Quaternary International 217 (2010) 43–52

Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Isotopes reveal limited effects of middle Pleistocene climate change on the ecology of mid-sized mammals

Robert S. Feranec [a,*], Elizabeth A. Hadly [b], Adina Paytan [c]

[a] New York State Museum, 3140 Cultural Education Center, Albany, NY 12230, USA
[b] Department of Biology, 371 Serra Mall, Stanford University, Stanford, CA 94305-5020, USA
[c] Institute of Marine Science, University of California Santa Cruz, Santa Cruz, CA 95064, USA

ARTICLE INFO

Article history:
Available online 7 August 2009

ABSTRACT

To better understand how past climatic change influenced mammalian communities, we used fossils from the Pit Locality of Porcupine Cave, to evaluate how two taxa responded to climatic events spanning two glacial–interglacial transitions of the middle Pleistocene in Colorado. We analyzed the isotopes of carbon, oxygen and strontium in 84 specimens of rabbits and marmots to infer (1) if feeding and habitat preferences differed across glacial–interglacial transitions, and (2) whether these taxa responded similarly and synchronously to climatic events. Our results showed no significant differences in any of the isotopic values within taxa across levels. Stable carbon isotope values revealed a C_3-dominated environment around Porcupine Cave during the middle Pleistocene, similar to what is present around the cave today. Oxygen isotopes did not change significantly across levels suggesting consistent water sources over time and preventing any correlation to the Marine Isotope Stages. Marmots did show significantly more positive oxygen isotope values than rabbits over most of the Pit levels likely indicative of hibernation. Lack of significant change in Sr isotopes indicates similarity in habitat range through time, or homogenization of landscape Sr values due to atmospheric inputs. These results suggest that middle Pleistocene climatic change had a negligible effect on the ecology of the sampled individuals around Porcupine Cave. The effects of climate on mammals are complex and these results cannot be extrapolated globally; research is needed to differentiate how global climate change affects mammals in different regions and of different life history to provide insight into how current global warming will affect extant species.

1. Introduction

Understanding the response of mammals to climate change is becoming increasingly important due to current global warming trends and the forecast of even greater climatic changes in the next few hundred years (Houghton et al., 2001; National Assessment Synthesis Team, 2001; Reilly et al., 2001; Wigley and Raper, 2001). Climate can have profound effects on mammals across spatial and temporal scales (Blois and Hadly, 2009). For example, short-term variation in the environment may lead to adjustments in individual behavior, movement patterns or access to resources in the environment, while large-scale environmental variation can induce changes to population size and the geographic range of species. One way to understand how climate change affects mammals is to explore how mammals responded to climatic changes of the past. Recognizing how species have reacted to climate change may also permit a better understanding of how ecosystems are assembled and how different species will interact in the future.

The fossil deposits of the Pit Locality in Porcupine Cave, South Park, Colorado, provide a unique opportunity to study the effects of Pleistocene climatic change on mammals. The deposits span two glacial–interglacial cycles, are likely older than 780 ka (probably corresponding to Marine Isotope Stages 21–22), and contain abundant taxa and specimens (Bell and Barnosky, 2000; Barnosky, 2004; Barnosky and Bell, 2004). Several taxa persist through these glacial–interglacial transitions, permitting a comparison of the ecology of the same taxa in different climatic periods (glacials vs. interglacials) and the ecologies of different taxa within the same climatic period.

Ratios of stable isotopes obtained from the tissues of ancient mammalian fossils have become useful for inferring ecological information in mammal taxa. Stable carbon isotopes of mammal tooth enamel have been shown to be useful in determining

---

* Corresponding author. Tel.: +1 518 474 5819; fax: +1 518 486 2034.
E-mail addresses: rferanec@mail.nysed.gov (R.S. Feranec), hadly@stanford.edu (E.A. Hadly), apaytan@ucsc.edu (A. Paytan).

1040-6182/$ – see front matter © 2009 Elsevier Ltd and INQUA. All rights reserved.
doi:10.1016/j.quaint.2009.07.018

paleodiets (Katzenberg, 1989; Quade et al., 1992; Bocherens et al., 1994; MacFadden and Cerling, 1996; Cerling et al., 1997; Cerling et al., 1998; Koch, 1998; Koch et al., 1998; MacFadden et al., 1999; Sponheimer et al., 1999; Bocherens, 2003; Kohn et al., 2005), while stable oxygen isotopes provide information about the source of ingested waters as well as physiological influences on body water (Land et al., 1980; Longinelli, 1984; Luz et al., 1984; Koch et al., 1989; Bryant and Froelich, 1995; Bryant et al., 1996; Fricke and O'Neil, 1996; Kohn, 1996; Kohn et al., 1996, 1998; Sponheimer and Lee-Thorp, 1999). Strontium isotopes present data on migration, home range use, and geographic source of a fossil deposit (Ezzo et al., 1997; Hoppe et al., 1999; English et al., 2001; Porder et al., 2003; Hodell et al., 2004; Reynolds et al., 2005; Feranec, 2007). In this study, we have analyzed the isotopes of carbon, oxygen, and strontium to get a better understanding of the effects of climate change (specifically food and water resources and habitat range) on different mid-sized (~1500 g) mammal taxa. Due to their abundance in the Pit Locality deposits, their similar body sizes, and relatively similar ecologies, we concentrated our analyses on two mid-sized mammals: rabbits (Leporinae) and marmots (*Marmota* sp.).

This study is an extension of the previous analysis by Feranec (2004), which focused solely on examining carbon and oxygen isotope changes in *Marmota* from the Pit. While this study uses the previous study's *Marmota* data set, the examination of an additional taxon (i.e., Leporinae) and an additional isotopic system (i.e., Sr), allows us to investigate additional aspects of ecology (e.g., home range use), extend comparisons further back in time, and compare and contrast results between taxa. For the present study we investigated (1) whether there were significant ecological changes, identified by changes in isotopic values, within these two taxa across the middle Pleistocene glacial–interglacial cycles in Colorado; and, (2) whether the two taxa responded similarly to the middle Pleistocene climate changes in Colorado. We expected that the middle Pleistocene glacial–interglacial changes will affect the ecology of the analyzed taxa similarly. We predict that both carbon and oxygen isotope values will increase during interglacials and decrease during glacials in response to the warmer and cooler temperatures. Data from this study would permit a better understanding of the effects of climate changes on the ecology of mid-sized mammals.

2. Background

2.1. Carbon isotopes

Animals reflect the carbon isotope value of their food in their tissues (DeNiro and Epstein, 1978a; Vogel, 1978; Tieszen et al., 1979). Carbon isotope values are useful for understanding animal diet because the different photosynthetic pathways used by plants, C_3, C_4, and Crassulacean Acid Metabolism (CAM), impart different $^{13}C/^{12}C$ ratios to plant tissues. C_3 plants (e.g., trees, shrubs, and grasses in regions with cool growing seasons) are relatively enriched in the light carbon isotope (^{12}C) and have a mean $\delta^{13}C$ value of −27.0‰, typically ranging from −22‰ to −35‰ (O'Leary, 1988; Farquhar et al., 1989; Ehleringer et al., 1991; Ehleringer and Monson, 1993). C_4 plants (e.g., warm-growing season grasses and sedges) are relatively enriched in the heavy carbon isotope (^{13}C). These plants have a mean $\delta^{13}C$ value of −13.0‰ and generally range from −9‰ to −19‰ (O'Leary, 1988; Farquhar et al., 1989; Ehleringer et al., 1991; Ehleringer and Monson, 1993). The third pathway, Crassulacean Acid Metabolism (CAM), is typical in succulents (e.g., cacti) and may yield values that range between C_3 and C_4 plants (O'Leary, 1988; Farquhar et al., 1989; Ehleringer et al., 1991; Ehleringer and Monson, 1993). Based on our understanding of the growth requirements and distribution of CAM plants and the feeding habits of the mammals investigated (Nowak, 1999), it is assumed that the taxa in this study did not consume CAM plants as a significant part of their diet, and the isotopic effects of CAM photosynthesis are not considered further for our study.

Studies using differences in the carbon isotope values from mammals generally focus on communities containing a mixture of C_3 and C_4 plants, which enables taxa to be distinguished based on the predominant forage included in their diet (DeNiro and Epstein, 1978b; Vogel, 1978; Tieszen, 1994; MacFadden and Cerling, 1996; Cerling et al., 1998; Koch, 1998; Kohn et al., 2005). However, Porcupine Cave is situated at high elevation in a dry montane plateau (>2900 m) and the vegetation in the vicinity of Porcupine Cave today is dominated by C_3 plants (Sage et al., 1999; Cooper, 2004). Based on the elevation and climate conditions in the area, we expect that the vegetation during the middle Pleistocene near Porcupine Cave also was dominated by C_3 plants. Thus, our analyses were focused on detecting variation in the $\delta^{13}C$ values derived from C_3 plants. Because different processes, such as light intensity, temperature, and water stress can produce variation in the $\delta^{13}C$ value of C_3 plants (Farquhar et al., 1989; O'Leary et al., 1992; Ehleringer and Monson, 1993; Koch, 1998; Heaton, 1999; Bocherens, 2003) these analyses should reveal climate related changes in plant physiology. Specifically, C_3 plants typically have more negative values in closed, forested habitats; while more open, drier habitats are characterized by more positive isotope values (Farquhar et al., 1989; van der Merwe and Medina, 1991; O'Leary et al., 1992; Ehleringer and Monson, 1993; Koch, 1998; Heaton, 1999; Bocherens, 2003). Recent studies have used these habitat differences to highlight the use of carbon isotopes in determining resource partitioning of herbivores in C_3-dominated environments (Quade and Cerling, 1995; Bocherens et al., 1997; Cerling et al., 1999; Bocherens et al., 2001; Bocherens, 2003; Drucker et al., 2003; Cerling et al., 2004; MacFadden and Higgins, 2004; Feranec and MacFadden, 2006) and we continue in this vein here.

2.2. Carbon isotopes in mid-sized mammals

Mid-sized herbivores reflect the carbon isotope values of plants they ingested, but the $\delta^{13}C$ value of the tooth enamel is further enriched by a consistent amount, about +12.8‰ ± 0.7‰ for animals of this size (Passey et al., 2005). Setting the fractionation from plant material to tooth enamel at +12.8‰, extant taxa that feed solely on C_3 plants will display enamel carbon isotope values between −22.2‰ and −9.2‰, while taxa that feed only on C_4 plants have enamel $\delta^{13}C$ values around 0.0‰ (Koch, 1998; Passey et al., 2005). The carbon in plants and ultimately enamel is derived from the atmosphere, and the $\delta^{13}C$ value of CO_2 in the atmosphere has decreased about −1.5‰, from −6.5‰ to about −8.0‰, due to fossil fuel burning over the last 200 years (Friedli et al., 1986; Marino and McElroy, 1991; Marino et al., 1992). A diet of pure C_3 plants would range from −20.7‰ to −7.7‰ in the enamel of Pleistocene herbivores. Isotope values more positive than −7.7‰ would imply incorporation of either C_4 or CAM plants into the diet. The −7.7‰ $\delta^{13}C$ value as indicative of C_4 or CAM plant incorporation into an herbivore diet is a very conservative estimate as previous studies on modern and fossil herbivores show that pure C_3 feeders rarely have values more positive than −8.0‰ (MacFadden and Cerling, 1996; Cerling et al., 1999; Cerling et al., 2004).

2.3. Oxygen isotopes in mammals

The oxygen isotopes in mammal tooth enamel depend on the isotopic composition of ingested water, the consistent fractionation of oxygen isotopes between body water and the tooth enamel, and the metabolism of the particular animal (Land et al., 1980;

Longinelli, 1984; Luz et al., 1984; Luz and Kolodny, 1985; Koch et al., 1989; Kohn, 1996; Kohn et al., 1996; Kohn et al., 1998). Mammals ingest water from two sources, either through drinking or from the food they consume. The isotopic signature of surface waters is affected by temperature and humidity, such that δ^{18}O values are more positive where and when it is warmer and more negative where and when it is colder (Dansgaard et al., 1982; Rozanski et al., 1992; Fricke and O'Neil, 1996; Kohn and Welker, 2005). Water in plant leaves which the studied taxa consume also varies and is typically more positive than the local surface waters due to evapotranspiration. Leaves enriched in δ^{18}O values are more pronounced in warmer and more arid conditions (Ometto et al., 2005; Yakir et al., 1990; Yakir, 1992). Thus, animals that occupy open habitats, or obtain most of their water from consumed vegetation, would be expected to ingest more positive δ^{18}O as compared to taxa foraging in a cooler, moister forested habitat, or those that regularly drink surface waters.

Body size and metabolism can also influence the oxygen isotope composition in tooth enamel. Large mammals that are obligate drinkers tend to have lower metabolisms and are most likely to track δ^{18}O values of ingested waters (Longinelli, 1984; Luz et al., 1984; Bryant and Froelich, 1995). The δ^{18}O values of smaller mammals are likely to be influenced to a larger degree by diet and physiology as well as ingested water (Bryant and Froelich, 1995; Kohn et al., 1996; Kohn et al., 1998; Podlesak et al., 2008).

2.4. *Strontium isotopes in mammals*

Bedrock geology and atmospheric inputs are the ultimate determinants of ^{87}Sr/^{86}Sr values of the landscape (Faure, 1986; Capo et al., 1998). Mammals will integrate the landscape ^{87}Sr/^{86}Sr ratios into their body tissues (Faure, 1986), over the area where they foraged (Porder et al., 2003). Different rock types display different ^{87}Sr/^{86}Sr values (Faure, 1986), and the local bedrock geology around Porcupine Cave is heterogeneous (Fig. 1; Raynolds, 2004). Therefore, if ^{87}Sr/^{86}Sr differences are observed across time or within taxa at Porcupine Cave, it might suggest variation in the use of particular areas or habitats in the past (Porder et al., 2003).

3. Materials and methods

3.1. *Porcupine Cave, the Pit Locality, and fossil material*

Porcupine Cave is located in central Colorado in the southwestern corner of Park County (38 43′ 45″N, 105 51′ 41″W) at 2900 m above sea level (Fig. 1; Barnosky et al., 2004a). The cave is host to over twenty major vertebrate fossil localities, and may be the largest collection of vertebrate fossils of middle Pleistocene age in North America (Barnosky et al., 2004a). Taphonomically, this material was likely gathered by woodrats (*Neotoma* sp.) and to a lesser degree carnivores (Barnosky et al., 2004a).

One of the major vertebrate localities in Porcupine Cave is the Pit Locality. Over 60 species are recognized from the Pit including at least 57 mammal species (Barnosky, 2004). This locality contains over 7000 specimens from at least 1500 individuals (Barnosky, 2004). Fourteen layers have been identified in the Pit deposits, and these strata have been placed into five glacial or interglacial episodes. Layers 11–14, 6–9, and 1–3 are placed within interglacial episodes, while layers 10 and 4–5 into glacial episodes (Bell and Barnosky, 2000; Barnosky, 2004). These strata are likely more than 780,000 years old (Barnosky and Bell, 2004). The stratified nature of the deposits and the large number of available specimens (NISP > 7200; MNI > 1500) make the Pit Locality ideal for studying the effects of climate on the ecology of mammals.

In this study we focus on two taxa, marmots (*Marmota* sp.; Polly, 2003) and rabbits (Leporinae). These taxa were chosen because the Pit Locality deposits contain abundant specimens. Further, these taxa have a similar body size and ecological requirements (Frase and Hoffman, 1980; Nowak, 1999). We attempted to sample teeth that mineralized after weaning. For marmots we concentrated on premolars and the third molar, although first and second molars were sampled when necessary. For the rabbits, we sampled the hypselodont (ever-growing) cheek teeth. The sampled rabbit teeth did not have any taxonomically diagnostic characteristics and it was not possible to identify the rabbit teeth to the species level. To reduce the possibility of sampling multiple species, we made attempts to sample only those teeth that were similar in size and appearance (large size). Even so, since different rabbit species have similar ecologies, we predict that climate change would affect all taxa in the same way.

3.2. *Isotope sample processing*

The method for sampling tooth enamel for C- and O-isotopes followed MacFadden and Cerling (1996) and Koch et al. (1997). Sampling involved removing all dentine from a piece of mammal tooth using a 0.5 mm or 0.3 mm carbide drill bit and a variable speed Dremel™ rotary tool. The remaining pristine enamel was then crushed to a powder using a mortar and pestle. Preparation of samples for analysis involved treating the enamel powder samples with 30% hydrogen peroxide for 24 h to remove organics. The hydrogen peroxide was then decanted and the enamel powder was washed with distilled water, and soaked in 0.1 N acetic acid for another 24 h to remove any adsorbed diagenetic carbonate. The following day the acetic acid was decanted and the enamel powder was washed with distilled water and air dried (under a laminar flow hood).

After treatment, Leporinae samples were analyzed using an ISOCARB automated carbonate preparation system attached to a Micromass Optima gas source mass spectrometer within the Geology Department at the University of California, Davis. About 1 mg samples were dissolved in 100% phosphoric acid at 90 °C to create CO_2. All samples were corrected to NBS-19 and UCD-SM92 a calibrated in-house marble standard. Precision for the Leporinae samples was 0.1‰ for both carbon and oxygen. *Marmota* samples were analyzed using similar equipment at the Department of Earth and Ocean Sciences, University of California, Santa Cruz. NBS-19 was used at both labs ensuring compatibility of the data. Precision for the marmot samples was also 0.1‰ for both carbon and oxygen. Isotopic results in this study are expressed in the standard δ-notation: $X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where X is the δ^{13}C or δ^{18}O value, and $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{18}\text{O}/{}^{16}\text{O}$, respectively. The δ^{13}C and δ^{18}O values are reported relative to the V-PDB standard.

For Sr-isotope analysis, a subset ($N = 30$) of the Leporinae samples that were prepared and analyzed for C- and O-isotopes was used. These samples were prepared for ^{87}Sr/^{86}Sr analysis following the protocol of Porder et al. (2003). After the C- and O-isotope treatment, the samples were dissolved in 2.5 N HCl. Sr was separated out of the sample using cation exchange techniques. ^{87}Sr/^{86}Sr ratios were analyzed using a Finnegan MAT 262 thermal ionization mass spectrometer (TIMS) in the Department of Geological and Environmental Science at Stanford University. The mean ^{87}Sr/^{86}Sr value for NBS-987 was 0.71030 ± 0.00005 (2σ), and data were normalized to ^{86}Sr/^{88}Sr = 0.1194 during the analyses. Sample data were corrected to the accepted ^{87}Sr/^{86}Sr value of 0.710235 for NBS-987. Due to the amount of sample powder available, it was not possible to obtain ^{87}Sr/^{86}Sr values for the marmot specimens.

Statistical analyses consisted of: (1) comparison within taxa across levels; (2) comparison within taxa with levels grouped into

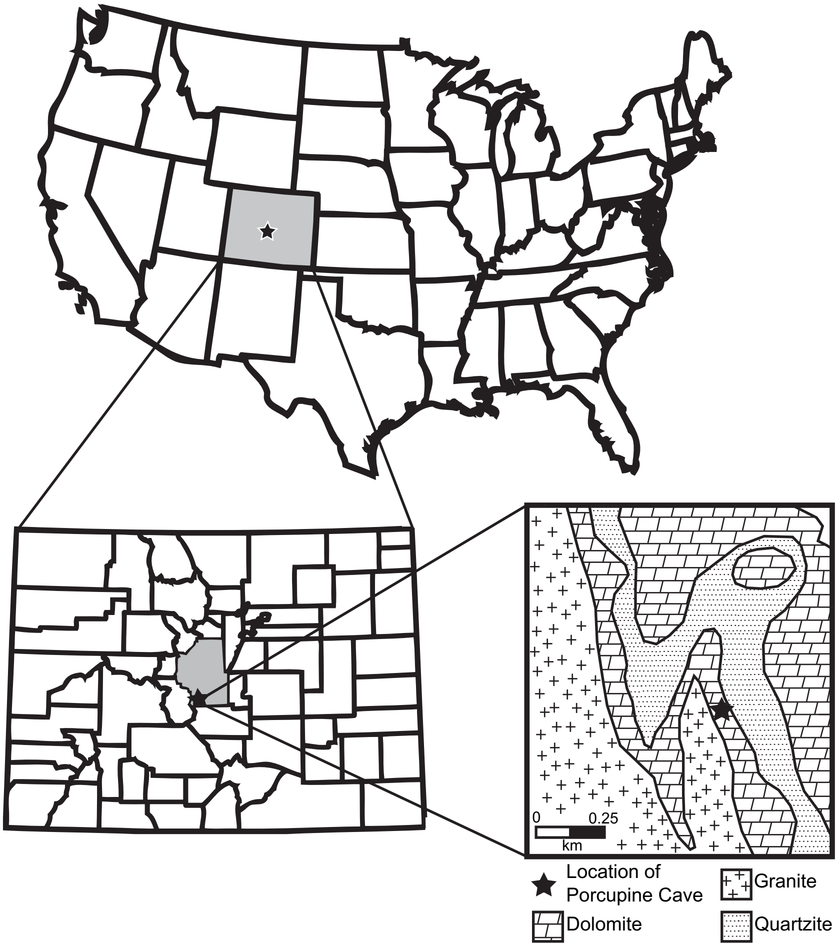

Fig. 1. Map of the location and the bedrock geology in the vicinity around Porcupine Cave.

glacial–interglacial intervals; (3) comparison between taxa within specific levels; and (4) comparison between taxa combining all levels. Mean differences in isotope values within and between taxa, as well as across levels were compared by ANOVA and post hoc Tukey's HSD tests. The post hoc Tukey's HSD tests are similar to *t*-tests but take into account multiple comparisons (using *t*-tests did not change the results obtained). Statistical analyses were run on JMP IN 5 For Students, with significance set at $p < 0.05$.

4. Results

In general few differences were observed between taxa or between levels in isotopic signatures. No significant differences within taxa were observed across levels for carbon (Leporinae, $p < 0.08$; *Marmota* sp., $p < 0.07$) and oxygen (Leporinae, $p < 0.70$; *Marmota* sp., $p < 0.31$) isotope values (Fig. 2, Tables 1 and 2). However, when data were pooled into glacial–interglacial levels, a significant difference in δ^{13}C values in marmots ($p < 0.01$) between pooled interglacial levels 6–7 and pooled interglacial levels 1–3 is seen. Over time, there is a correlation in marmots ($r^2 = 0.51$, $p < 0.0004$) for increasing δ^{13}C values, but this does not fluctuate with glacial cooling and interglacial warming.

Comparison of the isotopic values between taxa within levels did show some significant differences. For carbon isotopes, rabbits were significantly different from marmots only at level 5 ($p < 0.03$), with marmots (mean $= -10.3$‰) having a significantly more positive mean than rabbits (mean $= -11.3$‰). For oxygen, rabbits and marmots were significantly different at level 1 ($p < 0.04$), level 2 ($p < 0.01$), level 3 ($p < 0.001$), level 5 ($p < 0.02$), and level 7 ($p < 0.03$). In levels that had significant differences in δ^{18}O, marmots were always significantly more positive than the rabbits (Table 1). The oxygen isotope differences were more pronounced when combining the results from all levels (Fig. 3), showing that marmots had more positive δ^{18}O values than rabbits. A significant difference between rabbits and marmots emerged when comparing the ranges of δ^{18}O values across all levels ($p < 0.01$) between taxa, while no difference was observed in δ^{13}C values ($p < 0.10$). However, differences in the ranges of both carbon and oxygen isotope values between rabbits and marmots were significantly correlated to sample size (carbon, $r^2 = 0.26$, $p < 0.04$; oxygen, $r^2 = 0.66$, $p < 0.0001$).

Analysis of ^{87}Sr/^{86}Sr values within the rabbits showed no significant differences across levels ($p < 0.14$), or when levels were grouped into glacial to interglacial intervals ($p < 0.11$) (Fig. 2). ^{87}Sr/^{86}Sr values were not obtained for the marmot specimens due to the small amount of sample powder available.

5. Discussion

The lack of significant variation across all levels of the Pit Locality in δ^{13}C, δ^{18}O, or ^{87}Sr/^{86}Sr values within marmots or within rabbits implies that the climate change associated with the two

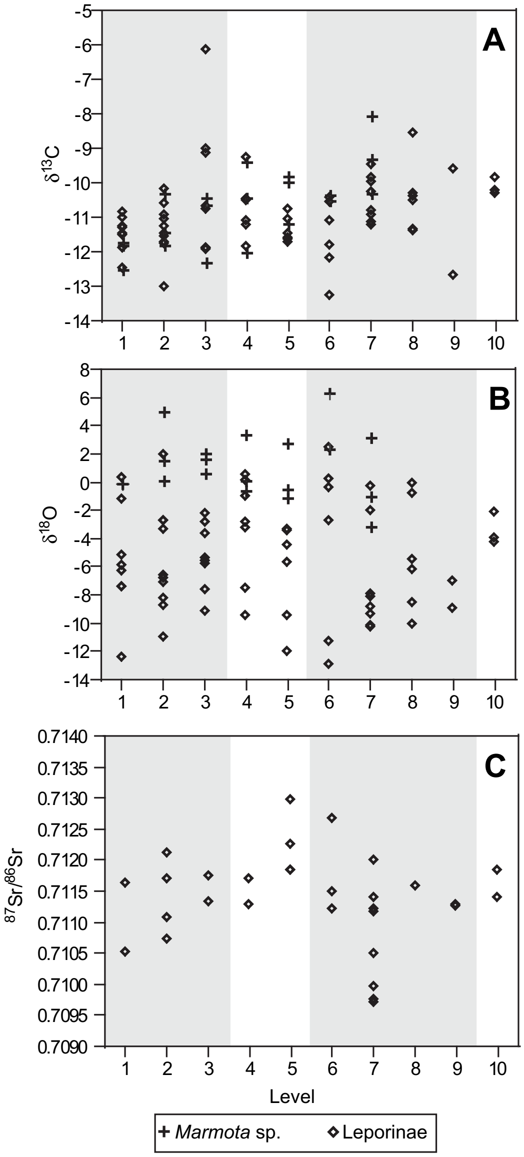

Fig. 2. Plot of carbon (A), oxygen (B), and strontium (C) isotope values for marmots (plus signs) and rabbits (diamonds) for each level in the Pit Locality of Porcupine Cave. Gray background, interglacial levels; white background, glacial levels.

inferred glacial–interglacial cycles represented in the Pit Locality deposits had a limited effect on these taxa. Carbon isotope values show that the ecosystem around Porcupine Cave during the middle Pleistocene was dominated by C_3 plants and that this food resource was available to the mammals sampled here. This is not surprising given the altitude of the cave (2900 m), and the C_3-dominated modern flora (Cooper, 2004). Although some C_4 plants are present on the landscape today and were probably also present in the past (e.g., *Distichlis stricta*), they do not at present and did not in the past form a dominant part of the diets of rabbits and marmots. Our data suggest that marmots and rabbits did not significantly change the food resources ingested as the climate changed. Further, while the sedimentology of the Pit Locality deposits suggests particular climatic regimes (Bell and Barnosky, 2000; Barnosky, 2004), our carbon isotope data do not reveal any significant turnover in vegetation (at least the vegetation consumed by rabbits and marmots) through time in the area around Porcupine Cave. These data are not necessarily inconsistent. One hypothesis is that these populations of rabbits and marmots were selecting particular types of food and were not consuming a generalist diet representative of the landscape as a whole. Additionally, although the isotopic values do not reveal any changes in resource use over the two glacial–interglacial cycles, this does not mean that the rabbit or marmot populations were not impacted by the climatic events. Rabbits and marmots may have responded to climate fluctuations by adjusting population sizes rather than changing food preferences. Indeed there is clear evidence of a change in relative abundance for these taxa in the Pit Locality (Barnosky, 2004). However, the changes in relative abundances for these taxa do not appear to be specifically associated with the glacial–interglacial cycles (Barnosky, 2004). Thus, we conclude that despite considerable climatic fluctuations due to glacial–interglacial cycles neither the food resources nor other ecological parameters that could affect carbon isotope values (e.g., water stress) in the sampled mammals were significantly altered.

Lack of significant differences in oxygen isotopes values within each taxon across levels also implies that climate change had limited effect on the water resources for rabbits and marmots over the time spanned by the Pit Locality deposits. However, our data do demonstrate a large range of oxygen isotope values (15.4‰ for rabbits, 9.4‰ for marmots), which may obscure potential changes in the landscape and suggest that several water sources are available locally and used by these mammals. This range is particularly high for these taxa compared to the range seen in mammals from nearby fossil sites (i.e., *Geomys* and *Thomomys* at SAM Cave and Hansen Bluff; Rogers and Wang, 2002). There are

Table 1
Carbon and oxygen isotope values for sampled rabbits and marmots by level within the Pit Locality from Porcupine Cave, South Park, Colorado. Bold values, interglacial levels; italics values, glacial levels.

Level	Leporinae							*Marmota* sp.						
	N	Mean δ^{13}C (‰)	δ^{13} C SD (‰)	δ^{13}C Range (‰)	Mean δ^{18}O (‰)	δ^{18}O SD (‰)	δ^{18} O Range (‰)	*N*	Mean δ^{13}C (‰)	δ^{13}C SD (‰)	δ^{13} C Range (‰)	Mean δ^{18}O (‰)	δ^{18} O SD (‰)	δ^{18} O Range (‰)
Total	64	−10.9	1.1	7.1	−5.3	3.8	15.4	20	−10.7	1.1	4.4	1.1	2.3	9.4
1	**8**	**−11.4**	**0.5**	**2.3**	**−5.6**	**4.0**	**12.8**	**3**	**−12.0**	**0.4**	**0.8**	**−0.1**	**0.0**	**0.0**
2	**10**	**−11.3**	**0.8**	**2.9**	**−5.5**	**3.8**	**8.9**	**3**	**−11.2**	**0.8**	**1.5**	**2.2**	**2.5**	**4.9**
3	**8**	**−10.1**	**2.0**	**5.8**	**−5.2**	**2.4**	**6.9**	**3**	**−11.1**	**1.0**	**1.9**	**1.4**	**0.7**	**1.4**
4	*7*	*−10.7*	*0.8*	*2.6*	*−3.2*	*3.8*	*10.0*	*3*	*−10.6*	*1.3*	*2.6*	*0.9*	*2.1*	*3.9*
5	*6*	*−11.3*	*0.4*	*1.0*	*−6.3*	*3.6*	*8.7*	*3*	*−10.3*	*0.8*	*1.4*	*0.4*	*2.1*	*3.9*
6	**6**	**−11.5**	**1.1**	**2.8**	**−4.0**	**6.4**	**15.4**	**2**	**−10.4**	**0.1**	**0.2**	**4.3**	**2.8**	**4.0**
7	**8**	**−10.4**	**0.7**	**1.8**	**−7.1**	**3.8**	**10.0**	**3**	**−9.2**	**1.1**	**2.2**	**−0.3**	**3.2**	**6.3**
8	**6**	**−10.4**	**1.0**	**2.9**	**−5.1**	**4.0**	**9.9**	–	–	–	–	–	–	–
9	**2**	**−11.1**	**2.2**	**3.0**	**−7.9**	**1.3**	**1.9**	–	–	–	–	–	–	–
10	*3*	*−10.1*	*0.2*	*0.5*	*−3.4*	*1.2*	*2.1*	–	–	–	–	–	–	–

Table 2
Strontium isotope values for rabbits by level within the Pit Locality from Porcupine, Cave, South Park, Colorado. Bold values, interglacial levels; italic values, glacial levels.

Leporinae			
Level	*N*	Mean $^{87}Sr/^{86}Sr$	$^{87}Sr/^{86}Sr$ SD
Total	30	0.71139	0.00076
1	**2**	**0.71110**	**0.00080**
2	**4**	**0.71142**	**0.00062**
3	**2**	**0.71156**	**0.00030**
4	*2*	*0.71151*	*0.00028*
5	*4*	*0.71225*	*0.00053*
6	**3**	**0.71181**	**0.00077**
7	**8**	**0.71073**	**0.00086**
8	**1**	**0.71161**	–
9	**2**	**0.71129**	**0.00001**
10	*2*	*0.71163*	*0.00031*

a number of possible reasons for the large range of oxygen isotope values observed in our results. First, the deposit may represent a time-averaged assemblage spanning possibly thousands to tens of thousands of years; thus the range of values may represent the range of $\delta^{18}O$ values occurring in that area over the time frame represented in each layer. Second, the range in values could represent ingestion of water from many different sources. Both marmots and rabbits are capable of ingesting significant quantities of water from surface water sources (e.g., stream water) and/or from vegetation (e.g., plant leaves, seeds, fruits). If these taxa regularly use a variety of sources to obtain necessary water, then the observed range in $\delta^{18}O$ values is possible as it represents variable contribution from these sources to the individuals sampled. Third, the sampled teeth in rabbits were the hypselodont (ever-growing) cheek teeth. The sampled portion of the teeth then may represent different times of the year, which combined with the fact that this is an assemblage deposit, would result in a higher range of values due to seasonal variability in water resources. Finally, the sampled teeth in rabbits were only identifiable to the Leporinae and not to particular species. While we tried to sample only larger individuals, it is possible that the sample represents different species that ingested water from numerous sources creating the wide range in $\delta^{18}O$ values. Because of the large range observed in *Marmota* sp. from Porcupine Cave, we suspect that the large range observed in the rabbits is more likely due to the depositional history of fossils in the Pit (i.e., time-averaging) and/or the rabbits sampling a variety of water sources rather than sampling different species or different times of the year in their hypselodont teeth.

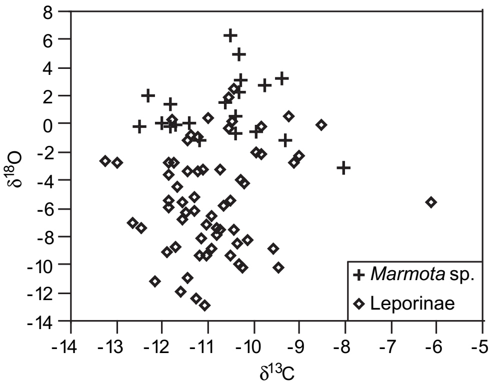

Fig. 3. Stable carbon and oxygen isotope results for all sampled marmots (plus signs) and rabbits (diamonds) in this study.

Although comparison within taxa across levels did not reveal any significant isotopic differences, we did find significant differences in the $\delta^{18}O$ values between the two taxa with marmots always being significantly more positive than rabbits. These results across all levels reveal either that marmots and rabbits consistently used different water resources, or that physiologically the two taxa were significantly different from one another. One reason for the observed differences could be physiological rather than ecological; *Marmota* sp. hibernates (Frase and Hoffman, 1980; Nowak, 1999), while rabbits do not (Nowak, 1999). The more positive $\delta^{18}O$ values in marmot tooth enamel could be attributed to low water turnover (Kohn et al., 1996) because during hibernation it is not possible for this taxon to drink from sources that have lower oxygen isotope values (e.g., stream water). This is similar to what is observed in drought tolerant species that drink only rarely (Kohn et al., 1996). Another reason for the observed $\delta^{18}O$ differences could be related to hibernation but not physiology. Because hibernation occurs during winter, marmots would be ingesting surface waters with more positive $\delta^{18}O$ values during the spring and summer and not ingesting the more negative $\delta^{18}O$ values of winter water resulting in higher annually averaged values.

Rogers and Wang (2002) revealed oxygen isotope differences in mammal teeth related to glacial–interglacial changes at the nearby localities SAM Cave and Hansen Bluff. These authors further suggested that their technique and the analysis of $\delta^{18}O$ values in mammals would be ideal for Porcupine Cave and would provide a better age control as well as provide information on the nature of the deposits and whether they represented actual “disharmonious assemblages” or merely a mixed assemblage due to taphonomic processes at the site (Rogers and Wang, 2002). Unfortunately, the lack of significant differences in $\delta^{18}O$ values across levels within each of the two taxa studied here precludes the possibility of using this technique to provide better age control and correlate the Pit Locality levels to the Marine Isotope Stages. In comparing the results we obtained from the Pit Locality to the results from SAM Cave and Hansen Bluff, we noticed some interesting similarities and differences. The mean $\delta^{18}O$ values for the Porcupine Cave Pit Locality rabbits are comparable to the values observed for SAM Cave/Hansen Bluff pocket gophers, although the range of values at the Pit Locality is much greater. The two SAM Cave/Hansen Bluff pocket gopher species show similar $\delta^{13}C$ values, but different $\delta^{18}O$ values. At SAM Cave/Hansen Bluff, *Geomys* has more positive $\delta^{18}O$ values than *Thomomys*. As with the observed differences between rabbits and marmots at the Pit Locality, we suspect this difference in isotopic values might relate to physiological differences or differences in water use between the different taxa.

Whereas other studies have been able to use $^{87}Sr/^{86}Sr$ values to discuss topics such as provenance of individuals, home range use, and migration (Ezzo et al., 1997; Hoppe et al., 1999; English et al., 2001; Hodell et al., 2004; Reynolds et al., 2005; Feranec, 2007), the lack of significant differences across levels in the Sr-isotope values of rabbits in the Pit Locality makes it impossible to assess such things. The lack of significant differences in $^{87}Sr/^{86}Sr$ values can result from either the rabbits using the same home range over the time period represented in the Pit Locality deposits, or from homogeneous values on the landscape. Although the bedrock geology around the cave is heterogeneous (Fig. 1; Raynolds, 2004), other factors (e.g., atmospheric input of Sr) can impact the strontium isotope levels creating more homogeneous values than expected from bedrock imprint (Faure, 1986; Capo et al., 1998). Future studies, such as the examination of biologically available (i.e., plant, soil) ^{87}Sr/^{86}Sr values, may help to distinguish between these two possibilities.

These results along with the results of previous studies (Bell and Barnosky, 2000; Barnosky et al., 2004b), indicates no clear relationship between climatic change and either ecological or morphological change in mid-sized mammals at Porcupine Cave during the middle Pleistocene. Studies that have shown ecological fluctuations with climatic change have primarily revealed changes in phenology, changes in population size, and geographic shifts in mammals associated with global warming (McCarty, 2001; Walther et al., 2002; Parmesan, 2006). Additionally, Martinez-Meyer et al. (2004) showed that some mammals have maintained particular ecological niches through intervals of climate change by shifting their geographic range. Phenological changes, changes in population size, and niche tracking would not necessarily result in isotopic changes in the tissues of mammals. However, while it does appear from relative taxon abundance data that certain taxa are favored at certain times around Porcupine Cave (Barnosky, 2004), the relation between change in abundance and climatic change is not apparent. It could be that climate change has not dramatically altered the ecological niches and requirements of these taxa or that these taxa have adapted to the climatic changes observed on glacial–interglacial timescales. It is also possible that the isotope variables that we have measured are not sensitive to these sorts of changes. From our data it appears that it is “business as usual” for rabbits and marmots in dealing with the glacial–interglacial changes at Porcupine Cave during the middle Pleistocene.

6. Conclusions

Isotope data from rabbits and marmots living in the mid Pleistocene show no significant differences within taxa across any of the Pit Locality levels suggesting that there was limited effect of climate change on the ecology of rabbit and marmot individuals living around Porcupine Cave during the middle Pleistocene. Carbon isotope data suggest a C$_3$-dominated environment, as is found in the area today. Because of the lack of significant differences across levels in oxygen isotope values, it was not possible to provide a more precise correlation of the Pit Locality levels to the Marine Isotope Stages, nor was it possible to better understand the nature of how the Pit assemblage formed or how it corresponds to data from other sites in the area. Significant differences were observed in oxygen isotope values between rabbits and marmots and are indicative of physiological differences, likely due to the fact that marmots typically hibernate a significant part of the year and rabbits do not. The lack of significant differences in strontium isotope values implies similar home range use in these taxa over time, or homogenization of strontium isotope values on the landscape resulting from input from allocthenous sources, such as the atmosphere. This study highlights the fact that climate and climatic change has variable effects on mammals and these effects may also vary spatially. While climate may have a large effect on certain taxa in certain places it may not have a demonstrable effect elsewhere. To tease apart how, where, and when climate effects mammals more research is needed.

Acknowledgements

We are honored to know Dr. Lundelius, his works, especially those on Pleistocene small mammals, and be able to participate in this issue of Quaternary International on behalf of him. We would like to thank A. Barnosky and P. Holroyd for permission to sample the specimens. C. Quang helped sample and prepare the rabbit specimens. We thank D. Winter of U.C. Davis and P. Koch of U.C. Santa Cruz for the carbon and oxygen results. We further thank S. Porder, J. Wooden, B. Weigand, and B. Ito for help with strontium sample preparation and analysis. This research was supported by grant EAR-0310337 from the National Science Foundation to E.A. Hadly and A. Paytan. Further support was provided by the Department of Integrative Biology at U.C. Berkeley, the Society of Vertebrate Paleontology and the N.Y. State Museum to R.S. Feranec. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

Appendix 1. Taxon, level, UCMP catalog number, isotope sample number, element, and carbon, oxygen and strontium isotope values for all specimens analyzed within this study

Taxon	Level	UCMP number	Sample no.	Element	δ^{13}C (‰)	δ^{18}O (‰)	^{87}SR/^{86}Sr
Leporinae	1	164061	RSF03268	Cheek tooth	−11.0	0.5	–
Leporinae	1	164064	RSF03255	Cheek tooth	−10.8	−7.3	–
Leporinae	1	164065	RSF03247	Cheek tooth	−11.2	−12.3	0.71166
Leporinae	1	164067	RSF03219	Cheek tooth	−12.4	−7.4	–
Leporinae	1	164104	RSF03279	Cheek tooth	−11.8	−5.8	0.71053
Leporinae	1	164121	RSF03269	Cheek tooth	−11.5	−6.2	–
Leporinae	1	164125	RSF03257	Cheek tooth	−11.4	−1.1	–
Leporinae	1	164129	RSF03265	Cheek tooth	−11.3	−5.1	–
Leporinae	2	164170	RSF03266	Cheek tooth	−11.5	−6.7	–
Leporinae	2	164171	RSF03245	Cheek tooth	−11.0	−7.1	–
Leporinae	2	164172	RSF03222	Cheek tooth	−10.9	−6.5	–
Leporinae	2	164179	RSF03278	Cheek tooth	−13.0	−2.7	0.71213
Leporinae	2	164181	RSF03280	Cheek tooth	−11.7	−8.7	0.71109
Leporinae	2	164184	RSF03270	Cheek tooth	−11.7	−2.6	–
Leporinae	2	164185	RSF03248	Cheek tooth	−11.4	−10.9	0.71172
Leporinae	2	164186	RSF03262	Cheek tooth	−10.5	2.0	0.71074
Leporinae	2	164187	RSF03260	Cheek tooth	−11.2	−3.3	–
Leporinae	2	164188	RSF03256	Cheek tooth	−10.1	−8.2	–
Leporinae	3	164305	RSF03229	Cheek tooth	−6.1	−5.5	–
Leporinae	3	164307	RSF03249	Cheek tooth	−11.8	−3.6	–
Leporinae	3	164310	RSF03246	Cheek tooth	−11.8	−5.3	–
Leporinae	3	164312	RSF03218	Cheek tooth	−11.9	−9.1	–

(continued on next page)

Appendix 1 (*continued*)

Taxon	Level	UCMP number	Sample no.	Element	δ^{13}C (‰)	δ^{18}O (‰)	^{87}SR/^{86}Sr
Leporinae	3	164315	RSF03238	Cheek tooth	−9.1	−2.7	–
Leporinae	3	164316	RSF03240	Cheek tooth	−10.7	−5.7	–
Leporinae	3	164317	RSF03242	Cheek tooth	−9.0	−2.2	0.71135
Leporinae	3	164318	RSF03239	Cheek tooth	−10.7	−7.5	0.71177
Leporinae	4	164425	RSF03271	Cheek tooth	−11.1	−3.1	–
Leporinae	4	164426	RSF03276	Cheek tooth	−10.5	−9.3	–
Leporinae	4	164429	RSF03259	Cheek tooth	−10.4	−7.5	–
Leporinae	4	164432	RSF03252	Cheek tooth	−9.2	0.6	–
Leporinae	4	164434	RSF03241	Cheek tooth	−11.2	−0.9	–
Leporinae	4	164436	RSF03216	Cheek tooth	−10.4	0.3	0.71131
Leporinae	4	164440	RSF03226	Cheek tooth	−11.8	−2.7	0.71171
Leporinae	5	164445	RSF03244	Cheek tooth	−11.0	−9.3	0.71187
Leporinae	5	164457	RSF03258	Cheek tooth	−10.7	−3.2	0.71228
Leporinae	5	164458	RSF03251	Cheek tooth	−11.6	−11.9	–
Leporinae	5	164459	RSF03235	Cheek tooth	−11.6	−5.6	–
Leporinae	5	164471	RSF03263	Cheek tooth	−11.7	−4.4	0.71299
Leporinae	5	164481	RSF03233	Cheek tooth	−11.4	−3.3	0.71185
Leporinae	6	164483	RSF03250	Cheek tooth	−10.5	−0.3	–
Leporinae	6	164488	RSF03220	Cheek tooth	−11.8	0.3	–
Leporinae	6	164506	RSF03227	Cheek tooth	−11.1	−12.8	0.71151
Leporinae	6	164511	RSF03277	Cheek tooth	−13.2	−2.6	–
Leporinae	6	164512	RSF03237	Cheek tooth	−10.4	2.5	0.71124
Leporinae	6	164515	RSF03230	Cheek tooth	−12.1	−11.2	0.71269
Leporinae	7	164517	RSF03236	Cheek tooth	−9.8	−0.2	0.71141
Leporinae	7	164524	RSF03221	Cheek tooth	−10.9	−8.8	0.70999
Leporinae	7	164525	RSF03272	Cheek tooth	−11.2	−9.3	0.70972
Leporinae	7	164526	RSF03224	Cheek tooth	−11.1	−8.1	0.70977
Leporinae	7	164528	RSF03225	Cheek tooth	−9.4	−10.2	0.71124
Leporinae	7	164529	RSF03275	Cheek tooth	−10.8	−7.8	0.71203
Leporinae	7	164535	RSF03234	Cheek tooth	−9.9	−2.0	0.71051
Leporinae	7	164536	RSF03215	Cheek tooth	−10.2	−10.1	0.71119
Leporinae	8	164558	RSF03253	Cheek tooth	−10.3	−8.5	–
Leporinae	8	164559	RSF03267	Cheek tooth	−11.4	−0.7	–
Leporinae	8	164563	RSF03223	Cheek tooth	−10.5	−5.4	–
Leporinae	8	164568	RSF03214	Cheek tooth	−11.3	−6.1	0.71161
Leporinae	8	164571	RSF03231	Cheek tooth	−10.3	−9.9	–
Leporinae	8	164572	RSF03243	Cheek tooth	−8.5	0.0	–
Leporinae	9	164593	RSF03217	Cheek tooth	−12.6	−7.0	0.71128
Leporinae	9	164594	RSF03212	Cheek tooth	−9.6	−8.9	0.7113
Leporinae	10	164576	RSF03213	Cheek tooth	−10.3	−3.9	0.71141
Leporinae	10	164582	RSF03232	Cheek tooth	−9.8	−2.0	0.71185
Leporinae	10	164588	RSF03254	Cheek tooth	−10.2	−4.2	–
Marmota sp.	1	181095	RSF001	LM1 or LM2	−11.8	−0.1	–
Marmota sp.	1	181117	RSF003	Rm1 or Rm2	−12.5	−0.1	–
Marmota sp.	1	181120	RSF002	Rm1 or Rm2	−11.7	−0.1	–
Marmota sp.	2	181176	RSF005	Rp4	−10.3	5.0	–
Marmota sp.	2	181180	RSF004	Lm1 or Lm2	−11.8	1.5	–
Marmota sp.	2	181194	RSF006	LM3	−11.4	0.1	–
Marmota sp.	3	93173	RSF008	Lm3	−12.3	2.1	–
Marmota sp.	3	181216	RSF007	LP4	−10.6	1.6	–
Marmota sp.	3	181304	RSF009	RP4	−10.4	0.7	–
Marmota sp.	4	181357	RSF012	LP4	−9.4	3.3	–
Marmota sp.	4	181403	RSF011	Lm1 or Lm2	−12.0	0.1	–
Marmota sp.	4	181476	RSF010	RP4	−10.4	−0.6	–
Marmota sp.	5	181723	RSF014	LP4	−10.0	−0.5	–
Marmota sp.	5	181764	RFS013	Lp4	−9.8	2.8	–
Marmota sp.	5	181866	RSF015	LP4	−11.2	−1.1	–
Marmota sp.	6	182040	RSF017	RP4	−10.5	6.3	–
Marmota sp.	6	182058	RSF018	RP4	−10.3	2.3	–
Marmota sp.	7	182086	RSF020	LP4	−9.3	−1.1	–
Marmota sp.	7	182088	RSF019	Lp4	−10.3	3.2	–
Marmota sp.	7	182159	RSF021	Rp4	−8.1	−3.1	–

References

Barnosky, A.D., 2004. Faunal dynamics of small mammals through the Pit sequence. In: Barnosky, A.D. (Ed.), Biodiversity Response to Climate Change in the Middle Pleistocene: the Porcupine Cave Fauna from Colorado. University of California, Berkeley, California, pp. 318–326.

Barnosky, A.D., Bell, C.J., 2004. Age and correlation of key fossil sites in Porcupine Cave. In: Barnosky, A.D. (Ed.), Biodiversity Response to Climate Change in the Middle Pleistocene: the Porcupine Cave Fauna from Colorado. University of California Press, Berkeley, California, pp. 64–73.

Barnosky, A.D., Bell, C.J., Raynolds, R.G., Taylor, L.H., 2004a. The Pleistocene fossils of Porcupine Cave, Colorado: spatial distribution and taphonomic overview. In: Barnosky, A.D. (Ed.), Biodiversity Response to Climate Change in the Middle Pleistocene: the Porcupine Cave Fauna from Colorado. University of California Press, Berkeley, California, pp. 6–26.

Barnosky, A.D., Kaplan, M.H., Carrasco, M.A., 2004b. Assessing the effect of Middle Pleistocene climate change on *Marmota* populations from the Pit locality. In: Barnosky, A.D. (Ed.), Biodiversity Response to Climate Change in the Middle Pleistocene: The Porcupine Cave Fauna from Colorado. University of California Press, Berkeley, California, pp. 332–340.

Bell, C.J., Barnosky, A.D., 2000. The microtine rodents from the Pit locality in Porcupine Cave, Park County, Colorado. Annals of Carnegie Museum 69, 93–134.

Blois, J.L., Hadly, E.A., 2009. Mammalian response to Cenozoic climatic change. Annual Review of Earth and Planetary Sciences 37, 181–208.

Bocherens, H., 2003. Isotopic biogeochemistry and the paleoecology of the mammoth steppe fauna. Deinsea 9, 57–76.

Bocherens, H., Billiou, D., Mariotti, A., Toussaint, M., Patou-Mathis, M., Bonjean, D., Otte, M., 2001. New isotopic evidence for dietary habits of Neandertals from Belgium. Journal of Human Evolution 40, 497–505.

Bocherens, H., Billiou, D., Patou-Mathis, M., Bonjean, D., Otte, M., Mariotti, A., 1997. Paleobiological implications of the isotopic signatures (^{13}C, ^{15}N) of fossil mammal collagen in Scladina Cave (Sclayn, Belgium). Quaternary Research 48, 370–380.

Bocherens, H., Fizet, M., Mariotti, A., 1994. Diet, physiology and ecology of fossil mammals as inferred from stable carbon and nitrogen isotope biogeochemistry: implications for Pleistocene bears. Palaeogeography, Palaeoclimatology, Palaeoecology 107, 213–225.

Bryant, J.D., Froelich, P.N., 1995. A model of oxygen isotope fractionation in body water of large mammals. Geochimica et Cosmochimica Acta 59, 4523–4537.

Bryant, J.D., Froelich, P.N., Showers, W.J., Genna, B.J., 1996. Biologic and climatic signals in the oxygen isotopic composition of Eocene–Oligocene equid enamel phosphate. Palaeogeography, Palaeoclimatology, Palaeoecology 126, 75–89.

Capo, R.C., Stewart, B.W., Chadwick, O.A., 1998. Strontium isotopes as tracers of ecosystem processes: theory and methods. Geoderma 82, 197–225.

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

Cerling, T.E., Harris, J.M., Leakey, M.G., 1999. Browsing and grazing in elephants: the isotope record of modern and fossil proboscideans. Oecologia 120, 364–374.

Cerling, T.E., Harris, J.M., MacFadden, B.J., 1998. Carbon isotopes, diets of North American equids, and the evolution of North American C4 grasslands. In: Griffiths, H. (Ed.), Stable Isotopes. BIOS Scientific Publishers Ltd., Oxford, pp. 363–379.

Cerling, T.E., Hart, J.A., Hart, T.B., 2004. Stable isotope ecology in the Ituri Forest. Oecologia 138, 5–12.

Cooper, D.J., 2004. The modern environment, flora, and vegetation of South Park, Colorado. In: Barnosky, A.D. (Ed.), Biodiversity Response to Climate Change in the Middle Pleistocene: the Porcupine Cave Fauna from Colorado. University of California Press, Berkeley, California, pp. 27–38.

Dansgaard, W., Clausen, H.B., Gundestrup, N., Hammer, C.U., Johnson, S.F., Kristinsdottir, P.M., Reeh, N., 1982. A new Greenland deep ice core. Science 218, 1273–1277.

DeNiro, M.J., Epstein, S., 1978a. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42, 495–506.

DeNiro, M.J., Epstein, S., 1978b. Carbon isotopic evidence for different feeding patterns in two hyrax species occupying the same habitat. Science 201, 906–908.

Drucker, D., Bocherens, H., Bridault, A., Billiou, D., 2003. Carbon and nitrogen isotopic composition of red deer (*Cervus elaphus*) collagen as a tool for tracking palaeoenvironmental change during the Late-Glacial and Early Holocene in the northern Jura (France). Palaeogeography, Palaeoclimatology, Palaeoecology 195, 375–388.

Ehleringer, J.R., Monson, R.K., 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. Annual Review of Ecology, Evolution and Systematics 24, 411–439.

Ehleringer, J.R., Sage, R.F., Flanagan, L.B., Pearcy, R.W., 1991. Climate change and the evolution of C_4 photosynthesis. Trends in Ecology and Evolution 6, 95–99.

English, N.B., Betancourt, J.L., Dean, J.S., Quade, J., 2001. Strontium isotopes reveal distant sources of architectural timber in Chaco Canyon, New Mexico. Proceedings of the National Academy of Sciences 98, 11891–11896.

Ezzo, J.A., Johnson, C.M., Price, T.D., 1997. Analytical perspectives on prehistoric migration: a case study from East-Central Arizona. Journal of Archaeological Science 24, 447–466.

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

Faure, G., 1986. Principles of Isotope Geology. Wiley & Sons Publishing, New York, 608 pp.

Feranec, R.S., 2004. Stable carbon and oxygen isotope analysis of marmot cheek teeth from the Pit Locality. In: Barnosky, A.D. (Ed.), Biodiversity Response to Climate Change in the Middle Pleistocene: the Porcupine Cave Fauna from Colorado. University of California Press, Berkeley, California, pp. 327–331.

Feranec, R.S., 2007. Determining landscape use of Holocene mammals using strontium isotopes. Oecologia 153, 943–950.

Feranec, R.S., MacFadden, B.J., 2006. Isotopic discrimination of resource partitioning among ungulates in C3-dominated communities from the Miocene of Florida and California. Paleobiology 32, 191–205.

Frase, B.A., Hoffman, R.S., 1980. *Marmota flaviventris*. Mammalian Species 135, 1–8.

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

Friedli, H., Lotscher, H., Oeschger, H., Siegenthaler, U., Stauffer, B., 1986. Ice core record of the ^{13}C/^{12}C ratio of atmospheric CO_2 in the past two centuries. Nature 324, 237–238.

Heaton, T.H.E., 1999. Spatial, species, and temporal variations in the ^{13}C/^{12}C ratios of C_3 plants: implications for paleodiet study. Journal of Archaeological Science 26, 637–649.

Hodell, D.A., Quinn, R.L., Brenner, M., Kamenov, G., 2004. Spatial variation of strontium isotopes (^{87}Sr/^{86}Sr) in the Maya region: a tool for tracking ancient human migration. Journal of Archaeological Science 31, 585–601.

Hoppe, K.A., Koch, P.L., Carlson, R.W., Webb, S.D., 1999. Tracking mammoths and mastodons: reconstruction of migratory behavior using strontium isotopes. Geology 27, 439–442.

Houghton, J.T., Ding, Y., Griggs, D.J., 2001. Climate Change 2001: the Scientific Basis. Cambridge University Press, New York.

Katzenberg, M.A., 1989. Stable isotope analysis of archaeological remains from southern Ontario. Journal of Archaeological Science 16, 319–329.

Koch, P.L., 1998. Isotopic reconstruction of past continental environments. Annual Review of Earth and Planetary Sciences 26, 573–613.

Koch, P.L., Fisher, D.C., Dettman, D., 1989. Oxygen isotope variation in the tusks of extinct proboscideans: a measure of season of death and seasonality. Geology 17, 515–519.

Koch, P.L., Hoppe, K.A., Webb, S.D., 1998. The isotopic ecology of late Pleistocene mammals in North America Part 1. Florida. Chemical Geology 152, 119–138.

Koch, P.L., Tuross, N., Fogel, M.L., 1997. The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite. Journal of Archaeological Science 24, 417–429.

Kohn, M.J., 1996. Predicting animal δ^{18}O: accounting for diet and physiological adaptation. Geochimica et Cosmochimica Acta 60, 4811–4829.

Kohn, M.J., McKay, M.P., Knight, J.L., 2005. Dining in the Pleistocene – who's on the menu? Geology 33, 649–652.

Kohn, M.J., Schoeninger, M.J., Valley, J.W., 1996. Herbivore tooth oxygen isotope compositions: effect of diet and physiology. Geochimica et Cosmochimica Acta 60, 3889–3896.

Kohn, M.J., Schoeninger, M.J., Valley, J.W., 1998. Variability in oxygen isotope compositions of herbivore teeth: reflections of seasonality or developmental physiology? Chemical Geology 152, 97–112.

Kohn, M.J., Welker, J.M., 2005. On the temperature correlation of δ^{18}O in modern precipitation. Earth and Planetary Science Letters 231, 87–96.

Land, L.S., Lundelius, E.L., Valastro, S., 1980. Isotopic ecology of deer bones. Palaeogeography, Palaeoclimatology, Palaeoecology 32, 143–151.

Longinelli, A., 1984. Oxygen isotopes in mammal bone phosphate: a new tool for paleohydrological and paleoclimatological research? Geochimica et Cosmochimica Acta 48, 385–390.

Luz, B., Kolodny, Y., 1985. Oxygen isotope variations in phosphate of biogenic apatites, IV. Mammal teeth and bones. Earth and Planetary Science Letters 75, 29–36.

Luz, B., Kolodny, Y., Horowitz, M., 1984. Fractionation of oxygen isotopes between mammalian bone-phosphate and environmental drinking water. Geochimica et Cosmochimica Acta 48, 1689–1693.

MacFadden, B.J., Cerling, T.E., 1996. Mammalian herbivore communities, ancient feeding ecology, and carbon isotopes; a 10 million-year sequence from the Neogene of Florida. Journal of Vertebrate Paleontology 16, 103–115.

MacFadden, B.J., Higgins, P., 2004. Ancient ecology of 15-million-year-old browsing mammals within C3 plant communities from Panama. Oecologia 140, 169–182.

MacFadden, B.J., Solounias, N., Cerling, T.E., 1999. Ancient diets, ecology, and extinction of 5 million-year-old horses from Florida. Science 283, 824–827.

Marino, B.D., McElroy, M.B., 1991. Isotopic composition of atmospheric CO_2 inferred from carbon in C_4 plant cellulose. Nature 349, 127–131.

Marino, B.D., McElroy, M.B., Salawitch, R.J., Spaulding, W.G., 1992. Glacial-to-interglacial variations in the carbon isotopic composition of atmospheric CO_2. Nature 357, 461–466.

Martinez-Meyer, E., Townsend, P.A., Hargrove, W.W., 2004. Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. Global Ecology and Biogeography 13, 305–314.

McCarty, J.P., 2001. Ecological consequences of recent climate change. Conservation Biology 15, 320–331.

National Assessment Synthesis Team, 2001. Climate Change Impacts on the United States: the Potential Consequences of Climate Variability and Change. Cambridge University Press, Cambridge.

Nowak, R.M., 1999. Walker's Mammals of the World. Johns Hopkins University Press, Baltimore.

O'Leary, M.H., Madhavan, S., Paneth, P., 1992. Physical and chemical basis of carbon isotope fractionation in plants. Plant, Cell and Environment 15, 1099–1104.

O'Leary, M.H., 1988. Carbon isotopes in photosynthesis. BioScience 38, 328–336.

Ometto, J.P.H., Flanagan, L.B., Martinelli, L.A., Ehleringer, J.R., 2005. Oxygen isotope ratios of waters and respired CO_2 in Amazonian forest and pasture ecosystems. Ecological Applications 15, 58–70.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution and Systematics 37, 637–669.

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

Podlesak, D.W., Torregrossa, A.-M., Ehleringer, J.R., Dearing, M.D., Passey, B.H., Cerling, T.E., 2008. Turnover of oxygen and hydrogen isotopes in the body water, hair, and enamel of a small mammal. Geochimica et Cosmochimica Acta 72, 19–35.

Polly, P.D., 2003. Paleophylogeography: the tempo of geographic differentiation in marmots (*Marmota*). Journal of Mammalogy 84, 369–384.

Porder, S.J., Paytan, A., Hadly, E.A., 2003. Mapping the origin of faunal assemblages using strontium isotopes. Paleobiology 29, 197–204.

Quade, J., Cerling, T.E., 1995. Expansion of C_4 grasses in the late Miocene of northern Pakistan: evidence form stable isotopes in paleosols. Palaeogeography, Palaeoclimatology, Palaeoecology 115, 91–116.

Quade, J., Cerling, T.E., Barry, J.C., Morgan, M.E., Pilbeam, D.R., Chivas, A.R., Lee-Thorp, J.A., van der Merwe, N.J., 1992. A 16-Ma record of paleodiet using carbon and oxygen isotopes in fossil teeth from Pakistan. Chemical Geology (Isotope Geosciences Section) 94, 183–192.

Raynolds, R.G., 2004. The geology and speleogenesis of Porcupine Cave. In: Barnosky, A.D. (Ed.), Biodiversity Response to Climate Change in the Middle Pleistocene: the Porcupine Cave Fauna from Colorado. University of California Press, Berkeley, California, pp. 51–56.

Reilly, J., Stone, P.H., Forest, C.E., Webster, M.D., Jacoby, H.D., Prinn, R.G., 2001. Uncertainty and climate change assessments. Science 293, 430–433.

Reynolds, A.C., Betancourt, J.L., Quade, J., Patchett, P.J., Dean, J.S., Stein, J., 2005. ^{87}Sr/^{86}Sr sourcing of ponderosa pine used in Anasazi great house construction at Chaco Canyon, New Mexico. Journal of Archaeological Science 32, 1061–1075.

Rogers, K.L., Wang, Y., 2002. Stable isotopes in pocket gopher teeth as evidence of a Late Matuyama climate shift in the Southern Rocky Mountains. Quaternary Research 57, 200–207.

Rozanski, K., Araguas-Araguas, L., Gonfiantini, R., 1992. Relation between long-term trends of Oxygen-18 isotope composition of precipitation and climate. Science 258, 981–985.

Sage, R.F., Wedin, D.A., Li, M., 1999. The Biogeography of C_4 Photosynthesis: Patterns and Controlling Factors. Academic Press, New York, 313–373 pp.

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

Sponheimer, M., Reed, K.E., Lee-Thorp, J.A., 1999. Combining isotopic and ecomorphological data to refine bovid paleodietary reconstruction: a case study from the Makapansgat Limeworks hominin locality. Journal of Human Evolution 36, 705–718.

Tieszen, L.L., 1994. Stable isotopes on the plains: vegetation analyses and diet determinations. In: Owsley, D.W., Jantz, R.L. (Eds.), Skeletal Biology in the Great Plains: Migration, Warfare, Health, and Subsistence. Smithsonian Institution Press, Washington D.C., pp. 261–282.

Tieszen, L.L., Hein, D., Qvortrup, S.A., Troughton, J.H., Imbamba, S.K., 1979. Use of δ^{13}C values to determine vegetation selectivity in East African herbivores. Oecologia 37, 351–359.

van der Merwe, N.A., Medina, E., 1991. The canopy effect, carbon isotope ratios and foodwebs in Amazonia. Journal of Archaeological Science 18, 249–259.

Vogel, J.C., 1978. Isotopic assessment of the dietary habits of ungulates. South African Journal of Science 74, 298–301.

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

Wigley, T.M.L., Raper, S.C.B., 2001. Interpretation of high projections for global-mean warming. Science 293, 451–454.

Yakir, D., 1992. Variations in the natural abundance of oxygen-18 and deuterium in plant carbohydrates. Plant, Cell and Environment 15, 1005–1020.

Yakir, D., DeNiro, M.J., Gat, J.R., 1990. Natural deuterium and oxygen-18 enrichment in leaf water of cotton plants grown under wet and dry conditions: evidence for water compartmentation and its dynamics. Plant, Cell and Environment 13, 49–56.