216.

Lee-Thorp, J.A., and van der Merwe, N.J. (1991) Aspects of the chemistry of modern and fossil biological apatites. Journal of Archaeological Science, V. 18, p. 343-354.

LeGeros, R.Z. (1981) Apatites in biological systems *in* Pamplin, B. *ed*., Inorganic biological crystal growth. New York, Pergamon Press, p. 1-45.

LeGeros, R.Z., Ito, A., Ishikawa, K., Sakae, T., LeGeros, J.P. (2009) Fundamentals of hydroxyapatite and related calcium phosphates *in* Basu, B., Katti, D., Kumar, A., *eds*., Advanced Biomaterials: Fundamentals, processing, and applications. John Wiley & Sons, Inc., p. 19-52.

Levin, N.E., Cerling, T.E., Passey, B.H., Harris, J.M., Ehleringer, J.R. (2006) A stable isotope aridity index for terrestrial environments. Proceedings of the National Academy of Sciences, v. 103, no. 30, p. 11201-11205.

Longinelli, A. (1984) Oxygen isotopes in mammal bone phosphate: A new tool for paleohydrological and paleoclimateological research? Geochimica et Cosmochimica Acta, v. 48, p. 385-390.

Longwell, C.R., Pampeyan, E.H., Bower, B., Roberts, R.J. (1965) Geology and mineral deposits of Clark County, Nevada. Nevada Bureau of Mines and Geology Bulletin, no. 62, p. 218.

Luz, B., Kolodny, Y., Horowitz, M. (1984) Fractionation of oxygen isotopes between mammalian bone-phosphate and environmental drinking water. Geochimica et Cosmochimica Acta, v. 126, p. 91-99.

MacFadden, B.J. (2000) Cenozoic mammalian herbivores from the Americas: Reconstructing ancient diets and terrestrial communities. Annual Review of Ecology, Evolution, and Systems, v. 31, p. 33-59.

MacFadden, B.J., DeSantis, L.R.G., Hochstein, J.L., Kamenov, G.D. (2010) Physical properties, geochemistry, and diagenesis of xenarthran teeth: Prospects for interpreting the paleoecology of extinct species. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 291, p. 180-189.

MacMahon, J.A. (1999) Warm Deserts *in* Barbour, M.G. and Billings, W.D., *eds*., North American Terrestrial Vegetation. Cambridge University Press, p. 285-322.

Marshall, L.G., Webb, S.D., Sepkoski, J.J., Raup, D.M. (1982) Mammalian evolution and the Great American Interchange. Science, v. 215, no. 4538, p. 1351-1357.

Marshall, L.G. (1988) Land mammals and the Great American Interchange. American Scientist, v. 76, p. 380-388.

Martin, P.S., Sabels, B.E., Shutler, D. (1961) Rampart Cave coprolite and ecology of the Shasta ground sloth. American Journal of Science, v. 259, no. 2, p. 102-107.

Martínez-Meyer, E., Peterson, A.T., Hargrove, W.W. (2004) Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. Global Ecology and Biogeography, v. 13, p. 305-314.

Maung-Thein, Z.M., Takai, M., Uno, H., Wynn, J.G., Egi, N., Tsubamoto, T., Htike, T., Soe, A.N., Maung, M., Nishimura, T., Yoneda, M. (2011) Stable isotope analysis of the tooth enamel of Chaingzauk mammalian fauna (Late Neogene, Myanmar) and its implication to paleoenvironment and paleogeography. Palaeogeography, Palaeoclimatology, and Palaeoecology, v. 300, p. 11-22.

Mawby, J.E. (1967) Fossil vertebrates of the Tule Springs site, Nevada *in* Wormington, H.M., and Ellis, D., *eds*., Pleistocene studies in southern Nevada. Nevada State Museum Anthropological Papers, v. 13, p. 105-128.

McDonald, H.G. (1996) Biogeography and paleoecology of ground sloths in California, Arizona and Nevada *in* Reynolds, R.E. and Reynolds, J., *eds*., Punctuated chaos in the southeastern Mojave Desert. San Bernardino County Museum Association Quarterly, v. 43, p. 61-66.

McDonald, H.G., Harington, C.R, De Iuliis, G. (2000) The ground sloth *Megalonyx* from Pleistocene deposits of the Old Crow Basin, Yukon, Canada. Arctic, v. 53, no. 3, p. 213-220.

McDonald, H.G. (2003) Sloth remains from North American caves and associated karst features *in* Schubert, B.W., Mead, J.I., Graham, R.W., *eds*., Ice Age cave faunas of North America. University of Indiana Press, Bloomington, Indiana, p. 1-16.

McDonald, H.G. (2005) Paleoecology of extinct Xenarthrans and the Great American Biotic Interchange. Bulletin of the Florida Museum of Natural History, v. 45, no. 4, p. 313-333.

McDonald, H.G. and Pelikan, S. (2006) Mammoths and mylodonts: Exotic species from two different continents in North America Pleistocene faunas. Quaternary International, v. 142-143, p. 229-241.

McDonald, H.G. and Jefferson, G.T. (2008) Distributions of Pleistocene *Nothrotheriops* (Xenarthra, Nothrotheridae) in North America. Natural History Museum of Los Angeles County Science Series, no. 41, p. 313-331.

McDonald, H.G. and Morgan, G.S. (2011) Ground sloths of New Mexico *in* Sullivan *et al*., *eds*. Fossil Record 3. New Mexico Museum of Natural History and Science, no. 53, p. 652-663.

McDonald, H.G., Dundas, R.G., Chatters, J.C (2012) Taxonomy, paleoecology and taphonomy of ground sloths (Xenarthra) from the Fairmead Landfill locality (Pleistocene: Irvingtonian) of Madera County, California. Quaternary Research, v. 79, no. 2, p. 215-227.

Mead, J.I., Agenbroad, L.D., Davis, O.K., Martin, P.S. (1986) Dung of *Mammuthus* in the arid Southwest, North America. Quaternary Research, v. 26, p. 121-127.

Mehringer, P.J. (1965) Late Pleistocene vegetation in the Mojave Desert of southern Nevada. Journal of the Arizona Academy of Sciences, v. 3, no. 3, p. 172-188.

Mehringer, P.J. (1967) Pollen analysis of the Tule Springs site, Nevada *in* Wormington, H.M., and Ellis, D., *eds*., Pleistocene studies in southern Nevada. Nevada State Museum Anthropological Papers, v. 13, p. 130-200.

Mehringer, P.J. (1967) The environment of extinction of the Late Pleistocene megafauna in the arid southwestern United States *in* Martin, P.S. and Wright, H.E., *eds*., Pleistocene Extinctions: The Search for a Cause. Yale University Press, p. 247-266.

Merriam, J.C. (1906) Recent cave exploration in California. American Anthropologist, v. 8, no. 2, p. 221-228.

Metcalfe, J.Z., Longstaffe, F.J., White, C.D. (2009) Method-dependent variations in stable isotope results for structural carbonate in bone apatite. Journal of Archaeological Science, v. 36, p. 110-121.

Michel, V., Ildefonse, P., Morin, G. (1995) Chemical and structural changes in *Cervus elephas* tooth enamel during fossilization (Lazaret Cave): A combined IR and XRD Rietveld analysis. Applied Geochemistry, v. 10, p. 145-159.

Naples, V.L. (1987) Reconstruction of cranial morphology and analysis of function in *Nothrotheriops shastense*. Contributions in Science, Los Angeles County Museum, v. 389, p. 1-21.

Naples, V.L. (1989) The feeding mechanism of the Pleistocene ground sloth, *Glossotherium*. Contributions in Science, Natural History Museum of Los Angeles, California, no. 415.

Naples, V.L. (1990) Morphological changes in the facial region and a model of dental growth and wear pattern development in *Nothrotheriops shastensis*. Journal of Vertebrate Paleontology, v. 10, no. 3, p. 372-389.

Nunez, E.E., MacFadden, B.J., Mead, J.I., Baez, A. (2010) Ancient forests and grasslands in the desert: Diet and habitat of Late Pleistocene mammals from Northcentral Sonora, Mexico. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 297, p. 391-400.

O'Leary, M.H. (1988) Carbon isotopes in photosynthesis. BioScience, v. 38, p. 328-336.

Oster, J.L. (2010) Reconstructing precipitation variability in California using Sierra Nevada speleothems. [Ph.D. Dissertation] University of California, Davis, p. 1-233.

Passey, B.H., Cerling, T.E. (2002) Tooth enamel mineralization in ungulates: Implications for recovering a primary isotopic time-series. Geochimica et Cosmochimica Acta, v. 66, p. 3225-3234.

Passey, B.H., Robinson, T.F., Ayliffe, L.K., Cerling, T.E., Sponheimer, M., Dearing, M.D., Roeder, B.L., Ehleringer, J.R. (2005) Carbon isotope fractionation between diet, breath CO_2, and bioapatite in different mammals. Journal of Archaeological Science, v. 32, p. 1459-1470.

Payen, L.A., and Taylor, R.E. (1976) Man and Pleistocene fauna at Potter Creek Cave, California. Journal of California Anthropology, v. 3, no. 1, p. 51-58.

Pellegrini, M., Lee-Thorp, J.A., Donahue, R.E. (2011) Exploring the variation of the $\delta^{18}O_p$ and $\delta^{18}O_c$ relationship in enamel increments. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 310, p. 71-83.

Pérez-Barbería, F.J., Gordan, I.J., Nores, C. (2001) Evolutionary transitions among feeding styles and habitats in ungulates. Evolutionary Ecology Research, v. 3, p. 221-230.

Person, A., Bocherens, H., Saliège, J.F., Paris, F., Zeitoun, V., Gérard, M. (1995) Early diagenetic evolution of one phosphate: An x-ray diffractometry analysis. Journal of Archaeological Science, v. 22, p. 211-221.

Piga, G., Santos-Cubedo, A., Solà, S., M., Brunetti, A., Malgosa, A., Enzo, S. (2009) An X-ray diffraction (XRD) and X-ray fluorescence (XRF) investigation in human and animal fossil bones from Holocene to Middle Triassic. Journal of Archaeological Science, v. 36, p. 1857-1868.

Poinar, H.N., Hofreiter, M., Spaulding, W.G., Martin, P.S., Stankiewicz, B.A, Bland, H., Evershed, R.P., Possnert, G., and Pääbo, S. (1998) Molecular coproscopy: Dung and diet of the extinct ground sloth, *Nothrotheriops shastensis*. Science, v. 281, no. 5375, p. 402-406.

Polyak, V.J., Asmerom, Y., Burns, S., Lachniet, M.S. (2012) Climatic backdrop to the terminal Pleistocene extinction of North American mammals. Geology, v. 40, no. 11, p. 1023-1026.

Quade, J. (1986) Late Quaternary environmental changes in the Upper Las Vegas Valley, Nevada. Quaternary Research, v. 26, p. 340-357.

Quade, J., Mifflin, M.D., Pratt, W.L., McCoy, W., Burckle, L. (1995) Fossil spring deposits in the southern Great Basin and their implications for changes in water-table levels near Yucca Mountain, Nevada during Quaternary time. Geological Society of America Bulletin, v. 107, no. 2, p. 213-230.

Quade, J., Rorester, R.M., Pratt, W.L., Carter, C. (1995) Black mats, spring-fed streams, and late glacial age recharge in the southern Great Basin. Quaternary Research, v. 49, no. 2, p. 129-148.

Quade, J., Forester, R.M., Whelan, J.F. (2003) Late Quaternary paleohydrologic and paleotemperature change in southern Nevada *in* Enzel, Y., Wells, S.G., Lancaster, N., *eds*., Paleoenvironments and paleohydrology of the Mojave and southern Great Basin Deserts. Geological Society of America Special Paper v. 368, p. 165-188.

Reiche, I., vignaud, C., Menu, M. (2002) The crystallinity of ancient bone and dentine: New insights by transmission electron microscopy. Archaeometry, v. 44, no. 3, p. 447-459.

Reynolds, R.E., Reynolds, R.L., and Bell, C.J. (1991) The Devil Peak sloth *in* Crossing the borders: Quaternary studies in eastern California and southwestern Nevada. San Bernardino County Museum Association Special Publication, Mojave Desert Quaternary Research Center Symposium, 91.

Ripple, W.J., Van Valkenburgh, B. (2010) Linking top-down forces to the Pleistocene megafaunal extinctions. BioScience, v. 60, no. 7, p. 516-526.

Rivals, F., Solounias, N., Mihlbachler, M.C. (2007) Evidence for geographic variation in the diets of Late Pleistocene and Early Holocene *Bison* in North America, and differences from the diets of recent *Bison*. Quaternary Research, v. 68, p. 338-346.

Rountrey, A.N., Fisher, D.C., Vartanyan, S., Fox, D.L. (2007) Carbon and nitrogen isotope analyses of a juvenile woolly mammoth tusk: Evidence of weaning. Quaternary International, v. 169, p. 166-173.

Rowland, S.M. and Needham, R.R. (2000) Ice Age ground sloths of southern Nevada. Clark County Museum Occasional Paper #2, p. 1-32.

Ruez, D.R. (2005) Diet of Pleistocene *Paramylodon harlani* (Xenarthra: Mylodontidae): Review of methods and preliminary use of carbon isotopes. Texas Journal of Science, v. 57, no. 4, p. 329-344.

Schoeninger, M.J., Halline, K., Reeser, H., Valley, J.W., Fournelle, J. (2003) Isotopic alteration of mammalian tooth enamel. International Journal of Osteoarchaeology, v. 13, p. 11-19.

Schubert, B.W., Graham, R.W., McDonald, H.G., Grimm, E.C., Stafford, T.W. (2004) Latest Pleistocene paleoecology of Jefferson's ground sloth (*Megalonyx jeffersonii*) and Elk-Moose (*Cervalces scotii*) in northern Illinois. Quaternary Research, v. 61, p. 213-240.

Schwarcz, H.P., Gibbs, L., Knyf, M. (1991) Oxygen isotope analysis as an indicator of place of origin *in* Pfeiffer, S. and Williamson, R.F., *eds*., Snake Hill: An investigation of a military cemetery from the War of 1812. Dundurn Press, Toronto, p. 263-268.

Scott, E., (2010) Extinctions, scenarios, and assumptions: Changes in latest Pleistocene large herbivore abundance and distribution in western North America. Quaternary International, v. 217, p. 225–239.

Severinghaus, C.W. (1949) Tooth development and wear as a criteria of age in white-tailed deer. Journal of Wildlife Management, v. 13, no. 2, p. 195-216.

Sharp, Z.D. and Cerling, T.E. (1998) Fossil isotope records of seasonal climate and ecology: Straight from the horse's mouth. Geology, v. 26, p. 219-222.

Shutler, R. (1967) Archeology of Tule Springs *in* Wormington, H.M., and Ellis, D., *eds*., Pleistocene studies in southern Nevada. Nevada State Museum Anthropological Papers, v. 13, p. 298-302.

Shutler, R. (1968) Tule Springs: Its implications to early man studies in North America. East New Mexico University Contributions in Anthropology, v. 1, no. 4, p. 19-26.

Sillen, A. (1989) Diagenesis in the inorganic phase of cortical bone *in* Price, T.D. *ed.* The chemistry of prehistoric human bone. New York, Cambridge University Press, p. 211-229.

Sillen, A., and LeGeros, R.Z. (1991) Solubility profiles of synthetic apatites and of modern and fossil bones. Journal of Archaeological Science, V. 18, p. 385-397.

Sillen, A., and Sealy, J.C. (1995) Diagenesis of strontium in fossil bone: A reconsideration of Nelson *et al*., (1986). Journal of Archaeological Science, v. 22, no. 2, p. 313-320.

Sinclair, W.J. (1903) A preliminary account of the exploration of the Potter Creek Cave, Shasta County, California. Science, v. 17, no. 435, p. 708-712.

Sinclair, W.J. (1904) The exploration of the Potter Creek Cave. University of California Publications in American Archeology and Ethnology, v. 2, no. 1, p. 1-27.

Smith, K.M. (2010) Life histories of female American mastodons (*Mammut americanum*): Evidence from tusk morphology, stable isotope records, and growth increments. [Ph.D. Dissertation] University of Michigan, Ann Arbor, Michigan, p. 1-239.

Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. Ecological Letters, v. 10, p. 1115-1123.

Spaulding, W.G. (1985) Vegetation and climate of the last 45,000 years in the vicinity of the Nevada Test Site, south-central Nevada. U.S. Geological Survey Professional Paper, v. 1329, p. 1-83.

Spaulding, W.G. (1990) Vegetation dynamics during the last deglaciation, southeastern Great Basin, U.S.A. Quaternary Research, v. 33, p. 188-203.

Spaulding, W.G. and Graumlich, L.J. (1986) The last pluvial climatic episodes in the deserts of southwestern North America. Nature, v. 320, p. 441-444.

Sponheimer, M. and Lee-Thorp, J.A. (1999) Oxygen isotopes in enamel carbonate and their ecological significance. Journal of Archaeological Science, v. 26, p. 723-728.

Sponheimer, M. and Lee-Thorp, J.A. (1999) Alteration of enamel carbonate environments during fossilization. Journal of Archaeological Science, v. 26, p. 143-150.

Sponheimer, M. and Lee-Thorp, J.A. (2006) Enamel diagenesis at South African Australopith sites: Implications for paleoecological reconstruction with trace elements. Geochimica et Cosmochimica Acta, v. 70, p. 1644-1654.

Springer, K., Sagebiel, C.J., Scott, E., Manker, C., Austin, C. (2005) Additions to the Late Pleistocene vertebrate paleontology of the Las Vegas Formation, Clark County, Nevada. Journal of Vertebrate Paleontology, Abstracts of Papers, v. 25, no. 3.

Springer, K., Scott, E., Sagebiel, C.J., Manker, C.R. (2010) The Tule Springs local fauna: Late Pleistocene vertebrates from the Upper Las Vegas Wash, Clark County, Nevada. Geological Society of America Abstracts with Programs, v. 42, no. 5, p. 250.

Springer K. and Manker C., (2010) Cool water tufas and black mats: Indicators of paleoenvironmental change in Late Pleistocene spring discharge deposits in the Upper Las Vegas Wash, Nevada. Geological Society of America, Abstracts with Programs, v. 42, no. 4, p. 77.

Springer, K., Manker C., Scott, E., Pigati, J., Mahan, S. (2011) Geochronologic and paleoenvironmental framework of the Late Pleistocene Tule Springs local fauna. Society of Vertebrate Paleontology Program and Abstracts, Seventy-First Annual Meeting.

Springer, K., Scott, E., Manker, C.R., Rowland, S.M. (2012) Vertebrate paleontology of Pleistocene lakes and groundwater discharge deposits of the Mojave desert and southern Great Basin. Nevada State Museum Paleontological Papers, no. 1, p. 157-232.

Stephan, E. (2000) Oxygen isotope analysis of animal bone phosphate: Method refinement, influence of consolidants, and reconstruction of palaeotemperatures for Holocene Sites. Journal of Archaeological Science, v. 27, p. 523-535.

Stock, C. (1917) Recent studies of the skull and dentition of *Nothrotherium* from Rancho La Brea. University of California Publications Bulletin of the Department of Geology, v. 10, no. 10, p. 137-164.

Stock, C. (1918) The Pleistocene fauna of Hawver Cave. University of California Publications, Bulletin of the Department of Geology, v. 10, no. 24, p. 461-515.

Stock, C. (1931) Problems of antiquity presented in Gypsum Cave, Nevada. The Scientific Monthly, v. 32, no. 1, p. 22-32.

Suvorova, E.I., and Buffat, P.A. (2001) Size effect in X-ray and electron diffraction patterns from hydroxyapatite particles. Crystallography Reports, v. 46, no. 5, p. 722-729.

Szpak, P., Gröcke, D.R., Debruyne, R., MacPhee, R.D.E., Guthrie, R.D., Froese, D., Zazula, G., Patterson, W.P., Poinar, H.N. (2010) Regional difference in bone collagen $\delta^{13}C$ and $\delta^{15}N$ of Pleistocene mammoths: Implications for paleoecology of the mammoth steppe. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 286, p. 88-96.

Tal, M., Oron, M., Gedalia, I., Ehrlich, J. (1976) X-ray diffraction and scanning electron microscope investigations of fluoride-treated dentine in man. Archives of Oral Biology, v. 21, p. 285-290.

Thompson, R.S., Van Devender, T.R., Martin, P.S., Foppe, T., Long, A. (1980) Shasta ground sloth (*Nothrotheriops shastense* Hoffstetter) at Shelter Cave, New Mexico: Environment, diet, and extinction. Quaternary Research, v. 14, p. 360-376.

Thompson, R.S., Whitlock, C., Bartlein, P.J., Harrison, S.P., and Spaulding, W.G. (1993) Climatic changes in the western United States since 18,000 yr B.P. *in* Wright Jr., H.E., Kutzbach, J.E., Webb III, T., Ruddiman, W.F., Street-Perrott, F.A., Bartlein, P.J., *eds*., Global climates since the Last Glacial Maxium. University of Minnesota Press, p. 468-513.

Thompson, R.S. and Anderson, K.H. (2000) Biomes of western North American at 18,000, 6000, and $0^{14}C$ yr BP reconstructed from pollen and packrat midden data. Journal of Biogeography, v. 27, no. 3, p. 555-584.

Tieszen, L.L., Boutton, T.W. (1989) Stable carbon isotopes in terrestrial ecosystem research *in* Rundel, P.W. *ed*., Stable isotopes in ecological research. New York, Springer-Verlag, p. 167-195.

Tieszen, L.L. (1994) Stable isotopes on the Plains: Vegetation analyses and diet determinations *in* Owsley, D.W., and Jantz, R.L., *eds*., Skeletal biology in the Great Plains: A multidisciplinary view. Washington D.C., Smithsonian Press, p. 261-282.

Tuross, N., Behrensmeyer, A.K., Eanes, E.D., Fisher, L.W., Hare, P.E. (1989) Molecular preservation and crystallographic alterations of a weathered sequence of wildebeest bones. Applied Geochemistry, v. 4, p. 261-270.

Tütken, T., Vennemann, T.W., Pfretzschner, H.U. (2008) Early diagenesis of bone and tooth apatite in fluvial and marine settings: Constraints from combined oxygen isotope, nitrogen and REE analysis. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 266, p. 254-268.

Ruddiman, W.F., Street-Perrott, F.A., and Bartlein, P.J. (1993) Global climates since the Last Glacial Maximum. University of Minnesota Press, p. 1-569.

Ungar, P.S. (2010) Mammal teeth: Origin, evolution, and diversity. The Johns Hopkins University Press, p. 1-304.

Uno, K.T. (2009) Extracting climate signals from a modern elephant tusk by carbon isotope and histological analyses. Geological Society of America Abstracts with Programs, v. 41, no. 7, p. 311.

Van der Merwe, N.J., Lee-Thorpe, J.A., Bell, R.H.V. (1988) Carbon isotopes as indicators of elephant diets and African environments. African Journal of Ecology, v. 26, p. 163-172.

Van Devender, T.R. (1987) Holocene vegetation and climate in the Puerto Blanco Mountains, southwestern Arizona. Quaternary Research, v. 27, p. 51-72.

Van Devender, T.R. and Spaulding, W.G. (1979) Development of vegetation and climate in the southwestern United States. Science, v. 204, p. 701-710.

Vaseenon, S. (2011) Relationship between caries-affected dentin mineral density and microtensile bond strength. [M.S. Thesis] University of Iowa, p. 1-128.

Vetter, L. (2007) Paleoecology of Pleistocene megafauna in southern Nevada, USA: Isotopic evidence for browsing on halophytic plants. [M.S. Thesis] University of Nevada, Las Vegas, p. 1-89.

Vetter, L., Griffing, C.Y., Loeschner, M.S., McLaurin, B.T., Rowland, S. M. (2007) Fluvial depositional environment of a Pleistocene megafaunal locality, Panaca, Nevada. Geological Society of America Abstracts with Programs, v. 39, no. 5, p. 14.

Visser, M.E. (2008) Keeping up with a warming world; Assessing the rate of adaptation to climate change. Proceedings of the Royal Society: Biological Sciences, v. 275, p. 649-659.

Vizcaíno, S.F., Bargo, M.S., Fariña, R.A. (2008) Form, function, and paleobiology in xenarthrans *in* Vizcaíno, S.F. and Loughry, W.L., *eds.* The biology of the Xenarthra. Gainesville, University Press of Florida, p. 86-99.

Vizcaíno, S.F. (2009) The teeth of the "toothless": Novelties and key innovations in the evolution of xenarthrans (Mammalia, Xenarthra). Paleobiology, v. 35, p. 343-366.

Vogel, J.C. (1978) Isotopic assessment of the dietary habitats of ungulates. South African Journal of Science, v. 74, p. 298-301.

Vogel, J.C., Eglington, B., Auret, J.M. (1990) Isotope fingerprints in elephant bone and ivory. Nature, v. 346, p. 747-749.

Wagner, J.D.M., Cole, J.E., Beck, J.W., Patchett, P.J., Henderson, G.M., Barnett, H.R. (2010) Moisture variability in the southwestern United States linked to abrupt glacial climate change. Nature Geoscience, v. 3, p. 110-113

Wallace, W.J. and Lathrap, D.W. (1952) An early implement assemblage from a limestone cavern in California. American Antiquity, v. 18, no. 2, p. 133-138.

Walther, G.R., Post, E., Convey, P., Menzels, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., Bairlein, F. (2002) Ecological responses to recent climate change. Nature, v. 416, p. 389-395.

Wang, Y. and Cerling, T.E. (1994) A model of fossil tooth and bone diagenesis: Implications for paleodiet reconstruction from stable isotopes. Palaeogeography, Palaeoclimatology, Palaeoecology, v. 107, p. 281-289.

Weiner, S. (2010) Microarchaeology: Beyond the visible archaeological record. University of Cambridge Press, p. 1-373.

West, J.B., Bowen, G.J., Cerling, T.E., Ehleringer, J.R. (2006) Stable isotopes as one of nature's ecological recorders. Trends in Ecology and Evolution, v. 21, no. 7, p. 408-414.

White, C.D., Spence, M.W., Stuart-Williams, H.L., Schwarcz, H.P. (1998) Oxygen isotopes and the identification of geographical origins: The Valley of Oaxaca versus the Valley of Mexico. Journal of Archaeological Science, v. 25, p. 643-655.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Davies, T.J., Grytnes, J.A., Harrison, S.P., Hawkins, B.A., Holt, R.D., McCain, C.M., Stephens, P.R. (2010) Niche conservatism as an emerging principle in ecology and conservation biology. Ecology Letters, v. 13, p. 1310-1324.

Yurtsever, Y. and Gat, J.R. (1981) Atmospheric waters *in* Gat, J.R. and Gonflantini, R., *eds*., Stable isotope hydrology: Deuterium and oxygen-18 in the water cycle. Technical Report Series no. 210, International Atomic Energy Agency, Vienna, pp. 103-142.

Zazzo, A., Balasse, M., Patterson, W.P. (2005) High resolution $\delta^{13}C$ intratooth profiles in bovine enamel: Implications for mineralization pattern and isotopic attenuation. Geochimica et Cosmochimica Acta, v. 69, p. 3631-3642.

Zazzo, A., Balasse, M., Patterson, W.P. (2006) The reconstruction of mammal individual history: Refining high-resolution isotope record in bovine tooth dentine. Journal of Archeological Science, v. 33, p. 1177-1187.

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Bonde, A.M., Rowland, S. (2011) Southern Great Basin Late Pleistocene seasonality and paleoenvironment recorded in *Bison latifrons* tooth enamel. Geological Society of America Abstracts with Programs, v. 43, no. 5, p. 262.

Bonde, J.W., Shirk, A.M., Druschke, P., Hilton, R. (2011) Frog taphonomy in a high elevation lake basin on the Nevadaplano, Late Cretaceous to Eocene, Sheep Pass Formation, east-central Nevada. Society of Vertebrate Paleontology Abstracts, 71st Annual Meeting.

Shirk, A.M., Bonde, J.W., Druschke, P., Hilton, R. (2009) Two distinct frog death assemblages from the Sheep Pass Formation (Maastritchian-Eocene), east-central Nevada. Geological Society of America Abstracts with Programs, v. 41, no. 7, p. 32.

Bonde, J.W., Varricchio, D.J., Jackson, F.D., Loope, D.B., and Shirk, A.M. (2008) Dinosaurs and dunes! Sedimentology and paleontology of the Mesozoic in the Valley of Fire State Park,

in Duebendorfer, E.M., and Smith, E.I., *eds*., Field Guide to plutons, volcanoes, faults, reefs, dinosaurs, and possible glaciation in selected areas of Arizona, California, and Nevada. Geological Society of America Field Guide 11, p. 249–262.

Bonde, J.W., Shirk, A.M., and Rowland, S. (2008) Taphonomy of the Gilcrease spring mound paleontological site, Clark County, Nevada, Geological Society of America Abstracts with Programs, v. 40, no. 1, p. 50.

Schweitzer, C.E., Shirk, A.M., Ćosović, V., Okan, Y., Feldmann, R.M., Hosgor, I. (2007) New Species of *Harpactocarcinus* from the Tethyan Eocene and their paleoecological setting. Journal of Paleontology, v. 81, no. 5, pp. 1091-1100.

Schweitzer, C.E., Feldmann, R.M., Shirk, A.M., Lazăr, I. (2007) Differential diversity in Jurassic sponge-algal and coralline communities, Romania. Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano, v. 35, no. 2, pp. 91-94.

Ćosović, V., Schweitzer, C.E., Premec Fucek, V., Feldmann, R.M., Shirk, A.M, Moroi, A. (2006) Orthophragminids and associated fossils in paleogeographic interpretation of transitional beds (Croatia). Anuário do Instituto de Geociências, v. 29, no. 1, pp. 647-648.

Shirk, A. M., Feldmann, R.M., Schweitzer, C.E., Lazăr, I. (2006) A novel assemblage of Decapod Crustacea from a Tithonian coral reef olistolith, Purcăreni, Romania. Geological Society of America 2006 Abstracts with Programs North Central Section, v. 38, no. 4, p. 56-57.

Lazăr, I.., Feldmann, R.M., Schweitzer, C.E., Shirk, A.M. (2005) Did sponges have crabs? The fauna of a unique sponge-algal cylindrical bioherm complex from the Upper Jurassic of Romania. Geological Society of America Abstracts with Programs, v. 37, no. 7, p. 57-24.

Waugh, D.A., Feldmann, R.M., Crawford, R.S., Kelley, B.M., Shirk, A.M., Conkle, L.N., Traugh, K. (2005) Role of age, gender, and sample location in the cuticular microstructure of a recent population of *Callinectes sapidus* and its implications for the study of fossil cuticle. Geological Society of America Abstracts with Programs, v. 37, no. 5, p. 33-9.

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