Quaternary Research 77 (2012) 408–417

Contents lists available at SciVerse ScienceDirect

Quaternary Research

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

Stable isotopes reflect the ecological stability of two high-elevation mammals from the late Quaternary of Colorado

Bryan S. McLean *, Steven D. Emslie

Department of Biology and Marine Biology, University of North Carolina Wilmington, Wilmington, NC, 28403, USA

ARTICLE INFO

Article history:
Received 26 September 2011
Available online 13 March 2012

Keywords:
Marmota flaviventris
Neotoma cinerea
Cement Creek Cave
Middle Wisconsin
Southern Rocky Mountains
Tooth enamel
$\delta^{13}C$
$\delta^{18}O$
Atmospheric CO_2

ABSTRACT

The vertebrate fossil record of Cement Creek Cave, Colorado, spans from >45,000 yr ago to the present and represents the richest stratified series of high-elevation (>2900 m) mammal remains known from the late Quaternary of North America. Stable carbon and oxygen isotope analyses of tooth enamel were used to assess potential ecological responses of two species found commonly throughout the cave, Yellow-bellied marmots (*Marmota flaviventris*) and Bushy-tailed woodrats (*Neotoma cinerea*), to late Quaternary climate and environmental changes of the Southern Rocky Mountains. Results indicate that despite such perturbations, the dietary ecologies of both species were maintained across this period. Neither taxon shifted to consuming C_4 taxa or different C_3 functional groups; similarly, no significant shifts in surface water use were detected. Variations in enamel $\delta^{13}C$ were observed, however, that represent the physiological responses of high-elevation plants to changing levels of late Quaternary atmospheric CO_2. While our findings extend both the geographic and elevational record of this plant CO_2 response, they simultaneously highlight the ecological stability of high-elevation *M. flaviventris* and *N. cinerea* during climate changes of late Quaternary magnitude.

© 2012 University of Washington. Published by Elsevier Inc. All rights reserved.

Introduction

Quaternary climate and environmental changes have affected Earth's biotas in various ways, and coherent fossil records remain essential for understanding these impacts. Cement Creek Cave (2950 m) is a limestone cave located in the Upper Gunnison Basin of southwestern Colorado that has produced the richest high-elevation mammalian fauna known from the late Pleistocene of North America, a diverse assemblage of small- and medium-sized montane taxa ranging in age from >45,000 ^{14}C yr BP to the present (Fig. 1; Emslie, 2002; S.D. Emslie et al., pers. comm., 2012). Prior to now, late Quaternary high-elevation mammal communities have remained poorly understood owing to a paucity of fossil material (Armstrong, 1972; Lundelius et al., 1983; Webb and Betancourt, 1990; Emslie, 2002). However, a deeper understanding of such communities is desirable as they are subject to unique environmental and ecological constraints and, therefore, may have responded uniquely to past climate change.

Late Quaternary environments of the Southern Rocky Mountains were characterized by changing temperatures and precipitation regimes (Barry, 1983; Thompson et al., 1993; Brugger, 2010), widespread alpine glacial activity (Richmond, 1986; Pierce, 2003; Brugger, 2007), fluctuations in treeline and formation of no-analog plant communities (Legg and Baker, 1980; Markgraf and Scott, 1981; Spaulding et al., 1983; Thompson et al., 1993; Fall, 1997; Briles et al., 2012). Many vertebrate faunas at lower elevations were also reassembled (Lundelius et al., 1983; Harris 1985; Graham et al., 1996; Stafford et al., 1999). In contrast, the small mammal community documented in Cement Creek Cave has shown remarkable continuity in composition and evenness across a range of late Pleistocene and Holocene climate changes (S.D. Emslie, pers. comm., 2012).

To better understand the mechanisms underlying this community persistence in the midst of a dynamically changing environment, we investigated the paleoecology of two species from Cement Creek Cave, Yellow-bellied marmots (*Marmota flaviventris*) and Bushy-tailed woodrats (*Neotoma cinerea*), using stable isotope analyses (SIA) of carbon and oxygen in tooth enamel. Specifically, SIA were used to reconstruct the diets and surface water use of *M. flaviventris* and *N. cinerea* across the past >45,000 yr and among three periods characterized by distinct climate regimes (middle Wisconsin, late Wisconsin, Holocene) in an effort to reveal potential ecological responses of these species. Results of these isotopic analyses are interpreted in the broader context of both global and regional paleoenvironmental and paleoecological proxy data, as well as the unique paleontological record of Cement Creek Cave.

Background

Tooth enamel biogeochemistry and paleoecological reconstruction

Fossil mammal teeth are commonly employed in paleoecological analyses as they are easily preserved, abundant in the fossil record, taxonomically distinctive, and because tooth enamel in particular consistently preserves original isotopic signatures (Wang and

* Corresponding author at: Department of Biology, University of New Mexico, Albuquerque, NM, 87131, USA. Fax: +1 505 277 0304.
E-mail address: mclean@unm.edu (B.S. McLean).

0033-5894/$ – see front matter © 2012 University of Washington. Published by Elsevier Inc. All rights reserved.
doi:10.1016/j.yqres.2012.02.001

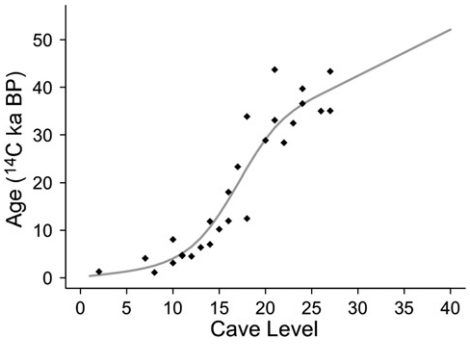

Figure 1. Accelerator mass spectrometry (AMS) radiocarbon ages obtained from fossil teeth and bone of various mammal taxa from Cement Creek Cave, Colorado (black diamonds, $N = 27$). Modeled ages for cave Levels 1–40 are plotted underneath (gray line). Cave levels are sequential 5-cm-deep excavation layers, and thus directly translatable into sedimentary depth (i.e., Level 1 = 0–5 cm of depth, and so forth. See text for additional model and excavation details).

Cerling, 1994; Koch et al., 1997). This preservation is largely due to the chemical and structural properties of enamel (>95% hydroxyapatite, highly crystalline, large crystal size), which render it less susceptible than either tooth dentin or bone (<80% hydroxyapatite, more porous, smaller crystal size) to diagenetic alteration (Land et al., 1980; Schoeninger and DeNiro, 1982; Wang and Cerling, 1994; Koch et al., 1997). Previous work has indicated that tooth enamel is capable of retaining original dietary signatures on the order of thousands (Van der Merwe, 1982; Koch et al., 1998; MacFadden et al., 1999) to millions (Quade et al., 1992; MacFadden and Cerling, 1996; Thewissen et al., 2007) of years.

In our analysis, enamel stable isotope signatures are reported following standard delta (δ) notation, where

$$\delta = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000 \quad (1)$$

and R_{sample} and $R_{standard}$ represent ratios of $^{13}C/^{12}C$ or $^{18}O/^{16}O$ in enamel samples and the Vienna Pee Dee Belemnite (VPDB) standard, respectively. Delta values are reported in parts per thousand, or per mil (‰).

Controls on carbon isotopes in bioapatite

Biogenic hydroxyapatite (bioapatite; $[Ca_{10}(PO_4)_6(OH)_2]$) has a few percent structural carbonate substitutions at both phosphate and hydroxyl sites and is thus an archive of dietary carbon inputs. Bioapatite $\delta^{13}C$ is mediated foremost by the primary producers fixing carbon in constituent ecosystems, specifically by the photosynthetic pathways they employ (C_3, C_4, CAM). Key molecular and enzymatic differences among pathways result in characteristic fractionations that render plant isotopic profiles distinguishable (O'Leary, 1981; Farquhar et al., 1989; Marshall et al., 2007).

The C_3 (Calvin) pathway is globally common among terrestrial plants and used by all trees and most shrubs, herbs and cool-season grasses. The modern flora around Cement Creek Cave is C_3-dominated. The $\delta^{13}C$ of C_3 plants is depleted, on average, by about 19‰ relative to atmospheric CO_2 (Farquhar et al., 1989; Marshall et al., 2007), resulting in median $\delta^{13}C$ values of −27‰ (range −35 to −22‰; Farquhar et al., 1989; Dawson et al., 2002; Marshall et al., 2007). The C_4 (Hatch-Slack) cycle, conversely, is employed by many warm-season and tropical grasses as well as some sedges and dicots. Relatively higher ^{13}C assimilation results in median $\delta^{13}C$ values around −14‰ for C_4 plants (range −19 to −9‰; Farquhar et al., 1989; Dawson et al., 2002; Marshall et al., 2007). The $\delta^{13}C$ values of CAM (Crassulacean Acid Metabolism) plants (a diverse array of mostly succulents) are intermediate between C_3 and C_4 plants (Marshall et al., 2007). Although *Neotoma* species are known to consume CAM plants elsewhere in the American Southwest (Vaughan, 1990), these are not thought to have contributed significantly to late Quaternary mammal diets in the Southern Rockies.

Certain environmental variables also influence $\delta^{13}C$ of plant tissues ($\delta^{13}C_{plant}$). For example, $\delta^{13}C$ of atmospheric CO_2 ($\delta^{13}C_{atm}$) contributes directly to $\delta^{13}C_{plant}$ (Farquhar et al., 1989; Marino and McElroy, 1991; Arens et al., 2000). Values of $\delta^{13}C_{atm}$ varied during the late Quaternary (Leuenberger et al., 1992; Marino et al., 1992; Sigman and Boyle, 2000) and have influenced $\delta^{13}C$ of C_3 plants for millions of years (Arens et al., 2000). Concentrations of atmospheric CO_2 (CO_{2atm}), which scaled closely with late Quaternary temperatures (Fig. 2) and continue to increase alongside them today (IPCC, 2007), also influence $\delta^{13}C$ of C_3 species by altering photosynthetic capacity (Farquhar et al., 1989; Marshall et al., 2007). Finally, certain microhabitat conditions affect $\delta^{13}C_{plant}$; lower $\delta^{13}C$ values are observed in plants growing in forested habitats ('canopy effect'; Vogel, 1978; Medina and Minchin, 1980; Farquhar et al., 1989), whereas plants growing in conditions of high irradiance, water stress, or high salinity may experience physiological responses which increase $\delta^{13}C_{plant}$ (Farquhar et al., 1989).

Mammalian bioapatite incorporates $\delta^{13}C$ of bulk diet (Ambrose and Norr, 1993), but with an enrichment due to isotopic fractionation along the cellular respiration/blood bicarbonate/structural carbonate pathway (Ambrose and Norr, 1993; Koch, 2007). These enrichments range between +9.5 and +13‰ for small to medium-sized rodents and lagomorphs in controlled trials (Ambrose and Norr, 1993; Passey et al., 2005; Sare et al., 2005). Herein, a diet-bioapatite $\delta^{13}C$ enrichment of 12.5‰ is assumed for *Marmota* and *Neotoma*, which lies slightly above experimental averages but may better reflect the dietary physiology of wild rodents (Sare et al., 2005; Koch, 2007). Feranec et al. (2010) used a similar enrichment value of +12.8‰ in their analysis of middle Pleistocene *Marmota* and Leporinae. Under this assumption, an average enamel $\delta^{13}C$ ($\delta^{13}C_{enamel}$) of −16‰ (range −22.5 to −9.5‰) or −1.5‰ (range −6.5 to +3.5‰) is expected for individuals consuming pure C_3 or C_4 diets, respectively.

Controls on oxygen isotopes in bioapatite

Oxygen in bioapatite is derived from several sources including dietary and inhaled oxygen and water vapor, with exact $\delta^{18}O$ values dependent on the isotopic composition of body water at the time of mineral precipitation (Longinelli, 1984; Luz et al., 1984; Bryant and Froelich, 1995). In terrestrial mammalian herbivores, dietary oxygen is obtained largely from surface waters used for drinking and as contained in plant forage (Bryant and Froelich, 1995; Kohn et al., 1996; Koch, 2007). Climate and geography are two primary controls on surface water $\delta^{18}O$ values (McGuire and McDonnell, 2007), and this makes

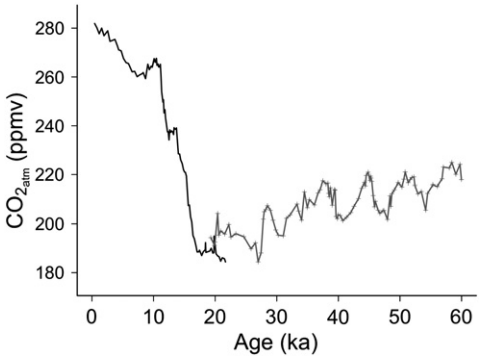

Figure 2. Atmospheric CO_2 concentrations (CO_{2atm}) over the past 60 ka as recorded in Antarctic ice. Graph is a composite of data from the Byrd (gray line; 90–20 ka; Ahn and Brook, 2008) and EPICA Dome C cores (black line; 21–0.5 ka; Monnin et al., 2001; Fluckiger et al., 2002). Byrd data are adjusted to the Greenland (GISP2) timescale as described in Ahn and Brook (2008).

isotopic analysis of mammalian bioapatite a potentially useful tool in both paleoclimatology and paleoecology (Longinelli, 1984; Luz et al., 1984; Bryant and Froelich, 1995; Fricke and O'Neil, 1996; Higgins and MacFadden, 2004).

The $\delta^{18}O$ of precipitation is more positive during warmer seasons and at lower latitudes and altitudes, while it is more negative during cooler seasons and at higher latitudes and altitudes (Yurtsever and Gat, 1981; Welker, 2000; Kohn and Welker, 2005; McGuire and McDonnell, 2007). Also, $\delta^{18}O$ of continental vapor masses and precipitation is typically lowered with distance traveled inland due to fractionation during rainout, and inland precipitation usually exhibits stronger seasonal fluctuations than in milder coastal areas (Welker, 2000; McGuire and McDonnell, 2007).

Apart from these meteoric influences, physiological and ecological characteristics of both herbivores and their plant foods are important considerations in oxygen isotopic analyses. Mammal taxa exhibit unique diet-bioapatite $\delta^{18}O$ fractionations that can be partially ascribed to physiological differences in oxygen flux (Longinelli, 1984; Luz et al., 1984; Bryant and Froelich, 1995; Kohn et al., 1996). Taxa also vary in water requirements such that some obligatorily consume large amounts of surface water while others (including *Marmota* and *Neotoma*) meet their water budgets solely with plant forage (Kohn et al., 1996). In the latter case, it is important that plant taxa exhibit leaf water $\delta^{18}O$ values which may differ as a result of variations in both physiology and growing conditions (Dongmann et al., 1974; Helliker and Ehleringer, 2000; Marshall et al., 2007).

Species biology and ecology

Marmots (Sciuridae: *Marmota*) are a clade of large-bodied ground squirrels distributed across the Holarctic (Wilson and Reeder, 2005). The Yellow-bellied marmot occurs across the western U.S. in open montane and intermontane habitats such as meadows and talus slopes (Frase and Hoffmann, 1980; Hall, 1981), and in the Southern Rocky Mountains can be found at a range of elevations in both mesic and xeric areas where suitable bouldery substrates exist (Armstrong, 1972; Fitzgerald et al., 1994). Remains of *M. flaviventris* are common throughout the Cement Creek Cave deposits and the species remains common in the region today, indicating it has been a persistent element of the high-elevation fauna at this site since approximately the middle of the Wisconsin glacial period.

M. flaviventris has a sciurid dental formula with moderately high-crowned, rooted molariform teeth and consumes a diet of grasses, forbs, and flowers in the Southern Rockies (Frase and Hoffmann, 1980). Like most other North American ground-dwelling sciurids, marmots have a strictly patterned phenology and reproduce once annually (Andersen et al., 1976; Frase and Hoffmann, 1980; Fitzgerald et al., 1994); much of the remainder of each year is spent in hibernation. This phenology ensures that post-weaning molariform teeth of marmots are formed in late summer when large amounts of plant material are being consumed in preparation for hibernation.

Woodrats (Cricetidae: *Neotoma*) are distributed across North America but reach highest species diversity in Mexico and the southwestern U.S. (Hall, 1981; Vaughan, 1990). The group is already responsible for major contributions to late Quaternary paleoecology from preservation of their accumulated middens (e.g., Betancourt et al., 1990), and this represents a rich body of knowledge to which isotopic analyses of *Neotoma* fossils would likely prove complementary. Bushy-tailed woodrats occur in a variety of western North American habitats (Hall, 1981; Vaughan, 1990; Smith, 1997) and are the most boreal-adapted and largest-bodied of their congeners (Hall, 1981; Smith, 1997). Modern *N. cinerea* are documented from most elevations and across several life zones in Colorado, with local presence dependent more on availability of rocky nesting substrates than specific environmental or dietary preferences (Finley, 1958; Armstrong, 1972; Fitzgerald et al., 1994). Similar to *M. flaviventris*, *N. cinerea* is a persistent element throughout the Cement Creek Cave record.

N. cinerea is a generalist herbivore (Vaughan, 1990; Fitzgerald et al., 1994) with adaptations for a low quality plant diet, specifically a cricetid dental formula with rooted, high-crowned molar teeth. Diets are comprised mostly of plants growing near nesting sites (although exceptions exist: Smith, 1997) and across Colorado appear flexible, including material from evergreen and coniferous trees, shrubs and forbs, among other plants, as available (Finley, 1958). *N. cinerea* is active year-round, and though its phenology is not as strict as that of *M. flaviventris*, it reproduces once or twice annually in the spring and summer months at higher elevations (Fitzgerald et al., 1994), providing some seasonal constraint on enamel isotopic signatures.

Materials and methods

Cement Creek Cave stratigraphy and dating

Cement Creek Cave is located south of the Elk Mountain Range in the East River valley, Colorado, and occupies an outcrop of Leadville limestone situated above Cement Creek, a tributary to the East River. Deposition of fossil material is attributed largely to the activity of *N. cinerea* and possibly also to small carnivores (Mustelidae), a pattern likely reinforced by the limited accessibility of the cave entrance. Excavations in Cement Creek Cave were conducted in 1998 (Emslie, 2002) and, more extensively, in 2007 (S.D. Emslie, pers. comm., 2012).

Material analyzed herein is from excavation of a 1×1.5 m pit in a small room inside Cement Creek Cave (Test Pit 2, Northeast Extension) in 2007. This excavation consisted of forty 5-cm levels to a depth of 2.2 m below the surface. Radiocarbon dates obtained from specimens in the upper two-thirds of this excavation (Fig. 1 and Table 1; Levels 1–27, $N = 19$ unique dates from 14 levels) are in reasonably good chronological order and record mostly continuous deposition spanning from at least 45 ka to the present (Fig. 1). Underlying strata (Levels 28–40), also rich in fossil material, exceed the upper limits of ^{14}C dating capabilities; no specimens from these levels have been successfully dated.

Sixteen dates from this series (three exclusions due to mixing and/or dating uncertainty, see Table 1) were pooled with eleven dates available from the 1998 test excavation (Emslie, 2002) and an age–depth model was developed using a cubic smoothing spline function implemented in the statistical computing program R (Fig. 1 and Table 2; R Development Core Team, 2011). Exclusion of the 1998 dates did not significantly alter model output. The default smoothing parameter value was used ($spar = 0.609$), which in R is calculated via initial assignment of a computational value λ to the dataset maximized via generalized cross-validation methods. The model contains no age reversals and captures major trends in depositional rates in the cave, which appear slowest during the late Wisconsin (specifically surrounding the Last Glacial Maximum [LGM]) but higher during the middle Wisconsin and Holocene. The model yielded ages for all upper cave levels (Levels 1–27) and was extrapolated to obtain ages for older levels without associated ^{14}C dates (Levels 28–40). Uncertainties associated with this extrapolation are treated further below.

To permit comparisons among time intervals with distinct climate histories, simple age bins were constructed as follows based on regional glacial chronologies (Richmond, 1986; Richmond and Fullerton, 1986; Pierce, 2003; Brugger, 2007): a middle Wisconsin bin (MW) at 65–35 ka, a late Wisconsin (LW) bin from 35–10 ka, and a Holocene (HOL) bin from 10 ka to the present. Cave levels were then partitioned into these bins based on modeled ages and the available ^{14}C record. Modern samples (see below) along with Levels 1–14 are assigned as HOL, Levels 19–23 as LW, and Levels 28–35 as MW age. These assignments are very conservative as they exclude a number of sampled

Table 1
Uncalibrated radiocarbon (^{14}C) ages of various mammal specimens from Cement Creek Cave. AMS radiocarbon dates from the 2007 excavation (above line) and the 1998 excavation (below line; Emslie, 2002) of Cement Creek Cave. Listed with each specimen are provenience, material analyzed and associated laboratory number. Depths of 1998 samples, corrected for use in the current study, are given in parentheses. All 2007 samples dated at the Keck Carbon Cycle AMS Facility, University of California Irvine (UCIAMS); all 1998 samples dated at Beta Analytic, Inc (BETA). Starred specimens were omitted in model construction.

Cave level	Taxon	Age (^{14}C yr BP)	Error (^{14}C yr)	Specimen	Laboratory number
2	*Marmota flaviventris*	1300	15	Lm3	53285
7	*Marmota flaviventris*	4105	15	RM1 or 2	53286
10	*Marmota flaviventris*	3120	15	LM1 or 2	53287
11	*Marmota flaviventris*	4780	20	Partial molar	56844
11	*Neotoma cinerea*	4630	15	RM1 (dentine) + partial maxilla	87756
13	*Marmota flaviventris*	6400	20	i1 + L mandible	56845
14	*Marmota flaviventris**	>44,800	–	Molar	56846
14	*Lepus americanus*	7035	20	Distal R femur	87758
15	*Marmota flaviventris**	>43,900	–	Rm3 + mandibular fragment	56847
15	*Lepus townsendii*	10,230	25	1st phalange	87757
16	*Marmota flaviventris*	18,040	70	Rm3	53288
17	*Marmota flaviventris**	>43,300	–	Rm3	53289
17	*Marmota flaviventris*	23,260	120	L premaxilla	85361
18	*Marmota flaviventris*	33,840	510	Lm3	53290
21	*Marmota flaviventris*	43,700	1900	LM1	53294
21	*Marmota flaviventris*	33,060	410	LI	85362
23	*Marmota flaviventris*	32,440	430	LM2	53291
24	*Marmota flaviventris*	36,560	720	Lm2 or 3	53292
27	*Marmota flaviventris*	35,040	590	Rm1 + mandibular fragment	53293
4(8)	*Marmota flaviventris*	1120	40	L i1	128214
5(10)	*Marmota flaviventris*	8070	50	L i1	125777
6(12)	*Odocoileus hemionus*	4520	50	R femur shaft fragment	135139
7(14)	*Thomomys talpoides*	11,870	110	Partial cranium	128215
8(16)	*Phenacomys intermedius*	11,970	50	Lm1+ Lm2 + L mandible	125780
9(18)	*Urocitellus (S.) elegans*	12,480	50	RP4 + RM2 + R maxilla	125781
10(20)	*Marmota flaviventris*	28,820	180	L partial tibia	129369
11(22)	*Lepus americanus*	28,330	170	Distal L tibia	125783
12(24)	*Lepus townsendii*	39,690	620	R ilium	125784
13(26)	*Marmota flaviventris*	34,980	600	L innominate	120098
13(26)	*Marmota flaviventris*	43,330	760	L I1	135140

intermediary levels due either to marginal modeled ages or an associated ^{14}C date(s) indicating mixing of sediments from different periods. Strata below Level 35 are also excluded from bins due to age uncertainties, but are assumed to be of middle Wisconsin age; these levels are instead considered individually. Throughout, age bins are referenced by the above designations (MW, LW, HOL) while actual geochronological divisions are spelled in full.

Table 2
Sample information. Samples of fossil *Marmota* and *Neotoma* used in this study with associated cave levels and modeled ages of those levels. The ages represent uncalibrated ^{14}C ages and are based on dates given in Table 1. Sample sizes for each taxon are followed in parentheses by either numbers of post-weaning teeth (*Marmota*) or numbers of first molars (*Neotoma*) comprising the sample. See text for additional details.

Cave level	Model age (^{14}C yr BP)	*Marmota* (*N*)	*Neotoma* (*N*)
11	5137	3 (1)	8 (7)
12	6546	2 (1)	–
15	13,369	–	4 (4)
17	19,735	5 (3)	–
18	23,026	–	5 (5)
19	26,170	4 (4)	5 (5)
20	29,034	4 (3)	7 (6)
21	31,484	4 (3)	4 (3)
23	35,048	4 (2)	4 (3)
25	37,521	5 (5)	5 (5)
26	38,526	–	4 (4)
27	39,500	4 (4)	–
28	40,472	5 (5)	5 (5)
30	42,415	5 (4)	5 (5)
32	44,358	5 (4)	5 (5)
33	45,330	3 (3)	5 (5)
35	47,273	4 (4)	–
36	48,245	5 (5)	5 (5)
38	50,188	–	5 (5)
39	51,159	5 (5)	–
40	52,131	3 (2)	3 (3)

Sample selection, processing, calibration and analysis

Teeth of *M. flaviventris* and *N. cinerea* were selected from throughout the Cement Creek Cave sequence for analysis (Table 2). When sufficient material was available, both species were sampled from within the same level to facilitate interspecies comparisons. Marmot ($N = 70$) and woodrat ($N = 79$) teeth were sampled from 17 and 16 different levels, respectively, and most cave levels were rich enough to permit analysis of at least 3–5 teeth of *M. flaviventris* and 4–5 of *N. cinerea*. Individuality of teeth within levels was ensured by sampling identical tooth positions (when possible) or via comparisons of molar wear and general preservation.

Body tissues formed while juvenile mammals are nursing are isotopically reflective of a maternally derived milk diet and tissues with little to no compositional turnover (e.g., tooth enamel) retain this signal indefinitely. For this reason, ecological investigations using mammalian tooth enamel often utilize post-weaning teeth. For Cement Creek Cave *Marmota*, post-weaning teeth (M3, P3, P4) were sampled where available (~76% of samples) while other tooth positions were included as necessary (I, M1, M2). Enamel sampled from *Marmota* incisors should also be taken as post-weaning, since these teeth are ever-growing and relative widths suggested they were of adult age (Munson, 1984).

Alternatively, molar teeth of *N. cinerea* (M1, M2, and portions of M3) are formed nearly simultaneously during nursing (Finley, 1958) and this may preclude integration of 'pure' adult ecological information in woodrat enamel. However, the theoretically constant fractionation rates between environments and female mammals and their young should maintain the utility of woodrat teeth in paleoecological investigation. Sampling of *Neotoma* was largely restricted to first upper and lower molars (M1; ~95% of samples), allowing for collection of sufficient enamel while minimizing confounding effects of isotopic variation along the mammalian toothrow.

In addition to fossil samples, a series of modern specimens of both species was assembled from field-collected and museum specimens. This sample included seven *N. cinerea* collected immediately below Cement Creek Cave and three *M. flaviventris* collected <1 mile west

of the cave between 2009 and 2010, as well as teeth from eleven additional *M. flaviventris* collected in the Upper Gunnison Basin (UGB) since 1973. Collection localities of all modern marmots ($N=14$) lie on a broad north–south transect in the UGB that spans an elevational gradient of approximately 2350 to 3350 m and includes the major habitats found in the region today. All field-collected specimens were obtained following protocols approved by the UNCW Institutional Animal Care and Use Committee and as outlined in the American Society of Mammalogists' guide to wild animal research (Sikes et al., 2011). Historical samples were obtained from intact crania or mandibles housed at Rocky Mountain Biological Laboratory (Gothic, Colorado) and Western State College (Gunnison, Colorado).

Pure enamel was isolated from all teeth using a dental micromotor (NSK America Corp., Schaumburg, IL, USA) fitted with a carbide tip sized between 0.3 and 0.5 mm, and then ground to a fine powder using a mortar and pestle. Chemical treatment of samples followed one protocol of Koch et al. (1997). Powders were first treated with 30% H_2O_2 for 24 h to remove organic material, and afterwards H_2O_2 was decanted and samples were rinsed three times with deionized (DI) water and isolated via microcentrifugation. Powders were then treated with 0.1 M CH_3COOH for an additional 24 h to remove possible adherent secondary carbonates, again rinsed and centrifuged three times, and allowed to air dry under a flow hood for 24 to 48 h. Pristine enamel powder was analyzed for carbonate composition via a GVI Optima mass spectrometer (Manchester, UK) at the University of California—Davis Dept. of Geology Stable Isotope Laboratory, where all samples were roasted under vacuum prior to analysis at 375°C for 0.5 h then reacted in a common H_3PO_4 bath at 90°C to yield CO_2. Average precision of measured carbon and oxygen isotope ratios was ±0.04 and 0.06‰, respectively, and all are reported relative to the V-PDB standard.

The systematic decrease in $\delta^{13}C_{atm}$ due to anthropogenic fossil-fuel combustion since the pre-industrial era (Suess effect) now totals between 1.5 and 2.0‰ (Keeling et al., 1979; Marino and McElroy, 1991; Keeling et al., 2005). To account for this, modern samples were corrected to pre-industrial values with yearly precision using ancient and historical measurements of $\delta^{13}C_{atm}$. Modern samples were first corrected to 1979 levels using data from Station La Jolla, California (Keeling et al., 1979; Keeling et al., 2005), then further corrected to match concurrent South Pole data (Keeling et al., 2005), thereby accounting for hemispheric differences in $\delta^{13}C_{atm}$. Values were then adjusted to pre-industrial values as observed in Antarctic ice (Friedli et al., 1986; Francey et al., 1999) by adding an additional 1.4‰. Total $\delta^{13}C$ corrections ranged between +1.4 and +1.98‰. For several samples with uncertain collection dates (*Marmota*, $N=3$), a total correction of +1.45‰ was applied, which assumes collection dates in the mid-1980s.

The failure of some age bins to meet assumptions of normality (i.e., small sample sizes and/or outliers) required the use of nonparametric methods in most statistical analyses. Where relevant, data are presented graphically with medians, quartiles, and outliers indicated. All statistical analyses were performed using R version 2.13.0 (R Development Core Team, 2011).

Results

Cave levels accounted for significant amounts of $\delta^{13}C$ variation in both *Marmota* (Fig. 3a; Kruskal–Wallis rank sum, $X^2=46.92$, $P\ll0.01$) and *Neotoma* (Fig. 4a; $X^2=30.95$, $P=0.01$). Pairwise cave-level comparisons (Student's t-tests) revealed consistent differences between Holocene samples and those of the Pleistocene. Modern *Marmota* $\delta^{13}C$ are lower relative to all Pleistocene levels ($P<0.05$), while modern *Neotoma* $\delta^{13}C$ are lower relative to all Pleistocene levels except 15 ($P<0.02$). Similarly, middle Holocene $\delta^{13}C$ (Level 11; Level 12 excluded hereafter due to small sample size) was lower relative to multiple Pleistocene levels in both taxa (*Marmota*, 9 of 15 levels, $P\leq0.04$; *Neotoma*, 7 of 15 levels, $P\leq0.04$) and these

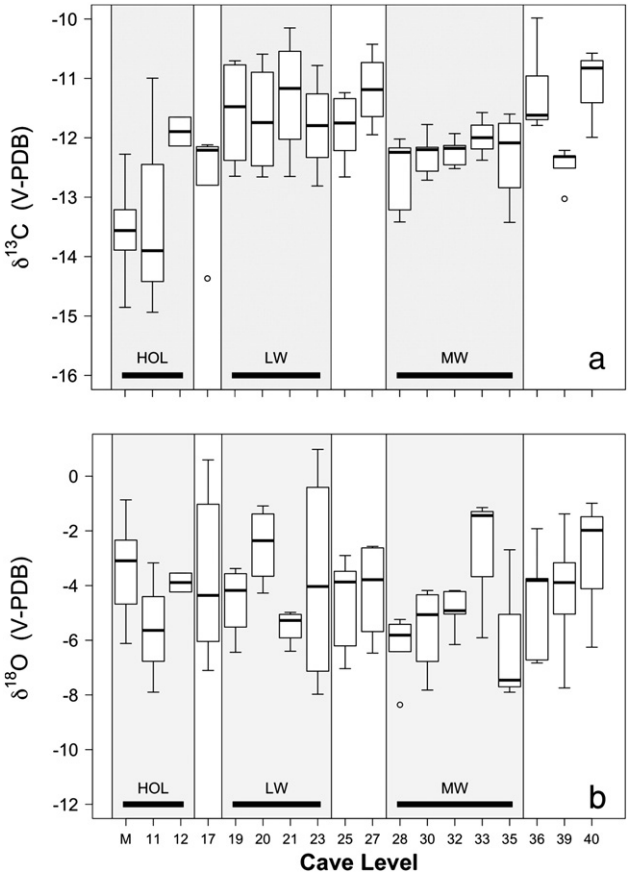

Figure 3. Measured $\delta^{13}C$ (a) and $\delta^{18}O$ (b) signatures of tooth enamel from fossil and modern ('M') *Marmota flaviventris*. Age bins are delineated by gray shading(HOL = Holocene, LW = late Wisconsin, MW = middle Wisconsin; see text for additional details). Here and in Figure 4, data are presented as boxplots where midline, boxes and whiskers represent the median, interquartile range (IQR) and most extreme value falling within the outlier criterion ($1.58^*(IQR/\sqrt{n})$). Data points identified as outliers using this criterion are given as open circles.

were indistinguishable from modern samples. Additional patterns were observed in *Marmota* from oldest cave levels; specifically, $\delta^{13}C$ from Levels 36 and 40 were higher than both an intervening level (39; $P\leq0.02$) and four and two MW levels, respectively ($P\leq0.05$).

Unlike for carbon signatures, cave levels did not account for significant amounts of variation observed in $\delta^{18}O$ in either *Marmota* (Fig. 3b; $X^2=22.30$, $P=0.17$) or *Neotoma* (Fig. 4b; $X^2=12.06$, $P=0.74$). Few significant pairwise $\delta^{18}O$ differences were found among cave levels in either species, but these included higher values in both modern and early LW (Level 20) *Marmota* $\delta^{18}O$ as compared to three of the five MW levels (28, 30, 35; $P<0.04$). Few differences and no patterns in $\delta^{18}O$ were observed among *Neotoma* from different cave levels.

When samples were pooled into MW, LW and HOL age bins, *Marmota* $\delta^{13}C$ differed significantly among each bin (Wilcoxon rank sum, $P<0.03$) with LW values highest, HOL values lowest, and MW intermediate (Fig. 5). *Neotoma* $\delta^{13}C$ differed only between each Wisconsin bin and the Holocene ($P\ll0.01$), with HOL values again lowest. The only significant $\delta^{18}O$ difference present among age bins was higher HOL values relative to MW *Marmota* ($P<0.01$); *Neotoma* $\delta^{18}O$ was invariant among bins. In support of the a priori delineation of age bins, relatively few intra-bin differences among individual levels were observed for either isotope system.

Finally, several comparisons were made to illuminate interspecies isotopic differences that may be reflective of ecological or physiological variation. When all modern and fossil specimens were pooled, $\delta^{13}C$ values were indistinct between species (Welch two sample test, $P=0.38$), but $\delta^{18}O$ was found to be marginally higher in *Marmota*

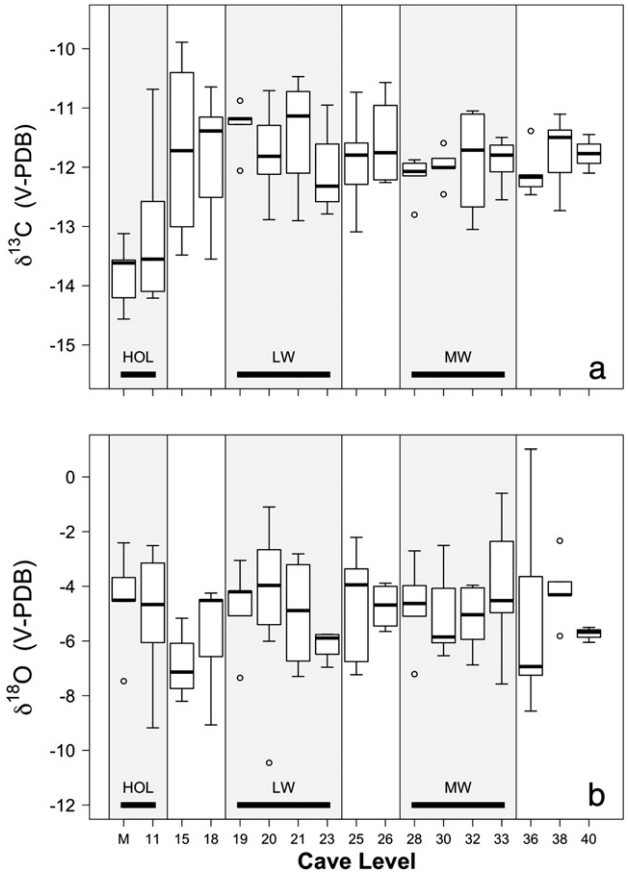

Figure 4. Measured $\delta^{13}C$ (a) and $\delta^{18}O$ (b) signatures of tooth enamel from fossil and modern ('M') *Neotoma cinerea*. Age bins and boxplots as in Figure 3.

($P = 0.056$). Additional comparisons among the three age bins revealed no significant differences in $\delta^{13}C$ or $\delta^{18}O$ between species (Fig. 5), although $\delta^{13}C$ of MW *Neotoma* was marginally higher than *Marmota* $\delta^{13}C$ from this same period ($P = 0.051$).

Discussion

Carbon composition of herbivore enamel

Tissues of ancient herbivores have proven invaluable not only for reconstructing species' diets and ecology, but also for revealing

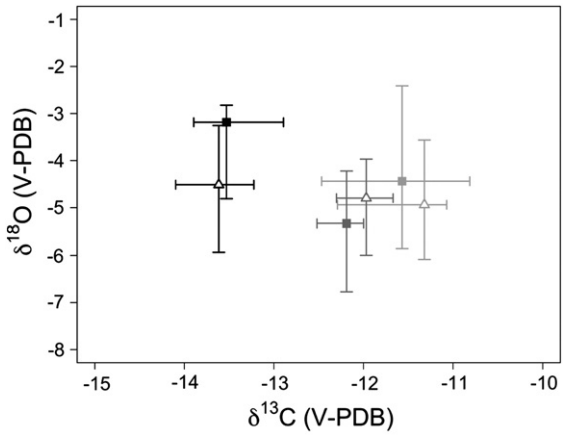

Figure 5. Median (center symbol) and interquartile range (bars) of age-binned enamel $\delta^{13}C$ and $\delta^{18}O$ signatures of *Marmota flaviventris* (closed squares) and *Neotoma cinerea* (open triangles); (HOL = black, LW = light gray, MW = dark gray).

major episodes of C_3/C_4 turnover in response to environmental change and contributing to a global paleochronology of C_4 grass expansion (Cerling et al., 1997; Ehleringer et al., 1997). Notable C_4 expansions did occur as recently as the late Pleistocene on some continents (Aucour et al., 1994; Street-Perrott et al., 1997; Huang et al., 1999), attributable to the competitive advantage of C_4 pathways under conditions of lowered CO_{2atm}. C_4 taxa comprise only a minor part of the flora across high elevations in Colorado today (Barrell, 1969; Cooper, 2004), but palynological evidence indicates their abundance may have been variable in the region of Cement Creek Cave during the late Quaternary (Fall, 1997). Thus, the possibility of a local C_4 increase at this high elevation site cannot be excluded. However, $\delta^{13}C_{enamel}$ values in the present study indicate C_4 plants never dominated the diets of Cement Creek Cave *Marmota* or *Neotoma*, and together with the available pollen record this suggests C_3 plants have remained the dominant photosynthetic pathway at this high-elevation site since the middle Wisconsin. A scenario of C_3 dominance is in agreement with known advantages of C_3 plants at high latitudes and altitudes (Teeri and Stowe, 1976) as well as model and isotopic data indicating late Pleistocene C_4 expansions were of limited scope in both the Americas (Collatz et al., 1998; MacFadden et al., 1999) and the American Southwest in particular (Connin et al., 1998; Holmgren et al., 2007). Additional high-elevation pollen records, and possibly paleobotanical analyses of Cement Creek Cave sediments, would be helpful in revealing the actual extent to which late Quaternary C_3/C_4 ratios varied in this region and in evaluating the influences of C_4 dietary incorporation versus C_3 plant CO_{2atm} response on isotopic signatures of herbivore tissues.

Differences in $\delta^{13}C_{enamel}$ among age bins are also inconsistent with dietary shifts of *Marmota* or *Neotoma* among C_3 plant groups. Boreal plant taxa vary in $\delta^{13}C$ relative to functional group (Brooks et al., 1997), yet invoking this variation to explain trends in $\delta^{13}C_{enamel}$ yields scenarios that are directly opposed to paleoecological records. For example, late Wisconsin $\delta^{13}C_{enamel}$ maxima could be explained by dietary shifts to include increasing amounts of trees and shrubs, yet this was a time when treelines were below the elevation of Cement Creek Cave and the region was dominated by an alpine sagebrush-steppe plant assemblage (Legg and Baker, 1980; Markgraf and Scott, 1981, Fall, 1997; Briles et al., 2012). Such an explanation would then require another to explain lowered HOL $\delta^{13}C_{enamel}$: namely, a return to forb-based diets. Although the latter is consistent with modern diets of these taxa, it would occur precisely when treelines rose and alpine tundra assemblages contracted (Armstrong, 1972; Legg and Baker, 1980; Markgraf and Scott, 1981; Fall, 1997; Briles et al., 2012).

Instead of changes in the diets of *Marmota* or *Neotoma*, the $\delta^{13}C_{enamel}$ data are fully consistent with effects of fluctuating CO_{2atm} on the physiology of montane C_3 plants consumed by these herbivores. Conditions of depleted CO_{2atm} reduce the ability of plant stomata to supply CO_2 necessary for optimal photosynthetic rates and the photosynthetic reaction as a result becomes CO_2-limited (O'Leary, 1981; Farquhar et al., 1989; Sage and Coleman, 2001; Marshall et al., 2007). C_3 plants grown under such conditions exhibit decreased water use efficiency and lowered concentrations of intracellular CO_2, resulting in systematic $\delta^{13}C$ increases of photosynthate and plant tissue (Farquhar et al., 1989). Such plant response has previously been observed in fossils of limber pine (*Pinus flexilis*) from the Great Basin spanning the past 30,000 yr (Van de Water et al., 1994) and juniper (*Juniperus*) from Rancho La Brea, California, dating from the past 50,000 yr (Ward et al., 2005). The present study extends the latitudinal, elevational and taxonomic record of this phenomenon in North America.

The dominant event recorded in $\delta^{13}C_{enamel}$ is the significant decrease of HOL signatures relative to those of MW and LW, which we interpret as a direct reflection of montane plant responses to rapid increases in CO_{2atm} following the late Pleistocene from 180–200 to

nearly 280 parts per million volume [ppmv] (Fig. 2; Leuenberger et al., 1992; Francey et al., 1999; Petit et al., 1999). Yet enamel signatures also reveal subtler responses to CO_{2atm} prior to this transition, indicating that montane plants, like those elsewhere in the western U.S. (Van de Water et al., 1994; Ward et al., 2005), tracked CO_{2atm} and temperature instabilities of the last glacial period (Fig. 2; Bond et al., 1993; Dansgaard et al., 1993; NGRIP, 2004). MW $\delta^{13}C_{enamel}$ averages less than during LW (though only significantly in *Marmota*), a result of elevated CO_{2atm} during the middle Wisconsin followed by a late Wisconsin global CO_{2atm} minimum. Additionally, *Marmota* from the oldest Cement Creek Cave sediments (Levels 36–40) exhibit significant intra-level differences, a pattern that matches the rapid CO_{2atm} fluctuations between 60 and 40 ka associated with Northern Hemispheric Dansgaard–Oeschger (D–O) and Heinrich events (Bond et al., 1993; Dansgaard et al., 1993; NGRIP, 2004). Modeled ages of these levels (53–48 ka) place them securely in this timeframe, and thus these data are not inconsistent with some level of CO_2 teleconnection between continental North America and the North Atlantic during these events followed by plant physiological response.

The $\delta^{13}C_{enamel}$ values of late Pleistocene *Marmota* and *Neotoma* fall within the expected range for herbivores living in open or xeric environments (MacFadden and Cerling, 1996). This agrees well with paleoecological records from the Southern Rockies, at least for the late Wisconsin, which indicate high-elevation environments were dominated by a no-analog sagebrush steppe-tundra at this time (Legg and Baker, 1980; Markgraf and Scott, 1981; Thompson et al., 1993; Fall, 1997). Enamel data suggest a similar assemblage occurred around Cement Creek Cave as well, which during the period was located above upper treeline and in proximity to large alpine glaciers (Fall, 1997; Brugger, 2007, 2010), and that this assemblage supplied the diets of both herbivore species examined here. However, little evidence exists on the exact nature of middle Wisconsin environments in the region, though temperatures had been mild enough to induce retreat of early Wisconsin glaciers (Richmond, 1986; Pierce, 2003). Similarity of MW and LW $\delta^{13}C_{enamel}$ apart from CO_{2atm} effects, however, is consistent with dominance of open alpine steppe vegetation at Cement Creek Cave throughout both the middle and late Wisconsin, and this assertion is supported by an abundance of characteristic steppe (*Lemmiscus*, *Urocitellus*) and alpine (*Phenacomys*, *Ochotona*) mammal taxa in MW and LW strata as well as absence of obligate forest taxa (*Tamiasciurus*, *Myodes*) prior to the latest Wisconsin (S.D. Emslie, pers. comm., 2012). If milder middle Wisconsin conditions did contribute to rising treelines or increased arboreal densities at this elevation, as could be inferred from a few marginal pollen sequences (Wright et al., 1973; Legg and Baker, 1980), it was probably as open parkland and failed to significantly affect diets or habitats of *Marmota* or *Neotoma*.

Climate warming at the end of the Pleistocene contributed to regional paleovegetative change in the Southern Rockies including contraction of alpine steppe assemblages, formation of denser montane forests and ascension of upper treelines between 300 and 700 m (Legg and Baker, 1980; Markgraf and Scott, 1981; Fall, 1997). Concomitant decreases in median $\delta^{13}C_{enamel}$ are ~2.0 and 2.3‰ for *Marmota* and *Neotoma*, respectively, between LW and HOL age bins (Figs. 3 and 4). However, these figures are more substantial than the ~1.5‰ decrease observed between late Wisconsin and Holocene needles of *Pinus flexilis* and attributed to CO_2 stress by Van de Water et al. (1994). They also exceed changes of similar direction recorded in bone collagen of dire wolves (*Canis dirus*), bison (*Bison antiquus*) and other megaherbivore taxa from Rancho La Brea (Coltrain et al., 2004; Bump et al., 2007), though it is noted these megafaunal records do not extend to 10 ka. If this discrepancy is real, it could reflect the increased water use efficiency of high-altitude plants (Marshall et al., 2007), a physiological adaptation that, during the late Wisconsin, would have contributed to more significant reductions in stomatal conductance and increases in $\delta^{13}C_{plant}$ as compared to lower-elevation forms. Marshall and Zhang (1994) found that woody plant ^{13}C discrimination decreased by ~1.2‰ with each km increase in altitude due to increasing water use efficiency. Alternatively, it is plausible that plant foods of *Marmota* and *Neotoma* were more water-stressed than those of other regions during the late Wisconsin due to reduced summer precipitation (Fall, 1997). Distinguishing between these two hypotheses is not yet possible.

It is true that LW-to-HOL $\delta^{13}C_{enamel}$ trends are, superficially, also consistent with canopy effects induced by Holocene forests on small mammal forage. In fact, the $\delta^{13}C$ values of *Marmota* and *Neotoma* in this study are only ~1‰ higher than those of bone apatite of modern Southern Red-backed voles (*Myodes gapperi*) from spruce-fir forests in Alberta, Canada (Sare et al., 2005). However, the modern environment immediately surrounding Cement Creek Cave consists mostly of steppe and scattered conifers growing on arid soils, and although dense subalpine forest does occur discontinuously in the region, the possibility of a canopy effect acting on our modern samples seems unlikely. Furthermore, because $\delta^{13}C_{enamel}$ is statistically indistinct between modern specimens and those from Level 11 (the best-sampled Holocene level), a canopy effect likely does not explain any of the lowered HOL values. Thus, while additional work is necessary to understand the prevalence of canopy effects in temperate ecosystems, $\delta^{13}C_{enamel}$ patterns in the present study can be fully explained as the acute physiological responses of montane plants to CO_{2atm} fluctuations.

Oxygen composition of herbivore enamel

Given the temperature and precipitation changes proposed for the Southern Rockies during and after the Wisconsin, it is interesting that few temporal patterns in $\delta^{18}O_{enamel}$ were found in either species. However, different meteoric factors (origin, seasonality and type of precipitation) could potentially have confounding effects on surface water $\delta^{18}O$ (McGuire and McDonnell, 2007), so such observations do not necessarily by themselves support a static late Quaternary temperature and precipitation regime. In *Marmota*, significant MW $\delta^{18}O_{enamel}$ decreases (relative to HOL) may reflect cooler temperatures or, alternatively, dietary intake of surface waters originating from waning early Wisconsin glaciers (Richmond, 1986; Pierce, 2003). On the other hand, LW $\delta^{18}O_{enamel}$ values remain indistinct from MW and HOL in both species, an unexpected result as late Wisconsin conditions were characterized by environmental changes that should have influenced surface waters. These include reduced summer and annual temperatures (Legg and Baker, 1980; Barry, 1983; Thompson et al., 1993; Fall, 1997), possible changes in summer precipitation (Fall, 1997), and the supposed extension of large alpine glaciers to within ~10 km of the cave (Brugger, 2010).

One weak pattern observed in the data is a $\delta^{18}O_{enamel}$ decrease in the interval between the LW (specifically, Level 20) and the start of the Holocene (Figs. 3 and 4). How this trend is best interpreted in a meteoric framework is not entirely clear, but it is consistent with increased levels of ^{18}O-depleted snowmelt resulting from local deglaciation after the LGM. The Sawatch and Elk mountain ranges surrounding Cement Creek Cave were glaciated during the late Pleistocene, as were the upper reaches of the Cement Creek drainage (Brugger, 2010), and melt from these glaciers could have altered surface water ^{18}O surrounding the cave. A comparable $\delta^{18}O_{enamel}$ decrease is observed between Levels 35–40 in *Marmota*, possibly reflective of analogous meltwater inputs from early Wisconsin glaciers. However, an alternative explanation for both these patterns is that $\delta^{18}O_{enamel}$ decreases were modulated by physiological responses of montane plants, as is observed in $\delta^{13}C_{enamel}$. Evapotranspiration typically results in ^{18}O-enrichment of leaf water, with the rate of evapotranspiration strongly dependent on environmental conditions. If increased stomatal conductance was a plant response to conditions of low Pleistocene CO_{2atm} and/or other variables like increased summer aridity (Fall, 1997), then leaf water $\delta^{18}O$ would have been elevated as a result and potentially recorded in herbivore enamel.

It has been suggested that larger-bodied mammals which are obligate drinkers record $\delta^{18}O$ of meteoric waters more faithfully than smaller taxa (e.g., Bryant and Froelich, 1995), and it is possible that the absence of strong temporal signals in $\delta^{18}O_{enamel}$ results from the limited extent and scope with which *Marmota* and *Neotoma* sample such waters. Also, growth time of molariform teeth generally decreases with taxon size, necessarily decreasing the ecological information recorded in any single small mammal tooth. Alternatively, the molariform teeth of modern *Marmota* appear to be capable of recording broad elevational trends in surface water $\delta^{18}O$ (B.S. McLean, unpublished data). Thus, while no major changes in surface water use of *Marmota* and *Neotoma* were detected across the late Quaternary at Cement Creek Cave, additional work should be directed at clarifying the usefulness of $\delta^{18}O_{enamel}$ analyses in these and similar taxa.

Comparative ecology, paleoecology and broader implications

Across both carbon and oxygen isotopes and in the specific context of this study (where diets of neither taxon appear significantly altered), *Marmota* is a more sensitive paleoecological indicator than *Neotoma*. This sensitivity is attributed largely to the dental morphology and strict phenology of *M. flaviventris*, which conspire to ensure post-weaning molariform teeth are formed in summer when montane plant stress (resulting in variations in $\delta^{13}C_{plant}$ and leaf water $\delta^{18}O$) is most likely to occur. Other biological and physiological differences between these taxa likely explain the marginally significant $\delta^{18}O_{enamel}$ increases of *Marmota* relative to *Neotoma*, a result that mirrors findings by Feranec et al. (2010). These differences are probably not directly related to hibernation, however, as molariform tooth enamel appears to be formed solely in months when animals are active. It also remains possible that this pattern is due not to physiological but phenological differences; the trends are consistent with late summer seasonal effects on dietary waters like precipitation $\delta^{18}O$- or leaf $\delta^{18}O$-enrichment. Future research on such interspecies isotopic differences should incorporate taxa employing a range of life history strategies that can be sampled across various temporal (i.e., seasonal) and spatial scales. Lastly, it should be noted that the lack of any further $\delta^{13}C_{enamel}$ and $\delta^{18}O_{enamel}$ differences between the taxa examined here should not be taken to indicate complete dietary similarities, as only pre-weaning molars of *Neotoma* were analyzed. Future studies could benefit from serially sampling entire mammalian toothrows instead of just single teeth.

The mammalian paleoecological record we report here compliments data from nearby Porcupine Cave located in central Colorado and at a nearly identical elevation (2900 m), which has produced the richest assemblage of middle Pleistocene vertebrate fossils in North America (Barnosky, 2004). Portions of these deposits date between >600 ka and ~1 Ma and are representative of at least two glacial–interglacial cycles (Barnosky, 2004; Barnosky et al., 2004). Analysis of tooth enamel of *Marmota* spp. and unidentified leporid spp. from the cave revealed that resource use of these taxa was not demonstrably affected by middle Pleistocene climate cycling (Feranec et al., 2010). Unfortunately, subtler isotopic variation between glacial and interglacial periods (e.g., due to CO_{2atm} effects) was not identified, which likely speaks to the tight stratigraphic control available in the Cement Creek Cave record. Nonetheless, when results of both studies are considered, they suggest that the dietary niches of multiple lineages of small mammals have been maintained in the Southern Rockies across long stretches of the Quaternary.

Lastly, these results also offer insight into patterns of community persistence previously observed in the Cement Creek Cave small mammal community (S.D. Emslie, pers. comm., 2012). *M. flaviventris* and *N. cinerea* have a dietary ecology uniquely adapted to high-elevation alpine environments, their vicissitudes, and the plant species they support which was stable across the late Quaternary. Similar adaptations in other high-elevation species could largely explain the observed community persistence. If these adaptations exist, they would in turn suggest that alpine environments, which have probably been common features of the Southern Rocky Mountains during the Pleistocene due to the number and length of glacial periods, have strongly shaped the evolutionary trajectories of these small mammal lineages. However, it is these same environments that are now acutely threatened by contemporary climate warming, the rate of which exceeds that observed at any point during the Quaternary (Barnosky et al., 2003; Beniston, 2003). Given insights from this study and the increasingly coherent Pleistocene paleoecological record from the Southern Rockies, future persistence of high-elevation small mammal species in the region likely depends on the extent to which current climate and environmental perturbations exceed those of the past 45,000 or even 1,000,000 yr.

Acknowledgments

This research was funded by the National Science Foundation (Grant EAR-0819678), Rocky Mountain Biological Laboratory (RMBL; Dr. Lee R.G. Snyder Fellowship), and both the UNCW Graduate School and Dept. of Biology and Marine Biology (Dr. James F. and Frances B. Parnell Fellowship). Valuable methodological guidance was provided by Robert Feranec (New York State Museum). We thank Catherine Mask and Leigh Ann Hunt (U.S. Forest Service) for their assistance in providing permit GUN627 to excavate at Cement Creek Cave, and gratefully acknowledge the considerable effort by researchers, graduate and undergraduate students involved in the excavation, cleaning and sorting of cave material. The 2007 excavations were supported in part by Quest Archaeological Research Program, Department of Anthropology, Southern Methodist University (SMU). Field research was supported by Mark Stiger and Patrick Magee (Western State College) and the North Carolina Museum of Natural Sciences and access to museum samples was granted by Ian Billick (RMBL) and Patrick Magee. David Meltzer (SMU), Chad Lane (UNCW), and Robert Feranec offered comments that greatly improved the quality of this manuscript.

References

Ahn, J., Brook, E.J., 2008. Atmospheric CO_2 and climate on millennial time scales during the last glacial period. Science 322, 83–85.
Ambrose, S., Norr, L., 1993. Experimental evidence for the relationship of carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In: Lambert, J., Grupe, G. (Eds.), Prehistoric Human Bone: Archaeology at the Molecular Level. Springer-Verlag, Berlin, pp. 1–37.
Andersen, D.C., Armitage, K.B., Hoffmann, R.S., 1976. Socioecology of marmots: female reproductive strategies. Ecology 57, 552–560.
Arens, N.C., Jahren, A.H., Amundson, R., 2000. Can C_3 plants faithfully record the carbon isotopic composition of atmospheric carbon dioxide? Paleobiology 26, 137–164.
Armstrong, D.M., 1972. Distribution of Mammals in Colorado. Museum of Natural History, University of Kansas, Lawrence, Kansas.
Aucour, A.-M., Hillaire-Marcel, C., Bonnefille, R., 1994. Late Quaternary biomass changes from ^{13}C measurements in a highland peatbog from equatorial Africa (Burundi). Quaternary Research 41, 225–233.
Barnosky, A.D. (Ed.), 2004. Biodiversity Response to Climate Change in the Middle Pleistocene. University of California Press, Berkeley.
Barnosky, A.D., Hadly, E.A., Bell, C.J., 2003. Mammalian response to global warming on varied temporal scales. Journal of Mammalogy 84, 354–368.
Barnosky, A.D., Bell, C.J., Emslie, S.D., Goodwin, H.T., Mead, J.I., Repenning, C.A., Scott, E., Shabel, A.B., 2004. Exceptional record of mid-Pleistocene vertebrates helps differentiate climatic from anthropogenic ecosystem perturbations. Proceedings of the National Academy of Sciences of the United States of America 101, 9297–9302.
Barrell, J., 1969. Flora of the Gunnison Basin: Gunnison, Saguache and Hinsdale Counties, Colorado; a Study in the Distribution of Plants. National Land Institute, Rockford, Illinois.
Barry, R.G., 1983. Late-pleistocene climatology. In: Porter, S.C. (Ed.), Late-Quaternary Environments of the United States, 1. University of Minnesota Press, Minneapolis, pp. 390–407.
Beniston, M., 2003. Climatic change in mountain regions: a review of possible impacts. Climatic Change 59, 5–31.
Betancourt, J.L., Van Devender, T.R., Martin, P.S. (Eds.), 1990. Packrat Middens: The Last 40,000 Years of Biotic Change. The University of Arizona Press, Tucson.
Bond, G., Broecker, W., Johnsen, S.J., McManus, J., Labeyrie, L., Jouzel, J., Bonani, G., 1993. Correlations between climate records from North Atlantic sediments and Greenland ice. Nature 365, 143–147.

Briles, C.E., Whitlock, C., Meltzer, D.J., 2012. Last glacial–interglacial environments in the southern Rocky Mountains, USA and implications for Younger Dryas-age human occupation. Quaternary Research 77, 96–103.
Brooks, J.R., Flanagan, L.B., Buchmann, N., Ehleringer, J.R., 1997. Carbon isotope composition of boreal plants: functional grouping of life forms. Oecologia 110, 301–311.
Brugger, K.A., 2007. Cosmogenic ^{10}Be and ^{36}Cl ages from late Pleistocene terminal moraine complexes in the Taylor River drainage basin, central Colorado, USA. Quaternary Science Reviews 26, 494–499.
Brugger, K.A., 2010. Climate in the southern Sawatch Range and Elk Mountains, Colorado, U.S.A., during the Last Glacial Maximum: inferences using a simple degree-day model. Arctic, Antarctic, and Alpine Research 42, 164–178.
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.
Bump, J.K., Fox-Dobbs, K., Bada, J.L., Koch, P.L., Peterson, R.O., Vucetich, J.A., 2007. Stable isotopes, ecological integration and environmental change: wolves record atmospheric carbon isotope trend better than tree rings. Proceedings of the Royal Society B: Biological Sciences 274, 2471–2480.
Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., Ehleringer, J.R., 1997. Global vegetation change through the Miocene/Pliocene boundary. Nature 389, 153–158.
Collatz, G.J., Berry, J.A., Clark, J.S., 1998. Effects of climate and atmospheric CO_2 partial pressure on the global distribution of C_4 grasses: present, past, and future. Oecologia 114, 441–454.
Coltrain, J.B., Harris, J.M., Cerling, T.E., Ehleringer, J.R., Dearing, M., Ward, J., Allen, J., 2004. Rancho La Brea stable isotope biogeochemistry and its implications for the palaeoecology of late Pleistocene, coastal southern California. Palaeogeography Palaeoclimatology Palaeoecology 205, 199–219.
Connin, S.L., Betancourt, J., Quade, J., 1998. Late Pleistocene C_4 plant dominance and summer rainfall in the southwestern United States from isotopic study of herbivore teeth. Quaternary Research 50, 179–193.
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, pp. 27–38.
Dansgaard, W., Johnsen, S.J., Clausen, H.B., Dahl-Jensen, D., Gundestrup, N.S., Hammer, C.U., Hvidberg, C.S., Steffensen, J.P., Sveinbjornsdottir, A.E., Jouzel, J., Bond, G., 1993. Evidence for general instability of past climate from a 250-kyr ice-core record. Nature 364, 218–220.
Dawson, T.E., Mambelli, S., Plamboeck, A.H., Templer, P.H., Tu, K.P., 2002. Stable isotopes in plant ecology. Annual Review of Ecology and Systematics 33, 507–559.
Dongmann, G., Nurnberg, H.W., Forstel, H., Wagener, K., 1974. On the enrichment of $H_2^{18}O$ in the leaves of transpiring plants. Radiation and Environmental Biophysics 11, 41–52.
Ehleringer, J.R., Cerling, T.E., Helliker, B.R., 1997. C_4 photosynthesis, atmospheric CO_2, and climate. Oecologia 112, 285–299.
Emslie, S.D., 2002. Fossil shrews (Insectivora: Soricidae) from the late Pleistocene of Colorado. The Southwestern Naturalist 47, 62–69.
Fall, P.L., 1997. Timberline fluctuations and late Quaternary paleoclimates in the Southern Rocky Mountains, Colorado. Geological Society of America Bulletin 109, 1306–1320.
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.
Feranec, R.S., Hadly, E.A., Paytan, A., 2010. Isotopes reveal limited effects of middle Pleistocene climate change on the ecology of mid-sized mammals. Quaternary International 217, 43–52.
Finley, R.B., 1958. The wood rats of Colorado: distribution and ecology. University of Kansas Publications, Museum of Natural History 10, 213–552.
Fitzgerald, J.P., Meaney, C.A., Armstrong, D.M., 1994. Mammals of Colorado. Denver Museum of Natural History and University Press of Colorado, Niwot.
Fluckiger, J., Monnin, E., Stauffer, B., Schwander, J., Stocker, T.F., Chappellaz, J., Raynaud, D., Barnola, J.-M., 2002. High-resolution Holocene N_2O ice core record and its relationship with CH_4 and CO_2. Global Biogeochemical Cycles 16, 1010.
Francey, R.J., Allison, C.E., Etheridge, D.M., Trudinger, C.M., Enting, I.G., Leuenberger, M., Langenfelds, R.L., Michel, E., Steele, L.P., 1999. A 1000-year high precision record of $\delta^{13}C$ in atmospheric CO_2. Tellus 51B, 170–193.
Frase, B.A., Hoffmann, 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, 234–238.
Graham, R.W., Lundelius, E.L., Graham, M.A., Schroeder, E.K., Toomey, R.S., 1996. Spatial response of mammals to late Quaternary environmental fluctuations. Science 272, 1601–1606.
Hall, E.R., 1981. The Mammals of North America. John Wiley and Sons, New York.
Harris, A.H., 1985. Late Pleistocene Vertebrate Paleoecology of the West. University of Texas Press, Austin.
Helliker, B.R., Ehleringer, J.R., 2000. Establishing a grassland signature in veins: ^{18}O in the leaf water of C_3 and C_4 grasses. Proceedings of the National Academy of Sciences of the United States of America 97, 7894–7898.
Higgins, P., MacFadden, B.J., 2004. "Amount effect" recorded in oxygen isotopes of late glacial horse (*Equus*) and bison (*Bison*) teeth from the Sonoran and Chihuahuan deserts, southwestern United States. Palaeogeography Palaeoclimatology Palaeoecology 206, 337–353.
Holmgren, C.A., Norris, J., Betancourt, J.L., 2007. Inferences about winter temperatures and summer rains from the late Quaternary record of C_4 perennial grasses and C_3 desert shrubs in the northern Chihuahuan Desert. Journal of Quaternary Science 22, 141–161.
Huang, Y., Street-Perrott, F.A., Perrott, R.A., Metzger, P., Eglinton, G., 1999. Glacial–interglacial environmental changes inferred from molecular and compound-specific ^{13}C analyses of sediments from Sacred Lake, Mt. Kenya. Geochimica et Cosmochimica Acta 63, 1383–1404.
IPCC, 2007. Climate change 2007: the physical science basis. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge and New York.
Keeling, C.D., Mook, W.G., Tans, P.P., 1979. Recent trends in the $^{13}C/^{12}C$ ratio of atmospheric carbon dioxide. Nature 277, 121–123.
Keeling, C.D., Piper, S.C., Bacastow, R.B., Wahlen, M., Whorf, T.P., Heimann, M., Meijer, H.A., 2005. Atmospheric CO_2 and $^{13}CO_2$ Exchange with the Terrestrial Biosphere and Oceans from 1978 to 2000: Observations and Carbon Cycle Implications. In: Ehleringer, J.R., Cerling, T.E., Dearing, M. (Eds.), A History of Atmospheric CO_2 and its Effects on Plants, Animals, and Ecosystems. Springer-Verlag, New York, pp. 83–113.
Koch, P.L., 2007. Isotopic study of the biology of modern and fossil vertebrates. In: Michener, R., Lajtha, K. (Eds.), Stable Isotopes in Ecology and Environmental Science. Blackwell Publishing, Malden, pp. 99–154.
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.
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.
Kohn, M.J., Welker, J.M., 2005. On the temperature correlation of $\delta^{18}O$ in modern precipitation. Earth and Planetary Science Letters 231, 87–96.
Kohn, M.J., Schoeninger, M.J., Valley, J.W., 1996. Herbivore tooth oxygen isotope compositions: effects of diet and physiology. Geochimica et Cosmochimica Acta 60, 3889–3896.
Land, L.S., Lundelius, E.L., Valastro, S., 1980. Isotopic ecology of deer bones. Palaeogeography Palaeoclimatology Palaeoecology 32, 143–151.
Legg, T.E., Baker, R.G., 1980. Palynology of Pinedale sediments, Devlins Park, Boulder County, Colorado. Arctic and Alpine Research 12, 319–333.
Leuenberger, M., Siegenthaler, U., Langway, C.C., 1992. Carbon isotope composition of atmospheric CO_2 during the last ice age from an Antarctic ice core. Nature 357, 488–490.
Longinelli, A., 1984. Oxygen isotopes in mammal bone phosphate: a new tool for paleohydrological and paleoclimatological research? Geochimica et Cosmochimica Acta 48, 385–390.
Lundelius, E.L., Graham, R.W., Anderson, E., Guilday, J., Holman, J.A., Steadman, D.W., Webb, S.D., 1983. Terrestrial vertebrate faunas. In: Porter, S.C. (Ed.), Late-Quaternary Environments of the United States, 1. University of Minnesota Press, Minneapolis, pp. 311–353.
Luz, B., Lolodny, 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., Cerling, T.E., Harris, J.M., Prado, J., 1999. Ancient latitudinal gradients of C_3/C_4 grasses interpreted from stable isotopes of New World Pleistocene horse (*Equus*) teeth. Global Ecology and Biogeography 8, 137–149.
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.
Markgraf, V., Scott, L., 1981. Lower timberline in central Colorado during the past 15,000 yr. Geology 9, 231–234.
Marshall, J.D., Zhang, J., 1994. Carbon isotope discrimination and water-use efficiency in native plants of the North-Central Rockies. Ecology 75, 1887–1895.
Marshall, J.D., Brooks, J.R., Lajtha, K., 2007. Sources of variation in the stable isotopic composition of plants. In: Michener, R., Lajtha, K. (Eds.), Stable Isotopes in Ecology and Environmental Science. Blackwell Publishing, Malden, pp. 22–60.
McGuire, K., McDonnell, J., 2007. Stable isotope tracers in watershed hydrology. In: Michener, R., Lajtha, K. (Eds.), Stable Isotopes in Ecology and Environmental Science. Blackwell Publishing, Malden, pp. 334–374.
Medina, E., Minchin, P., 1980. Stratification of $\delta^{13}C$ values of leaves in Amazonian rain forests. Oecologia 45, 377–378.
Monnin, E., Indermuhle, A., Dallenbach, A., Fluckiger, J., Stauffer, B., Stocker, T.F., Raynaud, D., Barnola, J.-M., 2001. Atmospheric CO_2 concentrations over the last glacial termination. Science 291, 112–114.
Munson, P.J., 1984. Teeth of juvenile woodchucks as seasonal indicators on archaeological sites. Journal of Archaeological Science 11, 395–403.
NGRIP Members, 2004. High-resolution record of Northern Hemisphere climate extending into the last interglacial period. Nature 431, 147–151.
O'Leary, M.H., 1981. Carbon isotope fractionation in plants. Phytochemistry 20, 553–567.
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.
Petit, J.R., Jouzel, J., Raynaud, D., Barkov, N.I., Barnola, J.M., Basile, I., Bender, M., Chappellaz, J., Davis, M., Delaygue, G., Delmotte, M., Kotlyakov, V.M., Legrand, M.,

Lipenkov, V.Y., Lorius, C., Pepin, L., Ritz, C., Saltzman, E., Stievenard, M., 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. Nature 399, 429–436.
Pierce, K.L., 2003. Pleistocene glaciations of the Rocky Mountains. Development in Quaternary Science 1, 63–76.
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 94, 183–192.
R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna http://www.R-project.org/.
Richmond, G.M., 1986. Stratigraphy and Correlation of Glacial Deposits of the Rocky Mountains, the Colorado Plateau and the Ranges of the Great Basin. In: Sibrava, V., Bowen, D.Q., Richmond, G.M. (Eds.), Quaternary Glaciations in the Northern Hemisphere. Pergamon Press, Elmsford, pp. 99–127.
Richmond, G.M., Fullerton, D.S., 1986. Summation of quaternary glaciations in the United States of America. In: Sibrava, V., Bowen, D.Q., Richmond, G.M. (Eds.), Quaternary Glaciations in the Northern Hemisphere. Pergamon Press, Elmsford, pp. 183–196.
Sage, R.F., Coleman, J.R., 2001. Effects of low atmospheric CO_2 on plants: more than a thing of the past. Trends in Plant Science 6, 18–24.
Sare, D.T.J., Millar, J.S., Longstaffe, F.J., 2005. Tracing dietary protein in red-backed voles (*Clethrionomys gapperi*) using stable isotopes of nitrogen and carbon. Canadian Journal of Zoology 83, 717–725.
Schoeninger, M.J., DeNiro, M.J., 1982. Carbon isotope ratios of apatite from fossil bone cannot be used to reconstruct diets of animals. Nature 297, 577–578.
Sigman, D.M., Boyle, E.A., 2000. Glacial/interglacial variations in atmospheric carbon dioxide. Nature 407, 859–869.
Sikes, R.S., Gannon, W.L., Animal Care and Use Committee of the American Society of Mammalogists, 2011. Guidelines of the American Society of Mammalogists for the use of wild animals in research. Journal of Mammalogy 92, 235–253.
Smith, F.A., 1997. *Neotoma cinerea*. Mammalian Species 564, 1–8.
Spaulding, W.G., Leopold, E.B., Van Devender, T.R., 1983. Late Wisconsin Paleoecology of the American Southwest. In: Porter, S.C. (Ed.), Late-Quaternary Environments of the United States, 1. University of Minnesota Press, Minneapolis, pp. 259–293.
Stafford, T.W., Semken, H.A., Graham, R.W., Klippel, W.F., Markova, A., Smirnov, N.G., Southon, J., 1999. First accelerator mass spectrometry ^{14}C dates documenting contemporaneity of nonanalog species in late Pleistocene mammal communities. Geology 27, 903–906.
Street-Perrott, F.A., Huang, Y., Perrott, R.A., Eglinton, G., Barker, P., Khelifa, L.B., Harkness, D.D., Olago, D.O., 1997. Impact of lower atmospheric carbon dioxide on tropical mountain ecosystems. Science 278, 1422–1426.
Teeri, J.A., Stowe, L.G., 1976. Climatic patterns and the distribution of C_4 grasses in North America. Oecologia 23, 1–12.
Thewissen, J.G.M., Cooper, L.N., Clementz, M.T., Bajpai, S., Tiwari, B.N., 2007. Whales originated from aquatic artiodactyls in the Eocene epoch of India. Nature 450, 1190–1194.
Thompson, R.S., Whitlock, C., Bartlein, P.J., Harrison, S.P., Spaulding, W.G., 1993. Climatic changes in the Western United States since 18,000 yr B.P. In: Wright, H.E., Kutzbach, J.E., Webb, T., Ruddiman, W.F., Street-Perrott, F.A., Bartlein, P.J. (Eds.), Global Climates since the Last Glacial Maximum. University of Minnesota Press, Minneapolis, pp. 468–513.
Van de Water, P.K., Leavitt, S.W., Betancourt, J.L., 1994. Trends in stomatal density and $^{13}C/^{12}C$ ratios of *Pinus flexilis* needles during last glacial–interglacial cycle. Science 264, 239–243.
Van der Merwe, N.J., 1982. Carbon isotopes, photosynthesis, and archaeology. American Scientist 70, 596–606.
Vaughan, T.A., 1990. Ecology of living packrats. In: Betancourt, J.L., Van Devender, T.R., Martin, P.S. (Eds.), Packrat Middens: the Last 40,000 Years of Biotic Change. The University of Arizona Press, Tucson, pp. 14–27.
Vogel, J., 1978. Recycling of carbon in a forest environment. Oecologia Plantarum 13, 89–94.
Wang, Y., Cerling, T.E., 1994. A model of fossil tooth and bone diagenesis: implications for paleodiet reconstruction from stable isotopes. Palaeogeography Palaeoclimatology Palaeoecology 107, 281–289.
Ward, J.K., Harris, J.M., Cerling, T.E., Wiedenhoeft, A., Lott, M.J., Dearing, M.-D., Coltrain, J.B., Ehleringer, J.R., 2005. Carbon starvation in glacial trees recovered from the La Brea tar pits, southern California. Proceedings of the National Academy of Sciences of the United States of America 102, 690–694.
Webb, R.H., Betancourt, J.L., 1990. The spatial and temporal distribution of radiocarbon ages from packrat middens. In: Betancourt, J.L., Van Devender, T.R., Martin, P.S. (Eds.), Packrat Middens: The Last 40,000 Years of Biotic Change. The University of Arizona Press, Tucson, pp. 85–102.
Welker, J.M., 2000. Isotopic ($\delta^{18}O$) characteristics of weekly precipitation collected across the USA: an initial analysis with application to water source studies. Hydrological Processes 14, 1449–1464.
Wilson, D.E., Reeder, D.M. (Eds.), 2005. Mammal Species of the World. Johns Hopkins University Press, Baltimore.
Wright, H.E., Bent, A.M., Hansen, B.S., Maher, L.J., 1973. Present and past vegetation of the Chuska Mountains, northwestern New Mexico. Geological Society of America Bulletin 84, 1155–1180.
Yurtsever, Y., Gat, J., 1981. Atmospheric water. In: Gat, J.R., Gonfiantini, R. (Eds.), Stable Isotope Hydrology, Deuterium and Oxygen-18 in the Water Cycle. International Energy Agency, Vienna, pp. 103–142.