

LATE QUATERNARY PALEOECOLOGY OF TWO HIGH-ELEVATION MAMMAL
SPECIES FROM THE SOUTHERN ROCKY MOUNTAINS, COLORADO, USA

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ABSTRACT

The Quaternary period has been characterized by global climate and environmental changes – changes that have impacted Earth’s biotas in various ways. Coherent fossil records remain a central resource in the continued understanding of these impacts. Cement Creek Cave, Colorado (2950m), located in the Southern Rocky Mountains, has provided an abundant and chronologically intact record of late Quaternary small mammal taxa which spans in age from >45,000 years ago to the present. This record helps to fill a prior gap in knowledge of high-elevation mammal faunas in North America during this time, and represents a unique opportunity to investigate how different small mammal species responded ecologically to the climate change, glaciation and reassembly of floral and faunal communities that characterized this particular region throughout the late Quaternary.

In this study, stable carbon and oxygen isotope analyses of tooth enamel of Yellow-bellied marmots (*Marmota flaviventris*) and Bushy-tailed woodrats (*Neotoma cinerea*) were used to reconstruct the diets and ecology of these mammals as well as the paleovegetation and paleohydrology at Cement Creek Cave across the late Quaternary. Results of these analyses indicate that, despite changing climates, plant community composition, location of upper treelines and the growth and recession of nearby alpine glaciers, such factors had minimal impacts on the diet and surface water use of these two species over the past >45,000 years. Instead, tooth enamel $\delta^{13}\text{C}$ was found to contain significant signals of montane plant CO_2 stress, a physiological response to fluctuating levels of atmospheric CO_2 that now appears to have been widespread in western North American plant communities during the late Pleistocene. Together, the stable isotope data suggest a high level of ecological resilience of *M. flaviventris* and *N. cinerea* to climate and environmental changes of late Quaternary magnitude.

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INTRODUCTION

Climate change is an inherent property of Earth history and capable of marked impacts on biological systems. The Quaternary period, or last 2.58 million years (Gibbard et al. 2010), has been a time of repeated fluctuations in climate, as well as in greenhouse gas concentrations, glacial ice volumes and related environmental variables (Fig. 1; Dawson 1992, Wright et al. 1993, Petit et al. 1999, EPICA 2004). While many of the broader impacts of Quaternary environmental changes on terrestrial organisms are characterized (Lundelius et al. 1983, Graham et al. 1996, Hewitt 2000, Blois and Hadly 2009), detailing this knowledge depends largely on the availability and analysis of relevant fossil material. Where coherent Quaternary fossil records exist and can be analyzed alongside the growing body of paleoenvironmental data, it should be possible to gain new insight into specific ecological and evolutionary responses of organisms to past changes. Such knowledge would also provide a framework within which to interpret responses to contemporary perturbations (e.g., Barnosky et al. 2011), among them climate warming.

The fossil record of Cement Creek Cave, Colorado, provides an exceptional opportunity to analyze impacts of Quaternary climate change on mammalian ecology. Cement Creek Cave is located at high elevation (2950m) in the Southern Rocky Mountains of central-southwestern Colorado and contains a rich assemblage of small mammal fossils spanning the late Quaternary, from greater than 45,000 radiocarbon years ago (Ka) to the present (Emslie 2002, unpub.). This record dates from the middle Wisconsin glacial period through the Holocene and represents the richest well-stratified, high-elevation fauna known from this timeframe in North America. As such the cave material helps fill a gap in knowledge of late Quaternary high-elevation mammal communities, which have remained particularly poorly understood across North America due to

a paucity of fossil material (Armstrong 1972, Lundelius et al. 1983, Webb and Betancourt 1990, Emslie 2002).

To date, few studies have documented significant ecological responses of mammal taxa to the various perturbations of the Quaternary, and none have focused on potential responses of high-elevation mammals over the timespan represented in Cement Creek Cave. However, a more complete understanding of high-elevation biotas is important because species living at high elevations are subject to unique environmental, ecological and phenological constraints; they therefore may have been uniquely impacted during episodes of late Quaternary climate change. It is known that late Quaternary environments of the Southern Rocky Mountains were characterized by changing temperatures and precipitation regimes (Barry 1983, Thompson et al. 1993, Brugger 2010), growth and recession of numerous alpine glaciers (Richmond 1986, Pierce 2003, Brugger 2007), fluctuations in treelines 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). Many vertebrate faunas at lower elevations were also reassembled (Lundelius et al. 1983, Harris 1985, Graham et al. 1996, Stafford et al. 1999). However, unlike these other faunas, the small mammal community documented in Cement Creek Cave shows relatively high continuity in species composition and evenness across several periods of late Pleistocene and Holocene climate change (Emslie unpub.). In what ways then, if any, were these species responding ecologically to persist in such a dynamically changing environment?

The goal of this study is to investigate the paleoecology of two montane mammal herbivores, Yellow-bellied marmots (*Marmota flaviventris*) and Bushy-tailed woodrats (*Neotoma cinerea*) from Cement Creek Cave using stable isotope analyses (SIA) of carbon and oxygen in tooth enamel. Specifically, SIA are used to reconstruct the diets and ecology of *M.*

flaviventris and *N. cinerea* across the past >45,000 years and during three distinct climate intervals (middle Wisconsin, late Wisconsin, Holocene) and to test the null hypothesis that these species exhibited no ecological responses to climate change from the middle Wisconsin to the present. *M. flaviventris* (a large, ground-dwelling sciurid) and *N. cinerea* (a rock-dwelling cricetid) are common throughout the cave series and remain prominent members of the mammalian community that characterizes the region today (Armstrong 1972, Fitzgerald et al. 1994, Emslie unpub.); they are thus well suited for examining how climate extremes across the late Quaternary potentially impacted mammal ecology. However, they remain ecologically and evolutionarily distinct and may be capable of adapting quite differently to such perturbations. Stable isotope analyses are also used to make inferences on late Quaternary paleovegetation and paleohydrology around the cave during this period and are interpreted in the context of regional and global paleoenvironmental proxy data as well as the unique paleontological record of Cement Creek Cave.

Tooth Enamel Biogeochemistry and Paleoecological Reconstruction

Stable isotope analyses of fossil vertebrate tissues can provide insight into a multitude of paleoclimatic, paleoenvironmental and paleobiological phenomena and have been used to study diet, ecology, migration, ontogeny and physiology of ancient animals (Koch 2007). Fossil teeth are among the most commonly analyzed mammalian tissues as they are easily preserved, abundant in the fossil record, taxonomically distinctive, and because tooth enamel in particular is highly resistant to diagenesis (Wang and Cerling 1994, Koch et al. 1997). Specifically, the chemical and structural properties of enamel (>95% hydroxyapatite, highly crystalline, large crystal size) render it less susceptible than either 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). It has been demonstrated that enamel is capable of retaining original isotopic signatures on the order of thousands (van der Merwe 1982, Koch et al. 1998, MacFadden et al. 1999) to millions (MacFadden and Cerling 1996, Quade et al. 1992, Thewissen et al. 2007) of years.

Throughout this study, stable isotope signatures are reported follow standard delta (δ) notation, where

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

and R_{sample} and R_{standard} represent ratios of $^{13}\text{C}/^{12}\text{C}$ or $^{18}\text{O}/^{16}\text{O}$ 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; $[\text{Ca}_{10}(\text{PO}_4)_6(\text{OH})_2]$) has a few percent structural carbonate substitutions at both phosphate and hydroxyl sites and is an archive of information on dietary carbon inputs. Bioapatite $\delta^{13}\text{C}$ is mediated foremost by the primary producers that are 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 fractionations which render isotopic profiles of these groups distinguishable (O'Leary 1981; Farquhar et al. 1989; Marshall et al. 2007).

The C_3 (Calvin) pathway is common among terrestrial plants worldwide and is employed by all trees, most shrubs and herbs, and cool-season grasses. C_3 plants exhibit average $\delta^{13}\text{C}$ of –

19‰ relative to atmospheric carbon $\delta^{13}\text{C}$ (Farquhar et al. 1989, Marshall et al. 2007), with the latter currently averaging near -8‰ (Keeling et al. 2005). As a result, median $\delta^{13}\text{C}$ values of modern C_3 plants are -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 a few dicots. C_4 plants assimilate more heavy carbon than C_3 plants; median $\delta^{13}\text{C}$ of their tissues is around -14‰ (range -19 to -9‰ ; Farquhar et al. 1989, Dawson et al. 2002, Marshall et al. 2007). Lastly, the CAM (Crassulacean Acid Metabolism) cycle is used by many succulents and is found least commonly worldwide. CAM plants were likely insignificant portions of late Quaternary mammal diets in the Southern Rockies, although they are used by some species in the American Southwest today (e.g., Vaughan 1990). They exhibit $\delta^{13}\text{C}$ values intermediate between C_3 and C_4 plants, but with characteristic δD enrichments (Marshall et al. 2007).

Environmental variables can influence $\delta^{13}\text{C}$ of plant tissues ($\delta^{13}\text{C}_{\text{plant}}$) and must be considered in isotopic analyses. A number of these variables have been in flux during the late Quaternary. For example, $\delta^{13}\text{C}$ of atmospheric CO_2 ($\delta^{13}\text{C}_{\text{atm}}$) contributes directly to $\delta^{13}\text{C}_{\text{plant}}$ (Farquhar et al. 1989, Marino and McElroy 1991, Arens et al. 2000). It is known that $\delta^{13}\text{C}_{\text{atm}}$ was variable during the late Quaternary (Leuenberger et al. 1992, Marino et al. 1992, Sigman and Boyle 2000) and that it has contributed significantly to $\delta^{13}\text{C}$ of C_3 plants throughout deep geologic time (Arens et al. 2000). Values of $\delta^{13}\text{C}_{\text{atm}}$ have also been historically depleted by emissions from anthropogenic fossil fuel combustion since the Industrial era owing to release of ancient ^{13}C -depleted CO_2 (Keeling et al. 1979). Concentrations of atmospheric CO_2 ($\text{CO}_{2\text{atm}}$), which scaled closely with temperature across the late Quaternary and are increasing alongside global temperatures today (IPCC 2007), can affect stomatal conductance, photosynthetic

performance and $\delta^{13}\text{C}$ in C_3 species (Farquhar et al. 1989, Marshall et al. 2007). Certain microhabitat conditions also affect $\delta^{13}\text{C}_{\text{plant}}$; for example, $\delta^{13}\text{C}$ depletions often occur in plants growing in forested habitats ('canopy effect'; Vogel 1978, Medina and Minchin 1980), likely reflecting at least some utilization of ^{13}C -depleted source air from soil respiration (Farquhar et al. 1989). Alternatively, plants grown in conditions of high irradiance, water stress, or high salinity may experience lowered stomatal conductance and/or photosynthetic rates, lowered fractionations and increases in $\delta^{13}\text{C}_{\text{plant}}$ (Farquhar et al. 1989).

Mammalian bioapatite incorporates the $\delta^{13}\text{C}$ of bulk dietary material and is consistently enriched over these dietary values due to fractionation along the respiration/blood bicarbonate/structural carbonate pathway (Ambrose and Norr 1993, Koch 2007). Diet-bioapatite $\delta^{13}\text{C}$ enrichments between +9.5 and +13‰ are documented for several small to medium-sized rodents and lagomorphs from controlled trials (Ambrose and Norr 1993, Sare et al. 2005, Passey et al. 2005). In the absence of taxon-specific diet-bioapatite fractionation values, I assume $\delta^{13}\text{C}$ enrichments in wild *Marmota* and *Neotoma* of +12.5‰, a value that lies slightly above the average across these trials and may better reflect the dietary physiology of wild rodents (Sare et al. 2005, Koch 2007). Feranec et al. (2010) used a similar enrichment of +12.8‰ for their analysis of middle Pleistocene *Marmota* and Leporinae. Applying this enrichment, an average enamel $\delta^{13}\text{C}$ ($\delta^{13}\text{C}_{\text{enamel}}$) of -16‰ (range -22.5 to -9.5‰) would be expected for either species if consuming pure C_3 diets, while an average $\delta^{13}\text{C}_{\text{enamel}}$ of -1.5‰ (range -6.5 to +3.5‰) would be expected for the same if consuming pure C_4 diets.

Controls on Oxygen Isotopes in Bioapatite

Oxygen in bioapatite is derived from several sources, namely dietary oxygen and inhaled oxygen and water vapor, with exact $\delta^{18}\text{O}$ 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 largely obtained from meteoric (surface) water used for drinking and as contained in plant forage (Bryant and Froelich 1995, Kohn et al. 1996, Koch 2007). The $\delta^{18}\text{O}$ values of meteoric waters are, in turn, modulated by climates and environments, making isotopic analysis of bioapatite a potentially useful tool in paleoclimatology and paleoecology (Luz et al. 1984, Longinelli 1984, Bryant and Froelich 1995, Fricke and O'Neil 1996, Higgins and MacFadden 2004).

Climate and geography exert primary controls on meteoric water $\delta^{18}\text{O}$ values (McGuire and McDonnell 2007). The $\delta^{18}\text{O}$ of meteoric waters is enriched both during warmer seasons and at lower latitudes and altitudes, while being relatively depleted during cooler seasons and at higher latitudes and altitudes (Yurtsever and Gat 1981, Welker 2000, Kohn and Welker 2005, McGuire and McDonnell 2007). The $\delta^{18}\text{O}$ of continental vapor masses and precipitation also typically becomes depleted with distance traveled inland due to fractionation during rainout. Inland precipitation has also been shown to exhibit stronger seasonal $\delta^{18}\text{O}$ fluctuations than in milder coastal areas (Welker 2000, McGuire and McDonnell 2007).

Physiological and ecological characteristics of both herbivores and their dietary plants are important considerations in oxygen isotopic studies. Different mammal taxa exhibit unique relationships between $\delta^{18}\text{O}$ of dietary water and that of bioapatite, which may be partially ascribed to physiological differences in oxygen flux (Luz et al. 1984, Longinelli 1984, Bryant and Froelich 1995, Kohn et al. 1996). Different mammals also vary in water requirements such

that some species consume large quantities of meteoric waters while others obtain most or all dietary water from plant forage (Kohn et al. 1996). It is important in the latter case that plant species exhibit distinct leaf water $\delta^{18}\text{O}$ due variation 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 is a charismatic species of the western United States and is found in a range of open montane and intermontane habitats, such as meadows and talus slopes (Frase and Hoffmann 1980, Hall 1981). In Colorado's Southern Rocky Mountains *M. flaviventris* occurs at nearly all elevations in both mesic and xeric areas where suitable bouldery substrate is found (Armstrong 1972, Fitzgerald et al. 1994). Remains of *M. flaviventris* are common throughout Cement Creek Cave and the species is common in the region today, indicating it has been a persistent faunal element at this high-elevation site since at least the middle Wisconsin period.

The ecology and life history of *Marmota flaviventris* is unique and well studied, and this provides a useful background for paleoecological study of the species. *M. flaviventris* in the Southern Rockies consumes a diet of grasses, forbs, and flowers (Frase and Hoffmann 1980). Like many ground squirrels it is semifossorial and spends large portions of each year in hibernation; its phenology is thus strictly patterned and includes a single annual spring reproductive event (Andersen et al. 1976, Frase and Hoffmann 1980, Fitzgerald et al. 1994). Marmots possess a sciurid dental formula with moderately high-crowned and rooted molariform

teeth, and post-weaning teeth are still being formed during late summer precisely when individuals are sampling large amounts of plant material in preparation for hibernation.

Woodrats (Cricetidae: *Neotoma*) are distributed across much of North America and reach highest species diversity in Mexico and the southwestern United States (Hall 1981, Vaughan 1990). As a group they are already responsible for large contributions to late Quaternary paleoecology from preservation of their accumulated middens. Contents of *Neotoma* paleomiddens have yielded time-transgressive insights into late Quaternary environmental and ecological change across western North America (Betancourt et al. 1990). This represents a rich body of knowledge to which SIA of *Neotoma* fossils, thus far lacking, would likely prove complementary.

The Bushy-tailed woodrat (*Neotoma cinerea*) occurs widely across western North America in a variety of habitats (Hall 1981, Vaughan 1990, Smith 1997). It is, however, the most boreal-adapted of its congeners, and the largest-bodied (Hall 1981, Smith 1997). In Colorado, modern *N. cinerea* is documented from most elevations and across several life zones, with local presence probably limited more by availability of suitable rocky nesting substrates than specific environmental or dietary preferences (Finley 1958, Armstrong 1972, Fitzgerald et al. 1994). Similar to *Marmota flaviventris*, Bushy-tailed woodrats are common throughout Cement Creek Cave and have remained a persistent element of the high-elevation fauna at this site throughout the late Quaternary.

Neotoma cinerea is a generalist herbivore (Vaughan 1990, Fitzgerald et al. 1994) with unique adaptations for a varied low quality plant diet, specifically a cricetid dental formula with rooted, high-crowned molar teeth. *N. cinerea* is active year-round, and though its phenology is not as strict as that of *Marmota flaviventris* the species usually reproduces once or twice in the

spring and summer months at higher elevations (Fitzgerald et al. 1994), providing some seasonal constraint on enamel isotopic signatures. Diets are comprised mostly of plants growing near nesting sites (although exceptions exist, see Smith 1997), and across Colorado appear flexible, including material from evergreen and coniferous trees, shrubs and forbs, among other plants, as available (Finley 1958). This dietary flexibility quite possibly allowed *N. cinerea* to adapt to a range of late Quaternary vegetation types found around the cave.

MATERIALS AND METHODS

Cement Creek Cave Stratigraphy and Dating

Cement Creek Cave (Fig. 2) is located south of the Elk Mountain Range in the East River valley, and occupies a section of limestone outcrop situated above Cement Creek, a tributary to the East River. Sediment deposition in the cave is attributed largely to the activity of woodrats (*Neotoma*) and possibly also to small carnivores (Mustelidae), a pattern reinforced by the limited accessibility of the cave entrance. Two separate excavations have been conducted in Cement Creek Cave to date, in 1998 and 2007 (Emslie 2002, unpub.).

Fossil material analyzed herein is from excavation of a 1x1.5m pit in a small room inside the cave (Test Pit 2, Northeast Extension). This pit consisted of forty 5cm levels and reached a total depth of 2.2m below the surface. Radiocarbon dates obtained from faunal specimens from this pit as well as an adjacent excavated pit ($N=27$ unique dates from 19 levels) indicate the upper two-thirds of cave strata (Levels 1-27) are in reasonably good chronological order and record mostly continuous deposition spanning from at least 45Ka to the present. 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.

An age-depth model was developed by fitting the series of 27 ^{14}C dates with a cubic smoothing spline function using the statistical computing program R (Fig. 3; R Development Core Team 2011). The default smoothing parameter value was used ($spar=0.609$), which in R was calculated by initially assigning a computational value λ to the dataset maximized via generalized cross-validation methods. The model contains no age reversals and captures the major trends in depositional rates in the cave, which were slower during the cooler late Wisconsin (specifically surrounding the last glacial maximum (LGM)) but higher during both the middle Wisconsin and Holocene. With this model, ages were interpolated for those upper cave levels (Levels 1–27) without associated ^{14}C dates ($n=8$) and extrapolated for older undated levels (Levels 28–40). However, extrapolation beyond levels of known age often involves high uncertainty and this is treated further below.

Late Quaternary age boundaries used herein were derived entirely from geochronological data (versus, for instance, biochronological data). The middle Wisconsin is dated 65–35Ka in accord with glaciations in North America and the Rocky Mountains (Richmond 1986, Richmond and Fullerton 1986, Pierce 2003) and corresponds with Marine Isotope Stage (MIS) 3. The late Wisconsin is dated 35–10Ka following Richmond and Fullerton (1986) and corresponds with MIS 2. Both periods are distinct features of deep-sea sediment (Bond et al. 1993, Kennett 1995) and ice (Petit et al. 1999, NGRIP 2004) cores. The Pleistocene-Holocene boundary is dated at 10Ka (though it likely began earlier in the Northern Hemisphere; Walker et al. 2009). Lastly, as it is not unambiguous from geological data when the LGM occurred either locally or in the Southern Rocky Mountains as a whole (Richmond 1986, Pierce 2003, Licciardi et al. 2004, Brugger 2007), an LGM date between 20–18Ka is assumed.

Samples were partitioned into age bins as follows, informed by both the ^{14}C record and age-depth model. Modern specimens (see below) along with Levels 1–14 are assigned as Holocene (HOL), Levels 19–23 as late Wisconsin (LW), and Levels 28–35 as middle Wisconsin age (MW). These divisions are considered conservative as they exclude a number of intermediary levels due to either marginal model ages or a ^{14}C date indicating mixing of sediments from different periods. Also, sediments older than Level 35 are excluded based on the uncertainty inherent in age extrapolation, though they are likely of middle Wisconsin age as well; these levels are instead considered individually. Throughout, abbreviations (MW, LW, HOL) are used specifically in reference to the above age bins, while any established geochronological divisions are spelled out in full.

Sample Selection, Processing, Calibration and Analysis

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

Body tissues that form while juvenile mammals are nursing are isotopically reflective of a maternally-derived milk diet, and for those tissues with little to no compositional turnover (e.g., tooth enamel) this isotopic signal is retained throughout life. Thus, ecological investigations

using isotopic signatures of 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) and other tooth positions were included as necessary (I, M1, M2). Since marmot incisors are ever-growing, the few sampled incisors also record post-weaning isotopic signatures; relative widths of these incisors suggested they were of adult age (Munson 1984).

The first two molar teeth of *Neotoma cinerea* are formed nearly simultaneously while nursing (Finley 1958), along with portions of the third, and this may preclude incorporation of ‘pure’ post-weaning ecological information in woodrat tooth enamel. However, since isotopic fractionations proceed at nearly constant rates between environment and female mammals and their young, woodrat molar enamel remains a theoretically useful archive of paleoecological information. Sampling was largely restricted to first upper and lower molars of *N. cinerea* (~95% of samples) which allowed a sufficient amount of enamel to be collected while minimizing the variation typically found along the mammalian toothrow due to ontogeny.

In addition to fossil analyses, a series of modern samples was assembled from field-collected and museum specimens. Seven *Neotoma cinerea* were collected immediately below Cement Creek Cave and three *Marmota flaviventris* were collected <1 mile west of the cave. These samples allow direct comparisons to fossil specimens found in the cave. In addition, teeth from eleven specimens of *M. flaviventris* collected in the Upper Gunnison Basin, Colorado (UGB) since 1973 were also analyzed. Collection localities of all modern marmots used in this study ($N=14$) lie on a broad transect running nearly north-south through the UGB and passing alongside Cement Creek Cave (Fig. 2). The samples span an elevational gradient from approximately 2350m to 3350m and represent individuals living in the several dominant habitat types currently found throughout this region. All field-collected specimens were obtained in

2009 and 2010 following protocols approved by the UNCW Institutional Animal Care and Use Committee, and whole teeth from museum specimens were obtained with permission from intact crania or mandibles housed in biological collections of the Rocky Mountain Biological Laboratory (Gothic, Colorado) and Western State College (Gunnison, Colorado).

Pure enamel was isolated from all teeth using a NSK Ultimate XL dental micromotor (NSK America Corp., Schaumburg, IL, USA) fitted with a carbide tip sized between 0.3 and 0.5mm. Enamel fragments were then ground to a fine powder using a mortar and pestle. Chemical treatment of all samples followed a protocol of Koch et al. (1997). Enamel powder was treated with 30% hydrogen peroxide (H_2O_2) for 24 hours to remove organic material. Afterwards all H_2O_2 was decanted and powders were rinsed three times with deionized (DI) water and isolated via microcentrifugation. Powders were treated for an additional 24 hours with 0.1M acetic acid (CH_3COOH) 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 hours. 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. All samples were roasted under vacuum prior to analysis at 375°C for 0.5hr, then reacted at 90°C in a common H_3PO_4 bath to yield CO_2 . Average precision of measured carbon and oxygen isotope ratios was ± 0.04 and 0.06‰ , respectively, and all values are reported relative to the VPDB standard.

The systematic decrease in $\delta^{13}\text{C}_{\text{atm}}$ due to anthropogenic fossil fuel combustion since the pre-Industrial era (aka Suess effect) now totals between 1.5-2.0‰ (Keeling et al. 1979, Marino and McElroy 1991, Keeling et al. 2005). To account for this, corrections were applied to all modern samples with yearly precision using measurements of $\delta^{13}\text{C}_{\text{atm}}$ taken since 1979 (Keeling

et al. 1979, Keeling et al. 2005) in combination with pre-Industrial records of $\delta^{13}\text{C}_{\text{atm}}$ from Antarctic ice core data (Friedli et al. 1986, Francey et al. 1999). Samples were first corrected to 1979 levels using $\delta^{13}\text{C}_{\text{atm}}$ measurements from Station La Jolla, California, and then further corrected to account for the modern difference in $\delta^{13}\text{C}_{\text{atm}}$ between North and South Poles. Next, an additional 1.4‰ was added as a correction to pre-Industrial values observed in Antarctic ice. Total $\delta^{13}\text{C}$ corrections for all specimens ranged between +1.40 and +1.98‰. Several samples (*Marmota*, $n=3$) had unknown collection dates and to these a total correction of +1.45‰ was applied, which assumes a mid-1980's collection date for these specimens.

Failure of some age bins to meet assumptions of normality required nonparametric methods to be used for 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 explained significant $\delta^{13}\text{C}$ variation in both *Marmota* (Kruskal-Wallis rank sum, $X^2=46.92$, $P<<0.01$) and *Neotoma* (Fig. 5; $X^2=30.95$, $P=0.01$). The $\delta^{13}\text{C}$ data (Figs. 4 and 5) and pairwise cave level comparisons (Student's t-tests; Tables 1 and 2) indicate consistent differences between Holocene and Pleistocene levels. Modern *Marmota* $\delta^{13}\text{C}$ was depleted relative to all Pleistocene levels ($P<0.05$), and modern *Neotoma* $\delta^{13}\text{C}$ was depleted relative to all Pleistocene levels except 15 ($P<0.02$). Middle Holocene (Level 11; Level 12 excluded due to small sample size) $\delta^{13}\text{C}$ was indistinguishable from modern values in both taxa and similarly depleted relative to multiple Pleistocene levels (*Marmota*, 9 of 15 levels, $P\leq 0.04$; *Neotoma*, 7 of 15 levels, $P\leq 0.04$). Some other patterns were observed in *Marmota* from oldest cave levels;

specifically, Levels 36 and 40 were enriched over both an intervening level (39; $P \leq 0.02$) and over four and two MW levels, respectively ($P \leq 0.05$).

Unlike for carbon signatures, cave levels did not account for significant amounts of variation in $\delta^{18}\text{O}$ in either *Marmota* ($X^2=22.30$, $P=0.17$) or *Neotoma* ($X^2=12.06$, $P=0.74$). Few significant $\delta^{18}\text{O}$ differences were found among cave levels in either species (Figs. 4 and 5, Tables 1 and 2), but these included enrichments in both modern and early LW (Level 20) *Marmota* $\delta^{18}\text{O}$ over three of five MW levels (28, 30, 35; $P < 0.04$). Few differences and no patterns in $\delta^{18}\text{O}$ were observed among *Neotoma* from different cave levels.

When data were pooled into MW, LW and HOL age bins, *Marmota* $\delta^{13}\text{C}$ differed significantly among each bin (Wilcoxon rank sum, $P < 0.03$) with LW values most enriched, HOL values most depleted, and MW intermediate (Fig. 6). *Neotoma* $\delta^{13}\text{C}$ differed between each Wisconsin bin and the Holocene ($P < 0.01$), with HOL values again most depleted. Among enamel $\delta^{18}\text{O}$ signatures, the only significant difference that emerged was enrichment of HOL over MW *Marmota* ($P < 0.01$); *Neotoma* $\delta^{18}\text{O}$ was invariant among age bins. In support of the *a priori* delineation of age bins, relatively few intra-bin differences were observed for either isotope system.

Lastly, comparisons were made to illuminate any interspecies variation which might be indicative of ecological or physiological differences. Values of $\delta^{13}\text{C}$ were indistinct between species when modern and fossil specimens were pooled (Welch two sample test, $P=0.38$) while $\delta^{18}\text{O}$ was marginally higher in *Marmota* than *Neotoma* ($P=0.056$). Comparisons among the three age bins revealed no significant differences between species in either $\delta^{13}\text{C}$ or $\delta^{18}\text{O}$, although $\delta^{13}\text{C}$ of MW *Neotoma* was marginally more enriched than *Marmota* $\delta^{13}\text{C}$ from this same period ($P=0.051$).

DISCUSSION

Carbon Composition of Herbivore Enamel

The $\delta^{13}\text{C}$ signatures of ancient herbivore tissues have proven invaluable not only for reconstructing species' diets and ecology, but for revealing major episodes of C_3/C_4 turnover correspondent with ancient environmental change and contributing to a global paleochronology of C_4 grass expansion during the Cenozoic (Ehleringer et al. 1997, Cerling et al. 1997). Notable C_4 expansions occurred as recently as the last glacial period on some continents (Aucour et al. 1994, Street-Perrott et al. 1997, Huang et al. 1999) and are attributed to competitive advantages of C_4 plants under conditions of lowered $\text{CO}_{2\text{atm}}$. However, no evidence was found that *Marmota flaviventris* or *Neotoma cinerea* from Cement Creek Cave consumed significant amounts of C_4 plants. Although the possibility of a local late Pleistocene C_4 increase cannot be fully excluded, the data suggest that C_3 plants have dominated the flora at this high-elevation site since the MW, just as they do today. This scenario of C_3 dominance is in agreement with the perceived advantage of C_3 plants at high latitudes and altitudes (Teeri and Stowe 1976) as well as model and isotopic data which suggest that a late Pleistocene C_4 expansion was 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).

Instead of dietary shifts in *Marmota* and *Neotoma*, observed temporal patterns in $\delta^{13}\text{C}$ are consistent with adverse effects of lowered Pleistocene $\text{CO}_{2\text{atm}}$ on the physiology of montane C_3 plants comprising herbivore diets. Lowered $\text{CO}_{2\text{atm}}$ generally reduces the ability of plant stomata to supply CO_2 sufficient for optimal photosynthetic rates and the photosynthetic reaction as a result becomes increasingly CO_2 -limited (O'Leary 1981, Farquhar et al. 1989, Sage and Coleman 2001, Marshall et al. 2007). C_3 plants grown under CO_2 stress typically exhibit lowered

concentrations of intracellular CO₂ and decreased ¹³C fractionation, leading to systematic δ¹³C enrichment of photosynthate and plant tissues (Farquhar et al. 1989). Direct evidence for this type of response to low late Pleistocene CO_{2atm} has been observed in fossils of both limber pine (*Pinus flexilis*) from the American southwest spanning the past 30,000 years (Van de Water et al. 1994) and juniper (*Juniperus*) from Rancho La Brea, California, which span the past 50,000 years (Ward et al. 2005).

Enrichments in δ¹³C_{enamel} during both MW and LW relative to HOL for both taxa are statistically significant and record montane plant response to levels of Pleistocene CO_{2atm} around 180-200 parts per million (ppm) followed by rapid increase to Holocene, pre-Industrial levels of ~280ppm (Leuenberger et al. 1992, Francey et al. 1999, Petit et al. 1999). The δ¹³C_{enamel} data also record subtler responses to changing CO_{2atm} prior to the Pleistocene-Holocene transition, thus tracking CO_{2atm} and temperature instabilities which were common features of the last glacial period (Bond et al. 1993, Dansgaard et al. 1993, NGRIP 2004). LW δ¹³C_{enamel} values average more enriched than MW values (though only significantly in *Marmota*), a result of elevated temperature and CO_{2atm} during portions of the middle Wisconsin followed by a global CO_{2atm} minimum surrounding the LGM. Additionally, *Marmota* from the oldest Cement Creek Cave sediments (Levels 36–40) exhibit significant intralevel differences, a pattern consistent with pronounced CO_{2atm} and temperature fluctuations between 60–40Ka associated with Dansgaard-Oeschger (D-O) and Heinrich events in the Northern Hemisphere (Fig. 1; Bond et al. 1993, Dansgaard et al. 1993, NGRIP 2004). The modeled ages of these levels (53–48Ka) place them securely within this timeframe, supporting a CO₂ teleconnection between continental North America and the North Atlantic during these events and resultant montane plant physiological response. These isotopic patterns support a middle Pleistocene age for the oldest Cement Creek

Cave sediments; however, it remains speculative to match these oldest levels with specific D-O or Heinrich events due to age uncertainties.

Little evidence exists on the exact composition of plant communities in the Southern Rockies during the middle Wisconsin, but it is known that temperatures were mild enough to contribute to retreat of early Wisconsin glaciers in the region (Richmond 1986, Pierce 2003). Conversely, the record of late Wisconsin plant communities for this same region is comparatively rich and provides strong evidence of a no-analog sagebrush steppe-tundra which dominated high-elevation environments (Legg and Baker 1980, Markgraf and Scott 1981, Thompson et al. 1993, Fall 1997). Such an assemblage likely occurred around Cement Creek Cave, which at the time was located above upper treeline and in proximity to alpine glaciers in the region (Fall 1997, Brugger 2007, 2010). The $\delta^{13}\text{C}_{\text{enamel}}$ values in the present study fall within the expected range for herbivores living in open or xeric environments (MacFadden and Cerling 1996), and similarity of $\delta^{13}\text{C}_{\text{enamel}}$ values between MW and LW apart from the aforementioned $\text{CO}_{2\text{atm}}$ effects is consistent with dominance of open alpine steppe vegetation at Cement Creek Cave throughout the period. This assertion is further supported by an abundance of characteristic steppe (*Lemmyscus*, *Uroditellus*) and alpine (*Phenacomys*, *Ochotona*) mammal taxa throughout MW and LW cave sediments as well as absence of obligate forest taxa (*Tamiasciurus*, *Myodes*) prior to the latest Wisconsin (Emslie unpub.). If milder conditions during the middle or early late Wisconsin did contribute to higher treelines or increased densities of arboreal plants near this site, as could be inferred from a few marginal high-elevation pollen sequences (Wright et al. 1973, Legg and Baker 1980), it was probably only as open parkland and did not contribute to significant changes in the habitat or diets of either *Marmota* or *Neotoma* living in the vicinity.

The Pleistocene-Holocene transition is the dominant event recorded in herbivore enamel from Cement Creek Cave. Pollen records indicate post-LGM warming contributed to regional paleovegetative change including contraction of high-elevation steppe-tundra assemblages, formation of denser montane forests and ascension of upper treelines between 300 and 700m (Legg and Baker 1980, Markgraf and Scott 1981, Fall 1997). Concomitant depletions in median $\delta^{13}\text{C}_{\text{enamel}}$ values are approximately 2.0 and 2.3‰ for *Marmota* and *Neotoma*, respectively, between LW and HOL age bins. Though interpreted as a result of plant physiological response to surging $\text{CO}_{2\text{atm}}$, the figures are more substantial than the $\sim 1.5\text{‰}$ depletion between the late Wisconsin and Holocene observed in *Pinus flexilis* needles and attributed to CO_2 stress by Van de Water et al. (1994). They are also greater than changes of the same direction recorded in $\delta^{13}\text{C}$ of bone collagen from dire wolves (*Canis dirus*), bison (*Bison antiquus*) and several other megaherbivore taxa from Rancho La Brea (Coltrain et al. 2004, Bump et al. 2007). However, the latter records do not extend to 10Ka. If the discrepancy between fossil plant data and those of the present study is real, it possibly reflects the increased water use efficiency of high-altitude plants (Marshall et al. 2007), a physiological adaptation which could have contributed to more significant reductions in stomatal conductance and increases in $\delta^{13}\text{C}_{\text{plant}}$ during the late Wisconsin as compared to lower-elevation forms. Marshall and Zhang (1994) found that woody plant ^{13}C discrimination decreased by $\sim 1.2\text{‰}$ with each km increase in altitude due to higher water use efficiencies. However, an equally plausible explanation is that plant foods of *Marmota* and *Neotoma* were water-stressed during a late Wisconsin with a more arid growing season, driving increases in $\delta^{13}\text{C}_{\text{plant}}$. Some paleoecological reconstructions include reduced summer precipitation during this period (Fall 1997). Confidently distinguishing between these two hypotheses is not yet fully possible.

The patterns of $\delta^{13}\text{C}_{\text{enamel}}$ change between MW/LW and HOL which are observed in this study are not inconsistent with a canopy effect induced by Holocene forests on $\delta^{13}\text{C}$ of herbivore forage. I note the $\delta^{13}\text{C}$ values of *Marmota* and *Neotoma* in this study are only $\sim 1\text{‰}$ more enriched than those measured in bone apatite of modern red-backed voles (*Myodes gapperi*) from spruce-fir forests in Alberta, Canada (Sare et al. 2005). However, the nature of the modern environment immediately surrounding Cement Creek Cave discounts a canopy effect hypothesis. This habitat consists mostly of steppe and scattered conifers growing on arid soils, and although dense subalpine forest does grow discontinuously in the region, these factors render the possibility of canopy effects on our modern samples unlikely and thus inadequate for explaining lowered HOL $\delta^{13}\text{C}_{\text{enamel}}$. Furthermore, because modern $\delta^{13}\text{C}_{\text{enamel}}$ is statistically indistinct from Level 11, the best-sampled Holocene cave level, a canopy effect probably does not explain depletions in any HOL samples. Thus, while additional work is necessary to refine the nature of canopy effects in temperate ecosystems, $\delta^{13}\text{C}_{\text{enamel}}$ patterns between MW/LW and HOL samples in this study are best explained as a function of the enhanced physiological responses of high-elevation plants to Quaternary $\text{CO}_{2\text{atm}}$ instead of a major change in canopy cover or herbivore resource use.

Oxygen Composition of Herbivore Enamel

Given the several temperature and precipitation changes proposed for the western U.S. during and after the Wisconsin period, it is interesting that few $\delta^{18}\text{O}_{\text{enamel}}$ patterns were found among time bins in either species. However, different physical factors (origin, seasonality and type of precipitation) could have confounding effects on meteoric water $\delta^{18}\text{O}$ (McGuire and McDonnell 2007), so observations of the present study may not by themselves support static late

Quaternary seasonality and precipitation regimes. Significant $\delta^{18}\text{O}_{\text{enamel}}$ depletion in MW relative to HOL *Marmota* may reflect cooler temperatures or, alternatively, intake of dietary waters originating from waning early Wisconsin glaciers (Richmond 1986, Pierce 2003). On the other hand, LW $\delta^{18}\text{O}_{\text{enamel}}$ values are not distinct from MW and HOL in either species, an unexpected result since late Wisconsin conditions were characterized by reduced summer and annual temperatures (Legg and Baker 1980, Barry 1983, Thompson et al. 1993, Fall 1997), possibly reduced summer precipitation (Fall 1997), and extension of large alpine glaciers to within ~10km of the cave (Brugger 2010).

A weak pattern in both species is depletion of $\delta^{18}\text{O}_{\text{enamel}}$ in the interval between the LW (specifically, Level 20) and the beginning of the Holocene. How this trend is best interpreted in a meteoric framework is not entirely clear, but results are consistent with inputs of ^{18}O -depleted snowmelt from regional deglaciation after the LGM. A similar decrease is seen in *Marmota* between Levels 35-40, possibly a reflection of analogous surface water inputs from early Wisconsin glaciers. An alternative explanation is that these $\delta^{18}\text{O}_{\text{enamel}}$ depletions were modulated by physiological responses of montane plants to changing $\text{CO}_{2\text{atm}}$, as is observed in $\delta^{13}\text{C}_{\text{enamel}}$. 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 $\text{CO}_{2\text{atm}}$ and/or other variables like increased summer aridity (Fall 1997), then leaf water $\delta^{18}\text{O}$ would have been elevated as a result and potentially also recorded in herbivore enamel.

It has been suggested that larger-bodied mammals which are obligate drinkers record $\delta^{18}\text{O}$ of meteoric waters more faithfully than smaller taxa (e.g., Bryant and Froelich 1995) and it remains possible that the absence of strong temporal signals in $\delta^{18}\text{O}$ of *Marmota* and *Neotoma*

enamel is simply a consequence of the limited extent and scope with which these taxa sample such waters. Also, the time required for molariform tooth formation generally decreases with taxon size, and this necessarily decreases the amount of paleohydrological information recorded in a single small mammal tooth. On the other hand, data from modern *Marmota* seem to indicate that molariform teeth actually are capable of recording broad elevational trends in surface water $\delta^{18}\text{O}$ (McLean unpub.). It is obvious that additional work will be necessary to distinguish if any of the $\delta^{18}\text{O}_{\text{enamel}}$ trends in the fossil data are real and, if so, how they are best explained.

Comparative Paleoecology and Broader Implications

Stable isotope analyses of tooth enamel fail to reveal any major changes in the diets or surface water use of high-elevation *Marmota flaviventris* or *Neotoma cinerea* over the past >45,000 years around Cement Creek Cave, Colorado. Across both carbon and oxygen isotopes and in the context of this study, *Marmota* appears to be a more sensitive paleoecological indicator than *Neotoma*. This sensitivity is attributed mostly to the dental morphology and strict phenology of marmots, which conspire to ensure post-weaning molariform teeth are being formed in summer when plant responses to $\text{CO}_{2\text{atm}}$ and aridity and, consequently, variation in $\delta^{13}\text{C}_{\text{plant}}$ and leaf water $\delta^{18}\text{O}$ are most likely to occur. In most cases, $\delta^{13}\text{C}_{\text{enamel}}$ and $\delta^{18}\text{O}_{\text{enamel}}$ signatures were similar between species, but this should not be taken to indicate a total lack of interspecific dietary or physiological differences as only pre-weaning molars of *Neotoma* were analyzed. It is currently unknown how $\delta^{13}\text{C}$ of post-weaning bioapatite in *Neotoma* would compare to that of *Marmota*. However, the marginally significant $\delta^{18}\text{O}_{\text{enamel}}$ enrichment of *Marmota* over *Neotoma* does support observations on marmots by Feranec et al. (2010). Though this is probably a result of real physiological differences, the trend is not completely inconsistent

with late summer effects on plant waters consumed by marmots (e.g., due to precipitation $\delta^{18}\text{O}$ - or leaf $\delta^{18}\text{O}$ -enrichment).

The ecological resilience of marmots and woodrats reported herein compliments data on small mammals from nearby Porcupine Cave, located in central Colorado and at a nearly identical elevation (2900m), which is reported to represent the largest collection of middle Pleistocene vertebrate fossils in North America. The deposits date between >600Ka and ~1 million years ago and are representative of at least two glacial-interglacial cycles (Barnosky 2004, Barnosky et al. 2004). Analysis of enamel $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ from *Marmota* spp. and unidentified leporid spp. from this site similarly revealed that resource use of these taxa was not demonstrably affected by climate changes during the middle Pleistocene (Feranec et al. 2010). The inability of the Porcupine Cave study to identify subtler isotopic variation among glacial-interglacial periods (e.g., due to $\text{CO}_{2\text{atm}}$ effects on local plants) likely speaks to the tight stratigraphic control available with the Cement Creek Cave series.

Finally, the Cement Creek Cave results provide a richer context within which to understand patterns of small mammal community stability which have been observed at this site across the late Quaternary (Emslie unpub.). Specifically, this stability may be the result of unique ecological adaptations of these mammals - like patterns of diet and water use – which permit existence in alpine environments. Conservation of the dietary niche in *Marmota flaviventris* and *Neotoma cinerea* across the late Quaternary suggests these species are remarkably well-adapted to life in such environments, and similar reasoning may explain the late Quaternary persistence of other species in this high-elevation small mammal community as well. Since alpine environments were probably common features of the Southern Rockies during the Pleistocene due to the number and length of glacial periods, they likely have been significant

forces operating in the evolutionary histories of these populations. However, these same environments and the species they support are now among those most acutely threatened by contemporary climate warming, the rate of which exceeds that observed at anytime during the glacial-interglacial cycles of the late Quaternary. The insights gained in this study, along with the increasingly coherent Pleistocene paleontological and paleoecological record of the Southern Rocky Mountains region, indicate that the future persistence of high-elevation small mammals here and elsewhere may be a function of the extent to which current changes exceed those of the past >45,000 or even 1 million years.

CONCLUSIONS

Stable carbon and oxygen isotope analyses of tooth enamel were used to investigate the paleoecology of two mammalian herbivores, *Marmota flaviventris* and *Neotoma cinerea*, from the late Quaternary fossil record of Cement Creek Cave, Colorado. This work provides the first such record of the ecology of high-elevation small mammals over the past >45,000 years known from North America. Results of these analyses reveal that the major climate and environmental changes that characterized the Southern Rocky Mountains during the late Quaternary caused no major shifts in the diet and water use of these two species. Temporal patterns in tooth enamel $\delta^{13}\text{C}$ were observed, however, and attributed to physiological responses of montane plants to fluctuating levels of $\text{CO}_{2\text{atm}}$. This extends the geographic record of this type of plant response to late Quaternary $\text{CO}_{2\text{atm}}$, suggesting the phenomenon was widespread among western North American plant communities. The ecological resilience of *M. flaviventris* and *N. cinerea* documented here is likely a mechanism behind their late Quaternary persistence around Cement Creek Cave, and may also explain the high levels of species continuity and evenness previously

observed in the Cement Creek Cave small mammal community. These findings contribute to a valuable time-transgressive framework within which observed responses of high-elevation species and ecosystems to contemporary climate change might be better understood.

LITERATURE CITED

- Ambrose, S. and 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. *Prehistoric Human Bone: Archaeology at the Molecular Level*. (J. Lambert and G. Grupe, eds.), pp. 1-37. Springer-Verlag, Berlin, Germany.
- Andersen, D.C., Armitage, K.B. and Hoffmann, R.S. (1976) Socioecology of marmots: female reproductive strategies. *Ecology*, 57, 552-560.
- Arens, N.C., Jahren, A.H. and Amundson, R. (2000) Can C₃ 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. and Bonnefille, R. (1994) Late Quaternary biomass changes from ¹³C 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, California.
- Barnosky, A.D., Bell, C.J., Emslie, S.D., Goodwin, H.T., Mead, J.I., Repenning, C.A., Scott, E. and 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.
- Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B. and Ferrer, E.A. (2011) Has the Earth's sixth mass extinction already arrived? *Nature*, 471, 51-57.
- Barry, R.G. (1983) Late-Pleistocene Climatology. *Late-Quaternary Environments of the United States, Vol. 1*. (S.C. Porter, ed.), pp. 390-407. University of Minnesota Press, Minneapolis, Minnesota.
- Betancourt, J.L., Van Devender, T.R. and Martin, P.S. (eds.). (1990) *Packrat Middens: The Last 40,000 Years of Biotic Change*. The University of Arizona Press, Tucson, Arizona.
- Blois, J.L. and Hadly, E.A. (2009) Mammalian response to Cenozoic climatic change. *Annual Review of Earth and Planetary Sciences*, 37, 181-208.
- Bond, G., Broecker, W., Johnsen, S.J., McManus, J., Labeyrie, L., Jouzel, J. and Bonani, G. (1993) Correlations between climate records from North Atlantic sediments and Greenland ice. *Nature*, 365, 143-147.
- 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.
- Brugger, K.A. (2007) Cosmogenic ¹⁰Be and ³⁶Cl ages from late Pleistocene terminal moraine complexes in the Taylor River drainage basin, central Colorado, USA. *Quaternary Science Reviews*, 26, 494-499.
- Bryant, J.D. and 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. and 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, 2471-80.
- Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V. and Ehleringer, J.R. (1997) Global vegetation change through the Miocene/Pliocene boundary. *Nature*, 389, 153-158.
- Collatz, G.J., Berry, J.A. and Clark, J.S. (1998) Effects of climate and atmospheric CO₂ partial pressure on the global distribution of C₄ 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. and 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. and Quade, J. (1998) Late Pleistocene C₄ plant dominance and summer rainfall in the southwestern United States from isotopic study of herbivore teeth. *Quaternary Research*, 50, 179-193.
- 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. and Bond, G. (1993) Evidence for general instability of past climate from a 250-kyr ice-core record. *Nature*, 364, 218-220.
- Dawson, A.G. (1992) *Ice Age Earth: Late Quaternary Geology and Climate* (K Richards, ed.). Routledge, New York, New York.

- Dawson, T.E., Mambelli, S., Plamboeck, A.H., Templer, P.H. and 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. and 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. and 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.
- EPICA Members. (2004) Eight glacial cycles from an Antarctic ice core. *Nature*, 429, 623-628.
- 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. and 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. and 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 Jr., 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. and Armstrong, D.M. (1994) *Mammals of Colorado*. Denver Museum of Natural History and University Press of Colorado, Niwot, Colorado.
- Francey, R.J., Allison, C.E., Etheridge, D.M., Trudinger, C.M., Enting, I.G., Leuenberger, M., Langenfelds, R.L., Michel, E. and Steele, L.P. (1999) A 1000-year high precision record of $\delta^{13}\text{C}$ in atmospheric CO_2 . *Tellus*, 51B, 170-193.
- Frase, B.A. and Hoffmann, R.S. (1980) *Marmota flaviventris*. *Mammalian Species*, 135, 1-8.
- Fricke, H.C. and O'Neil, J.R. (1996) Inter- and intra-tooth variation in the oxygen isotope composition of mammalian tooth enamel phosphate: implications for palaeoclimatological and palaeobiological research. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 126, 91-99.
- Friedli, H., Lotscher, H., Oeschger, H., Siegenthaler, U. and Stauffer, B. (1986) Ice core record of the $^{13}\text{C}/^{12}\text{C}$ ratio of atmospheric CO_2 in the past two centuries. *Nature*, 324, 234-238.
- Gibbard, P.L., Head, M.J., Walker, M.J.C. and the Subcommission on Quaternary Stratigraphy. (2010) Formal ratification of the Quaternary System/Period and the Pleistocene Series/Epoch with a base at 2.58 Ma. *Journal of Quaternary Science*, 25, 96-102.
- Graham, R.W., Lundelius Jr., E.L., Graham, M.A., Schroeder, E.K. and 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, New York.
- Harris, A.H. (1985) *Late Pleistocene Vertebrate Paleocology of the West*. University of Texas Press, Austin, Texas.
- Helliker, B.R. and 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.
- Hendy, I.L. and Kennett, J.P. (2000) Stable Isotope Stratigraphy and Paleoclimatology of the Last 170 K.Y.: Site 1014, Tanner Basin, California. *Proceedings of the Ocean Drilling Program, Scientific Results, Vol. 167*. (M. Lyle, I. Koizumi, C. Richter and T.C. Moore, Jr., eds.), pp. 129-140.
- Hewitt, G. (2000) The genetic legacy of the Quaternary ice ages. *Nature*, 405, 907-913.
- Higgins, P. and MacFadden, B.J. (2004) "Amount Effect" recorded in oxygen isotopes of late glacial horse (*Equus*) and bison (*Bison*) teeth from the Sonoran and Chihuahuan deserts, southwestern United States. *Palaeogeography Palaeoclimatology Palaeoecology*, 206, 337 - 353.
- Holmgren, C.A., Norris, J. and 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. and 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. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller, eds.). Cambridge University Press, Cambridge, United Kingdom and New York, New York.

- Keeling, C.D., Mook, W.G. and Tans, P.P. (1979) Recent trends in the $^{13}\text{C}/^{12}\text{C}$ 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. and Meijer, H.A. (2005) Atmospheric CO_2 and $^{13}\text{CO}_2$ Exchange with the Terrestrial Biosphere and Oceans from 1978 to 2000: Observations and Carbon Cycle Implications. *A History of Atmospheric CO_2 and its Effects of Plants, Animals, and Ecosystems*. (J.R. Ehleringer, T.E. Cerling and M. Dearing, eds.), pp. 83-113. Springer-Verlag, New York, New York.
- Koch, P.L. (2007) Isotopic Study of the Biology of Modern and Fossil Vertebrates. *Stable Isotopes in Ecology and Environmental Science*. (R. Michener and K. Lajtha, eds.), pp. 99-154. Blackwell Publishing, Malden, Massachusetts.
- Koch, P.L., Hoppe, K.A. and 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. and 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., Schoeninger, M.J. and Valley, J.W. (1996) Herbivore tooth oxygen isotope compositions: effects of diet and physiology. *Geochimica et Cosmochimica Acta*, 60, 3889-3896.
- Kohn, M.J. and Welker, J.M. (2005) On the temperature correlation of $\delta^{18}\text{O}$ in modern precipitation. *Earth and Planetary Science Letters*, 231, 87-96.
- Land, L.S., Lundelius Jr., E.L. and Valastro Jr., S. (1980) Isotopic ecology of deer bones. *Palaeogeography Palaeoclimatology Palaeoecology*, 32, 143-151.
- Legg, T.E. and Baker, R.G. (1980) Palynology of Pinedale sediments, Devlins Park, Boulder County, Colorado. *Arctic and Alpine Research*, 12, 319-333.
- Leuenberger, M., Siegenthaler, U. and 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.
- Licciardi, J.M., Clark, P.U., Brook, E.J., Elmore, D. and Sharma, P. (2004) Variable responses of western U.S. glaciers during the last deglaciation. *Geology*, 32, 81-84.
- 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 Jr., E.L., Graham, R.W., Anderson, E., Guilday, J., Holman, J.A., Steadman, D.W. and Webb, S.D. (1983) Terrestrial Vertebrate Faunas. *Late-Quaternary Environments of the United States, Vol. 1*. (S.C. Porter, ed.), pp. 311-353. University of Minnesota Press, Minneapolis, Minnesota.
- Luz, B., Lolodny, Y. and 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. and 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. and 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. and 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. and Spaulding, W.G. (1992) Glacial-to-interglacial variations in the carbon isotopic composition of atmospheric CO_2 . *Nature*, 357, 461-466.
- Markgraf, V. and Scott, L. (1981) Lower timberline in central Colorado during the past 15,000 yr. *Geology*, 9, 231-234.
- Marshall, J.D., Brooks, J.R. and Lajtha, K. (2007) Sources of Variation in the Stable Isotopic Composition of Plants. *Stable Isotopes in Ecology and Environmental Science*. (R. Michener and K. Lajtha, eds.), pp. 22-60. Blackwell Publishing, Malden, Massachusetts.
- Marshall, J.D. and Zhang, J. (1994) Carbon isotope discrimination and water-use efficiency in native plants of the North-Central Rockies. *Ecology*, 75, 1887-1895.
- McGuire, K. and McDonnell, J. (2007) Stable Isotope Tracers in Watershed Hydrology. *Stable Isotopes in Ecology and Environmental Science*. (R. Michener and K. Lajtha, eds.), pp. 334-374. Blackwell Publishing, Malden, Massachusetts.
- Medina, E. and Minchin, P. (1980) Stratification of $\delta^{13}\text{C}$ values of leaves in Amazonian rain forests. *Oecologia*, 45, 377-378.

- 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. and Ehleringer, J.R. (2005) Carbon isotope fractionation between diet, breath CO₂, 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. and 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. and 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, Austria. <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. *Quaternary Glaciations in the Northern Hemisphere*. (V. Sibrava, D.Q. Bowen and G.M. Richmond, eds.), pp. 99-127. Pergamon Press, Elmsford, NY.
- Richmond, G.M. and Fullerton, D.S. (1986) Summation of Quaternary Glaciations in the United States of America. *Quaternary Glaciations in the Northern Hemisphere*. (V. Sibrava, D.Q. Bowen and G.M. Richmond, eds.), pp. 183-196. Pergamon Press, Elmsford, NY.
- Sage, R.F. and Coleman, J.R. (2001) Effects of low atmospheric CO₂ on plants: more than a thing of the past. *TRENDS in Plant Science*, 6, 18-24.
- Sare, D.T.J., Millar, J.S. and 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. and 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. and Boyle, E.A. (2000) Glacial/interglacial variations in atmospheric carbon dioxide. *Nature*, 407, 859-869.
- Smith, F.A. (1997) *Neotoma cinerea*. *Mammalian Species*, 564, 1-8.
- Spaulding, W.G., Leopold, E.B. and Van Devender, T.R. (1983) Late Wisconsin Paleoeecology of the American Southwest. *Late-Quaternary Environments of the United States, Vol. 1*. (S.C. Porter, ed.), pp. 259-293. University of Minnesota Press, Minneapolis, Minnesota.
- Stafford, T.W., Semken, H.A., Graham, R.W., Klippel, W.F., Markova, A., Smirnov, N.G. and Southon, J. (1999) First accelerator mass spectrometry ¹⁴C 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. and Olago, D.O. (1997) Impact of lower atmospheric carbon dioxide on tropical mountain ecosystems. *Science*, 278, 1422-1426.
- Teeri, J.A. and Stowe, L.G. (1976) Climatic patterns and the distribution of C₄ grasses in North America. *Oecologia*, 23, 1-12.
- Thewissen, J.G.M., Cooper, L.N., Clementz, M.T., Bajpai, S. and 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. and Spaulding, W.G. (1993) Climatic Changes in the Western United States since 18,000 yr B.P. *Global Climates since the Last Glacial Maximum*. (H.E. Wright Jr., J.E. Kutzbach, T. Webb III, W.F. Ruddiman, F.A. Street-Perrott and P.J. Bartlein, eds.), pp. 468-513. University of Minnesota Press, Minneapolis, Minnesota.
- Van de Water, P.K., Leavitt, S.W. and Betancourt, J.L. (1994) Trends in stomatal density and ¹³C/¹²C ratios of *Pinus flexilis* needles during last glacial-interglacial cycle. *Science*, 264, 239-43.
- Van der Merwe, N.J. (1982) Carbon isotopes, photosynthesis, and archaeology. *American Scientist*, 70, 596-606.
- Vaughan, T.A. (1990) Ecology of Living Packrats. *Packrat Middens: The Last 40,000 Years of Biotic Change*. (J.L. Betancourt, T.R. Van Devender and P.S. Martin, eds.), pp. 14-27. The University of Arizona Press, Tucson.

- Vogel, J. (1978) Recycling of carbon in a forest environment. *Oecologia Plantarum*, 13, 89-94.
- Walker, M., Johnsen, S., Rasmussen, S.O., Popp, T., Steffensen, J., Gibbard, P., Hoek, W., Lowe, J., Andrews, J., Björck, S., Cwynar, L.C., Hughen, K., Kershaw, P., Kromer, B., Litt, T., Lowe, D.J., Nakagawa, T., Newnham, R. and Schwander, J. (2009) Formal definition and dating of the GSSP (Global Stratotype Section and Point) for the base of the Holocene using the Greenland NGRIP ice core, and selected auxiliary records. *Journal of Quaternary Science*, 24, 3-17.
- Wang, Y. and Cerling, T.E. (1994) A model of fossil tooth and bone diagenesis: implications for paleodiet reconstruction from stable isotopes. *Palaeogeography Palaeoclimatology Palaeoecology*, 107, 281-289.
- Ward, J.K., Harris, J.M., Cerling, T.E., Wiedenhoeft, A., Lott, M.J., Dearing, M-D., Coltrain, J.B. and 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, 690-4.
- Webb, R.H. and Betancourt, J.L. (1990) The Spatial and Temporal Distribution of Radiocarbon Ages from Packrat Middens. *Packrat Middens: The Last 40,000 Years of Biotic Change*. (J.L. Betancourt, T.R. Van Devender and P.S. Martin, eds.), pp. 85-102. The University of Arizona Press, Tucson, Arizona.
- Welker, J.M. (2000) Isotopic ($\delta^{18}\text{O}$) 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. and Reeder, D.M. (eds.). (2005) *Mammal Species of the World*. Johns Hopkins University Press, Baltimore, Maryland.
- Wright Jr., H.E., Bent, A.M., Hansen, B.S. and Maher Jr., L.J. (1973) Present and past vegetation of the Chuska Mountains, northwestern New Mexico. *Geological Society Of America Bulletin*, 84, 1155-1180.
- Wright Jr., H.E., Kutzbach, J.E., Webb III, T., Ruddiman, W.F., Street-Perrott, F.A. and Bartlein, P.J. (eds.). (1993) *Global Climates since the Last Glacial Maximum*. Minneapolis, Minnesota.
- Yurtsever, Y. and Gat, J. (1981) Atmospheric Water. *Stable Isotope Hydrology, Deuterium and Oxygen-18 in the Water Cycle*. (J.R. Gat and R. Gonfiantini, eds.), pp. 103-142. International Energy Agency, Vienna, Austria.

Cave Level Pairwise Comparisons, *Marmota flaviventris*

		$\delta^{13}\text{C}$															
	MODERN	11	12	17	19	20	21	23	25	27	28	30	32	33	35	36	39
11	.587	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	.006	.055	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17	.047	.335	.203	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19	<.001	.005	.635	.030	-	-	-	-	-	-	-	-	-	-	-	-	-
20	<.001	.009	.754	.048	.843	-	-	-	-	-	-	-	-	-	-	-	-
21	<.001	.001	.365	.007	.596	.468	-	-	-	-	-	-	-	-	-	-	-
23	<.001	.015	.883	.077	.689	.839	.353	-	-	-	-	-	-	-	-	-	-
25	<.001	.013	.934	.074	.611	.764	.288	.931	-	-	-	-	-	-	-	-	-
27	<.001	<.001	.295	.004	.481	.367	.860	.270	.213	-	-	-	-	-	-	-	-
28	.024	.244	.272	.814	.050	.078	.013	.120	.120	.008	-	-	-	-	-	-	-
30	.003	.083	.552	.365	.178	.254	.059	.353	.371	.039	.501	-	-	-	-	-	-
32	.002	.071	.594	.324	.204	.287	.070	.394	.416	.046	.451	.935	-	-	-	-	-
33	.002	.045	.901	.192	.493	.615	.241	.752	.802	.183	.269	.599	.649	-	-	-	-
35	.006	.103	.549	.411	.191	.266	.068	.362	.381	.046	.547	.975	.913	.596	-	-	-
36	<.001	<.001	.293	.003	.483	.363	.885	.262	.201	.967	.006	.032	.039	.175	.040	-	-
39	.010	.160	.374	.606	.088	.133	.025	.196	.200	.016	.778	.695	.636	.388	.736	.012	-
40	<.001	.001	.283	.006	.454	.353	.796	.265	.213	.924	.011	.046	.054	.182	.052	.891	.020

		$\delta^{18}\text{O}$															
	MODERN	11	12	17	19	20	21	23	25	27	28	30	32	33	35	36	39
11	.088	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	.707	.375	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17	.789	.193	.862	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19	.291	.517	.715	.492	-	-	-	-	-	-	-	-	-	-	-	-	-
20	.507	.057	.446	.443	.170	-	-	-	-	-	-	-	-	-	-	-	-
21	.066	.957	.375	.175	.521	.046	-	-	-	-	-	-	-	-	-	-	-
23	.689	.257	.947	.896	.598	.394	.244	-	-	-	-	-	-	-	-	-	-
25	.197	.565	.640	.397	.911	.120	.572	.504	-	-	-	-	-	-	-	-	-
27	.468	.371	.883	.684	.790	.267	.364	.794	.694	-	-	-	-	-	-	-	-
28	.008	.653	.175	.045	.221	.009	.581	.077	.238	.134	-	-	-	-	-	-	-
30	.033	.965	.314	.121	.432	.028	.912	.182	.474	.287	.640	-	-	-	-	-	-
32	.140	.660	.558	.316	.795	.089	.676	.415	.876	.589	.306	.576	-	-	-	-	-
33	.722	.109	.576	.617	.281	.843	.097	.553	.219	.405	.026	.067	.173	-	-	-	-
35	.011	.609	.168	.048	.212	.010	.542	.078	.229	.132	.927	.594	.290	.028	-	-	-
36	.228	.524	.679	.438	.964	.136	.528	.547	.944	.744	.212	.432	.820	.243	.205	-	-
39	.382	.382	.837	.616	.830	.217	.373	.733	.728	.947	.129	.289	.615	.352	.128	.782	-
40	.864	.143	.667	.734	.354	.726	.131	.660	.284	.496	.039	.093	.228	.886	.040	.313	.440

TABLE 1.

Pairwise $\delta^{13}\text{C}$ (above) and $\delta^{18}\text{O}$ (below) comparisons among *Marmota flaviventris* from 17 cave levels and a modern sample (Student's t-tests). Bold values are significant at $\alpha=0.05$.

Cave Level Pairwise Comparisons, *Neotoma cinerea*

		$\delta^{13}\text{C}$														
	MODERN	11	15	18	19	20	21	23	25	26	28	30	32	33	36	38
11	.197	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15	.073	.172	-	-	-	-	-	-	-	-	-	-	-	-	-	-
18	.016	.086	.885	-	-	-	-	-	-	-	-	-	-	-	-	-
19	<.001	.004	.666	.381	-	-	-	-	-	-	-	-	-	-	-	-
20	<.001	.019	.961	.869	.228	-	-	-	-	-	-	-	-	-	-	-
21	.014	.037	.773	.574	.870	.596	-	-	-	-	-	-	-	-	-	-
23	.014	.104	.683	.720	.146	.499	.342	-	-	-	-	-	-	-	-	-
25	.004	.055	.836	.940	.228	.758	.484	.736	-	-	-	-	-	-	-	-
26	.005	.025	.900	.699	.569	.747	.801	.398	.589	-	-	-	-	-	-	-
28	<.001	.063	.610	.591	.011	.224	.250	.878	.557	.247	-	-	-	-	-	-
30	<.001	.033	.752	.814	.027	.462	.360	.807	.846	.398	.431	-	-	-	-	-
32	.006	.062	.823	.921	.232	.739	.475	.763	.976	.577	.595	.881	-	-	-	-
33	<.001	.027	.818	.918	.060	.636	.425	.693	.983	.496	.337	.758	.987	-	-	-
36	<.001	.051	.664	.676	.021	.319	.291	.999	.667	.304	.788	.649	.705	.502	-	-
38	<.001	.022	.951	.885	.246	.977	.589	.522	.781	.735	.270	.514	.761	.678	.365	-
40	<.001	.018	.938	.896	.148	.942	.555	.503	.780	.689	.180	.416	.759	.626	.274	.970

		$\delta^{18}\text{O}$														
	MODERN	11	15	18	19	20	21	23	25	26	28	30	32	33	36	38
11	.608	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15	.022	.082	-	-	-	-	-	-	-	-	-	-	-	-	-	-
18	.251	.504	.348	-	-	-	-	-	-	-	-	-	-	-	-	-
19	.705	.885	.061	.416	-	-	-	-	-	-	-	-	-	-	-	-
20	.931	.779	.109	.420	.860	-	-	-	-	-	-	-	-	-	-	-
21	.660	.976	.177	.584	.881	.783	-	-	-	-	-	-	-	-	-	-
23	.031	.194	.320	.736	.139	.228	.360	-	-	-	-	-	-	-	-	-
25	.803	.861	.103	.447	.956	.909	.857	.226	-	-	-	-	-	-	-	-
26	.672	.828	.034	.344	.960	.874	.841	.040	.982	-	-	-	-	-	-	-
28	.746	.853	.060	.400	.964	.888	.854	.136	.986	.996	-	-	-	-	-	-
30	.547	.945	.094	.536	.826	.735	.978	.222	.811	.757	.795	-	-	-	-	-
32	.369	.806	.082	.594	.670	.628	.871	.181	.688	.545	.640	.863	-	-	-	-
33	.774	.537	.075	.274	.599	.763	.562	.150	.663	.592	.624	.499	.408	-	-	-
36	.727	.940	.364	.732	.875	.797	.959	.580	.855	.852	.857	.971	.960	.623	-	-
38	.741	.427	.015	.172	.500	.768	.513	.020	.627	.421	.539	.376	.220	.929	.622	-
40	.069	.348	.163	.972	.252	.341	.519	.300	.350	.094	.244	.388	.375	.218	.720	.042

TABLE 2.

Pairwise $\delta^{13}\text{C}$ (above) and $\delta^{18}\text{O}$ (below) comparisons among *Neotoma cinerea* from 16 cave levels and a modern sample (Student's t-tests). Bold values are significant at $\alpha=0.05$.

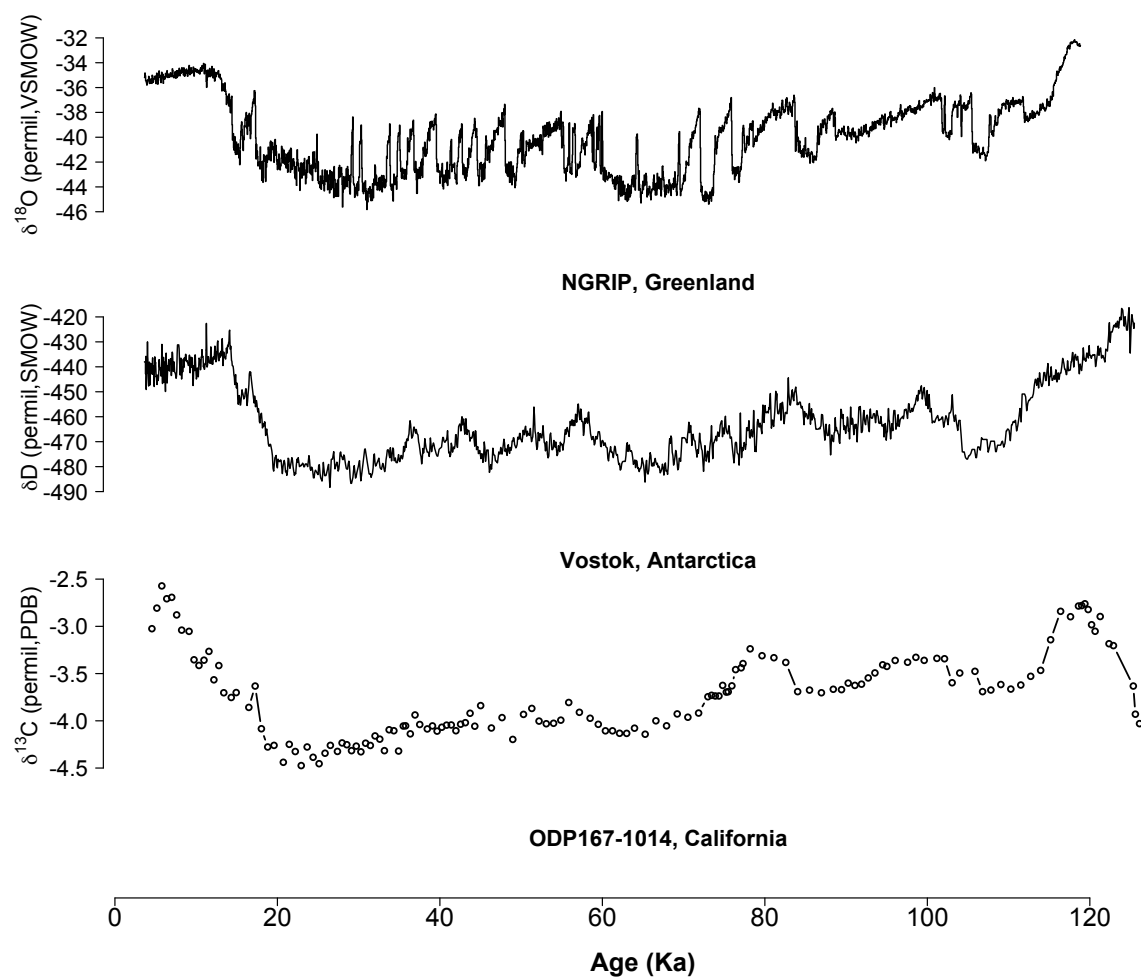


FIGURE 1.

Three late Quaternary paleotemperature records spanning the last ~130Ka: **a)** $\delta^{18}\text{O}$ record from the NGRIP ice core, central Greenland (NGRIP 2004); **b)** δD record from the Vostok, Antarctica ice core (Petit et al. 1999), and **c)** $\delta^{13}\text{C}$ record from planktonic foraminifera from deep sea sediment core ODP167-1014, Tanner Basin, California (Hendy and Kennett 2000).

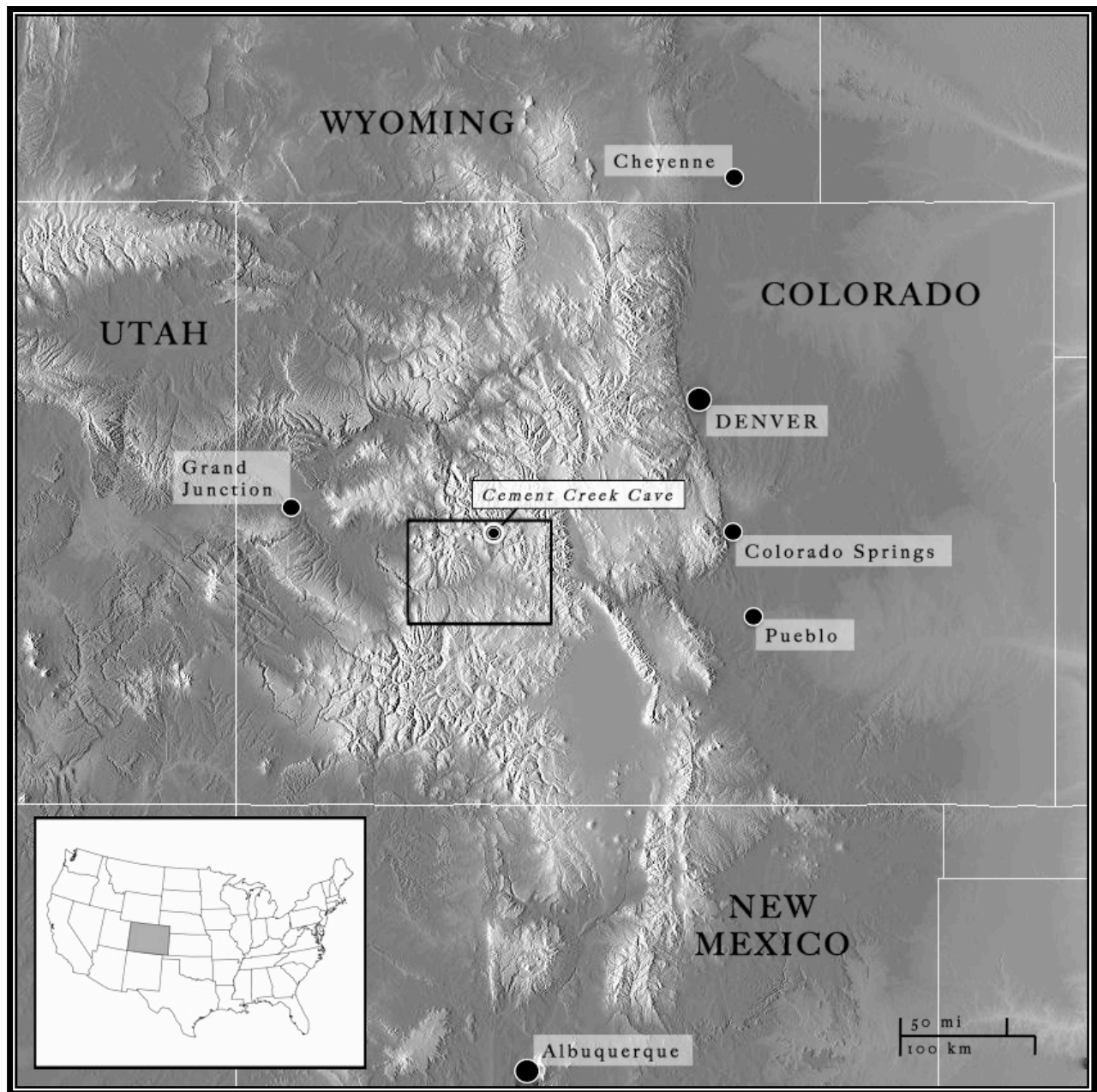


FIGURE 2.

Map of the Southern Rocky Mountains in Colorado, USA. The Gunnison Basin is indicated by a black box and Cement Creek Cave is marked with concentric circles.

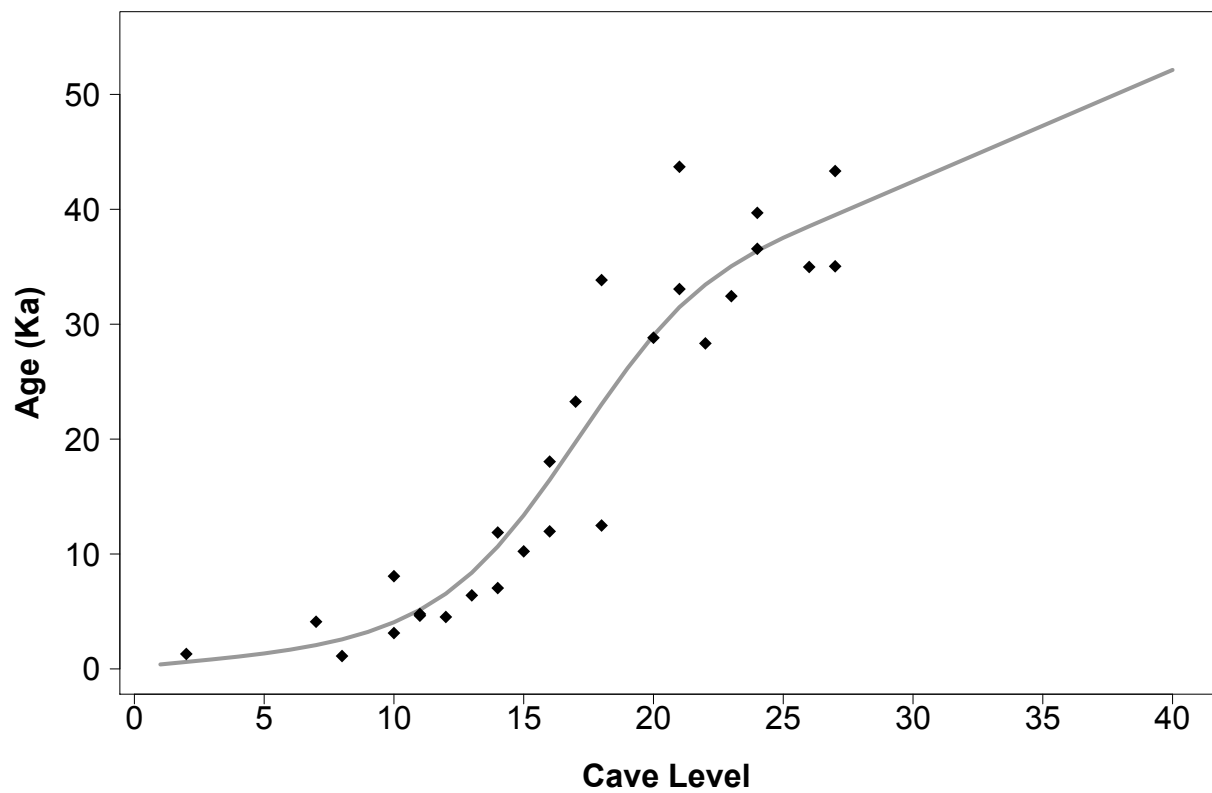


FIGURE 3.

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 the forty excavated cave levels (TP2, Northeast Extension) are plotted beneath (gray line; see text for model details).

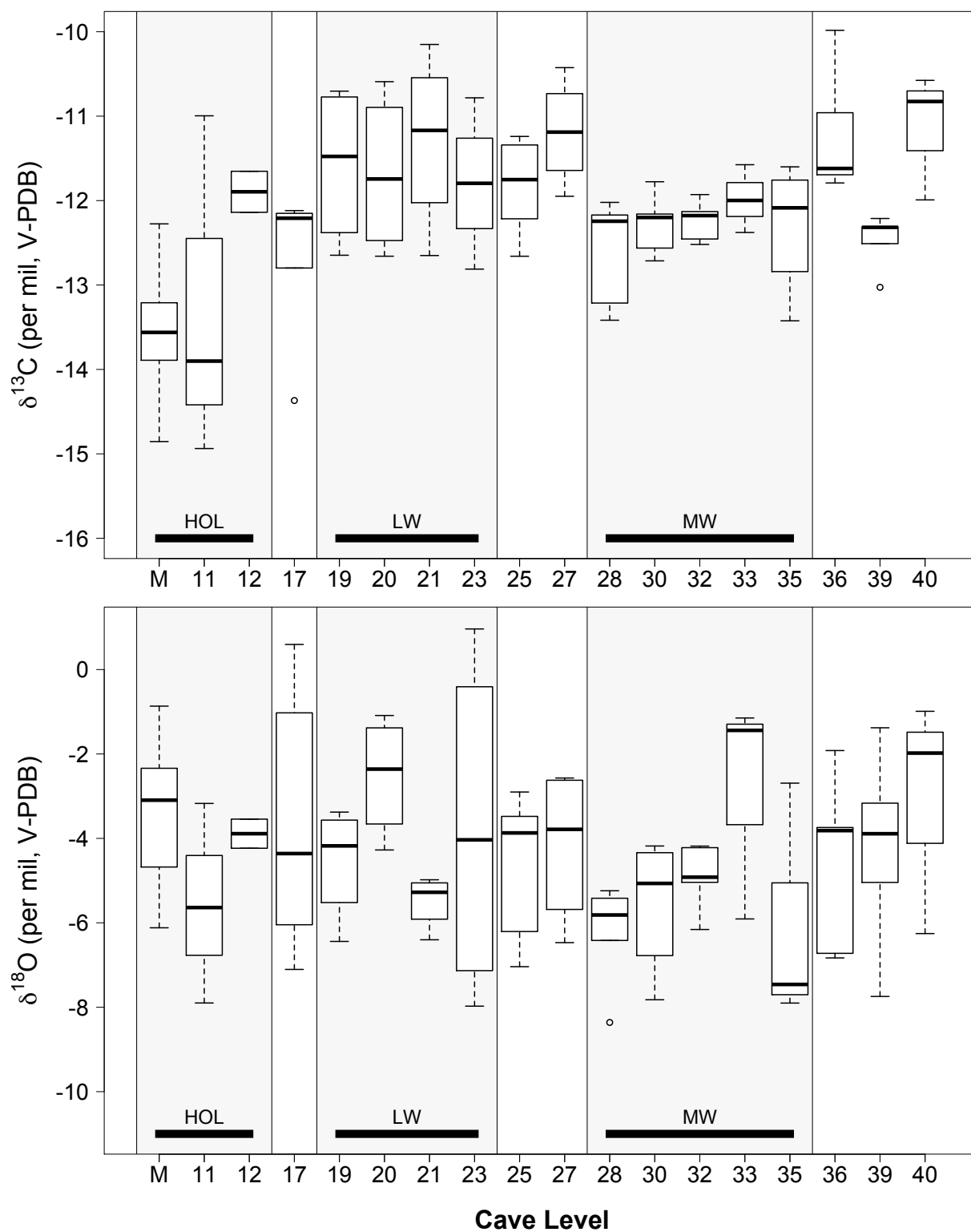


FIGURE 4.

Stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) of tooth enamel from fossil and modern ('M') *Marmota flaviventris*. Age bins used in this study are indicated by gray shading and are based on geochronological data (**HOL**=Holocene, **LW**=late Wisconsin, **MW**=middle Wisconsin; see text for details).

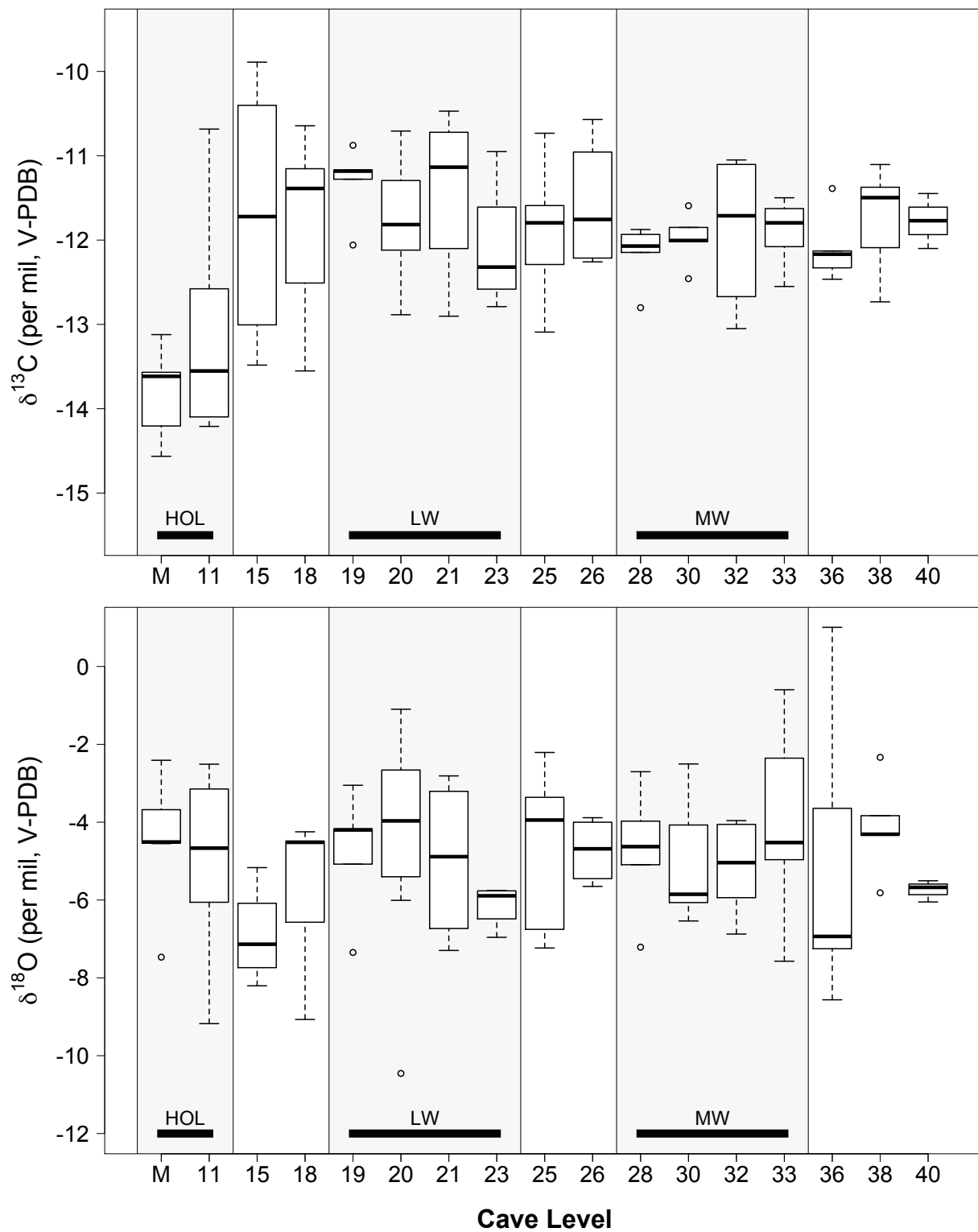


FIGURE 5.

Stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) of tooth enamel from fossil and modern ('M') *Neotoma cinerea*. Age bins defined as in Fig. 4; see text for further details.

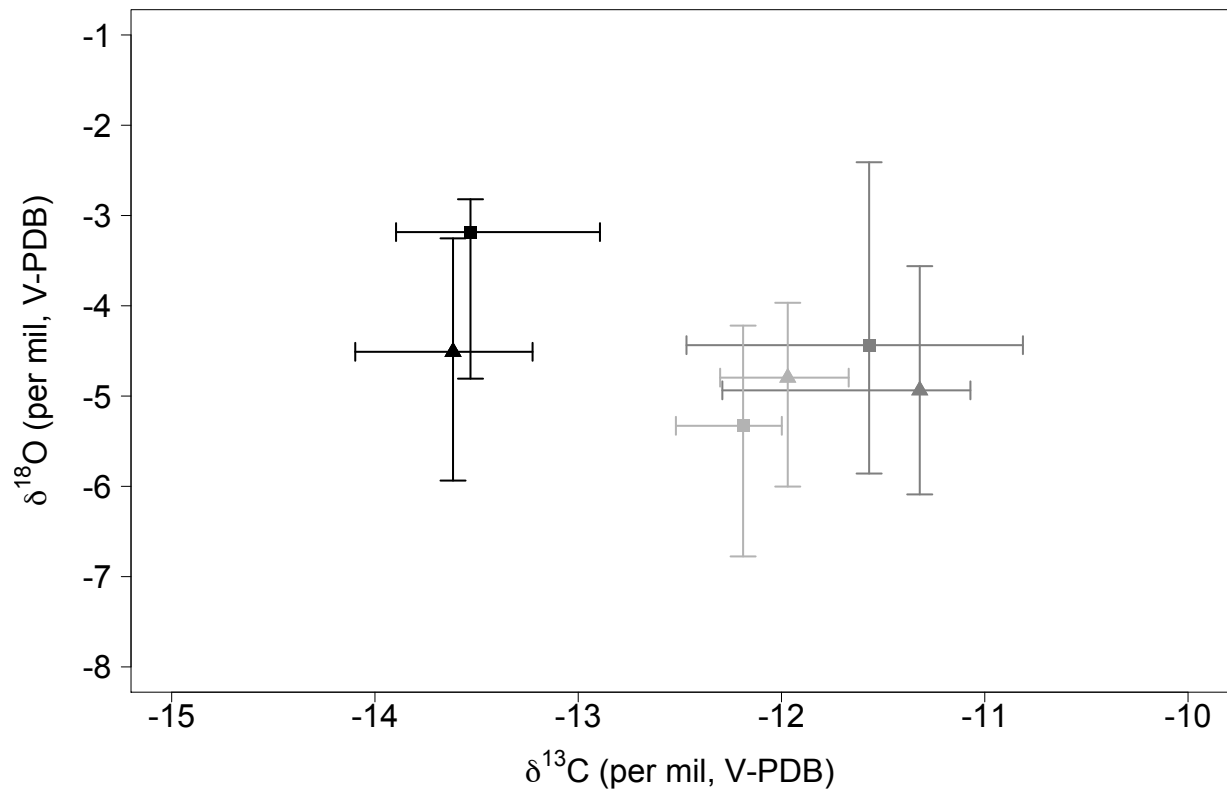


FIGURE 6.

Plot of tooth enamel stable isotope signatures ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) of *Marmota flaviventris* (filled squares) and *Neotoma cinerea* (filled triangles) from the three age bins used in this study (HOL=black, LW=dark gray, MW=light gray; see text for details). Data for each bin are presented with medians (center) and first and third quartiles (bars).