1-1-2007

Paleoecology of Pleistocene megafauna in southern Nevada, Usa: Isotopic evidence for browsing on halophytic plants

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PALEOECOLOGY OF PLEISTOCENE MEGAFAUNA IN SOUTHERN NEVADA, USA: ISOTOPIC EVIDENCE FOR BROWSING ON HALOPHYTIC PLANTS

by

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Bachelor of Science
University of Chicago
2002

A thesis submitted in partial fulfillment
of the requirements for the

Master of Science Degree in Geoscience
Department of Geoscience
College of Sciences

Graduate College
University of Nevada, Las Vegas
May 2007

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Thesis Approval

The Graduate College
University of Nevada, Las Vegas

April 16, 2007

The Thesis prepared by

Lael Vetter

Entitled

Paleoecology of Pleistocene megafauna in southern Nevada, USA:
Isotopic evidence for browsing on halophytic plants

is approved in partial fulfillment of the requirements for the degree of

Master of Science in Geoscience

Examination Committee Chair

Dean of the Graduate College

Examination Committee Member

Examination Committee Member

Graduate College Faculty Representative

1017-53

ABSTRACT

Paleoecology of Pleistocene megafauna in southern Nevada, USA: isotopic evidence for browsing on halophytic plants

by

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Stable isotopic techniques are emergent as a powerful reconstructive tool in Neogene paleoecology. The Las Vegas Valley in southern Nevada contains one of few diverse Late Pleistocene fossil assemblages in the Mojave Desert. This study investigates the diet of four megafaunal genera (*Mammuthus*, *Equus*, *Bison*, and *Camelops*) using $\delta^{13}C$ signatures preserved in tooth enamel. Results from serial sampling are also presented as a subannual record of dietary variation and seasonality. During the Last Glacial Maximum, the three grazing genera (*Mammuthus*, *Equus*, and *Bison*) consumed C_3 and C_4 grasses in the naturally occurring proportion, which consisted primarily of C_3 grasses. *Camelops* $\delta^{13}C$ values indicate the highest dietary proportion of C_4 plants; I interpret that these animals consumed browse material with a high proportion of the halophytic C_4 shrub *Atriplex*, a substantial component of modern Mojave Desert vegetation. This study provides new insight into stable isotopic applications for reconstruction of arid paleoenvironments.

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ACKNOWLEDGEMENTS

This project would not have been possible without the assistance, guidance, and support of several individuals and institutions. I would like to thank my advisor, Dr. Steve Rowland, for his guidance and introduction to this thesis topic. I would also like to thank my committee members, Dr. Ganqing Jiang and Dr. Matt Lachniet, for their support and stable isotope expertise, and Dr. Brett Riddle, for his comments and extensive discussion. Conversations with several other individuals contributed to the design and evolution of this project, including Bob Feranec, Eric Scott, Kathleen Springer, Paul Koch, and Henry Fricke.

John Southon, Guaciara Dos Santos, and Rachel Moores from the radiocarbon laboratory at UC Irvine and Dave Winter from the stable isotope laboratory at UC Davis provided facilities, expertise, and guidance. Dr. Brian Hedlund in the UNLV Biology Department graciously allowed me use of his laboratory facilities and equipment for sample preparation. Mr. Bill Gilcrease and the Gilcrease Bird Sanctuary provided access to the fossils.

Funding for this research was generously provided by a Geological Society of America student research grant, UNLV Geoscience scholarships from the Edwards and Olswang and Bernada E. French funds, and a UNLV Graduate and Professional Student Association grant. The UNLV James F. Adams scholarship allowed me to complete this project.

Finally, I would like to thank Tom Muntean, Alex Roy, and other graduate students who contributed support and extensive scientific discussion. I would like to thank Richard Power, Ben Newton, Charlie Hull, Jeff Haemer, Bob Kopp, and other friends and family who supported me throughout this degree and patiently listened to a considerable volume of commentary about large extinct mammals. Jena Barchas Lichtenstein and Dave Fike provided editing and comments. I would not have attended graduate school in the first place without encouragement from my mother, Dr. Debby Filler.

CHAPTER 1

INTRODUCTION

Overview

The end of the Pleistocene Epoch (11,500 calendar years before present, or 11.5 ka) marked the extinction of a unique "megafauna" of large mammals on almost every continent (Barnosky et al., 2004). The precise causes of this extinction have long been debated, and are still controversial. Current research suggests that both rapid climate change and human hunting may have played a significant role (Barnosky et al., 2004; Grayson and Meltzer, 2002, 2003; Martin, 1984; Mosiman and Martin, 1975).

The preferential extinction of large mammals, in concert with rapid climate change during deglaciation, suggests that nutritional stress may have had effects on multiple trophic levels and possibly played a role in extinction (Guthrie, 1984). Numerous recent studies have explored niche partitioning and dietary variation in taxa of extinct megafauna using stable isotopic variation (Feranec and MacFadden, 2000; Hoppe et al., 1999; Koch et al., 1998; MacFadden et al., 1996). Traditional paleontological reconstructions of diet rely primarily on dental morphology. In herbivores, grazing and browsing habits are delineated by hypsodonty (high-crowned teeth) versus brachydonty (low-crowned teeth), and further identified by the shape of the occlusal or chewing surface (Webb, 1974). Bison, mammoths, and horses all have hypsodont teeth with

relatively flat occlusal surfaces, and are interpreted as grazers; mastodons and antilocaprids have low-crowned teeth and are interpreted as browsers (Webb, 1974).

Isotopic discrimination between C_4 grasses and C_3 browse material permits more detailed reconstruction of the dietary preferences of herbivores. In some cases, as with equids, the evolution of hypsodonty mirrors the expansion of C_4 grasslands in the Late Miocene, as revealed by stratigraphic isotopic data (Cerling et al., 1989; Quade et al., 1989; Quade et al., 1992). These studies permit paleoecological reconstructions in mammalian diet and behavior at a level of complexity previously unattainable for the fossil record.

In low latitudes with sufficient moisture, browse plants are almost entirely C_3 and grasses are almost exclusively C_4, and isotopic values in tooth enamel can be directly correlated to dietary preferences. Because of the simplicity of assigning isotopic end-members to corresponding dietary end-members, most of these studies focused on low-latitude paleoecosystems with abundant rainfall. As a result, little work has produced reconstructions of this type in western North America. In the absence of these customary isotopic end-members for diet, other paleoecological questions may still be addressed and answered using isotopic data.

A diverse assemblage of fossil megafauna was recovered from the Las Vegas Valley in southern Nevada, located in the Central Basin and Range. Previous work has been primarily descriptive (de Narvaez, 1995; Haynes, 1967; Mawby, 1967), although some studies have analyzed species assemblages in an attempt to reconstruct population dynamics (de Narvaez, 1995; Vetter et al., 2005).

Objectives and Predictions

The Late Pleistocene assemblage of megaherbivore teeth recovered from the Gilcrease spring mound, Las Vegas Valley, Nevada, provided an opportunity to test hypotheses about isotopic reconstruction of diet in different taxa and seasonal variability within individual animals. In addition, absolute dating tests provided a means of evaluating the taphonomy of the site, and whether the fossils represent a time-averaged accumulation or a single mass death event. This project evaluated four genera of extinct large herbivores: *Mammuthus*, *Equus*, *Bison*, and *Camelops*.

This project evaluated the relative proportions of C_3 and C_4 vegetation in herbivore diets using stable carbon isotope values. Modern bison are obligate grazers and consume almost no browse material. Bison do not exhibit preference for C_3 or C_4 grasses and consume grass in the naturally-occurring C_3/C_4 ratio, and are thus passive recorders of the relative abundances of C_3 and C_4 grasses (Hoppe et al., 2006). I measured the carbon isotopic values from bison teeth and used these values, in conjunction with independent vegetation records, to approximate a baseline abundance of each type of grass. Recent evidence suggests that Pleistocene *Equus* and *Mammuthus* were both facultative grazers; Pleistocene *Camelops* was putatively a browser. I predicted that the carbon isotopic values of these three taxa would differ from values from bison, indicating differences in diet.

I also measured several serial samples along the growth axis of a single tooth for each individual. I predicted cyclic variability in both carbon and oxygen isotope values measured along the growth axis. These cyclic variations are interpreted as seasonal variation in diet. Since vegetation is highly variable on small spatial scales in the Basin

and Range, I predicted a broader range of intra-species carbon isotopic values between individuals than has been demonstrated for other Pleistocene herbivores.

Radiocarbon tests were performed on six *Mammuthus* molars from six individuals. I predicted that the absolute dates obtained from these analyses would span a range of values, indicating that these fossils accumulated over several thousand years.

Significance

The modern Mojave Desert is extremely arid and has a low vegetation density; as a result, it supports a very low density of modern large animals. The Pleistocene-to-Holocene transition in the Mojave Desert was a particularly dramatic climatic shift: the mean annual temperature approximately doubled, while the mean annual precipitation decreased by about a factor of two (Thompson et al., 1999). Data from the relatively small number of Quaternary fossil localities in the Mojave Desert indicate that a diverse fauna was present in the Late Pleistocene.

Southwestern North America is the historic location of megafaunal kill sites that unequivocally indicate interactions between human Paleoindian hunters and animals that are now extinct (Haury, 1953; Haury et al., 1959; Stock and Bode, 1937; Warnica, 1966). Recent evidence indicates the presence of humans in the Las Vegas Valley and surrounding area during the early Holocene (Heidi Roberts, 2006 personal comm. to S. Rowland). Interaction between human hunters and extinct megafauna in the Las Vegas Valley has been suggested based on stratigraphic association of archaeological artifacts with fossil remains (Harrington, 1933; Haynes, 1967). Although human-megafaunal interactions have not been conclusively proven, these interactions could have increased

the considerable environmental stress that resulted from changing climate and vegetation regimes.

In the Late Pleistocene faunal assemblage from the La Brea tar pits in southern California, studies have inferred environmental and nutritional stress from dietary shifts, indicated by both morphological (Van Valkenburgh and Hertel, 1993) and isotopic data (Fox-Dobbs and Koch, 2003). Faunal records from the Las Vegas Valley span the time interval from the Last Glacial Maximum to the end-Pleistocene megafaunal extinction, and thus record the paleoecology and paleoenvironmental interactions of these animals immediately prior to their extinction. In this study, I reconstruct resource partitioning and seasonal variability in dietary habits of Pleistocene herbivores in the Mojave Desert immediately prior to their extinction, and test for potential resource competition and environmental sources of nutritional stress.

CHAPTER 2

PREVIOUS RESEARCH

Geologic Background

The Las Vegas Valley is one of several fault-bounded intermontane basins in the Basin and Range, a region of continental extension in western North America (Longwell et al., 1965). Extension in the Central Basin and Range was initiated in the Late Miocene, and the Neogene sedimentary record extends into the Holocene (Faulds et al., 2001). Pleistocene sediments in the Las Vegas Valley consist primarily of coarse alluvial fans and fan remnants adjacent to mountain fronts; areas more distal from range fronts are characterized by finer sands and silts (Haynes, 1967). Drainage in the Las Vegas Valley runs generally from northwest to southeast, and terminates in Lake Mead and the Colorado River (Figure 1; Longwell et al., 1965).

The Pleistocene Epoch (~1.8 Ma to 10 ka) was characterized by frequent alternation between glacial and interglacial conditions, resulting from cyclical variation in orbital patterns (Hays et al., 1976). During glacial stages, pluvial conditions were prevalent in the Basin and Range, with considerably more precipitation than in the modern interglacial stage (Smith and Street-Perrott, 1983). Many closed intermontane basins were filled with lakes during Pleistocene pluvial intervals, and multiple pluvial events are recorded in thick lacustrine sedimentary sequences within some basins (Snyder et al., 1964). Other hydrologically open basins accumulated interbedded coarse and fine

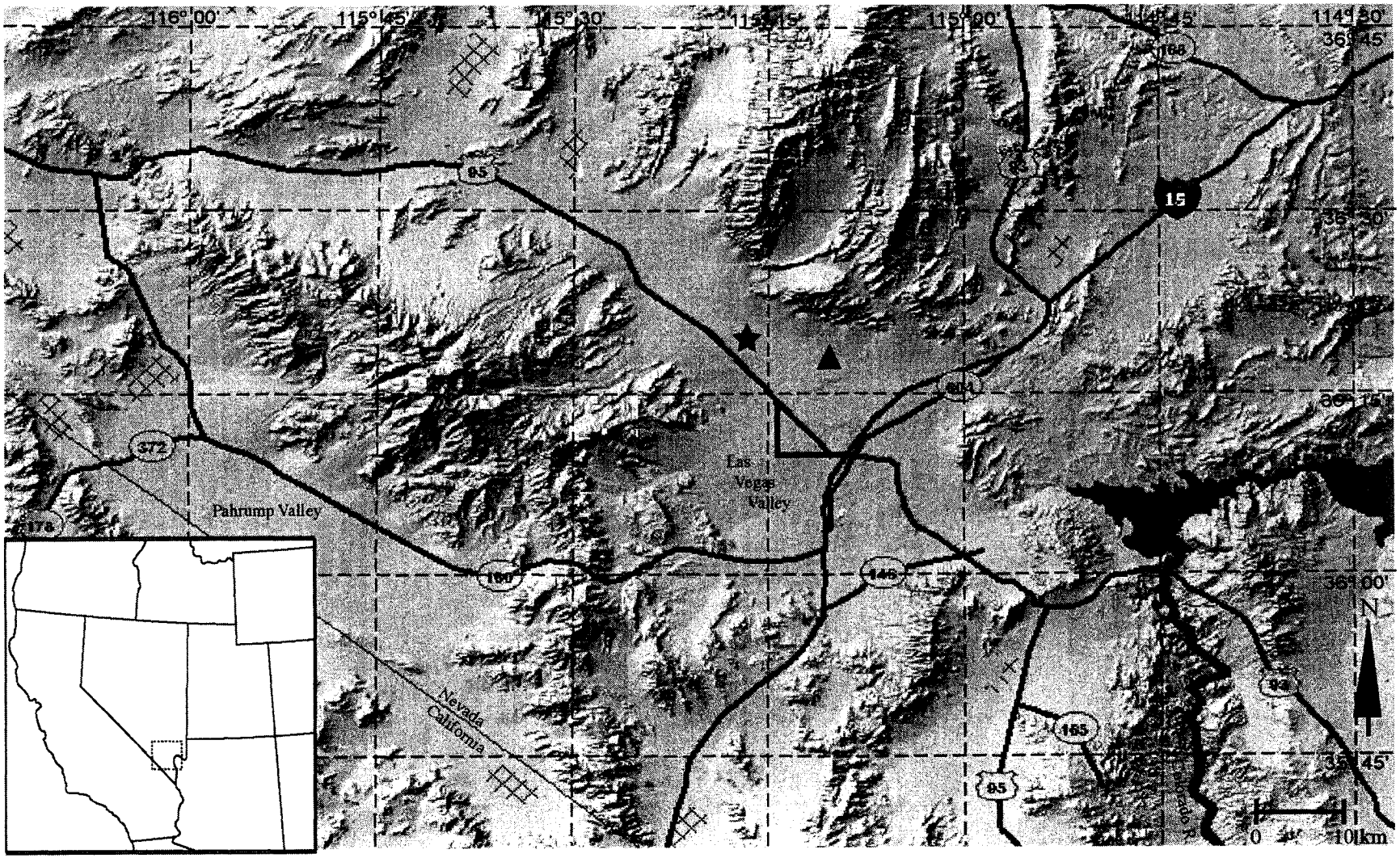

Figure 1. Map of the Las Vegas Valley, southern Nevada. ▲ = Tule Springs excavation, ★ = Gilcrease property and spring mound (modified from USGS, 2007).

deposits that reflect disparate precipitation and weathering between pluvial and interpluvial climatic regimes (Mifflin and Wheat, 1979). Pleistocene sediments in the Las Vegas Valley consist of interbedded gravels, sands, silt and mudstones, and paleosols (Quade, 1983). Reconstructed depositional environments are fluvial during drier intervals and paludal or marsh systems during wetter intervals (Quade, 1986).

The Tule Springs excavation, an interagency research effort that took place in 1962-63, mechanically exposed Late Pleistocene sediments (Haynes, 1967). Haynes (1967) identified and described seven stratigraphic units, labeled A through G, which provide context and continuity for Quaternary sediments in the region. Stratigraphic age control for these units was determined using radiocarbon dates from a variety of materials, including wood, mollusc shells, tufa carbonates, organic-rich tufa deposits, and bone material (Table 1; Haynes, 1967). Units A and C are primarily coarse-grained fluvial facies. Units B and D consist of greenish calcareous mudstone (Haynes, 1967); these two units are interpreted as paludal or marsh facies, deposited during wetter pluvial intervals (Quade, 1986). These mudstone units are also characterized by abundant burrows from cicada larvae, which in modern environments are linked with wetter conditions and a vegetation regime with abundant sagebrush (*Artemisia* spp.) (Quade, 1986). Unit D, which is correlative with the Last Glacial Maximum, is marked by the presence of abundant nodules of secondary soil carbonate (Quade, 1986). Subunit E_1 consists of cross-bedded alluvium, organic-rich black mats, and areally restricted green clays; subunit E_2 is interpreted as a drier environment consisting of hardpan and occasional marshes of limited extent. Units F and G consist primarily of fine-grained deposits and are interpreted as aeolian sediments deposited under very arid conditions; within these

units, black organic-rich mats and green clays are found only in association with modern springs (Quade, 1986).

Table 1. Selected stratigraphic units and ages of Quaternary sediments in the Las Vegas Valley; units from (Haynes, 1967; Mehringer, 1967; Quade, 1986). Absolute ages are inferred from radiocarbon dates of various interbedded materials.

Unit	Age range (ka)	Description	Features
G	1.0 – present	Fine-grained Aeolian deposits	
F_2	4.0 – 1.5	Fine-grained Aeolian deposits	
F_1	5.0 – 4.0	Fine-grained Aeolian deposits	
E_2	11.0 – 6.0	Cross-bedded alluvium	Hardpan
E_1	14.0 – 11.5	Cross-bedded alluvium	Black mats, occasional green clays
D	30.0 – 16.0	Greenish calcareous mudstone	Cicada larvae, carbonate nodules
B_2	> 40	Greenish calcareous mudstone	Cicada larvae

The Gilcrease Flat and Kyle Canyon alluvial fan are located ~4 km west of the Tule Springs excavation (Figure 1). Units C and D extend into the subsurface of the Kyle Canyon fan. The surface of the fan is correlative with the upper part of Unit D, and local paleosols are believed to be correlative with Unit E (de Narvaez, 1995). Several active springs have deposited topographic mounds (~100 to 500 m across and 4 to 15 m in height; Haynes, 1967). The Gilcrease and Stilwell alignments are parallel, north-south trending traces of a normal fault at the base of the Spring Mountains; these are marked by linear occurrence of a series of these spring mounds (Haynes, 1967). Spring discharge initiates when fan drainage is interrupted by impermeable, fine-grained fault gouge along the active fault (Haynes, 1967). Placement of these springs above local erosional surfaces at the top of Unit D, below Unit E_1, constrains initiation of movement along these faults to 22 ka to 14 ka, when spring discharge began (Haynes, 1967). More detailed examination of spring stratigraphy indicates that these springs were vigorously active beginning in the Late Pleistocene (~18 ka) and that discharge declined into the Holocene

(Quade, 1986). Several of the springs were active into historical time and discharge ceased in response to groundwater extraction from urban development in the Las Vegas Valley (Quade et al., 1995). The spring mounds measure approximately 30-150 m in diameter and 3-7 m in height, and accumulated a high diversity of megafaunal remains (Haynes, 1967).

Faunal Records

There is an overall paucity of published Pleistocene vertebrate localities in the Mojave Desert region. The modern abundance of large mammals is low due to resource limitation, and abundances may have been low in the Pleistocene as well. In addition, preservation potential is poor in arid environments, and much of the region is undeveloped or used for rangeland. A high diversity of large and small vertebrates and invertebrates is preserved at a few sites, but most published faunal records tend to describe isolated individual fossils. In contrast to most Pleistocene faunal localities in the Mojave Desert, the Las Vegas Valley contains a diverse fossil assemblage (de Narvaez, 1995; Glowiak, 2007; Mawby, 1967).

The Tule Springs fauna was recovered from the northwestern Las Vegas Valley and provides the most complete Pleistocene faunal record for the area (Haynes, 1967). The Tule Springs excavation yielded fossil material of invertebrates (primarily molluscs), amphibians, reptiles, birds, small mammals, and large carnivores and herbivores. Some pollen was also recovered from the Tule Springs excavation (Mehringer, 1967); these palynological data are discussed with other vegetation records below. The faunal assemblage is composed primarily of large mammals, in part due to large-scale methods

of excavation and inattention to smaller fossil material (Haynes, 1967). Most of these large mammals are herbivores, with few representatives of the carnivore guild (Table 2; Mawby, 1967).

Table 2. Large mammals from the Tule Springs fossil assemblage (Mawby, 1967). G = grazer, B = browser, C = carnivore. See Table 1 for correlation with stratigraphic units.

Family	Taxon	Common name	Diet	Stratigraphic unit
Proboscidea	*Mammuthus columbi*	Columbian mammoth	G	B_2, D, E_1
Equidae	*Equus* sp. (large morph—*E. occidentalis?*)	Horse	G	B_2, E_1
	E. conversidens	Horse	G	B_2, E_1
Camelidae	*Camelops hesternus*	Yesterday's camel	B	B_2, D, E_1
Bovidae	*Bison antiquus*	Antique bison	G	B_2
Cervidae	*Odocoileus* sp.	Deer	B	E_1
Ovidae	*Ovis Canadensis*	Mountain sheep	B	
Antilocapridae	*Tetrameryx* sp.	Pronghorn	B	E_1
Xenarthra	*Megalonyx* sp.	Giant ground sloth	B	B_2, E_1
	Nothrotheriops shastensis	Shasta ground sloth	B	B_2
Carnivora	*Felis* or *Lynx*	Small predatory cat	C	B_2
	Panthera atrox	American lion	C	B_2
	Puma sp.	Puma	C	E_1
	Canis latrans	Coyote	C	E_1

Additional Pleistocene vertebrate material in the Las Vegas Valley was recovered from Gypsum Cave, 22 km east of the Tule Springs locality. Initial excavations yielded the remains of several extinct and extant large mammals (Harrington, 1933). Radiocarbon analyses of dung samples of the Shasta ground sloth (*Nothrotheriops shastensis*) from

Gypsum Cave produced a range of ages from 8,400 to 11,700 yr BP (Heizer and Berger, 1970). Subsequent identification and analysis of the Gypsum Cave assemblage has yielded a minimum number of individuals for each taxon (Table 3; Glowiak, 2007), consistent with the distribution within the Tule Springs assemblage.

A specimen of *Nothrotheriops shastensis* was also recovered from a pitfall cave trap at Devil Peak in the Spring Mountains, ~80 km south of the Las Vegas Valley (Gromny, 2003). Isolated proboscidean and ungulate fossils are also reported from the region. Various localities include *Mammuthus columbi* from Pahrump Valley (NV), Cactus Springs (NV), and Valley Wells (CA); *Equus* sp. and *Camelops* sp. from Corn Creek Flat (NV); *Equus* sp. from Lathrop Wells (NV) and Kokoweef Cave (CA); and *Camelops* sp. from Sunshine Lake (NV) (Connin et al., 1998).

Table 3. Large mammals from the Gypsum Cave assemblage (Glowiak, 2007).

Order	Taxon	Common Name	Status	MNI (Juvenile/Adult)
Artiodactyla	*Hemiauchenia macrocephala*	Stilt-legged llama	Extinct	1/2
	Camelops hesternus	Yesterday's camel	Extinct	1/1
	Ovis canadensis	Bighorn sheep	Extant	1/8
	Odocoileus hemionus	Mule deer	Extant	1/6
Perissodactyla	*Equus* sp. 1	Horse	Extinct	1/4
	Equus sp. 2	Horse	Extinct	
Xenarthra	*Nothrotheriops shastensis*	Shasta ground sloth	Extinct	2/4
Carnivora	*Urocyon cinereoargenteus*	Gray fox	Extant	0/1
	Vulpes macrotus	Kit fox	Extant	0/4
Felidae (Family)	*Lynx rufus*	Bobcat	Extant	1/0

Vegetation Records

Plants can be categorized by either functional type (e.g., shrubs, herbaceous plants, grasses, etc.) or by photosynthetic mechanism. The C_3 photosynthetic pathway is utilized by most plants, including trees, shrubs, herbaceous plants, and some cool-season bunch grasses (e.g., *Amphipogon*, *Festuca*). The C_4 photosynthetic pathway is utilized by warm-season grasses (e.g., *Spartina*, *Sorghum*, *Bouteloua*; Watson and Dallwitz, 2005). The presence of C_3 or C_4 plants is discernible from isotopic analysis of organic matter, soil carbonate, and mammalian tooth enamel. Modern vegetation in the Las Vegas Valley consists primarily of C_3 shrubs and C_3 grasses (Mehringer, 1967; Quade et al., 1987). Components of the modern Mojave Desert plant community that utilize the C_4 photosynthetic pathway include occasional warm-season (C_4) grasses and *Atriplex* spp. (shadscale or saltbush), one of few C_4 shrubs (Quade et al., 1987). Modern vegetation in the Las Vegas Valley is composed of approximately 93-95% C_3 plants; this is corroborated by isotopic measurements of soil carbonate (Quade et al., 1987).

Temperature and moisture regimes in the Basin and Range are delimited by altitude. Extreme topographic relief in the Basin and Range results in high variability in plant communities on small spatial scales (Vasek and Barbour, 1977). Fluctuations in climatic conditions thus result in both altitudinal and latitudinal shifts in vegetation ranges. Modern vegetation in the Las Vegas Valley consists in part of taxa that exploit and colonize disturbed areas, so pre-disturbance analogs are necessary to evaluate modern plant species distributions based on climate variables alone. Reconstruction of plant species distribution during the different climatic conditions of the LGM and late glacial time is difficult using any single vegetation record or proxy. Multiple vegetation records

are discussed below; consideration of all of these records provides a more detailed basis for evaluation of Pleistocene herbivore diet.

Conventionally preserved plant macrofossils are infrequently recovered from coarse-grained terrestrial sedimentary sequences. However, arid environments contain plant macrofossils with a unique mode of preservation. Rodents of the species *Neotoma* sp. (packrats) colonize rocky habitats, acquire plant material from their surroundings, and incorporate the material into middens or nests (Finley, 1958).

Material in the middens is desiccated and preserved, and radiocarbon dates may be obtained from fecal pellets within the middens (Wells and Jorgensen, 1964). Packrats only collect material from a distance of approximately 100 m from their nests. Middens thus provide a site-specific record of vegetation that may be precisely dated, although the geographic and temporal range of any single midden is limited in scope. However, some evidence suggests that midden contents may not accurately represent total floral diversity at a given site, and that packrats may exhibit selectivity when collecting material for middens (e.g., Dial and Czaplewski, 1990).

Vegetation reconstructions using packrat middens demonstrate significant change in the composition of plant communities in the Basin and Range throughout the Pleistocene (Spaulding, 1983; Spaulding and Graumlich, 1986; van Devender and Spaulding, 1979). However, because packrats preferentially dwell in upland habitats, midden records are not directly applicable to reconstructions of valley floor vegetation in the Las Vegas Valley. Climate-induced range shifts were specific to individual plant species, so the overall species composition of plant communities fluctuated throughout the Pleistocene. The LGM and late glacial plant communities represented by macrofossils are

fundamentally different from modern communities (van Devender and Spaulding, 1979). Midden analyses suggest a minimum downward vertical shift in plant communities of 1065 m to 1200 m and indicate that a rapid transition to present-day desert scrub vegetation was underway by ~14 ka (Spaulding, 1985).

Preservation of pollen is generally poor in sediments deposited in arid environments. Some well-preserved Pleistocene palynological records for the Basin and Range exist in lacustrine sequences (Mensing, 2001), but palynological data are generally sparse in the Mojave Desert. The Tule Springs excavation yielded some pollen records from both alluvial and spring deposits, although poor preservation may result in a biased representation of Pleistocene vegetation communities (Mehringer, 1967). *Pinus* spp. pollen is overrepresented with respect to absolute abundance in pollen spectra due to the preferential long-distance transport of *Pinus* pollen (Solomon and Silkworth, 1986). The pine problem is potentially a confounding factor in determining absolute relative abundances of plant taxa from the Tule Springs pollen assemblage (Mehringer, 1967).

No single vegetation proxy supplies sufficient information for a complete reconstruction of Pleistocene plant communities. Because of the incomplete information provided by each vegetation proxy, I used packrat midden analyses and pollen data in conjunction with a stepwise regression model based on climate parameters to produce estimates of the percent abundance of C_4 grasses and other vegetation (Appendix 1). On the basis of these analyses I concluded that during the LGM in southern Nevada, C_4 grass abundance was approximately 4 to 13%, the abundance of non-grass C_4 plants (e.g. *Atriplex* spp., *Amaranthus*) was approximately 5%, and total C_4 biomass during the LGM ranged from 9 to 18%.

Previous Study of the Gilcrease Ranch Spring Mound

The Gilcrease Ranch spring mound (Cauldron 2; de Narvaez, 1995) is one of the fault-bounded springs located along the Gilcrease alignment on the Kyle Canyon fan (Haynes, 1967). Cauldron 2 (hereinafter referred to as "the spring mound") is located at 36.309°N/115.271°W, on the present site of the Gilcrease Nature Sanctuary, 8103 Racel Road, Las Vegas, Nevada. Active spring discharge is reported from historical times and ceased in approximately 1955 in response to urban development and groundwater extraction in the Las Vegas Valley. Fossil material was initially recovered from the site by the property owner, Mr. Bill Gilcrease, in 1985. From 1990 to 1995 the Fossil Club of Las Vegas excavated an area approximately 20 m in diameter to a depth of 6.5 m (de Narvaez, 1995).

The spring mound is located on a surface of the Kyle Canyon fan that is correlative with the Tule Springs Unit D (Quade, 1986). The sedimentology and stratigraphy of Cauldron 2 were described during the excavation (de Narvaez, 1995). Several black organic-rich mats are interbedded with spring deposits. Radiocarbon ages for the lower black mats are 12,727 to 12,178 cal yr BP and 11,801 to 10,963 cal yr BP (de Narvaez, 1995). A black mat from approximately the middle of the spring strata was dated to 9,615 to 9,582 cal yr BP, and a mat near the top of the spring mound was dated to 1,183 to 939 cal yr BP (de Narvaez, 1995). The placement of these dates implies that most deposition of sediments in the spring occurred during the latest Pleistocene and early Holocene.

An extensive collection of faunal material that consisted almost entirely of teeth from extinct large mammals was recovered from the spring mound (de Narvaez, 1995). Vigorous spring discharge resulted in a complex depositional pattern, precluding

stratigraphic age correlation of fossil material (de Narvaez, 1995). The dental assemblage recovered from the site consists of *Mammuthus columbi*, *Equus* sp. (one large and one small morph), *Camelops* sp., *Hemiauchenia* sp., *Bison antiquus*, and one small and one large unidentified carnivore. Seven partial *Mammuthus* tusks were also recovered, although preservation is extremely poor and this material is not well articulated (de Narvaez, 1995). Some skeletal material is present but has not been identified and is not demonstrably Pleistocene in age; it may instead be from modern fauna, since the spring was active into historic time (Haynes, 1967).

The unusual taphonomy of this site is likely a result of high pH in spring water from dissolved $CaCO_3$ (Paul Koch, 2006 personal comm.). Regional bedrock consists primarily of Paleozoic carbonates; aeolian dust is predominantly carbonate material, and groundwater also passes through carbonate aquifers, increasing sodium and calcium cation concentration and groundwater alkalinity. Deposition in aerobic environments with high pH is not conducive to preservation of organic material (e.g., bone collagen) (Nicholson, 1998). Tooth apatite is a more robust biogenic mineral and is thus preserved in the spring mound.

Radiocarbon (^{14}C) Dating

Radiocarbon (^{14}C) is a naturally-occurring cosmogenic isotope of carbon formed by interaction of N_2 in the troposphere with incoming cosmic rays. ^{14}N undergoes an n,p reaction to produce ^{14}C, and ^{14}C decays by β emission to ^{14}N with a half-life of 5730 yr (Bradley, 1999). Radiocarbon in organic matter from living organisms is equilibrated with the environment; when an organism dies, enzymatic equilibration ceases and net

radiocarbon decay begins. Abundances of radiocarbon in Pleistocene materials are measurable using accelerator mass spectrometry (AMS) techniques and provide absolute ages up to approximately 50 ka (van der Plicht et al., 2004).

Organic materials are rich in carbon. The high concentration of carbon allows precise AMS measurements of trace amounts of ^{14}C to produce a radiocarbon age. Soft animal tissues are rarely fossilized; radiocarbon ages are typically measured from the collagen-rich inner layer of fossil bones. The outer (cortical) bone is a denser, inorganic mineral matrix that is less organic rich, and is more difficult to date. Tooth apatite [$Ca_5(PO_4,CO_3,OH)_3(F,OH)$] is a phosphatic biogenic mineral with ~4% carbonate in the mineral lattice. This inherently low concentration of carbon in apatite leads to difficulty and the potential for significant error in measurement of trace amounts of ^{14}C in tooth enamel.

Stable Isotope Fractionation

Carbon and oxygen both have multiple naturally occurring stable isotopes. Carbon has two stable isotopes, ^{12}C and ^{13}C. On Earth, ^{12}C comprises 98.9% and ^{13}C comprises 1.1% of all stable carbon (Faure and Mensing, 2005). Oxygen has three stable isotopes: ^{16}O, ^{17}O, and ^{18}O. ^{16}O and ^{18}O are the two most abundant isotopes: ^{16}O accounts for 99.76%, and ^{18}O comprises approximately 0.20% (Faure and Mensing, 2005). The relative abundances of each of these isotopic species are fixed on the Earth's surface. Since light elements have a relatively high mass difference between isotopes, these elements are subject to isotopic mass fractionation by different geochemical processes, including evaporation, condensation, photosynthesis, and metabolism. Records of stable

isotope fluctuations provide key insight into the roles of various processes in biological and geochemical systems in the geologic past. Stable isotope abundance is expressed in per mil notation, relative to a standard. For example,

$$\delta^{18}O = \left(\frac{\left({}^{18}O/{}^{16}O \right)_{sample}}{\left({}^{18}O/{}^{16}O \right)_{standard}} - 1 \right) \times 1000$$

Carbon isotopic composition and the oxygen isotopic composition of carbonate solids are both typically reported with respect to the Vienna Pee Dee Belemnite (VPDB).

Oxygen isotopic values in different materials are primarily influenced by the $\delta^{18}O$ value of various water sources. Evaporation is the primary mechanism for isotopic differentiation of individual water bodies, although several different effects are observed within the realm of evaporative differentiation. The oxygen isotopic value of the modern ocean is defined as $\delta^{18}O$ = 0‰ VSMOW (-29.94‰ VPDB). Water evaporated from the ocean is isotopically lighter (has a lower $\delta^{18}O$) with respect to the ocean (Dansgaard, 1964). Subsequent rainout is isotopically heavy with respect to the producing vapor (Dansgaard, 1964). In continental environments with significant topographic relief, the "orographic effect" results in isotopically heavier water precipitating on windward sides of mountain ranges (Dansgaard, 1964).

The oxygen isotopic composition of modern rainfall in southern Nevada varies from about -13 to -1‰ (Friedman et al., 2002b). Geographic and temporal variation in $\delta^{18}O$ values of precipitation occurs as along spatial and altitudinal gradients, as well as seasonally (Friedman et al., 1992; Friedman et al., 2002b; Smith et al., 1992; Smith et al., 2002). Oxygen isotopic values of rainfall vary by about 2-3‰ from summer to winter (Friedman et al., 2002b). Over local changes in altitude >450m, precipitation $\delta^{18}O$ values

decrease 2-3‰/km (Friedman et al., 2002b). There is little isotopic variation from west to east across the Great Basin (Friedman et al., 2002a; Ingraham and Taylor, 1991), although a systematic isotopic depletion from south to north occurs regionally; this is interpreted as evidence of most precipitation for the region originating in the subtropical Pacific (Friedman et al., 2002a). Smith et al. (2002) conclude that the isotopic compositions of groundwater and precipitation in southern Nevada do not vary more than 1-2‰ for oxygen isotopes (~20‰, δD values), and that recharge is rapid on geologic timescales. Modern surface water $\delta^{18}O$ values are similar to values from precipitation and groundwater, and exhibit similar ranges of variability (Coplen and Kendall, 2000).

Mammalian tooth enamel $\delta^{18}O$ values are equilibrated with environmental signals and provide a record of the $\delta^{18}O$ of ingested water in tooth enamel phosphate (Bryant and Froelich, 1995; Kohn, 1996). The $\delta^{18}O$ values of structural carbonate (CO_3) in apatite are offset from phosphate $\delta^{18}O$ values and also record a faithful signal of environmental $\delta^{18}O$ (Bryant et al., 1996). Water sources include surface water, groundwater, and leaf water from ingested plants; for large mammals, the isotopic signal of leaf water is a negligible contributor to tooth enamel $\delta^{18}O$ (Bryant and Froelich, 1995). Variation in $\delta^{18}O$ values in tooth enamel structural carbonate thus record environmentally-mediated changes in the oxygen isotopic value of water ingested by an animal.

In terrestrial environments, carbon is fractionated by plants during photosynthesis; different photosynthetic mechanisms result in different fractionations and resultant $\delta^{13}C$ values (O'Leary, 1981). Plants that use the C_3 pathway produce organic matter with $\delta^{13}C$ values ranging from -24‰ to -31‰ (Figure 2; O'Leary, 1988). C_4 plants are more efficient at photosynthesis and thus fractionate carbon to a lesser extent; typical $\delta^{13}C$

values for C_4 plants are about -13‰ (Figure 2; O'Leary, 1988). Atmospheric $\delta^{13}C$ values have varied on glacial/interglacial timescales, producing an offset of +0.5‰ for the LGM and up to +1.3‰ for late glacial times (Marino et al., 1992). However, this offset was relatively constant over the span of mineralization time (years) of a single tooth, and is small compared to dietary variation. The isotopic composition of vegetation ingested by herbivores is recorded in trace carbonate in the tooth enamel with a metabolic offset of +13.5‰ to +14‰ (Bocherens et al., 1996).

Use of Stable Isotopes in Paleoecological Reconstruction

Carbon isotopic values preserved in fossil tooth enamel permit reconstruction of the relative proportion of C_3 and C_4 vegetation in the diets of individual herbivores (DeNiro and Epstein, 1978). The same isotopic data in faunal assemblages may be used to evaluate different paleoecological questions by interpreting two primary types of information: information about paleoenvironment and vegetation as recorded in tooth enamel (e.g., Connin et al., 1998; Higgins and MacFadden, 2004), and information about the diet and behavior of individual animals and clades (Koch, 1998).

Analyses of $\delta^{13}C$ values from individuals of several different taxa permit dietary reconstruction for animals that lived contemporaneously in the same ecosystem (Figure 2); because of the potential range in values between individuals, at least five specimens of the same taxon are necessary to provide corroboration of $\delta^{13}C$ values (Clementz and Koch, 2001). Niche spaces occupied by different clades of animals in an ancient ecosystem can be discerned from clustering of $\delta^{13}C$ and $\delta^{18}O$ values in related individuals and taxa. Browsers are identified by lighter, more negative carbon isotopic values, which

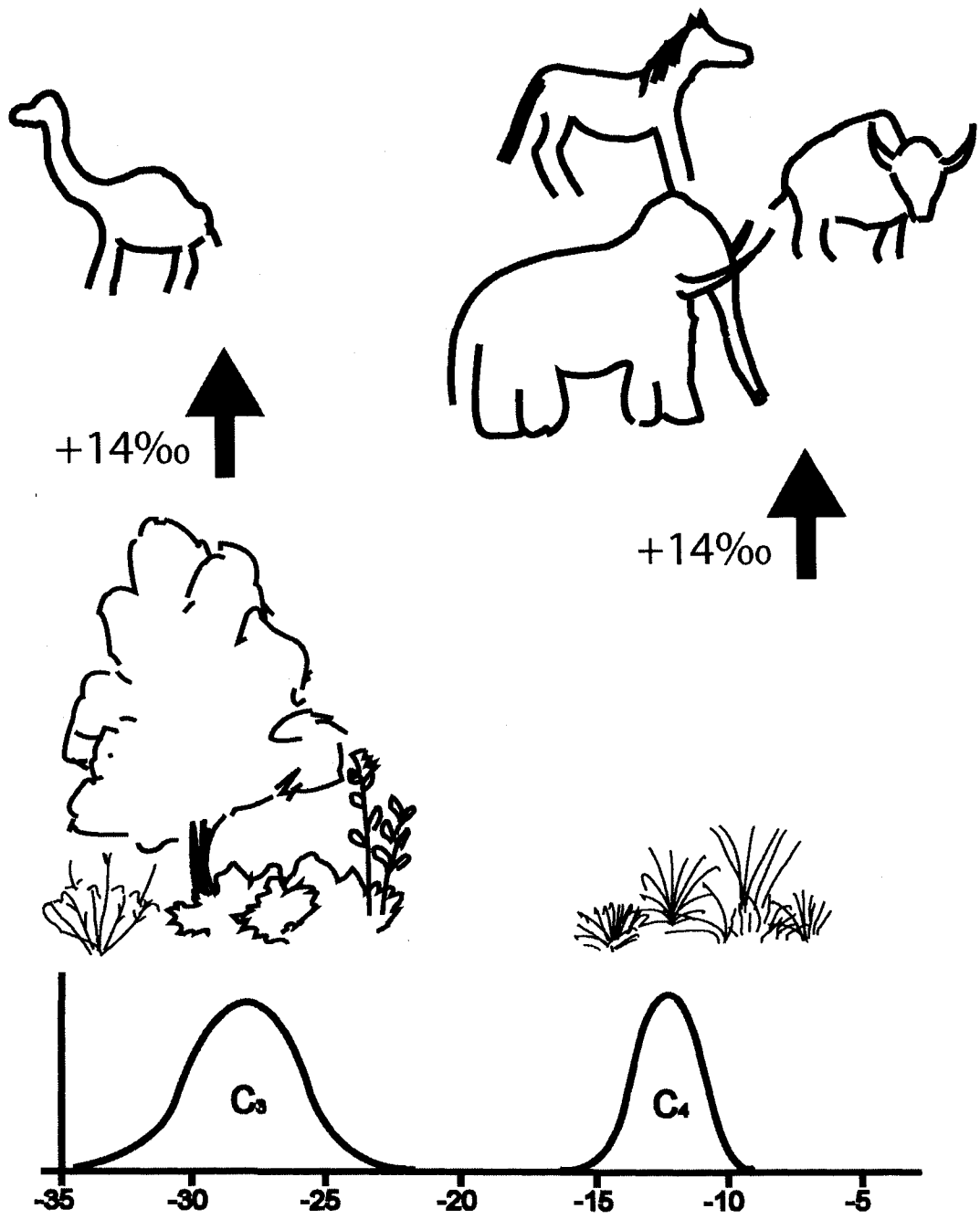

Figure 2. Stable isotope fractionation in C_3 and C_4 plants. Bimodal distribution of $\delta^{13}C$ values is recorded in the organic matter of plants with different photosynthetic mechanisms. Herbivores consume C_3 plants, C_4 plants, or a mixture of both, and $\delta^{13}C$ values from plants are recorded in the tooth enamel with a constant offset of +14‰.

correspond with ingestion of C_3 browse material. Further isotopic differentiation is possible between open, savanna-like habitats with C_3 plants (~ -27‰) and closed-canopy forests (~ -31‰)(Ehleringer et al., 1987), and in corresponding herbivory and forage habits of animals in these habitats (Ambrose and DeNiro, 1986).

Clustering of $\delta^{13}C$ values is usually interpreted as a taxon-specific dietary preference for a certain proportion of grass and browse material. Intra-generic $\delta^{13}C$ variation has been interpreted in two ways: as an adaptive response to resource limitation, or as an indication of variation in the geographic range of unrelated individuals within a fossil assemblage. High variability in $\delta^{13}C$ values in mammoths, with respect to contemporaneous browsers, is interpreted as ecological generalization and C_3/C_4 dietary mixing; this anomalous behavior is interpreted as a potential response to resource limitation (Koch et al., 1998). Hoppe (2004) found that demonstrable mammoth family groups from catastrophic death assemblages exhibited very low variability in $\delta^{13}C$ values between individuals. Deposits with time-averaged accumulations of fossils showed higher $\delta^{13}C$ value variability between individuals (Hoppe, 2004).

A variety of hypotheses about herbivore diet and resource partitioning in ancient ecosystems have been tested using stable isotopic analysis (Feranec and MacFadden, 2000; Koch et al., 1998; MacFadden, 2000; MacFadden et al., 1996). Examination of Cenozoic herbivore assemblages documents a shift in dietary habits in response to the evolution of C_4 grasses in the Late Miocene (MacFadden et al., 1996). Isotopic studies also demonstrate geographic variation in mammalian diet as both ecological adaptations to new habitats (Sánchez et al., 2004) and passive response to ecological change in the composition of plant communities (Fox and Koch, 2003). Another study of a Late

Pleistocene assemblage in Florida demonstrated no inter- or intra-generic differences in diet and feeding strategy in any herbivore taxa in response to ecological pressure from the arrival of *Bison*, a grazer (Feranec and MacFadden, 2000).

Although most isotopic reconstructions of Pleistocene ecosystems in North America focused on the eastern and central United States, Connin et al. (1998) analyzed the $\delta^{13}C$ and $\delta^{18}O$ values of several Late Pleistocene herbivore teeth from the American southwest and used these values to reconstruct paleovegetation. Some specimens from the Tule Springs excavation in the Las Vegas Valley were included in this dataset and provide a basis for interpretation of the isotopic values of other Late Pleistocene fossils from this area (Table 4; Connin et al., 1998). A qualitative assessment of these data suggests a shift from a C_4-rich plant community during B_2 deposition to a mixed C_3/C_4 vegetation regime during E_1 deposition.

Intra-generic $\delta^{18}O$ values from fossil herbivores often exhibit a higher σ than the level of variability recorded in modern ecosystems (e.g., Feranec and MacFadden, 2000). In modern, non-migrating herbivores, intra-generic variation in $\delta^{18}O$ values does not exceed a standard deviation (σ) of 1.1‰; for grazers, $\sigma < 0.9$‰, while for browsers $\sigma < 1.3$‰ (Bocherens et al., 1996). In fossil assemblages, $\delta^{18}O$ variability and σ may be interpreted in two ways. The pattern of fossil isotopic data could represent temporal mixing of individuals from different time periods that ingested meteoric water with different isotopic values; fossil assemblages with poor age constraints could thus be time-averaged accumulations (Koch et al., 1998). Alternatively, this intra-generic isotopic variation could represent geographic mixing of individuals whose tooth enamel mineralized in different contemporaneous climates, with one or more individuals migrating over large

distances (Koch et al., 1998). Intra-tooth variability in $\delta^{18}O$ values is demonstrated to either match the amplitude of local seasonal variation or to be damped due to a time lag from a hydrologic process with a longer residence time (Sharp and Cerling, 1998).

Table 4. $\delta^{13}C$ and $\delta^{18}O$ data for large extinct herbivores from the Tule Springs assemblage (Connin et al., 1998).

Taxon	Unit	Age (ka)	$\delta^{13}C$ VPDB (‰)	$\delta^{18}O$ VSMOW (‰)
Antilocapridae	E_1	14.0-11.5	-10.8	29.5
Tetrameryx spp.	E_1	14.0-11.5	-10.9	24.2
Tetrameryx spp.	E_1	14.0-11.5	-9.9	28.4
Equus spp.	E_1	14.0-11.5	-6.3	25.1
Equus spp.	E_1	14.0-11.5	-8.8	24.0
Camelops spp.	E_1	14.0-11.5	-9.6	24.8
Camelops spp.	E_1	14.0-11.5	-8.0	25.8
Mammuthus spp.	E_1	14.0-11.5	-8.3	20.6
Mammuthus spp.	E_1	14.0-11.5	-9.0	20.6
Mammuthus spp.	D	22.0-17.0	-6.4	22.8
Bison spp.	B_2	≥40.0	-4.9	20.3
Bison spp.	B_2	≥40.0	-3.4	25.0
Mammuthus spp.	B_2	≥40.0	-6.4	19.3
Equus spp.	B_2	≥40.0	-1.6	22.5

Recovery of Isotopic Time-Series from Tooth Enamel

Isotopic analyses from teeth sampled serially along the primary growth axis produce an isotopic record of seasonality (Cerling and Sharp, 1996; Fricke and O'Neil, 1996). Mineralization time for tooth enamel varies between taxa, but generally takes 1 to 3 years for large ungulates and proboscideans (Kohn et al., 1998). As with bulk isotopic values from fossil mammals, serial sampling of fossil mammal teeth is used to address two primary types of questions: paleoenvironmental and paleobiological (Fricke and O'Neil, 1996). Paleoenvironmental reconstructions based on serially sampled teeth provide a subannual record of climate and vegetation change (Fricke et al., 1998; Fricke and

O'Neil, 1996; Sharp and Cerling, 1998). Intra-tooth isotopic variation also provides insight into subannual cyclicity in the habits of individual animals and may be used to infer seasonal or cyclic behavior and other biological aspects of extinct animals (Feranec and MacFadden, 2000; Hoppe, 2004; Koch et al., 1998). Several serial sampling studies have examined seasonal variability in fossil ungulate and proboscidean teeth (Feranec and MacFadden, 2000; Fricke et al., 1998; Koch et al., 1998; MacFadden, 2000). For example, Koch et al. (1998) identified $\delta^{18}O$ minima concurrent with tightly spaced growth structures and interpreted these minima to correspond with a winter season of slow growth and drinking water that was less evaporatively enriched in ^{18}O.

Koch et al. (1998) measured intratooth isotopic variation in a mammoth molar and showed a $\delta^{13}C$ range of only 0.5‰. They concluded that low within-individual variability made bulk samples particularly well-suited to faithfully tracking the average $\delta^{13}C$ value of an individual animal. However, Feranec and MacFadden (2000) measured intra-tooth variation and found that $\delta^{13}C$ value ranges within individuals varied considerably more. Their results show $\delta^{13}C$ ranges of 1.7‰ to 1.8‰ for *Mammuthus* and 0.9‰ to 3.1‰ for *Equus*. The range in intratooth $\delta^{13}C$ values for *Bison* was less than 0.8‰ for three specimens and 4.8‰ for a fourth *Bison* specimen (Feranec and MacFadden, 2000).

Use of isotopic microsamples to infer paleoenvironmental or paleobiological conditions has raised important questions about the validity of isotopic time series recovered from a single tooth, and whether these time series faithfully record a true environmental signal (Hoppe et al., 2004a; Sharp and Cerling, 1998). Recent studies of intra-tooth isotopic variation indicate that the process of enamel mineralization (amelogenesis) can take up to two weeks, potentially damping the record of a primary

environmental signal of isotopic variation (Passey and Cerling, 2002). Other studies suggest that total amelogenesis in modern equids may continue for 6 to 12 months after eruption (Hoppe et al., 2004b). Furthermore, individual enamel layers form at a 5° to 10° angle with the enamel-dentine junction (EDJ) and then rotate to become parallel to the growth axis (Figure 3b; Hoppe et al., 2004b); sampling methods that bore deeply into the outer enamel surface are then perpendicular to the mineralization front and may average isotopic signatures. Modeling of attenuation of isotopic signals in ever-growing teeth demonstrates a faithful record of intra-tooth isotopic variation, although the primary signal is damped (Passey and Cerling, 2002).

Sampling strategy is thus of crucial importance when addressing paleoenvironmental and paleobiological questions with serial enamel samples. Initial attempts to recover primary isotopic time series from teeth were sampled along the outer surface of the enamel at regular intervals (Feranec and MacFadden, 2000; Fricke and O'Neil, 1996; MacFadden, 2000). However, this method does not account for averaging of the isotopic signal along the outer enamel surface due to rotation of the mineralization front. Zazzo et al. (2005) demonstrated that serial sampling along the enamel-dentine junction produced the least-attenuated signal with respect to primary isotopic variability (Figure 3a).

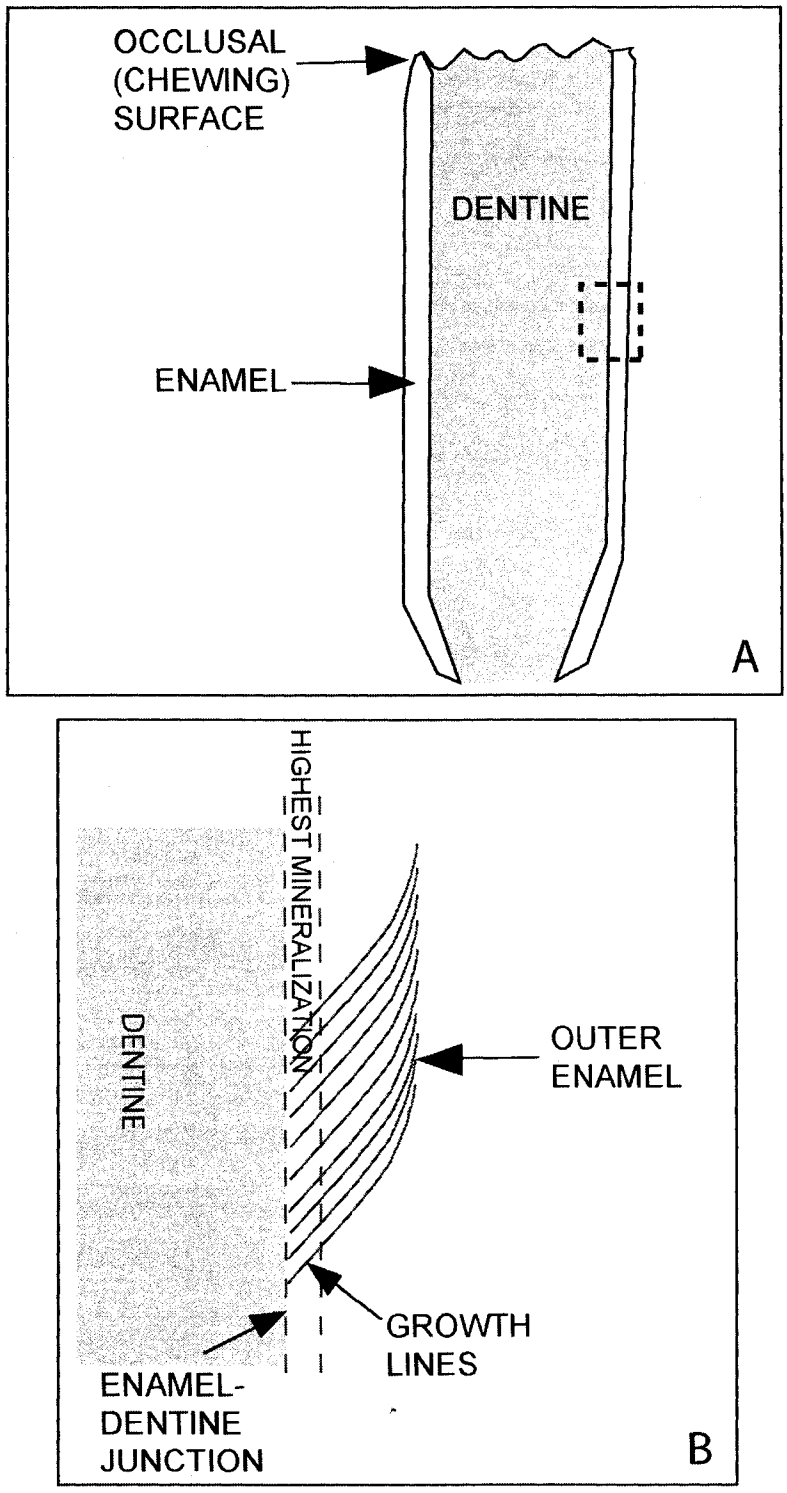

Figure 3. A) Cross-section of a typical ungulate tooth (box is shown magnified in B). B) Cross-section of enamel-dentine junction, showing highest degree of mineralization where growth lines are most perpendicular to growth direction.

CHAPTER 3

METHODS

Radiocarbon Dating

Six total *M. columbi* molars were selected for radiocarbon analysis (Table 5). Proboscideans grow six deciduous sets of molars over the course of their life spans; at any given time, one or two molars are present in each quadrant of the mouth. To avoid duplication between individuals, five of the teeth selected for analysis were right mandibular molars of M1 to M3 designation (fourth through sixth of six deciduous molars)(Haynes, 1991). One selected tooth (GIL MT-78) was a left mandibular molar of dP3 to M1 designation; this range encompasses the second through fourth of the set of deciduous molars, and this individual is thus of a different age (Haynes, 1991). Dentine samples were mechanically removed from between enamel plates.

Table 5. *Mammuthus columbi* molars selected for radiocarbon analysis. GIL numbers are from original excavation of the Gilcrease spring mound. Sample numbers correspond to numbering for stable isotopic analyses performed in this study.

GIL #	Sample #	Size	Quadrant
MT 65	MAM 1	M1-M2	R Mandible
MT 72	MAM 2	M1-M2	R Mandible
MT 8103	MAM 3	M1-M2	R Mandible
MT 73	MAM 4	M3	R Mandible
MT 78	MAM 5	dP3-M1	L Mandible
MT 7	--	M1	R Mandible

For each specimen, one dentine and two enamel samples were analyzed for radiocarbon dates. The dentine samples were prepared using a method developed for bone (dos Santos, 2006). Samples were treated with 0.5N HCl for 24 hours. Visual inspection indicated that no humic contaminants were present, so an alkali treatment step was omitted. Samples were hydrolyzed with 0.01N HCl at 70°C for 10 hours; the resulting gelatinized solution was then centrifuged through ultra-filters to remove excess water. The gelatinized solution was freeze-dried and centrifuged in an evacuated chamber for 8 hours. After cryogenic treatment and freeze-drying, no collagen remained for further analysis. This is consistent with the taphonomic properties of the Gilcrease site and the poor preservation of organic-rich skeletal components.

Enamel samples were leached with 0.01N HCl at 80°C to remove secondary carbonates. Samples were then acidified with 85% H_3PO_4 in vacuum tubes and heated to produce CO_2. The CO_2 from each sample was graphitized at 550°C using a hydrogen reduction method with Fe powder as a catalyst. Graphite samples were analyzed for radiocarbon on an NEC 0.5MV 1.5SDH-2 AMS particle accelerator. Initial enamel samples from each specimen consisted of approximately 15 mg of apatite and yielded very little CO_2 after acidification. Additional enamel samples from the same specimens were prepared with approximately 50 to 60 mg of initial apatite material. All sample preparation and analysis took place at the Keck Carbon Cycle AMS facility at the University of California, Irvine. Results are in radiocarbon years (RCyBP); calendar year age calibrations were performed using CALIB software version 5.0.1 (Stuiver and Reimer, 1993). Calendar year ages are calibrated for post-nuclear testing ages to the IntCal04 curve for terrestrial radiocarbon ages 26 ka to present (Reimer et al., 2004).

Stable Isotope Analysis

Five molars each were selected from four genera: *Mammuthus*, *Equus*, *Bison*, and *Camelops*. *Mammuthus* molars were selected from the radiocarbon analyses described above; for the other three genera, specimens were selected on the basis of disparate size to decrease the potential of repeated sampling of the same individual. Each tooth was mechanically prepared for serial sampling along the growth axis at the enamel-dentine junction (EDJ). Dentine was removed with a Dremel tool and the enamel surface was cleaned with alcohol. *M. columbi* molars were sampled with a Sherline 5410 microdrill at 5 mm interval along the EDJ. Other ungulate teeth were sampled with a Foredom rotary tool and a dental burr along the EDJ at sampling intervals that varied from 2 to 3 mm (Figure 4).

From tooth enamel carbonate-apatite $[Ca_5(PO_4,CO_3,OH)_3(F,OH)]$, the carbonate component was analyzed for $\delta^{13}C$ and $\delta^{18}O$ values. For each sample, 3-5 mg powdered enamel was treated with 30% H_2O_2 overnight to remove organic material. Samples were rinsed with deionized water and treated with 0.1N acetic acid to remove diagenetic carbonate, then rinsed with ethanol and air-dried. Apatite samples were then pre-roasted in a vacuum at 75°C for 30 minutes. For stable isotope analysis, 400-1000 μg of sample were reacted in a phosphoric acid bath at 90°C and analyzed on the directly coupled dual inlet of a GV Instruments Optima isotope ratio mass spectrometer at the University of California, Davis. Isotopic ratios are reported in VPDB values. One σ error is +/- 0.04 per mil for $\delta^{13}C$ and +/-0.06 per mil for $\delta^{18}O$.

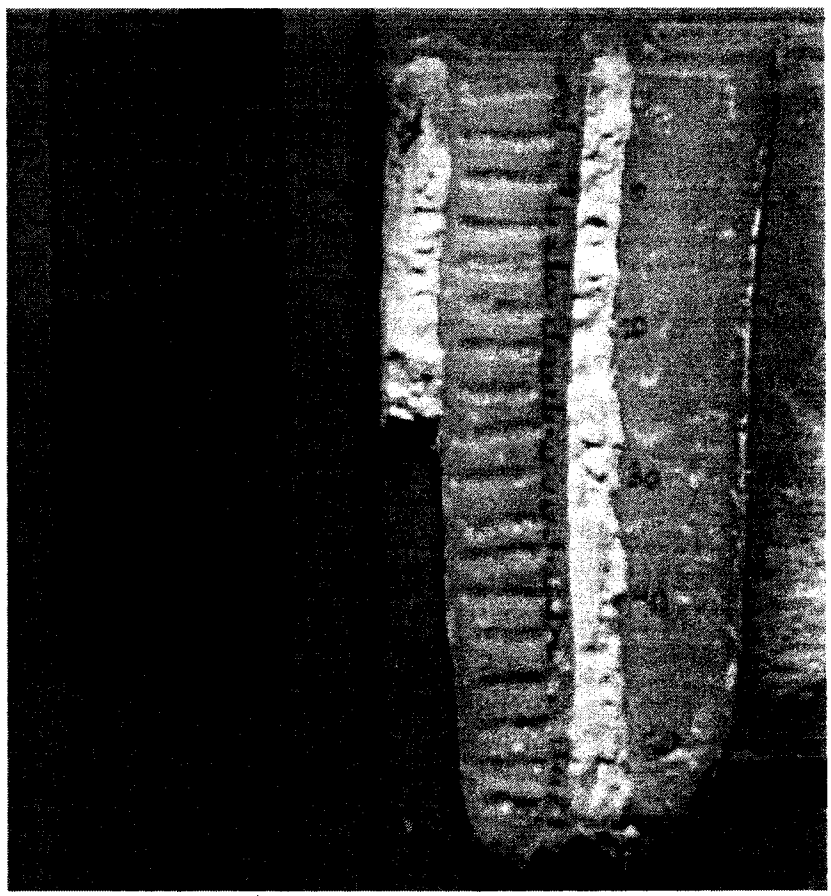

Figure 4. Photograph of sampling technique for ungulate teeth. Dentine was mechanically removed from interior of tooth; samples were collected at 2 to 3 mm intervals along the enamel-dentine junction.

The mean differences between genera were compared using ANOVA. The Student-Newman-Keuls multiple comparisons test was used to compare means between different genera. The GraphPad InStat 3 Macintosh version was used to calculate the statistics.

Methods for Vegetation Reconstruction

Vegetation records are available for the Pleistocene in the form of macroscopic fossils (packrat middens) and pollen data (from both sedimentary deposits and packrat middens). Packrats usually colonize rocky, upland habitats. Thus, packrat middens preferentially record vegetation from high-altitude, mountainous regions, and are less suitable for reconstructions of valley vegetation (Finley, 1990). Pollen data are available from sediments at the Tule Springs site (Mehringer, 1967) and from low-elevation packrat middens at other Mojave Desert localities (Koehler et al., 2005). However, identification of grass pollen at the genus level is difficult and rarely attempted, and pollen spectra usually only report percent abundance of the grass family (Poaceae or Gramineae). Determination of the percent abundance of C_3 and C_4 grasses is therefore not possible from palynological analyses alone.

In addition to some grasses, a few other plants utilize the C_4 pathway, and may affect the isotopic value of vegetation as a whole. Pollen spectra record the presence of plants in the family Chenopodiaceae. In southwestern North America, this group is primarily represented by *Atriplex* spp. (shadscale), a shrub that uses the C_4 pathway. Pollen records also indicate the presence of *Amaranthus* (Amaranthaceae), another C_4 plant. Isotopic reconstructions of the absolute proportion of C_3 and C_4 plants for this region should also account for the presence of these non-grass C_4 plants. Interpretations of herbivore diet

and feeding strategy from isotopic data in this study thus incorporate the estimated abundances of C_3 and C_4 plants of several different functional types.

Plants that utilize the Crassulacean Acid Metabolism (CAM) have $\delta^{13}C$ values intermediate between C_3 and C_4 plants; these include *Yucca* spp. and other succulent plants common in modern vegetation assemblages in southwestern North America. However, palynological records indicate that CAM plants were not present north of 36°N latitude in the Mojave Desert during the LGM (Koehler et al., 2005). Furthermore, CAM plants are not a demonstrable component of the diets of modern large herbivores; since there is little reason to assume that these plants were preferentially selected by Pleistocene herbivores, CAM plants are not discussed further here.

Several workers have presented predictive models for C_4 abundance. These models were formulated by testing the dependence of C_4 abundance on several different climatic variables, statistically identifying the variables with the most influence, and then producing a model based on these variables. Most of these models were calculated for a much lower mean annual temperature (MAT) and much higher mean annual precipitation (MAP) than observed in modern-day southern Nevada. Predictive models must be used with some caution, although calculations from modern climate data do concur with vegetation results for some models.

To estimate the percentage of C_4 plants present in the Las Vegas Valley during the Last Glacial Maximum, I used a predictive statistical model that calculated an estimate using independent paleoclimatic data. First, I present a model commonly used in association with isotopic studies of herbivore diet in wetter climates (Teeri and Stowe, 1976). This method produces an estimate of C_4 grasses for the modern climate in

southern Nevada that is not consistent with modern vegetation assemblages, and is thus a poor estimator of C_4 grass abundance in the Pleistocene. I then present a second method that incorporates different climate parameters, including precipitation, and provides an estimate of modern C_4 grass abundance consistent with observed vegetation.

The estimate from the Paruelo and Lauenroth (1996) model is then combined with palynological data from the Tule Springs assemblage to estimate the total percentage of C_4 grass in the Las Vegas Valley during the LGM. In addition, I used the Tule Springs pollen spectra to calculate percent abundance of plants in the Chenopodiaceae family and of the genus *Amaranthus*, and used this value as an estimate for the abundance of non-grass C_4 plants. The combined percentage of C_4 grasses and C_4 shrubs provide the total C_4 plant biomass for the Las Vegas Valley during the LGM.

Calculation of $\%C_4$ Grass from Reconstructed Climate Parameters

Teeri and Stowe (1976) used a multiple stepwise regression to determine the roles of various climatic variables in determining the relative abundance of C_3 and C_4 grasses. They found that the abundance of C_4 grasses in modern ecosystems was dependent on three primary climatic variables, all functions of temperature, and produced the following equation:

$$\%C4 = (1.60 \times TJM) + (0.0086 \times D\mu) - (8.98 \times \log F\mu) - 22.44$$

where T_{JM} = normal July minimum temperature (°F)

D_μ = mean annual degree days above 65°F

F_μ = mean annual freeze-free period (days)

Modern climate data for the Las Vegas Valley have values for these variables of T_{JM} = 73.2°F, D_μ = 2968, and F_μ = 302 days (WRCC, 2007); this produces an estimate of 97% C_4 grass abundance using the Teeri and Stowe (1976) model. Modern vegetation surveys do not support the value produced by this model (Quade et al., 1987).

Initial estimates of mean annual temperature (MAT) for the LGM range from 6.5°C to 7.5°C, a 6 to 7°C drop from present MAT values (Spaulding, 1985). These estimates were based on data compiled from several packrat midden analyses, using the modern ranges of plant taxa observed in the middens. More recent analysis of these data using new techniques yields MAT values of 7.9°C to 8.5°C for the LGM, a 4.9 to 5.5°C drop from the present MAT value (Thompson et al., 1999). I used both estimates of temperature change in my reconstruction of paleoclimatic variables for this exercise to produce a range of possible $\%C_4$ values (Table 6).

Table 6. Calculated climate variables for the Las Vegas Valley during the LGM using estimates of MAT from various datasets, and predicted %C4 values.

Reference	Time	Temp. drop °C	Temp. drop °F	T_{JM} (°F)	D_μ	F_μ	$\%C_4$
WRCC, 2007	Modern	0	0	73.2	2903	302	97
Thompson et al., 1999	LGM max	4.9	8.82	64.4	1443	238	72
Thompson et al., 1999	LGM min	5.5	9.9	63.3	1291	231	69
Spaulding, 1985	LGM max	6	10.8	62.4	1169	227	66
Spaulding, 1985	LGM min	7	12.6	60.6	948	208	62

Several studies have used the Teeri and Stowe (1976) model to estimate or calculate percent C_4 grass abundance. However, this method accounts for only two functional types of vegetation: C_3 and C_4 grasses. In pure grasslands, this model is appropriate and applicable (Fox and Koch, 2003); in areas with mixed plant communities, other vegetation types may dominate that are not accounted for by this model. In addition, the model is based solely on temperature. In the Mojave Desert, where aridity is a substantial factor in determining vegetation communities, the predictive power of this model is poor.

Paruelo and Lauenroth (1996) developed a model for the abundance of several plant functional types in western North America that predicted percent productivity and absolute productivity. They identified five plant functional types: C_3 grasses, C_4 grasses, shrubs, herbaceous plants, and succulents. They then used a multiple stepwise regression to determine the relationship between the abundance of each plant functional type and several climatic variables. The climatic factors that were most influential were MAT, mean annual precipitation (MAP), and the proportion of MAP that occurred during the summer months (JJA/MAP). According to this model, C_4 grass abundance is determined by the following equation:

$$\%C4 = -0.9837 + (0.000594 \times MAP) + (1.3528 \times JJA/MAP) + (0.2710 \times \ln(MAT))$$

where MAP = Mean annual precipitation (mm)

JJA/MAP = Proportion of mean annual precipitation that occurs during June, July, and August

MAT = Mean annual temperature (°C)

Modern climate data for the Las Vegas Valley have values for these variables of MAT = 19.2°C, MAP = 125 mm, and JJA/MAP = 0.16 (WRCC, 2007); this produces an estimate of 9% C_4 grass abundance using the Paruelo and Lauenroth (1996) model. Modern vegetation surveys are in approximate agreement with this estimate (Quade et al., 1987). To assess a range of possible values for $\%C_4$ vegetation, I used a range of estimates of MAP, and of net decreases in MAT (Table 7; Spaulding, 1985; Thompson et al., 1999). Climate circulation models for the LGM are highly debated, and reconstructions of seasonality of precipitation for this interval are controversial (Connin et al., 1998). I estimated the proportion of summer precipitation to be approximately equal to modern precipitation (Paruelo and Lauenroth, 1996).

Table 7. Calculated climate variables for the Las Vegas Valley during the LGM using estimates of MAT, MAP, and seasonality of precipitation. Predicted %C4 abundance is also reported, using the Paruelo and Lauenroth (1996) model.

Reference	Interval	MAT (°C)	MAP (mm)	JJA/MAP	$\%C_4$
WRCC, 2007	Modern	19.2	125	0.15	9
Thompson et al., 1999	LGM max T	14.3	266	0.15	10
Thompson et al., 1999	LGM max T	14.3	321	0.15	13
Thompson et al., 1999	LGM min T	13.7	266	0.15	9
Thompson et al., 1999	LGM min T	13.7	321	0.15	12
Spaulding, 1985	LGM max T	13.2	246	0.15	6
Spaulding, 1985	LGM max T	13.2	265	0.15	8
Spaulding, 1985	LGM min T	12.2	246	0.15	4
Spaulding, 1985	LGM min T	12.2	265	0.15	5

This model for prediction of vegetation using several plant functional types is more inclusive of potential shrub, succulent, and forb components; I therefore use the range of

$\%C_4$ abundance calculated here to estimate the abundance of C_4 grasses in the Las Vegas Valley during the LGM.

Correlation with Other Vegetation Data

Mehringer (1967) identified pollen types from various stratigraphic levels within the Tule Springs excavation that were correlated with radiocarbon dates. Fossil pollen spectra were reported for Unit D (31,300 to 22,600 yr BP) and Unit E_1 (9920 yr BP and younger). Spring Mound 4A is correlated between Units D and E_1, and also provides a pollen spectrum for the interval between the top of Unit D and the base of Unit E_1. The high volume of *Pinus* pollen from preferential aerial transport (up to 80% in Unit D and 60% in Spring Mound 4A) may result in an underrepresentation of other taxa (Solomon and Silkworth, 1986). The percent abundance of grass pollen ranged from 0 to 8% in Unit D, had a value of ~10% in Spring Mound 4A, which correlates between Units D and E_1, and had a value of 8% at the base of Unit E. These values estimate the total abundance of C_3 and C_4 grasses combined, and may underestimate this abundance. Given the potential for underrepresentation of grass abundance from pollen data alone, and since palynologically-derived abundance values are approximately equal to C_4 abundances predicted by the Paruelo and Lauenroth (1996) model, I used estimates from the model of 4 to 13% C_4 grass at the LGM.

Modern "Cheno-am" pollen rain (from the family Chenopodiaceae and the genus *Amaranthus*) is approximately 8% on the Kyle Canyon fan; this value fluctuates in an altitudinal transect of the Spring Mountains and reaches a peak abundance of 20% at 1500 m (Mehringer, 1967). Cheno-am pollen counts ranged from 1 to 6% in Unit D, had

a value of ~3% in Spring Mound 4A, and had a value of 5% at the base of Unit E_1. Cheno-am abundances of 10% are reported from pollen spectra in LGM-age packrat middens for other nearby Mojave Desert localities (Koehler et al., 2005). As with all data recovered from pollen spectra, the abundances of non-*Pinus* taxa may be under-reported.

I used a conservative estimate of 5% abundance of non-grass C_4 taxa for the LGM to late glacial transition. With the inclusion of estimated abundance of C_4 grasses of 4 to 13%, estimates of total $\%C_4$ plant abundance for the LGM therefore range from 9 to 18%. These abundances of C_4 plants of various functional types are used in conjunction with interpretations of feeding habits from dental morphology to interpret Pleistocene mammal diet from $\delta^{13}C$ values.

CHAPTER 4

RESULTS

Radiocarbon Dates

The radiocarbon ages of mammoth molars from enamel samples are summarized in Table 8. The lack of collagen in pre-treatment of dentine for radiocarbon analysis is consistent with the poor or nonexistent preservation of bones in the spring deposit. Two samples from each tooth were analyzed, except in cases of sample loss. Radiocarbon ages are reported in both ^{14}C yr BP and as ranges in thousands of years ago (ka) (Reimer et al., 2004).

Table 8. Radiocarbon ages of mammoth molars from analysis of enamel samples. Both radiocarbon ages (BP) and calibrated ages (ka) are reported.

Sample	UCIAMS #	^{14}C age (BP)	IntCal04 CAL range (ka)
MAM 1	28539	13960 ± 80	16424 – 16852
MAM 1	28548	15270 ± 35	18621 – 18724
MAM 2	28540	15880 ± 110	18951 – 19176
MAM 2	28549	17630 ± 45	20618 – 20950
MAM 3	28542	14210 ± 80	16730 – 17182
MAM 3	28551	14975 ± 40	18113 – 18381
MAM 4	28538	13360 ± 70	15654 – 16046
MAM 5	28541	15290 ± 110	18595 – 18774
MAM 5	28550	15015 ± 35	18141 – 18359
MT 7	28537	18350 ± 160	21572 – 22119
MT 7	28547	18200 ± 50	21499 – 21885

Duplicate samples from the same tooth fail to yield consistent radiocarbon ages within one standard deviation; therefore, these data are suspect. Low carbon content in tooth enamel carbonate-apatite resulted in significantly lower precision in AMS dates,

and these data demonstrate that high-resolution dating is difficult if not impossible using tooth enamel alone. However, the span of radiocarbon ages from 22.2 ka to 16.4 ka is consistent with the hypothesis that these fossils are a time-averaged accumulation, and provides a range of ages for context of further paleoenvironmental interpretations.

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

Mean isotopic data from tooth enamel analyses are displayed in Table 9 and Figure 5. Values displayed are the calculated means of intra-tooth analyses for each individual animal, and are reported with respect to VPDB. The $\delta^{13}C$ and $\delta^{18}O$ values of individuals from each genus are displayed in Figures 6 through 9 with one σ error bars for each individual. The average $\delta^{13}C$ value for *Mammuthus* is -8.45‰ with a standard deviation of 0.54‰, and the range of $\delta^{13}C$ values is -9.18‰ to -8.00‰. The average $\delta^{13}C$ value for *Equus* is -8.14‰ with a standard deviation of 0.48‰. The range of $\delta^{13}C$ values for *Equus* is -8.83‰ to -7.42‰.

Table 9. Mean isotopic values for carbon and oxygen isotopes and percent C_4 plants in the diet from tooth enamel samples, Gilcrease spring mound, Las Vegas Valley, Nevada.

		$\delta^{13}C$ VPDB (‰)			$\delta^{18}O$ VPDB (‰)			
Taxon	n	Average	S.D.	Range	Average	S.D.	Range	% C_4
Mammuthus	5	-8.44	0.54	-9.18 to -8.00	-14.42	0.54	-15.32 to -13.96	12 – 23
Equus	5	-8.16	0.59	-8.83 to -7.42	-11.07	0.61	-11.71 to -10.08	15 – 28
Bison	5	-8.72	1.70	-10.22 to -5.97	-13.21	1.56	-15.42 to -11.13	3 – 41
Camelops	5	-6.54	1.24	-8.49 to -5.23	-11.65	0.82	-12.54 to -10.67	18 – 48

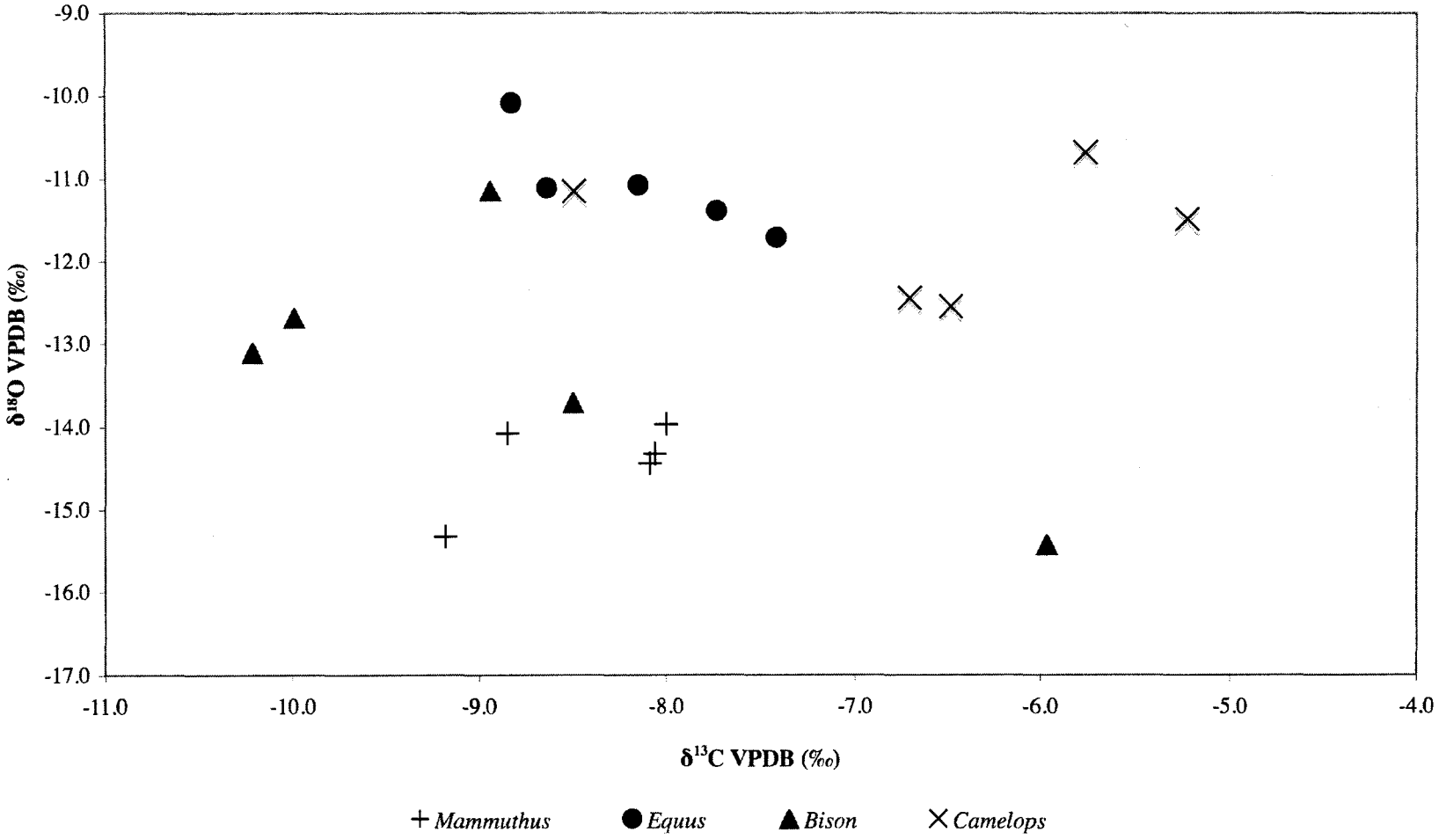

Figure 5. Bulk carbon and oxygen isotope values for *Mammuthus*, *Equus*, *Bison*, and *Camelops*. Dietary variation between taxa is indicated by differences in carbon isotopic values.

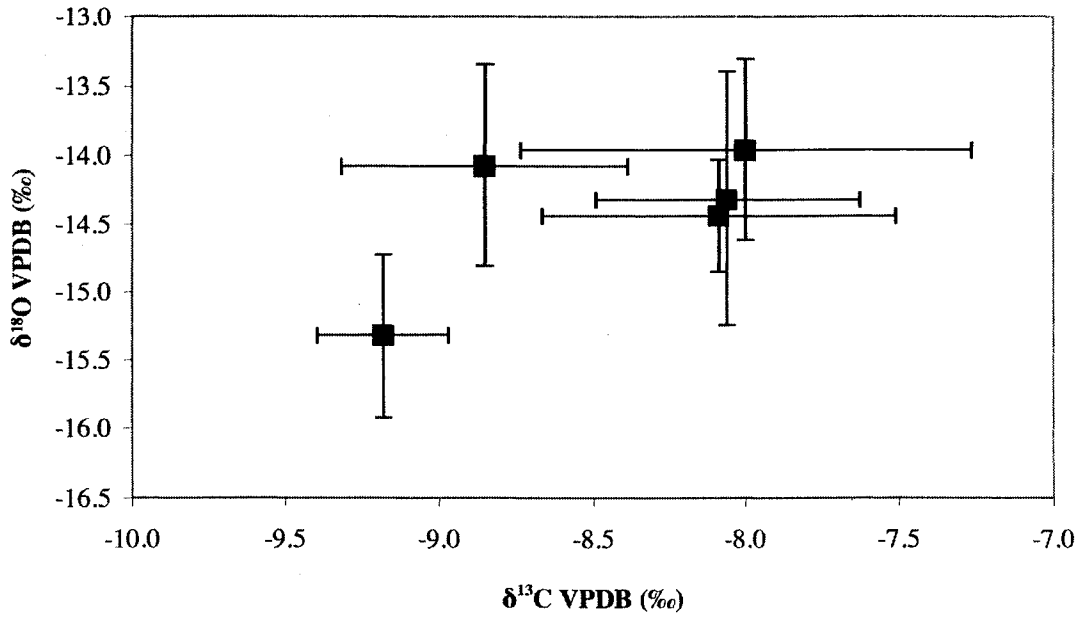

Figure 6. Mean $\delta^{13}C$ and $\delta^{18}O$ values for *Mammuthus*. Error bars show one standard deviation as calculated using the range of intratooth values from each individual.

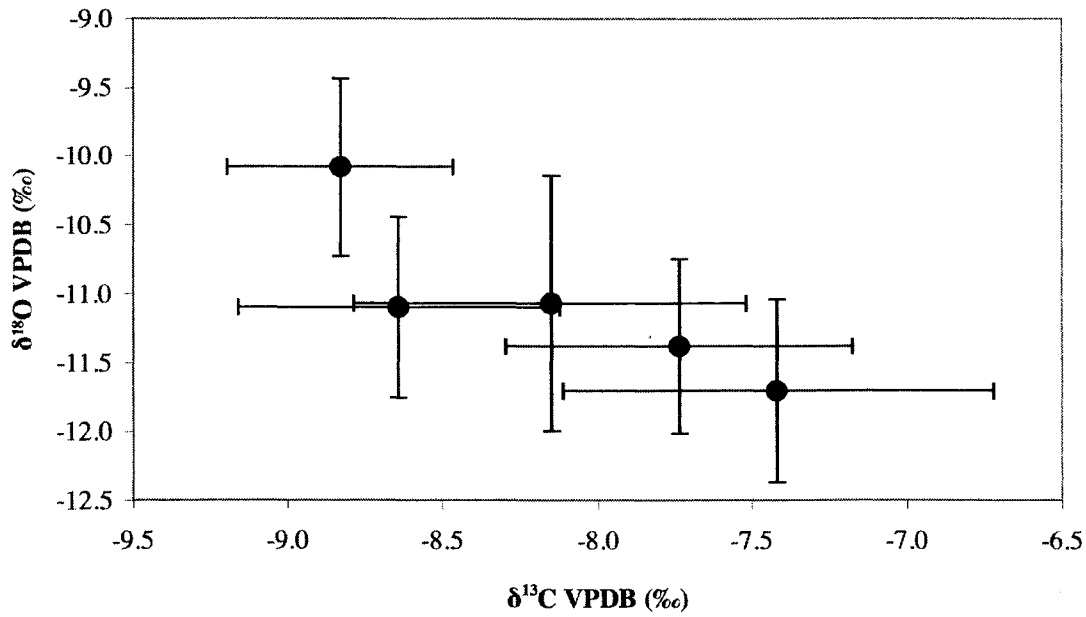

Figure 7. Mean $\delta^{13}C$ and $\delta^{18}O$ values for *Equus*. Error bars show one standard deviation as calculated using the range of intratooth values from each individual.

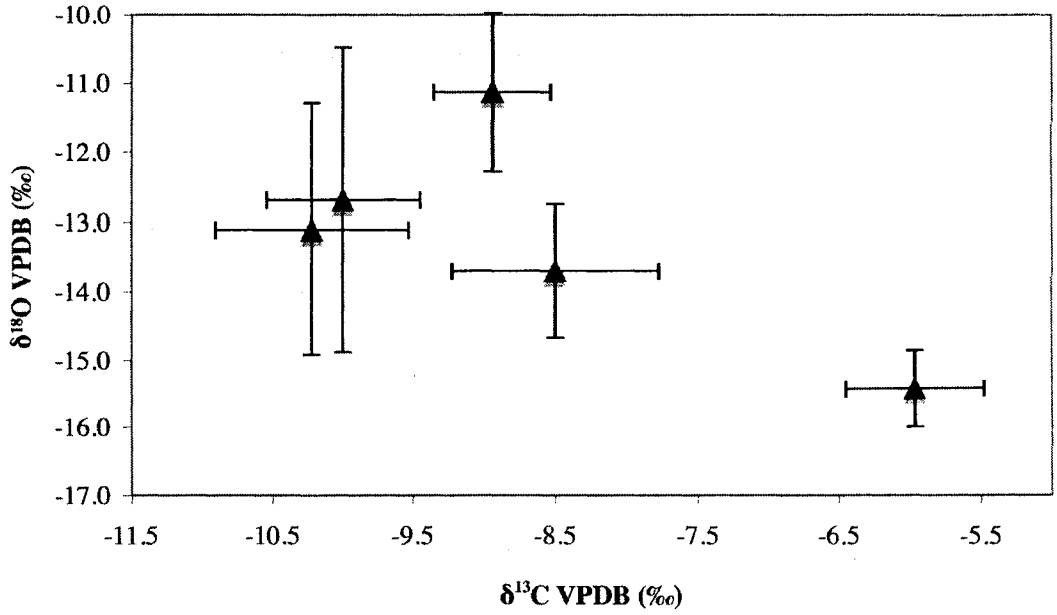

Figure 8. Mean $\delta^{13}C$ and $\delta^{18}O$ values for *Bison*. Error bars show one standard deviation as calculated using the range of intratooth values from each individual.

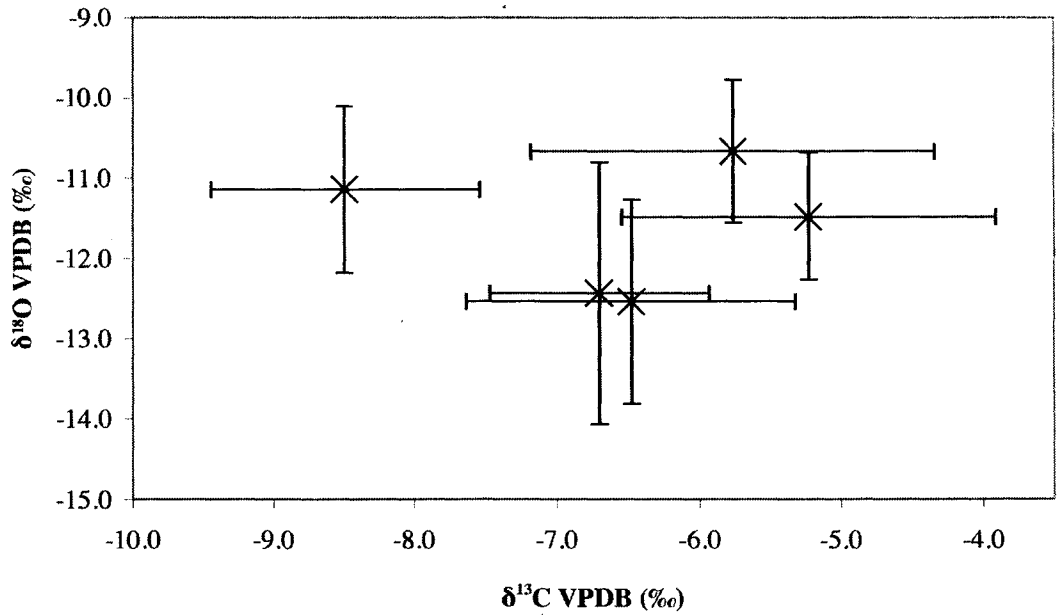

Figure 9. Mean $\delta^{13}C$ and $\delta^{18}O$ values for *Camelops*. Error bars show one standard deviation as calculated using the range of intratooth values from each individual.

Carbon isotope values vary considerably more between individuals for the *Bison* and *Camelops* specimens analyzed (Figure 5). The average $\delta^{13}C$ value for *Bison* is -8.72‰ with a standard deviation of 1.70‰, and the range of $\delta^{13}C$ values for *Bison* is -10.22‰ to -5.97‰. The average $\delta^{13}C$ value for *Camelops* is -6.53‰ with a standard deviation of 1.24‰, and the range of $\delta^{13}C$ values for *Camelops* is -8.49‰ to -5.23‰.

Oxygen isotope values are also reported as the calculated means of all intra-tooth analyses for each individual animal; values are reported here with respect to VPDB (Table 9). The average $\delta^{18}O$ value for *Mammuthus* is -14.42‰ with a standard deviation of 0.54‰; values range from -15.32‰ to -13.96‰. The average $\delta^{18}O$ value for *Equus* is -11.07‰ with a standard deviation of 0.61‰; values range from -11.17‰ to -10.08‰. The average $\delta^{18}O$ value for *Bison* is -13.21‰ with a standard deviation of 1.56‰; values range from -15.42‰ to -11.13‰. The average $\delta^{18}O$ value for *Camelops* is -11.65‰ with a standard deviation of 0.82‰; values range from -12.54‰ to -10.67‰.

Statistical Analysis of Bulk Isotopic Data

Statistical analysis of differences in $\delta^{13}C$ values between genera was performed using ANOVA; the Student-Newman-Keuls post-test was used to evaluate differences in $\delta^{13}C$ values between individual pairs of genera. Significant differences in $\delta^{13}C$ values are observed between genera ($P<0.03$). Paired comparisons between *Mammuthus*, *Equus*, and *Bison* show that there are no significant differences between any two of these taxa. *Mammuthus*, *Equus*, and *Bison* all exhibit average $\delta^{13}C$ values that indicate ≤20% proportion of C_4 plants in the diet. Individual paired comparisons between *Camelops* and

each of these three taxa show significant differences ($P<0.05$). The carbon isotopic values for *Camelops* indicate that this taxon had the highest proportion of C_4 plants in its diet.

Intra-Tooth Variation in Isotopic Values

Serial tooth enamel samples were collected from five individuals from each genus (Tables 10 and 11). Average values from each individual were treated as bulk samples and are reported in the Mean $\delta^{13}C$ and $\delta^{18}O$ Values section above. The serial sample isotopic data display some intra-tooth cyclicity; this pattern is more pronounced for some genera than others (Figures 10 through 29).

Variation in carbon and oxygen isotopes in *Mammuthus* is displayed in Figures 10 through 14. All intratooth $\delta^{13}C$ variations in *Mammuthus* have similar means (Table 10). The range of $\delta^{13}C$ values for a single individual varies from 0.85‰ to 2.58‰; the average range is 1.71‰. The average within-individual standard deviation is 0.49‰. For all *Mammuthus* specimens, $\delta^{13}C$ values show little correlation with $\delta^{18}O$ values. MAM 4 shows approximately two cycles of isotopic variation in carbon and oxygen (Figure 13). Specimens MAM 1, MAM 2, and MAM 5 show two to three cycles of variation (Figures 10, 11, and 14). MAM 3 shows three to four cycles of variation (Figure 12).

Carbon and oxygen isotope variations for *Equus* are displayed in Figures 15 through 19. Mean values of intratooth variations are similar between individual *Equus* specimens (Tables 10 and 11). Ranges of $\delta^{13}C$ values for individuals vary from 1.27‰ to 2.65‰, with an average range of 1.95‰. The average within-individual standard deviation is 0.55‰. Most *Equus* specimens show some inverse correlation between $\delta^{13}C$ and $\delta^{18}O$ values. Specimens EQS 2, EQS 4, and EQS 5 all show one to two cycles of variation

(Figures 16, 18, and 19). EQS 3 shows approximately four complete cycles of isotopic variation (Figure 17). Intratooth isotopic data for EQS 1 follow no particular trend (Figure 15).

Intratooth measurements of carbon and oxygen isotope values for *Bison* are displayed in Figures 20 through 24. Mean values of intratooth $\delta^{13}C$ variation vary considerably between individuals, from -10.22‰ to -5.97‰ (Table 10). The range of $\delta^{13}C$ values in a single individual varies from 1.44‰ to 2.24‰, with an average range of 1.80‰. The average intratooth standard deviation is 0.57‰. The total span of $\delta^{13}C$ values between individuals is much greater than the $\delta^{13}C$ range for any given individual. All *Bison* specimens show inverse variation between $\delta^{13}C$ and $\delta^{18}O$ values; r^2 values range from 0.41 to 0.91 for four specimens (BIS 2, BIS 3, BIS 4, and BIS 5). BIS 1 displays two to three potential cycles in carbon and oxygen isotope variation (Figure 20). BIS 2, BIS 4, and BIS 5 all show one to two cycles (Figures 21, 23, and 24). BIS 3 shows less than one full cycle of variation (Figure 22).

Variation in carbon and oxygen isotopic values in *Camelops* is displayed in Figures 25 through 29. Mean values of intratooth $\delta^{13}C$ variation vary from -8.49‰ to -5.23‰, although with the exception of CAM 5 ($\delta^{13}C_{mean}$= -8.49‰), mean values for *Camelops* are > -7‰. Ranges of $\delta^{13}C$ values for individuals vary from 2.35‰ to 4.78‰, with an average range of 3.30‰. The average within-individual standard deviation is 1.12‰. Although the range of intratooth $\delta^{13}C$ values for any given individual is relatively high with respect to other taxa in this study, these ranges overlap within the span of mean values for each individual (Figure 9). Some *Camelops* specimens show approximate inverse variation between $\delta^{13}C$ and $\delta^{18}O$ values. CAM 1 and CAM 2 display greater than

one cycle in oxygen and carbon isotope variation (Figures 25 and 26). CAM 4 displays one to two cycles (Figure 28); CAM 3 displays two complete cycles (Figure 27). CAM 5 displays one complete cycle in $\delta^{18}O$ values, but no apparent cyclicity in $\delta^{13}C$ values (Figure 29).

Table 10. Serial sample results for carbon isotope values in tooth enamel of *Mammuthus*, *Equus*, *Bison*, and *Camelops*.

		$\delta^{13}C$ VPDB (‰)					Averages of individual intratooth values		
Specimen	n	Mean	S.D.	Max.	Min.	Range	Mean	S.D.	Range
MAM 1	21	-8.00	0.74	-6.88	-9.46	2.58			
MAM 2	19	-8.06	0.43	-7.34	-8.93	1.59			
MAM 3	21	-8.09	0.58	-7.20	-15.29	1.90	-8.44	0.49	1.71
MAM 4	22	-9.18	0.21	-8.77	-9.62	0.85			
MAM 5	17	-8.85	0.46	-7.76	-9.40	1.64			
EQS 1	16	-7.74	0.56	-6.04	-8.25	2.21			
EQS 2	17	-8.15	0.63	-7.36	-9.33	1.97			
EQS 3	24	-8.83	0.36	-8.12	-9.39	1.27	-8.16	0.55	1.95
EQS 4	18	-7.42	0.70	-5.84	-8.49	2.65			
EQS 5	15	-8.64	0.52	-7.83	-9.49	1.66			
BIS 1	18	-8.94	0.41	-7.99	-9.44	1.44			
BIS 2	16	-9.99	0.55	-9.16	-10.82	1.66			
BIS 3	15	-8.50	0.72	-7.78	-10.03	2.24	-8.72	0.57	1.80
BIS 4	15	-5.97	0.49	-5.21	-6.79	1.57			
BIS 5	16	-10.22	0.69	-9.47	-11.57	2.09			
CAM 1	15	-6.48	1.16	-4.92	-7.94	3.01			
CAM 2	13	-5.23	1.32	-3.45	-7.21	3.75			
CAM 3	20	-6.70	0.77	-5.17	-7.77	2.60	-6.54	1.12	3.30
CAM 4	16	-5.76	1.42	-3.16	-7.94	4.78			
CAM 5	18	-8.49	0.95	-7.20	-9.55	2.35			

Table 11. Serial sample results for oxygen isotope values in tooth enamel of *Mammuthus*, *Equus*, *Bison*, and *Camelops*

		$\delta^{18}O$ VPDB (‰)					Averages of individual intratooth values		
Specimen	n	Mean	S.D.	Max.	Min.	Range	Mean	S.D.	Range
MAM 1	21	-13.96	0.65	-11.86	-15.07	3.21			
MAM 2	19	-14.32	0.92	-12.66	-16.09	3.44			
MAM 3	21	-14.44	0.41	-13.68	-15.29	1.61	-14.42	0.67	2.73
MAM 4	22	-15.32	0.60	-14.11	-16.50	2.38			
MAM 5	17	-14.08	0.73	-12.59	-15.60	3.01			
EQS 1	16	-11.38	0.63	-10.52	-12.78	2.26			
EQS 2	17	-11.07	0.92	-8.96	-12.34	3.38			
EQS 3	24	-10.08	0.65	-9.02	-11.32	2.29	-11.07	0.70	2.55
EQS 4	18	-11.71	0.66	-10.67	-12.79	2.12			
EQS 5	15	-11.10	0.66	-10.17	-12.87	2.71			
BIS 1	18	-11.13	1.12	-9.72	-13.73	4.01			
BIS 2	16	-12.68	2.13	-7.89	-15.01	7.12			
BIS 3	15	-13.70	0.94	-11.78	-14.90	3.12	-13.21	1.30	4.34
BIS 4	15	-15.42	0.55	-14.09	-16.22	2.13			
BIS 5	16	-13.11	1.76	-10.00	-15.33	5.33			
CAM 1	15	-12.54	1.23	-11.27	-14.62	3.35			
CAM 2	13	-11.48	0.77	-9.46	-11.98	2.52			
CAM 3	20	-12.44	1.58	-9.96	-14.68	4.72	-11.65	1.09	3.45
CAM 4	16	-10.67	0.86	-9.22	-11.94	2.72			
CAM 5	18	-11.14	1.01	-9.01	-12.94	3.93			

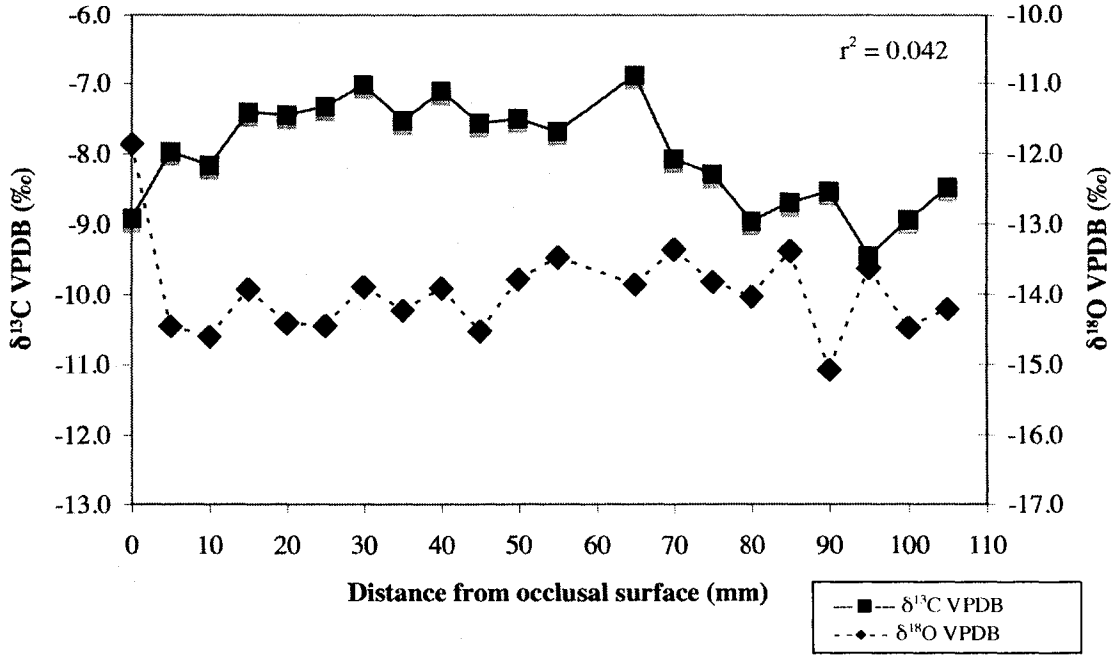

Figure 10. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Mammuthus* specimen MAM 1.

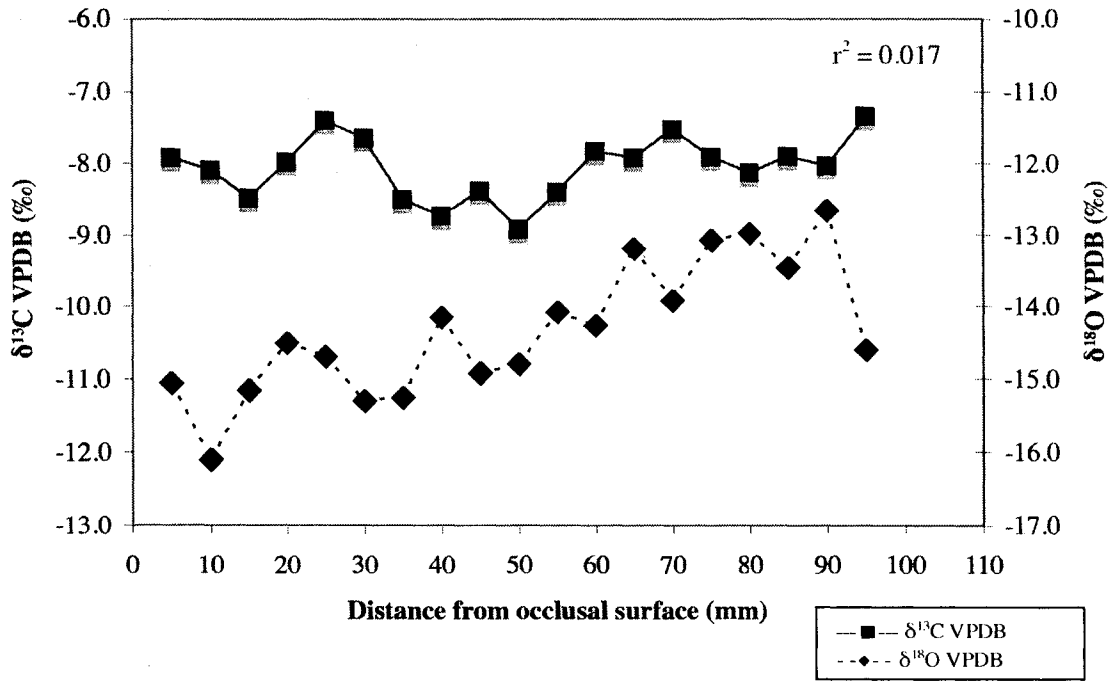

Figure 11. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Mammuthus* specimen MAM 2.

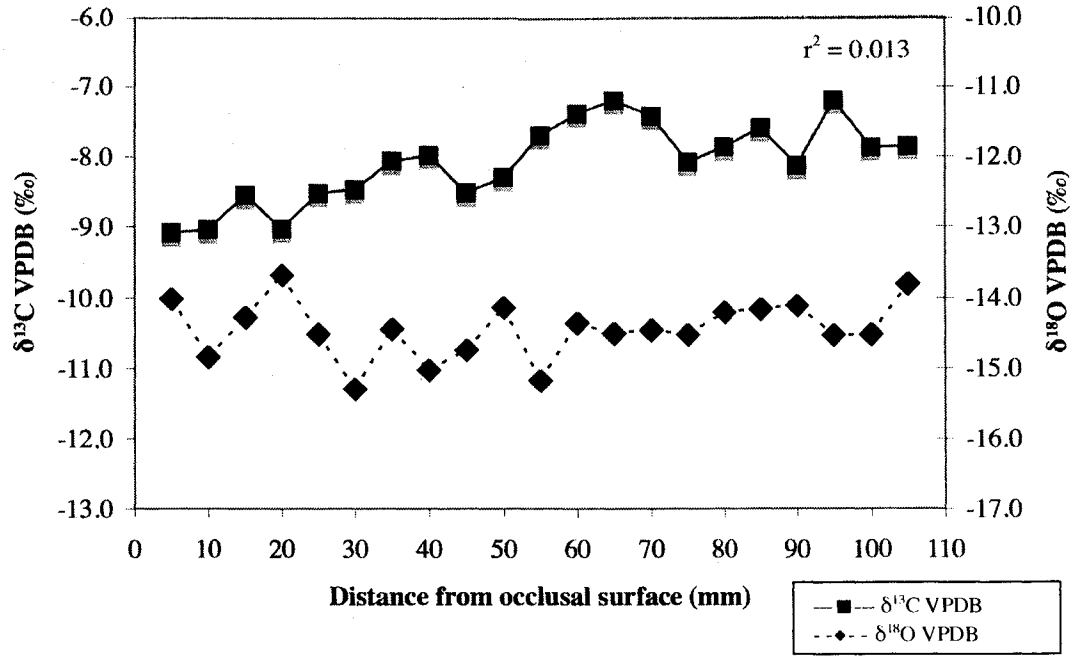

Figure 12. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Mammuthus* specimen MAM 3.

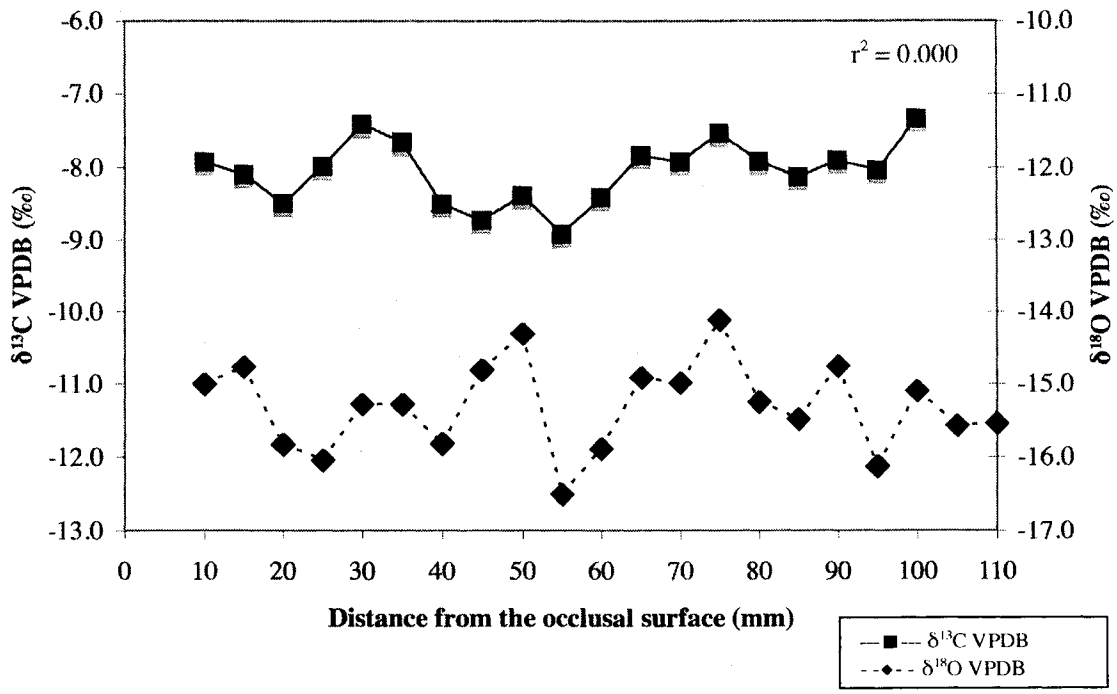

Figure 13. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Mammuthus* specimen MAM 4.

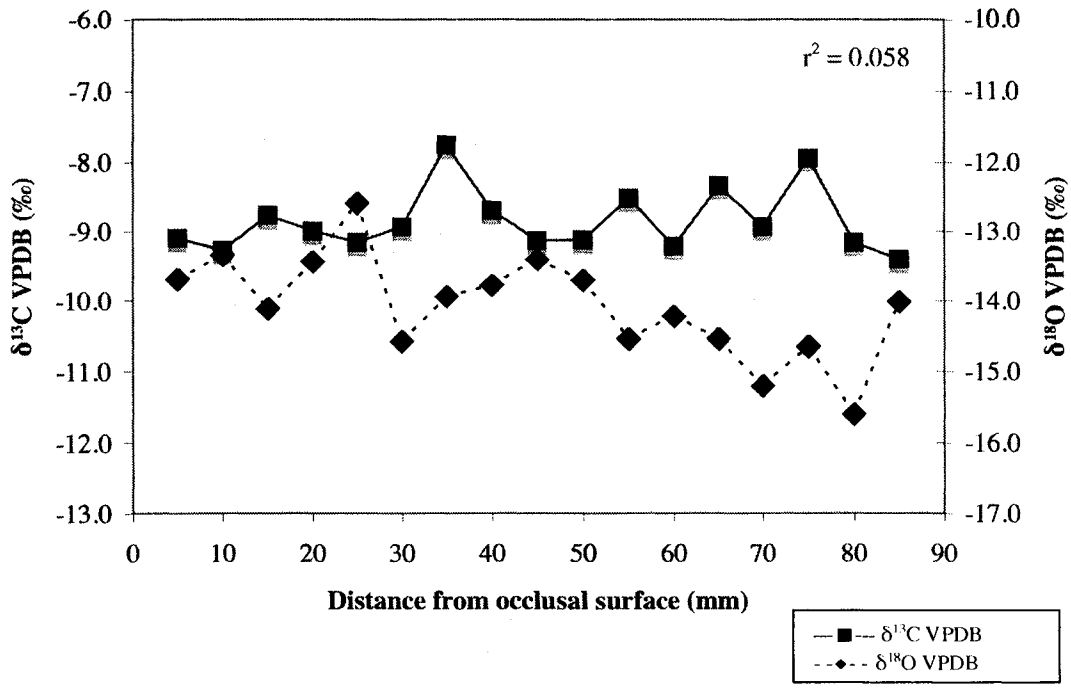

Figure 14. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Mammuthus* specimen MAM 5.

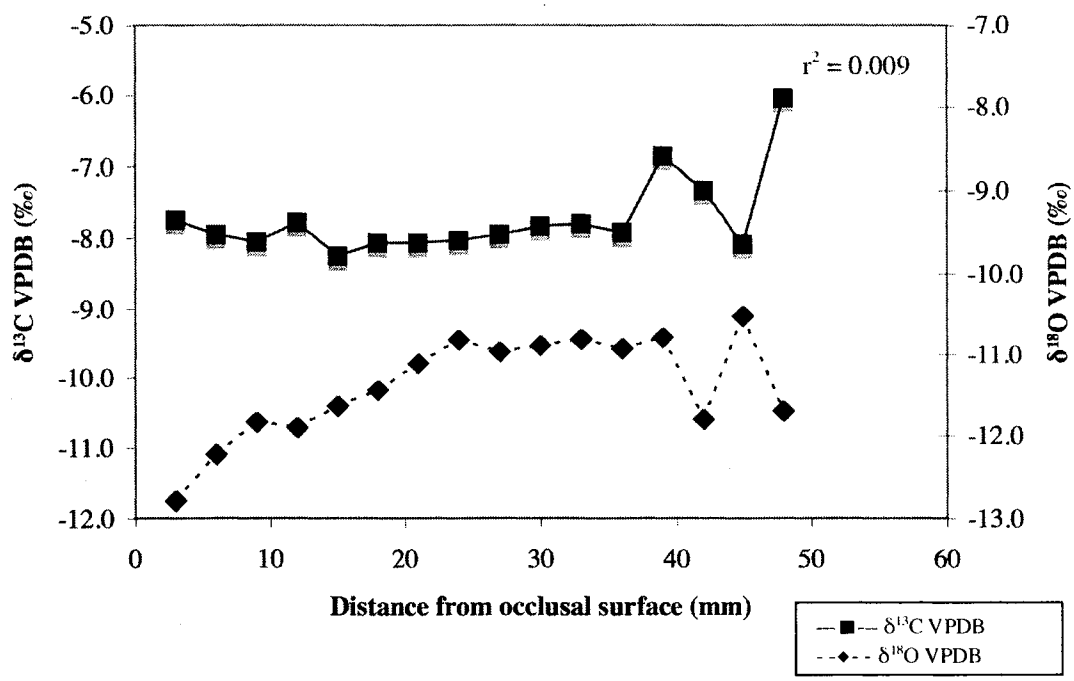

Figure 15. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Equus* specimen EQS 1.

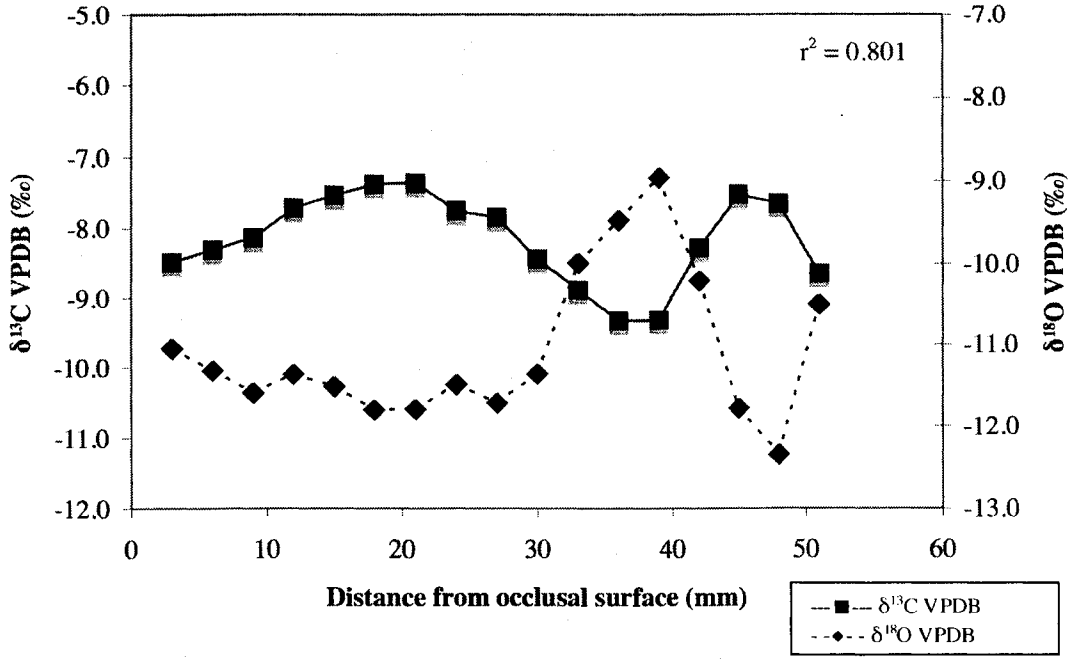

Figure 16. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Equus* specimen EQS 2.

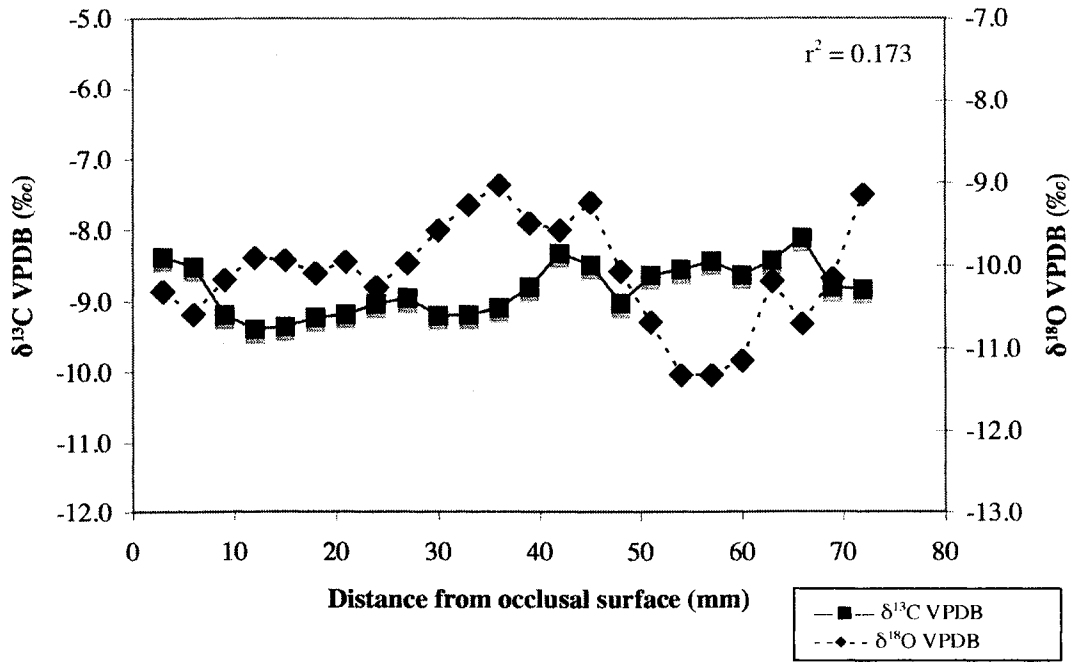

Figure 17. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Equus* specimen EQS 3.

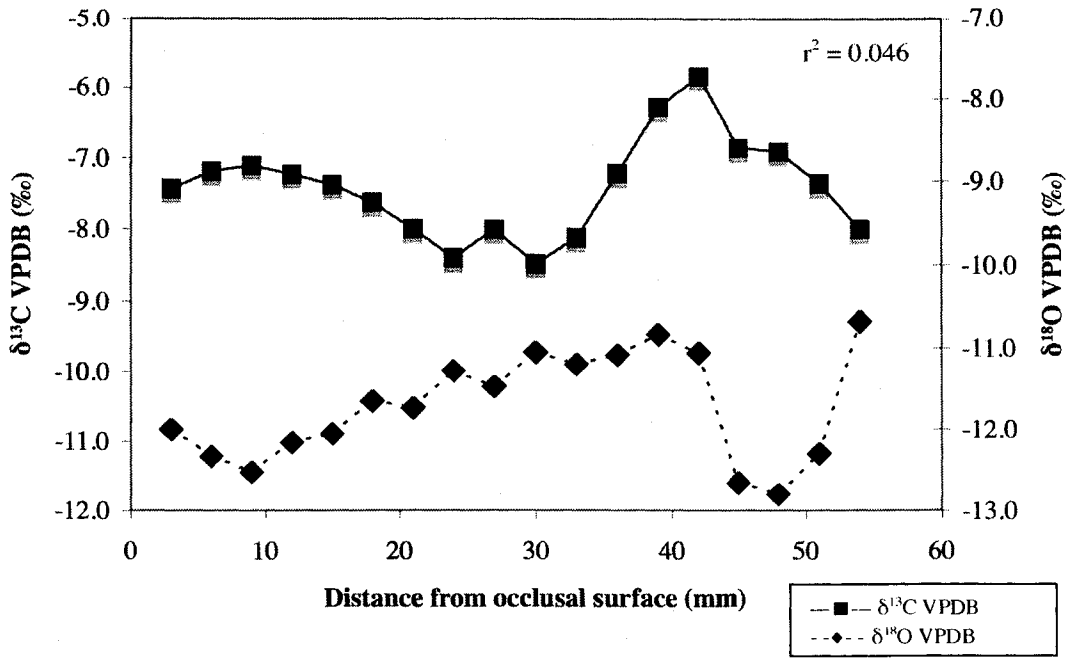

Figure 18. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Equus* specimen EQS 4.

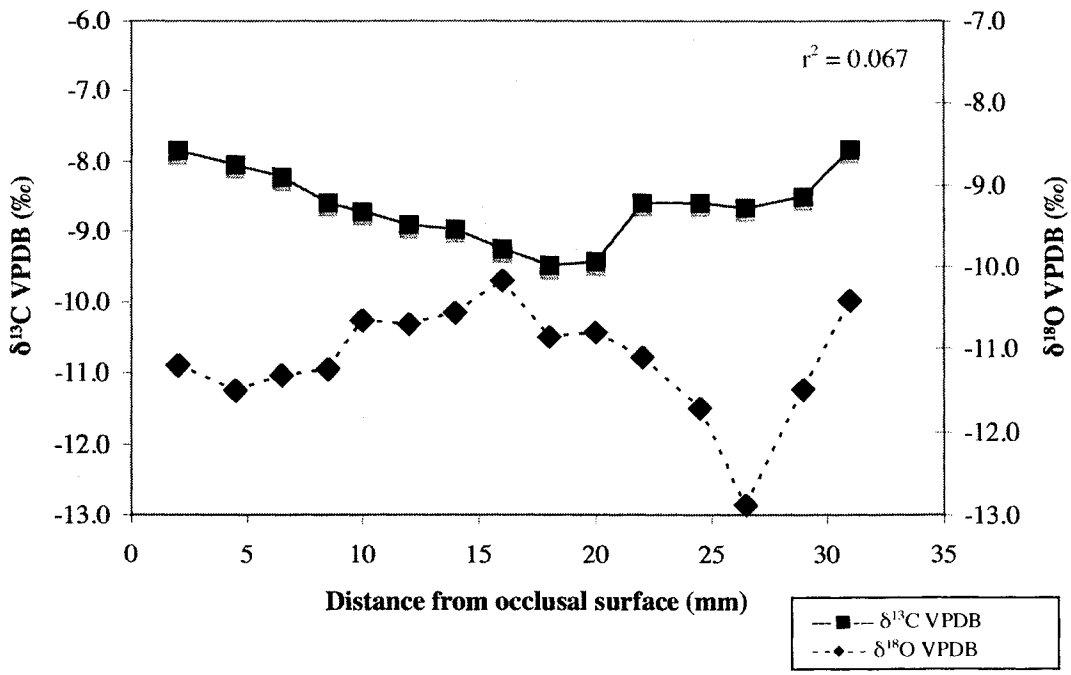

Figure 19. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Equus* specimen EQS 5.

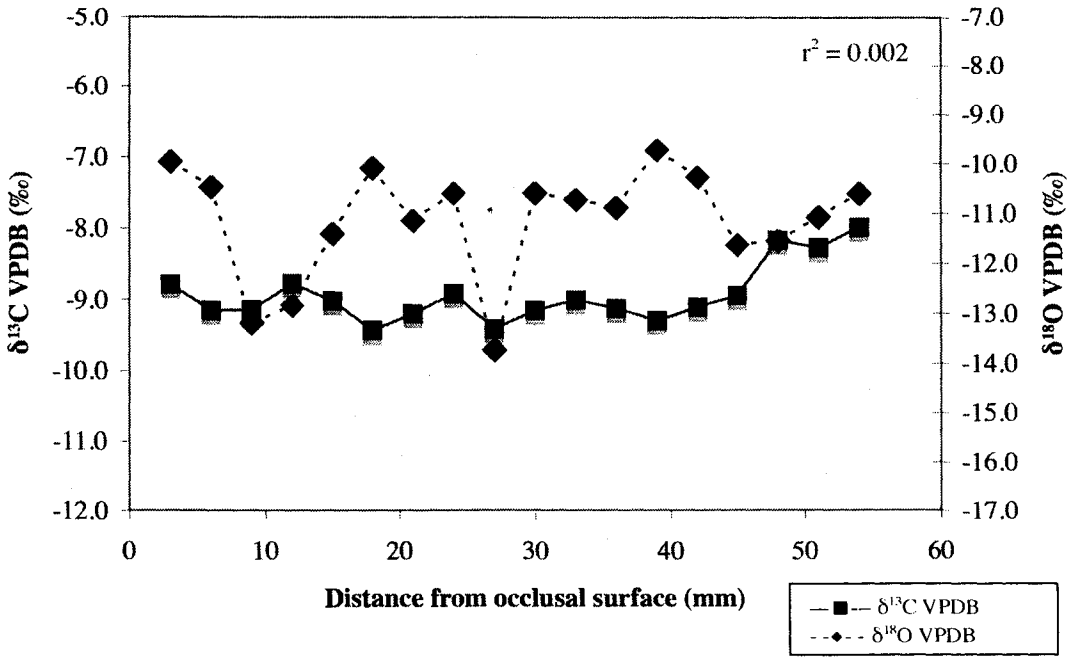

Figure 20. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Bison* specimen BIS 1.

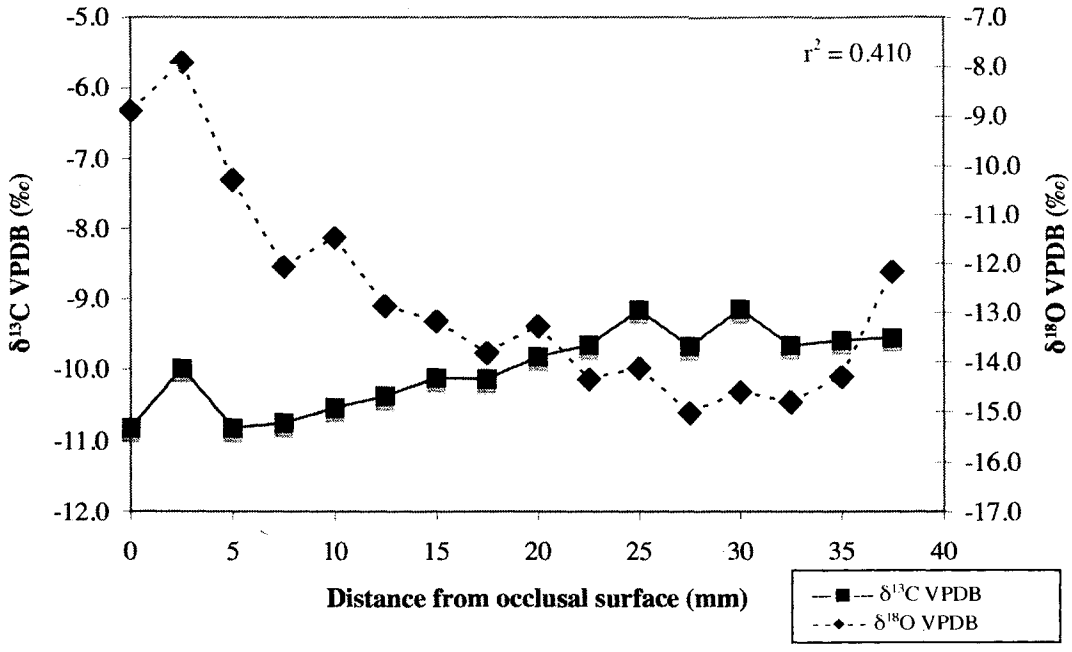

Figure 21. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Bison* specimen BIS 2.

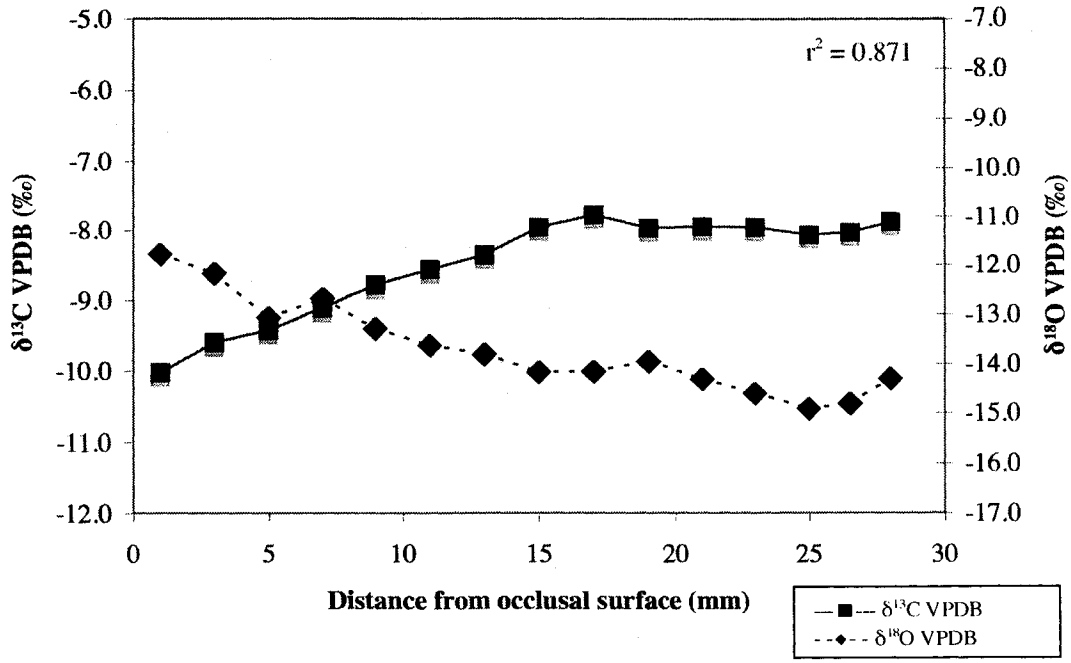

Figure 22. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Bison* specimen BIS 3.

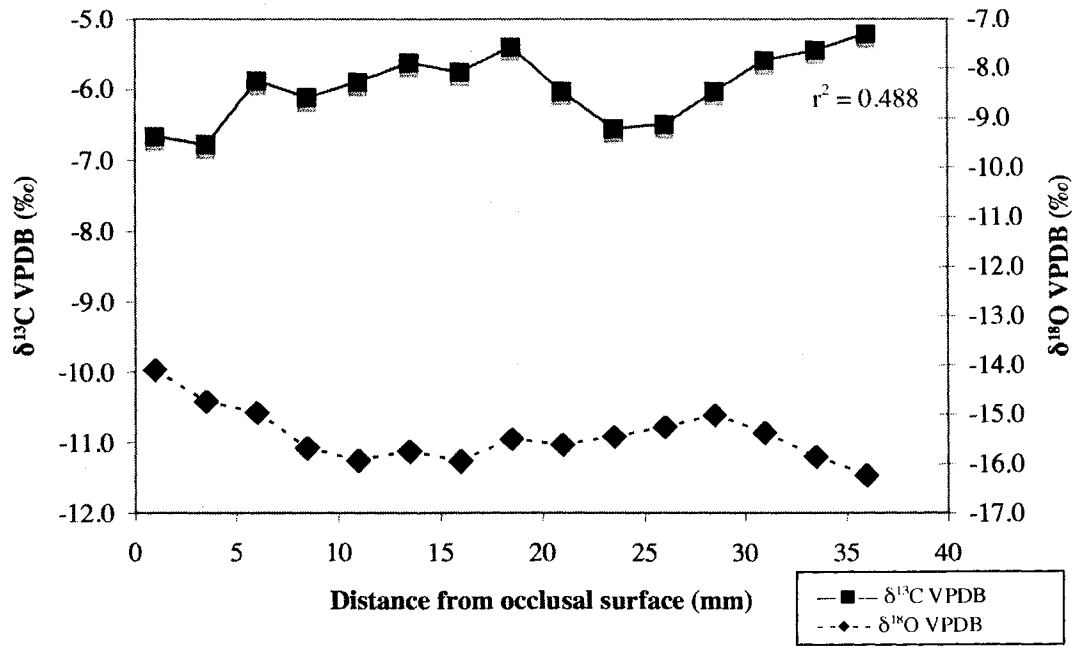

Figure 23. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Bison* specimen BIS 4.

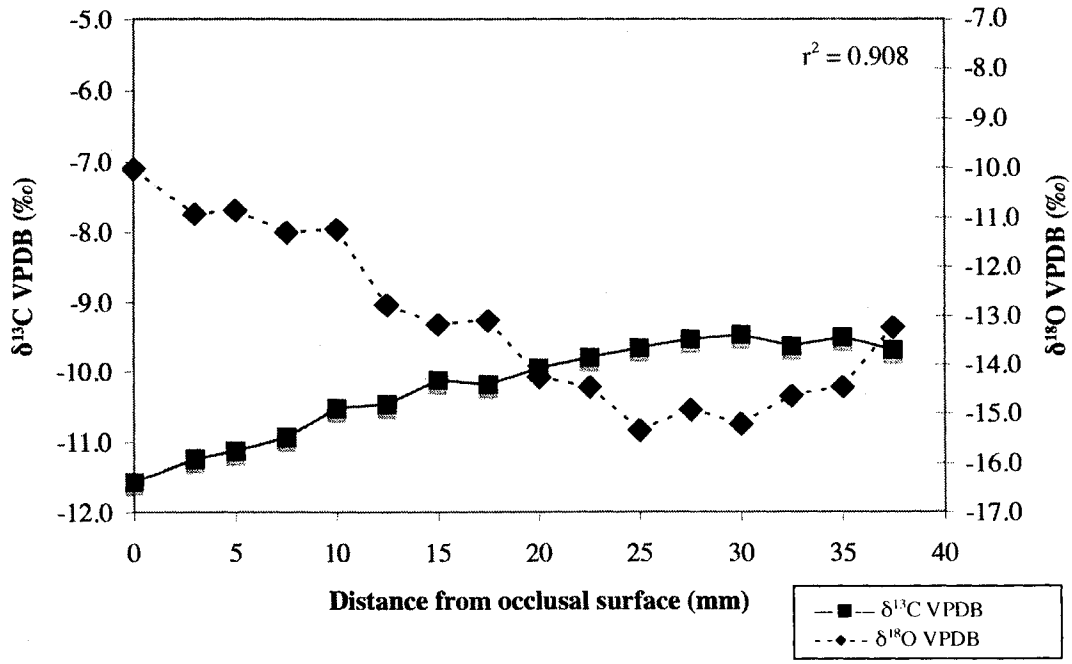

Figure 24. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Bison* specimen BIS 5.

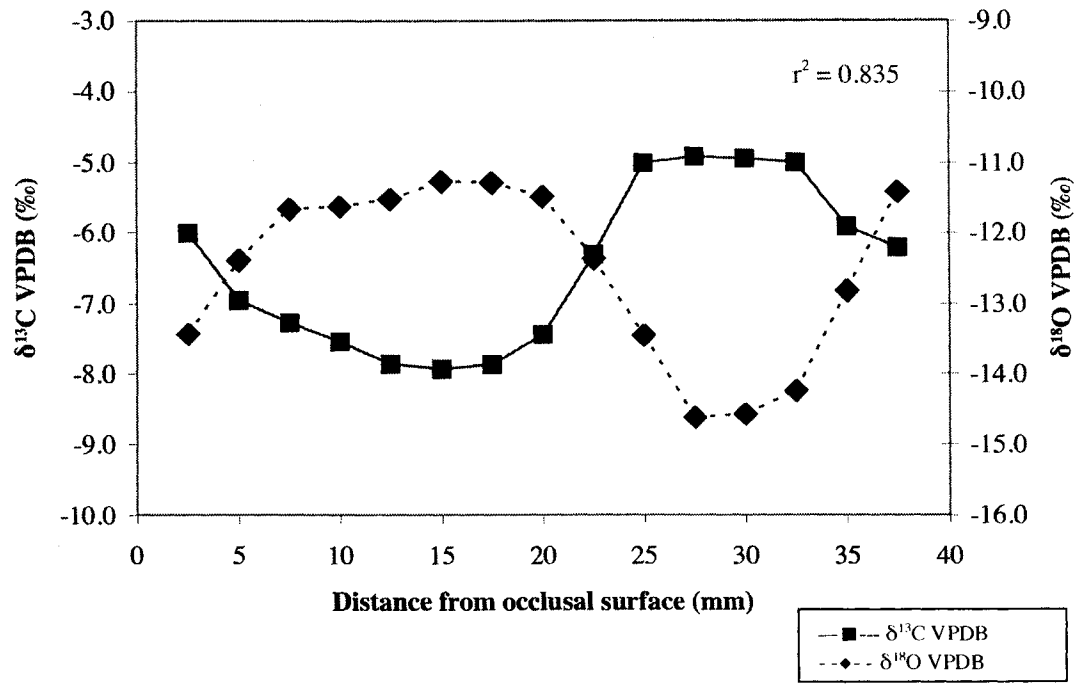

Figure 25. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Camelops* specimen CAM 1.

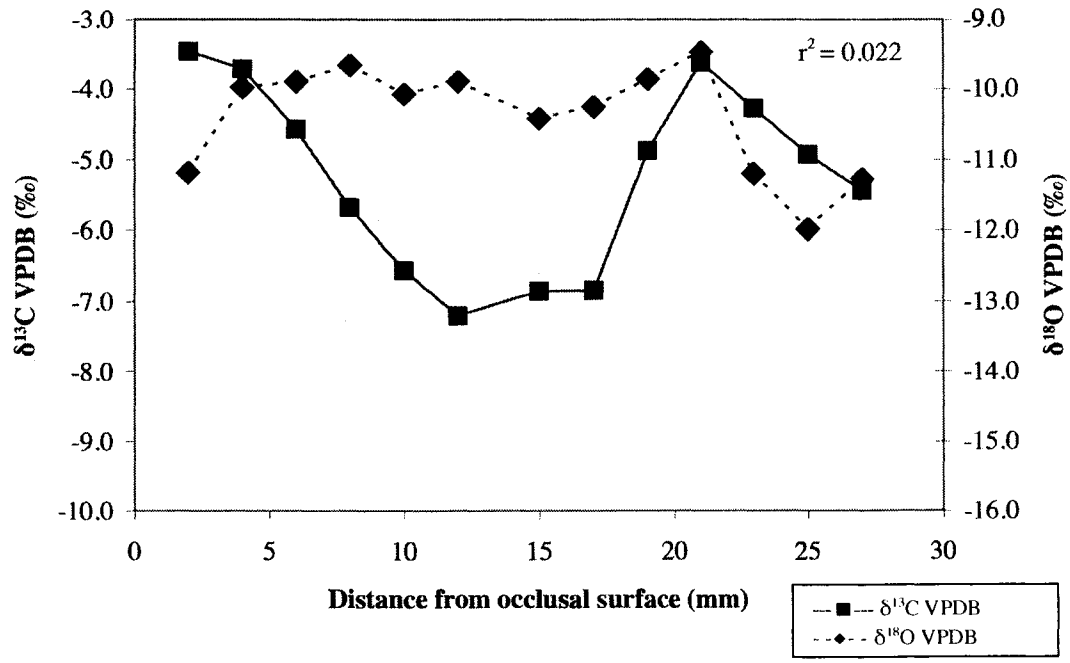

Figure 26. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Camelops* specimen CAM 2.

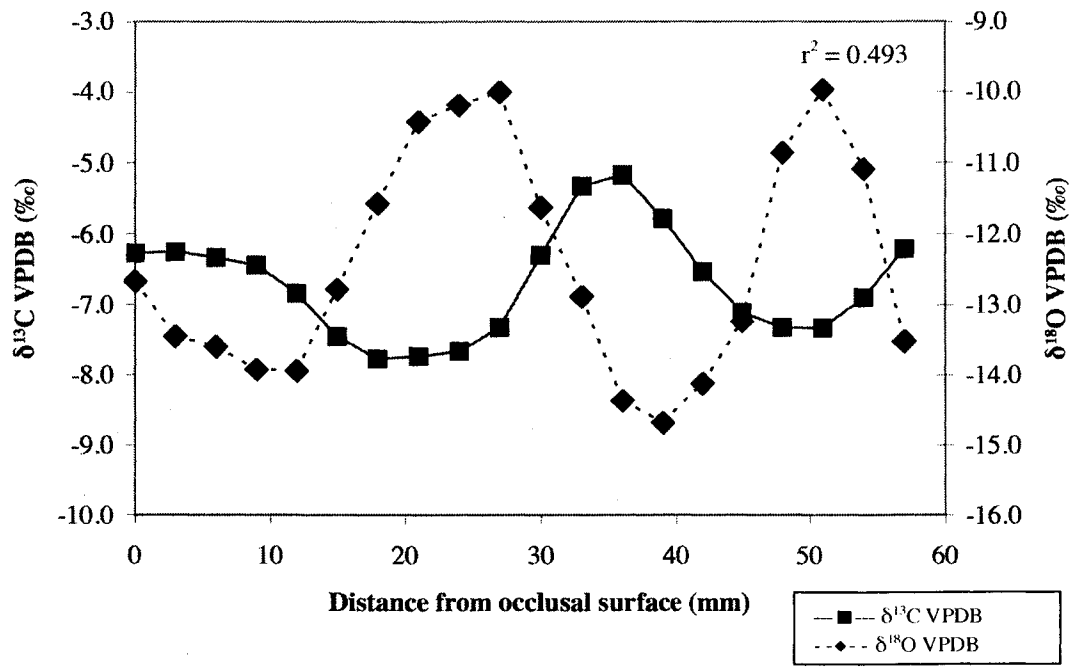

Figure 27. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Camelops* specimen CAM 3.

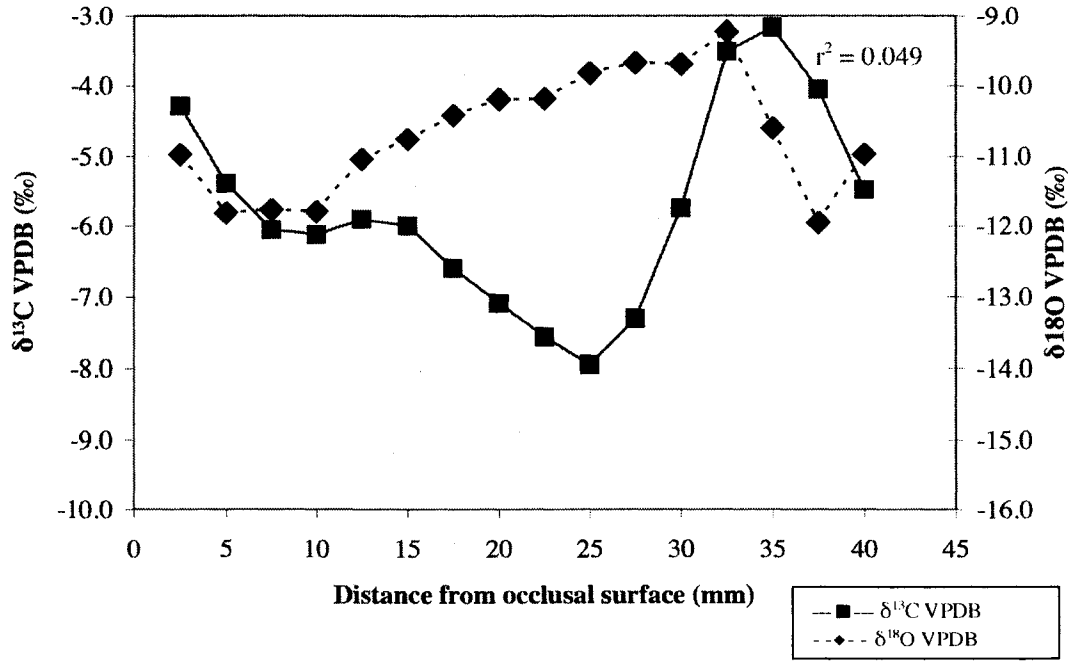

Figure 28. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Camelops* specimen CAM 4.

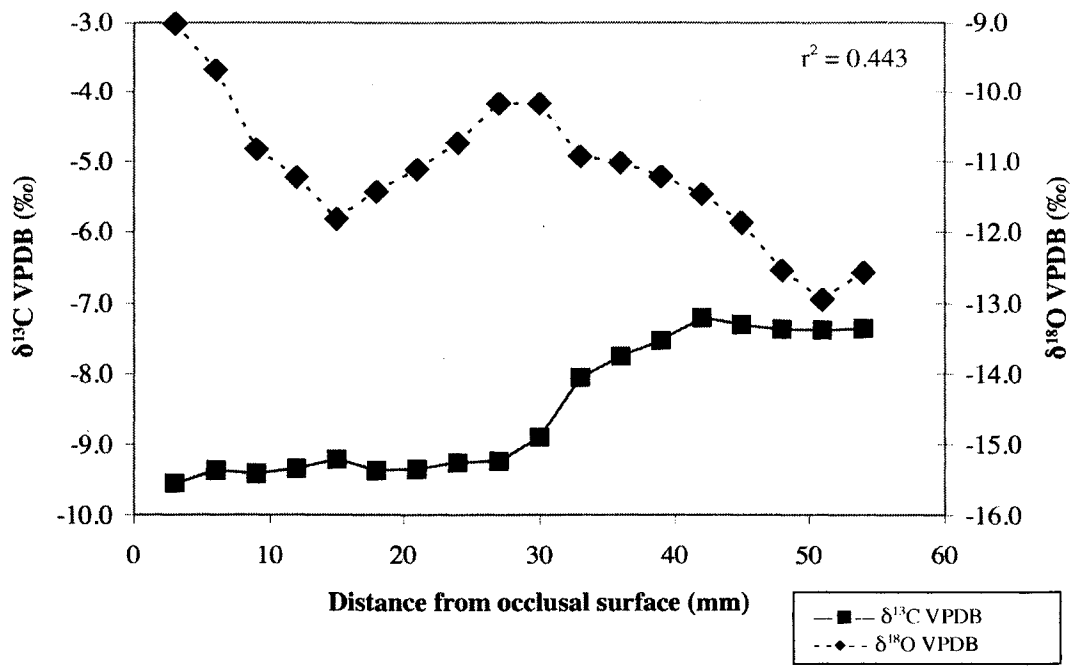

Figure 29. Intra-tooth variation in $\delta^{13}C$ and $\delta^{18}O$ values, *Camelops* specimen CAM 5.

CHAPTER 5

DISCUSSION

Isotopic Reconstruction of Diet and Range

The relative proportions of C_3 and C_4 plants in the diets of each individual were calculated using isotopic end-member values for tooth enamel of pure C_3 and pure C_4 feeders. The average $\delta^{13}C$ value for *Mammuthus* was -8.45‰, which suggests that it was primarily a C_3 feeder with an average proportion of 19% C_4 plants (Figure 5). Similarly, the average $\delta^{13}C$ value for *Equus* was -8.14‰, which suggests that it was also primarily a C_3 feeder, with an average proportion of 21% C_4 plants (Figure 5).

Both *Bison* and *Camelops* exhibit a broader range of $\delta^{13}C$ values between individuals than *Mammuthus* or *Equus*. The $\delta^{13}C$ values for *Bison* range from -10.22‰ to -5.97‰, and the calculated proportion of C_4 material in the diet is 16%, ranging from 3% to 41% (Table 9; Figure 5). Results from *Camelops* exhibit similar variability: $\delta^{13}C$ values range from -8.49‰ to -5.23‰, and the calculated proportion of C_4 plants in *Camelops* diet is 36%, ranging from 18% to 48% (Table 9; Figure 5).

Of all taxa analyzed in this study, bison have the highest preference for grazing, and indiscriminately consume C_3 and C_4 grasses in the proportion in which they occur on the landscape (Hoppe et al., 2006). Evaluation of *Bison* $\delta^{13}C$ values, excluding the outlier BIS 4, indicate ingestion of 3 to 18% C_4 material. Since *Bison* is an obligate grazer and a passive recorder of the relative C_3/C_4 grass abundance, the results from this study suggest

an abundance of C_4 grasses of 3 to 18% at the LGM in southern Nevada. This value is also consistent with estimated abundances of C_4 grasses from other vegetation data.

The feeding habits of *Bison* from the Gilcrease spring mound vary considerably between individuals, as inferred from isotopic values (Figure 8). Average $\delta^{13}C$ values for this taxon generally indicate ≤20% C_4 plants in the diet. The single individual with a greater proportion of C_4 grasses in its diet (BIS 4; Figure 5) was possibly migrating to areas further to the south (e.g., Arizona) where a higher percentage of C_4 grasses have been documented for the LGM (Connin et al., 1998; Liu et al., 1996). An alternative, more likely explanation lies in the intermittent activity of the Gilcrease spring through late glacial and Holocene times. A higher percentage of C_4 grass has been documented in the area for later intervals (Connin et al., 1998; Mehringer, 1967; Spaulding, 1985); BIS 4 could represent an individual from this later time period. This is also confirmed by isotopic data from late glacial herbivores from Unit E_1 of the Tule Springs assemblage (Connin et al., 1998).

The $\delta^{13}C$ values recorded in *Camelops* tooth enamel indicate that the average individual diet contained a higher proportion of C_4 plant material than any of the other herbivores analyzed (Table 9; Figure 5). Conventional interpretations of camelids place them in a browsing or mixed-feeding niche, although they have hypsodont teeth (Dompierre and Churcher, 1996). Recent isotopic studies allow more detailed reconstruction of diet and suggest ecological generalization in intermediate feeding with a preference for browse (Feranec, 2003). Of all taxa analyzed in this study, *Camelops* has the highest preference for browsing, although $\delta^{13}C$ values here indicate the greatest consumption of C_4 plant material.

Modern camels are highly adapted for survival in arid environments. Nutritional studies of modern camels demonstrate that they show a strong preference for salty plants (halophytes) (Farid, 1989; Wardeh, 2004; Wilson, 1989), and identify *Atriplex* spp. and other halophytic taxa among their most preferred browse plants (Farid, 1989; Wilson, 1989). *Atriplex*, a C_4 shrub, is a member of the Chenopodiaceae family, and is abundant in the modern Great Basin in several forms, including *A. confertifolia* (shadscale) and *A. canescens* (fourwing saltbush) (Mozingo, 1987). *Atriplex* spp. provides an important source of winter browse material for a variety of modern large mammals, including both livestock and range animals (Blaisdell and Holmgren, 1984; Cook and Harris, 1968; Tipton, 1994). Chenopod pollen is present in sedimentary records from this interval, although it is not abundant (Mehringer, 1967). However, other vegetation records from the Mojave Desert indicate a high percentage of chenopods (Koehler et al., 2005). Because of the browsing feeding habit demonstrated for both modern and fossil camelids and the preference of modern Old World camels for the salty browse plant *Atriplex*, I interpret that the high $\delta^{13}C$ values in *Camelops* teeth record preferential browsing on the C_4 shrub *Atriplex*.

The $\delta^{13}C$ values for each of two grazers, *Mammuthus* and *Equus*, are approximately consistent with reconstructed abundances of C_4 vegetation on the landscape during the LGM to late glacial transition. The $\delta^{13}C$ values of *Mammuthus* and *Equus* are slightly higher than those of *Bison* from this study, indicating a slightly higher percentage of C_4 plants ingested. Some evidence has suggested a mixed-feeding habit for *Mammuthus* and *Equus*, in contrast to traditional interpretations of pure grazing (Koch et al., 1998). I interpret that the diets of *Mammuthus* and *Equus* were composed primarily of C_3 grasses,

with a preference for a small percentage of browse, composed of the C_4 shrub *Atriplex*. This is consistent both with interpretations for *Camelops* and with newer evidence from other studies suggesting facultative grazing in these taxa.

Oxygen isotopic variability between individuals can be used to evaluate whether individual fossils accumulated over a short or long time span. In modern large herbivores in Africa, the average within-species standard deviation of $\delta^{18}O$ is ±1.3‰ for browsers, ±0.9‰ for pure grazers, and ±1.1‰ for mixed feeders (Bocherens et al., 1996). Koch et al. (1998) concluded that within-species variability exceeding 1.1‰ to 1.3‰ should be considered significant, and interpreted as an assemblage composed of individuals from different geographic or temporal populations. The within-clade standard deviations of $\delta^{18}O$ in *Mammuthus* (0.54‰), *Equus* (0.61‰), and *Camelops* (0.82‰) do not approach this critical limit. The $\delta^{18}O$ standard deviation in *Bison* is 1.56‰, which indicates that in this assemblage, individual animals most likely came from different populations.

Low intra-taxon ranges of $\delta^{18}O$ values for both *Mammuthus* and *Equus* suggest that these individuals did not migrate considerable distances over the time interval of tooth growth. It is possible that these individuals represent an accumulation over a long time span. However, coincident low variability in $\delta^{13}C$ values for both taxa suggests either an accumulation of individuals over a short time span or no change in diet concurrent with the increase in C_4 plants during the transition to late glacial flora. A broader range of $\delta^{18}O$ values in *Bison* suggests a broader geographic range for individuals, or that *Bison* accumulated in the spring mound over a longer time span than *Mammuthus* or *Equus*. A wide range of $\delta^{18}O$ values for *Camelops* suggests a wider range that could reflect either

geographic or altitudinal variation. The interpretation of preferential feeding on *Atriplex* may have led *Camelops* to range farther up slopes in search of forage.

Isotopic Records of Seasonal Variations

Intra-tooth variation in $\delta^{13}C$ values for *Mammuthus*, *Equus*, and *Bison* all exhibit ranges similar to previously documented ranges in these Pleistocene taxa in other locations. The low intra-tooth variability for each individual of these taxa suggests less seasonal variation in diet, and little seasonal partitioning of resources discernible from isotopic analysis. Instead, individuals consumed grass in the naturally occurring C_3/C_4 proportion. *Mammuthus* and *Equus* may have consumed a small amount of C_4 browse, as discussed above; this preference for a small amount of browse does not vary notably between individuals. The ranges of intra-tooth variation in *Camelops* are consistently higher, suggesting a more seasonally varied diet. A browsing habit with a high proportion of seasonally available halophytic C_4 species would produce an isotopic pattern with higher seasonal variability in $\delta^{13}C$ values.

The high range of $\delta^{18}O$ values in modern seasonal precipitation (Friedman et al., 2002b) makes distinction of secular or seasonal trends in ^{18}O difficult for any single individual. In general, $\delta^{18}O$ values of precipitation are higher in the summer because of ^{18}O enrichment through evaporation (Dansgaard, 1964). In the Basin and Range, summer $\delta^{18}O$ values are additionally higher because the dominant source of summer precipitation, the summer monsoon, originates in the ^{18}O-enriched Gulf of California (Friedman et al., 2002a). Over seasonal timescales, $\delta^{13}C$ and $\delta^{18}O$ values should covary: an increase in warm-season grasses should correspond to an increase in temperature. In the taxa

analyzed in this study that do show demonstrable correlation, $\delta^{13}C$ values vary inversely with $\delta^{18}O$ values, which is contrary to the expected pattern. *Atriplex* is a preferred winter browse plant for modern rangeland herbivores (Monzigo, 1987; Tipton, 1994) and livestock (Blaisdell and Holmgren, 1984; Cook and Harris, 1968). Increased winter consumption of nondeciduous browse such as *Atriplex* may have produced the inverse relationship between $\delta^{13}C$ and $\delta^{18}O$ exhibited by *Mammuthus*, *Equus*, *Bison*, and *Camelops*. The amplitude and pattern of seasonality is strongest in *Camelops*, which I interpret consumed the highest proportion of *Atriplex*.

Implications for Interpretation of Isotopic Data

This study underscores the importance of correlating isotopic data with independent records of paleovegetation. Isotopic values from tooth enamel have been used to reconstruct changes in vegetation through time. Studies of this type often use $\delta^{13}C$ values from grazers to approximate the percent C_4 grass on the landscape, and assume passive recording of the naturally-occurring abundance of C_3 and C_4 grasses. These results demonstrate that isotopic values indicative of C_4 plants may not always correlate to the grass functional type, depending on the feeding habits of the animal. Reconstructions of vegetation in the Mojave Desert and other arid regions should approach interpretation of tooth enamel isotopic values with caution, and consider both the abundance of drought-tolerant C_4 shrubs and the feeding habits of the animal.

High intra-tooth variability is also documented here for the browser *Camelops*. While this provides high-resolution paleobiological information, it calls into question the use of bulk tooth enamel samples, rather than a mean of values mineralized over the course of

one or several years. Interpretation of vegetation regimes from bulk isotopic sampling alone should consider potential intra-tooth variability as a significant source of error or bias. Intratooth samples provide high-resolution data of subannual variation in vegetation and potentially in climate; mean values calculated from intratooth samples provide a more accurate representation of the vegetation consumed by an individual.

CHAPTER 6

SUMMARY

This study uses stable isotopic methods to reconstruct the paleoecology and resource partitioning of megafauna in southern Nevada at the LGM and during the LGM-late glacial transition. Radiocarbon data are suspect, but the dates obtained confirm stratigraphic placement of the spring mound fossils in the LGM and late glacial intervals. These dates corroborate the hypothesis that these fossils accumulated over several thousand years during the LGM and late glacial time. High variability in $\delta^{18}O$ values further suggests that individual animals preserved at the site lived during different time intervals.

Resource partitioning between Late Pleistocene herbivores is demonstrated here between grazer taxa and one browsing taxon. Potential resource partitioning between obligate grazers (*Bison*) and facultative grazers (*Equus* and possibly *Mammuthus*) is demonstrated isotopically through small amounts of seasonal $\delta^{13}C$ variation in *Equus* coupled with more positive mean $\delta^{13}C$ values than the naturally-occurring proportion of C_3 and C_4 grasses would predict. Results indicate that *Camelops* ingested the highest proportion of C_4 plants, interpreted as a preference for browsing on the C_4 shrub *Atriplex*. Vegetation records indicate the presence of *Atriplex*; studies of modern camels indicate a strong preference for this plant, here discernible in fossil taxa as well.

The results of this study highlight the importance of detailed knowledge of the diets and feeding preferences of modern herbivores in reconstructions of the paleodiet of extinct animals. Isotopic values of herbivore tooth enamel are traditionally interpreted with respect to end-member plant functional types. Here, the C_4 isotopic signal may come from multiple plant functional types; the dietary preferences of each animal provide a basis for interpretation of isotopic data from herbivore tooth enamel. The selective feeding habits of some animals, such as the preferential grazer *Bison*, permit the naturally-occurring abundance of C_4 grasses to be passively recorded in *Bison* teeth. This provides a basis for evaluation of enrichment of C_4 plants in the diets of other herbivores, which may be interpreted as an indication of feeding on non-grass C_4 plants. Furthermore, selective or preferential herbivory on specific plants may enhance the isotopic signal of diet preserved in mammalian tooth enamel, depending on the feeding habits of the animal. This may affect interpretations of paleovegetation using herbivore tooth enamel alone.

The identification of the isotopic signature of *Atriplex*, in conjunction with its association with arid, alkaline growing conditions, combine into an isotopically distinct paleoenvironmental indicator with many potential applications. In arid environments too dry and too cold to support C_4 grasses, the presence of *Atriplex* may be discerned through isotopic analyses; in areas with a low proportion of C_4 grasses, such as southern Nevada during the LGM, careful use of isotopic analysis in conjunction with herbivore feeding habits may be used to demonstrate the presence of *Atriplex* and associated alkali desert scrub vegetation. Several avenues of future research are possible using this proxy: in paleobiological dietary reconstructions, vegetation reconstructions using tooth enamel

isotopic values, and as potential paleoenvironmental indicators of soil chemistry, aridity, and other variables.

APPENDIX 1

STABLE ISOTOPE DATA

Sample	Dist. from occlusal surface (mm)	$\delta^{13}C$ VPDB (‰)	$\delta^{18}O$ VPDB (‰)	$\delta^{18}O$ VSMOW (‰)
MAM 1-01	0	-8.92	-11.86	18.64
MAM 1-02	5	-7.97	-14.45	15.97
MAM 1-03	10	-8.17	-14.59	15.82
MAM 1-04	15	-7.41	-13.92	16.52
MAM 1-05	20	-7.44	-14.40	16.02
MAM 1-06	25	-7.33	-14.44	15.98
MAM 1-07	30	-7.02	-13.88	16.56
MAM 1-08	35	-7.53	-14.22	16.21
MAM 1-09	40	-7.11	-13.91	16.53
MAM 1-10	45	-7.57	-14.52	15.89
MAM 1-11	50	-7.50	-13.78	16.66
MAM 1-12	55	-7.69	-13.47	16.98
MAM 1-13	65	-6.88	-13.86	16.58
MAM 1-14	70	-8.08	-13.36	17.09
MAM 1-15	75	-8.29	-13.81	16.63
MAM 1-16	80	-8.97	-14.02	16.41
MAM 1-17	85	-8.70	-13.37	17.08
MAM 1-18	90	-8.55	-15.07	15.33
MAM 1-19	95	-9.46	-13.62	16.82
MAM 1-20	100	-8.95	-14.47	15.95
MAM 1-21	105	-8.49	-14.20	16.23
MAM 2-01	5	-7.92	-15.05	15.35
MAM 2-02	10	-8.10	-16.09	14.27
MAM 2-03	15	-8.49	-15.14	15.25
MAM 2-04	20	-7.98	-14.50	15.91
MAM 2-05	25	-7.40	-14.69	15.72
MAM 2-06	30	-7.65	-15.29	15.10
MAM 2-07	35	-8.51	-15.24	15.15
MAM 2-08	40	-8.73	-14.14	16.28
MAM 2-09	45	-8.39	-14.92	15.49
MAM 2-10	50	-8.93	-14.80	15.61

Sample	Dist. from occlusal surface (mm)	$\delta^{13}C$ VPDB (‰)	$\delta^{18}O$ VPDB (‰)	$\delta^{18}O$ VSMOW (‰)
MAM 2-11	55	-8.41	-14.07	16.35
MAM 2-12	60	-7.84	-14.26	16.16
MAM 2-13	65	-7.93	-13.19	17.26
MAM 2-14	70	-7.53	-13.92	16.51
MAM 2-15	75	-7.91	-13.07	17.38
MAM 2-16	80	-8.13	-12.98	17.48
MAM 2-17	85	-7.91	-13.45	16.99
MAM 2-18	90	-8.03	-12.66	17.81
MAM 2-19	95	-7.34	-14.60	15.81
MAM 3-01	5	-9.09	-14.01	16.42
MAM 3-02	10	-9.05	-14.83	15.57
MAM 3-03	15	-8.55	-14.28	16.14
MAM 3-04	20	-9.03	-13.68	16.76
MAM 3-05	25	-8.52	-14.51	15.90
MAM 3-06	30	-8.47	-15.29	15.10
MAM 3-07	35	-8.06	-14.44	15.98
MAM 3-08	40	-7.98	-15.02	15.38
MAM 3-09	45	-8.51	-14.74	15.67
MAM 3-10	50	-8.30	-14.14	16.28
MAM 3-11	55	-7.70	-15.17	15.22
MAM 3-12	60	-7.38	-14.35	16.06
MAM 3-13	65	-7.20	-14.50	15.92
MAM 3-14	70	-7.42	-14.45	15.96
MAM 3-15	75	-8.08	-14.52	15.90
MAM 3-16	80	-7.86	-14.20	16.22
MAM 3-17	85	-7.59	-14.16	16.26
MAM 3-18	90	-8.13	-14.11	16.31
MAM 3-19	95	-7.20	-14.53	15.88
MAM 3-20	100	-7.87	-14.52	15.89
MAM 3-21	105	-7.86	-13.81	16.63
MAM 4-01	10	-9.62	-15.00	15.40
MAM 4-02	15	-9.07	-14.76	15.64
MAM 4-03	20	-9.10	-15.82	14.55
MAM 4-04	25	-9.27	-16.03	14.33
MAM 4-05	30	-9.42	-15.28	15.11
MAM 4-06	35	-9.44	-15.27	15.11
MAM 4-07	40	-9.38	-15.82	14.55
MAM 4-08	45	-9.09	-14.80	15.60
MAM 4-09	50	-8.86	-14.30	16.11
MAM 4-10	55	-8.77	-16.50	13.85
MAM 4-11	60	-9.26	-15.89	14.48
MAM 4-12	65	-9.28	-14.91	15.49
MAM 4-13	70	-9.07	-14.98	15.42

Sample	Dist. from occlusal surface (mm)	$\delta^{13}C$ VPDB (‰)	$\delta^{18}O$ VPDB (‰)	$\delta^{18}O$ VSMOW (‰)
MAM 4-14	75	-9.36	-14.11	16.31
MAM 4-15	80	-9.02	-15.25	15.14
MAM 4-16	85	-9.40	-15.48	14.90
MAM 4-17	90	-8.94	-14.76	15.65
MAM 4-18	95	-9.32	-16.12	14.24
MAM 4-19	100	-9.06	-15.09	15.30
MAM 4-20	105	-9.16	-15.57	14.81
MAM 4-21	110	-8.94	-15.54	14.84
MAM 4-22	115	-9.15	-15.82	14.55
MAM 5-01	5	-9.10	-13.68	16.75
MAM 5-02	10	-9.27	-13.34	17.11
MAM 5-03	15	-8.77	-14.11	16.31
MAM 5-04	20	-8.99	-13.43	17.01
MAM 5-05	25	-9.16	-12.59	17.88
MAM 5-06	30	-8.94	-14.57	15.84
MAM 5-07	35	-7.76	-13.94	16.49
MAM 5-08	40	-8.70	-13.78	16.66
MAM 5-09	45	-9.14	-13.40	17.05
MAM 5-10	50	-9.13	-13.70	16.73
MAM 5-11	55	-8.53	-14.53	15.88
MAM 5-12	60	-9.21	-14.22	16.20
MAM 5-13	65	-8.35	-14.54	15.88
MAM 5-14	70	-8.93	-15.20	15.19
MAM 5-15	75	-7.95	-14.65	15.77
MAM 5-16	80	-9.16	-15.60	14.78
MAM 5-17	85	-9.40	-14.01	16.42
EQS 1-01	3	-7.75	-12.78	17.69
EQS 1-02	6	-7.96	-12.22	18.26
EQS 1-03	9	-8.05	-11.83	18.67
EQS 1-04	12	-7.78	-11.90	18.60
EQS 1-05	15	-8.25	-11.63	18.87
EQS 1-06	18	-8.07	-11.44	19.07
EQS 1-07	21	-8.07	-11.11	19.41
EQS 1-08	24	-8.03	-10.81	19.72
EQS 1-09	27	-7.95	-10.96	19.56
EQS 1-10	30	-7.84	-10.88	19.65
EQS 1-11	33	-7.80	-10.81	19.72
EQS 1-12	36	-7.93	-10.92	19.60
EQS 1-13	39	-6.86	-10.78	19.75
EQS 1-14	42	-7.34	-11.80	18.70
EQS 1-15	45	-8.08	-10.52	20.02
EQS 1-16	48	-6.04	-11.70	18.81
EQS 2-01	3	-8.49	-11.04	19.48

Sample	Dist. from occlusal surface (mm)	$\delta^{13}C$ VPDB (‰)	$\delta^{18}O$ VPDB (‰)	$\delta^{18}O$ VSMOW (‰)
EQS 2-02	6	-8.31	-11.31	19.20
EQS 2-03	9	-8.13	-11.59	18.92
EQS 2-04	12	-7.72	-11.36	19.15
EQS 2-05	15	-7.54	-11.51	18.99
EQS 2-06	18	-7.38	-11.80	18.70
EQS 2-07	21	-7.36	-11.79	18.71
EQS 2-08	24	-7.75	-11.49	19.02
EQS 2-09	27	-7.84	-11.71	18.79
EQS 2-10	30	-8.43	-11.35	19.16
EQS 2-11	33	-8.88	-9.99	20.57
EQS 2-12	36	-9.33	-9.47	21.10
EQS 2-13	39	-9.32	-8.96	21.63
EQS 2-14	42	-8.28	-10.21	20.34
EQS 2-15	45	-7.53	-11.77	18.73
EQS 2-16	48	-7.65	-12.34	18.14
EQS 2-17	51	-8.65	-10.50	20.04
EQS 3-01	3	-8.38	-10.31	20.24
EQS 3-02	6	-8.52	-10.58	19.96
EQS 3-03	9	-9.19	-10.17	20.38
EQS 3-04	12	-9.39	-9.90	20.66
EQS 3-05	15	-9.36	-9.94	20.62
EQS 3-06	18	-9.23	-10.09	20.46
EQS 3-07	21	-9.18	-9.95	20.60
EQS 3-08	24	-9.04	-10.26	20.29
EQS 3-09	27	-8.96	-9.96	20.59
EQS 3-10	30	-9.20	-9.57	21.00
EQS 3-11	33	-9.19	-9.26	21.31
EQS 3-12	36	-9.10	-9.02	21.56
EQS 3-13	39	-8.80	-9.49	21.08
EQS 3-14	42	-8.33	-9.57	21.00
EQS 3-15	45	-8.50	-9.24	21.34
EQS 3-16	48	-9.03	-10.06	20.49
EQS 3-17	51	-8.64	-10.67	19.86
EQS 3-18	54	-8.56	-11.32	19.20
EQS 3-19	57	-8.44	-11.31	19.20
EQS 3-20	60	-8.64	-11.14	19.38
EQS 3-21	63	-8.43	-10.19	20.35
EQS 3-22	66	-8.12	-10.70	19.83
EQS 3-23	69	-8.81	-10.16	20.39
EQS 3-24	72	-8.84	-9.14	21.44
EQS 4-01	3	-7.44	-11.99	18.50
EQS 4-02	6	-7.19	-12.33	18.15
EQS 4-03	9	-7.11	-12.52	17.96

Sample	Dist. from occlusal surface (mm)	$\delta^{13}C$ VPDB (‰)	$\delta^{18}O$ VPDB (‰)	$\delta^{18}O$ VSMOW (‰)
EQS 4-04	12	-7.23	-12.15	18.34
EQS 4-05	15	-7.38	-12.04	18.45
EQS 4-06	18	-7.62	-11.64	18.86
EQS 4-07	21	-8.00	-11.72	18.78
EQS 4-08	24	-8.40	-11.27	19.25
EQS 4-09	27	-8.01	-11.46	19.05
EQS 4-10	30	-8.49	-11.04	19.48
EQS 4-11	33	-8.12	-11.19	19.33
EQS 4-12	36	-7.23	-11.08	19.44
EQS 4-13	39	-6.28	-10.83	19.70
EQS 4-14	42	-5.84	-11.05	19.47
EQS 4-15	45	-6.87	-12.65	19.62
EQS 4-16	48	-6.92	-12.79	17.68
EQS 4-17	51	-7.38	-12.29	18.19
EQS 4-18	54	-8.01	-10.67	19.86
EQS 5-01	2	-7.84	-11.19	19.33
EQS 5-02	4.5	-8.04	-11.49	19.02
EQS 5-03	6.5	-8.22	-11.31	19.20
EQS 5-04	8.5	-8.59	-11.24	19.28
EQS 5-05	10	-8.71	-10.64	19.89
EQS 5-06	12	-8.91	-10.70	19.84
EQS 5-07	14	-8.97	-10.55	19.99
EQS 5-08	16	-9.25	-10.17	20.38
EQS 5-09	18	-9.49	-10.85	19.68
EQS 5-10	20	-9.43	-10.79	19.74
EQS 5-11	22	-8.59	-11.10	19.42
EQS 5-12	24.5	-8.59	-11.71	18.79
EQS 5-13	26.5	-8.66	-12.87	17.59
EQS 5-14	29	-8.50	-11.48	19.03
EQS 5-15	31	-7.83	-10.41	20.14
BIS 1-01	3	-8.78	-9.95	20.60
BIS 1-02	6	-9.16	-10.45	20.09
BIS 1-03	9	-9.14	-13.19	17.27
BIS 1-04	12	-8.78	-12.84	17.63
BIS 1-05	15	-9.02	-11.38	19.13
BIS 1-06	18	-9.44	-10.07	20.48
BIS 1-07	21	-9.20	-11.13	19.40
BIS 1-08	24	-8.92	-10.58	19.95
BIS 1-09	27	-9.42	-13.73	16.70
BIS 1-10	30	-9.16	-10.59	19.95
BIS 1-11	33	-9.02	-10.72	19.81
BIS 1-12	36	-9.13	-10.87	19.66
BIS 1-13	39	-9.30	-9.72	20.84

Sample	Dist. from occlusal surface (mm)	$\delta^{13}C$ VPDB (‰)	$\delta^{18}O$ VPDB (‰)	$\delta^{18}O$ VSMOW (‰)
BIS 1-14	42	-9.11	-10.26	20.28
BIS 1-15	45	-8.95	-11.62	18.88
BIS 1-16	48	-8.18	-11.54	18.97
BIS 1-17	51	-8.28	-11.06	19.46
BIS 1-18	54	-7.99	-10.59	19.94
BIS 2-01	0	-10.82	-8.89	21.70
BIS 2-02	2.5	-9.99	-7.89	22.73
BIS 2-03	5	-10.82	-10.27	20.28
BIS 2-04	7.5	-10.75	-12.05	18.44
BIS 2-05	10	-10.55	-11.45	19.06
BIS 2-06	12.5	-10.38	-12.85	17.62
BIS 2-07	15	-10.12	-13.15	17.31
BIS 2-08	17.5	-10.15	-13.81	16.63
BIS 2-09	20	-9.83	-13.27	17.19
BIS 2-10	22.5	-9.67	-14.33	16.09
BIS 2-11	25	-9.17	-14.11	16.32
BIS 2-12	27.5	-9.68	-15.01	15.39
BIS 2-13	30	-9.16	-14.59	15.82
BIS 2-14	32.5	-9.68	-14.80	15.61
BIS 2-15	35	-9.60	-14.30	16.12
BIS 2-16	37.5	-9.57	-12.16	18.33
BIS 3-01	1	-10.03	-11.78	18.72
BIS 3-02	3	-9.60	-12.17	18.32
BIS 3-03	5	-9.43	-13.06	17.40
BIS 3-04	7	-9.12	-12.68	17.79
BIS 3-05	9	-8.79	-13.29	17.17
BIS 3-06	11	-8.57	-13.63	16.82
BIS 3-07	13	-8.36	-13.80	16.64
BIS 3-08	15	-7.96	-14.16	16.27
BIS 3-09	17	-7.78	-14.15	16.28
BIS 3-10	19	-7.97	-13.94	16.49
BIS 3-11	21	-7.95	-14.31	16.12
BIS 3-12	23	-7.96	-14.59	15.82
BIS 3-13	25	-8.07	-14.90	15.51
BIS 3-14	26.5	-8.03	-14.80	15.61
BIS 3-15	28	-7.88	-14.29	16.13
BIS 4-01	1	-6.67	-14.09	16.34
BIS 4-02	3.5	-6.79	-14.73	15.68
BIS 4-03	6	-5.88	-14.96	15.44
BIS 4-04	8.5	-6.11	-15.68	14.70
BIS 4-05	11	-5.90	-15.92	14.45
BIS 4-06	13.5	-5.63	-15.74	14.64
BIS 4-07	16	-5.76	-15.94	14.43

Sample	Dist. from occlusal surface (mm)	$\delta^{13}C$ VPDB (‰)	$\delta^{18}O$ VPDB (‰)	$\delta^{18}O$ VSMOW (‰)
BIS 4-08	18.5	-5.40	-15.50	14.89
BIS 4-09	21	-6.04	-15.62	14.77
BIS 4-10	23.5	-6.56	-15.45	14.94
BIS 4-11	26	-6.49	-15.25	15.14
BIS 4-12	28.5	-6.03	-15.01	15.39
BIS 4-13	31	-5.59	-15.37	15.02
BIS 4-14	33.5	-5.45	-15.85	14.53
BIS 4-15	36	-5.21	-16.22	14.14
BIS 5-01	0	-11.57	-10.00	20.56
BIS 5-02	3	-11.24	-10.91	19.62
BIS 5-03	5	-11.13	-10.83	19.70
BIS 5-04	7.5	-10.94	-11.28	19.23
BIS 5-05	10	-10.52	-11.22	19.30
BIS 5-06	12.5	-10.47	-12.76	17.71
BIS 5-07	15	-10.12	-13.16	17.30
BIS 5-08	17.5	-10.18	-13.08	17.38
BIS 5-09	20	-9.96	-14.25	16.17
BIS 5-10	22.5	-9.80	-14.45	15.97
BIS 5-11	25	-9.67	-15.33	15.07
BIS 5-12	27.5	-9.54	-14.92	15.48
BIS 5-13	30	-9.47	-15.20	15.19
BIS 5-14	32.5	-9.64	-14.64	15.78
BIS 5-15	35	-9.51	-14.45	15.96
BIS 5-16	37.5	-9.69	-13.23	17.23
CAM 1-01	2.5	-6.01	-13.42	17.02
CAM 1-02	5	-6.95	-12.38	18.10
CAM 1-03	7.5	-7.28	-11.66	18.84
CAM 1-04	10	-7.55	-11.63	18.88
CAM 1-05	12.5	-7.87	-11.51	19.00
CAM 1-06	15	-7.94	-11.27	19.25
CAM 1-07	17.5	-7.87	-11.28	19.23
CAM 1-08	20	-7.45	-11.48	19.03
CAM 1-09	22.5	-6.32	-12.37	18.11
CAM 1-10	25	-5.01	-13.45	17.00
CAM 1-11	27.5	-4.92	-14.62	15.79
CAM 1-12	30	-4.94	-14.57	15.84
CAM 1-13	32.5	-5.00	-14.23	16.19
CAM 1-14	35	-5.92	-12.81	17.65
CAM 1-15	37.5	-6.21	-11.41	19.11
CAM 2-01	2	-3.45	-11.17	19.35
CAM 2-02	4	-3.71	-9.97	20.58
CAM 2-03	6	-4.57	-9.88	20.68
CAM 2-04	8	-5.68	-9.65	20.92

Sample	Dist. from occlusal surface (mm)	$\delta^{13}C$ VPDB (‰)	$\delta^{18}O$ VPDB (‰)	$\delta^{18}O$ VSMOW (‰)
CAM 2-05	10	-6.57	-10.06	20.49
CAM 2-06	12	-7.21	-9.88	20.68
CAM 2-07	15	-6.86	-10.41	20.14
CAM 2-08	17	-6.84	-10.24	20.31
CAM 2-09	19	-4.88	-9.85	20.71
CAM 2-10	21	-3.61	-9.46	21.11
CAM 2-11	23	-4.26	-11.19	19.33
CAM 2-12	25	-4.93	-11.98	18.51
CAM 2-13	27	-5.44	-11.27	19.25
CAM 3-01	0	-6.27	-12.67	17.80
CAM 3-02	3	-6.25	-13.45	17.00
CAM 3-03	6	-6.33	-13.60	16.85
CAM 3-04	9	-6.44	-13.92	16.51
CAM 3-05	12	-6.84	-13.94	16.50
CAM 3-06	15	-7.45	-12.78	17.69
CAM 3-07	18	-7.77	-11.56	18.94
CAM 3-08	21	-7.74	-10.41	20.13
CAM 3-09	24	-7.66	-10.17	20.37
CAM 3-10	27	-7.32	-10.00	20.56
CAM 3-11	30	-6.29	-11.61	18.89
CAM 3-12	33	-5.33	-12.87	17.59
CAM 3-13	36	-5.17	-14.36	16.05
CAM 3-14	39	-5.78	-14.68	15.73
CAM 3-15	42	-6.53	-14.11	16.31
CAM 3-16	45	-7.11	-13.24	17.21
CAM 3-17	48	-7.33	-10.86	19.67
CAM 3-18	51	-7.34	-9.96	20.59
CAM 3-19	54	-6.91	-11.09	19.43
CAM 3-20	57	-6.22	-13.52	16.92
CAM 4-01	2.5	-4.28	-10.96	19.56
CAM 4-02	5	-5.39	-11.81	18.69
CAM 4-03	7.5	-6.05	-11.76	18.73
CAM 4-04	10	-6.12	-11.79	18.71
CAM 4-05	12.5	-5.91	-11.03	19.49
CAM 4-06	15	-6.00	-10.75	19.78
CAM 4-07	17.5	-6.59	-10.40	20.14
CAM 4-08	20	-7.10	-10.18	20.37
CAM 4-09	22.5	-7.57	-10.17	20.38
CAM 4-10	25	-7.94	-9.81	20.75
CAM 4-11	27.5	-7.31	-9.66	20.90
CAM 4-12	30	-5.75	-9.68	20.88
CAM 4-13	32.5	-3.51	-9.22	21.36
CAM 4-14	35	-3.16	-10.59	19.95

Sample	Dist. from occlusal surface (mm)	$\delta^{13}C$ VPDB (‰)	$\delta^{18}O$ VPDB (‰)	$\delta^{18}O$ VSMOW (‰)
CAM 4-15	37.5	-4.05	-11.94	18.55
CAM 4-16	40	-5.49	-10.96	19.56
CAM 5-01	3	-9.55	-9.01	21.58
CAM 5-02	6	-9.37	-9.67	20.89
CAM 5-03	9	-9.41	-10.82	19.71
CAM 5-04	12	-9.34	-11.22	19.30
CAM 5-05	15	-9.21	-11.81	18.69
CAM 5-06	18	-9.37	-11.42	19.09
CAM 5-07	21	-9.35	-11.11	19.41
CAM 5-08	24	-9.26	-10.73	19.81
CAM 5-09	27	-9.24	-10.16	20.39
CAM 5-10	30	-8.91	-10.16	20.39
CAM 5-11	33	-8.05	-10.92	19.61
CAM 5-12	36	-7.74	-11.01	19.51
CAM 5-13	39	-7.52	-11.21	19.31
CAM 5-14	42	-7.20	-11.46	19.05
CAM 5-15	45	-7.30	-11.86	18.64
CAM 5-16	48	-7.37	-12.53	17.95
CAM 5-17	51	-7.37	-12.94	17.53
CAM 5-18	54	-7.36	-12.56	17.91

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