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The effect of Holocene temperature fluctuations on the evolution and ecology of *Neotoma* (woodrats) in Idaho and northwestern Utah

Felisa A. Smith[a,*] and Julio L. Betancourt[b]

[a] *Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA*
[b] *U.S. Geological Survey, Desert Laboratory, 1675 West Anklam Road, Tucson, AZ 85745, USA*

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Abstract

Animals respond to climatic change by adapting or by altering distributional patterns. How an animal responds is influenced by where it is positioned within its geographic range; the probability of extirpation is increased near range boundaries. Here, we examine the impact of Holocene climatic fluctuations on a small mammalian herbivore, the bushy-tailed woodrat (*Neotoma cinerea*), at five locations within south central Idaho and northwestern Utah. Previous work demonstrated that woodrats adapt to temperature shifts by altering body size. We focus here on the relationship between body mass, temperature, and location within the geographic range. Body mass is estimated by measuring fossil fecal pellets, a technique validated in earlier work. Overall, we find the predicted phenotypic response to climate change: animals were larger during cold periods, and smaller during warmer episodes. However, we also identify several time periods when changes in environmental temperature exceeded the adaptive flexibility of *N. cinerea.* A smaller-bodied species, the desert woodrat (*N. lepida*) apparently invaded lower elevation sites during the mid-Holocene, despite being behaviorally and physically subordinate to *N. cinerea.* Analysis of contemporary patterns of body size and thermal tolerances for both woodrat species suggests this was because of the greater heat tolerance of *N. lepida*. The robust spatial relationship between contemporary body size and ambient temperature is used as a proxy to reconstruct local climate during the Holocene.

Keywords: Bergmann's rule; Body mass; Species replacement; *Neotoma lepida*; *Neotoma cinerea*; Late Quaternary; Global warming

Introduction

Biologists agree that global warming is likely to produce changes in the diversity and distribution of species, but the magnitude, timing and nature of such responses remains unclear (e.g. Holt, 1990; Mooney, 1991; Field et al., 1992; Shugart et al., 1992; Smith and Buddemeier, 1992; Webb and Bartlein, 1992). Animals may be affected directly by altered temperature and/or moisture regimes, for example, or indirectly through associated vegetation changes (Birch, 1957; Smith and Buddemeier, 1992). For herbivores in particular, direct effects are likely to be compounded by vegetation changes, especially in the case of animals with specialized habitat affinities or relatively small home ranges (Webb and Bartlein, 1992). Climatic change may also occur too rapidly for animals to adapt, or they may be unable to adapt because of physiological or phylogenetic constraints (Peters and Darling, 1985; but see Hoffmann and Blows, 1993). Under such circumstances, species may become locally extinct. Estimating the potential range of adaptive response to climatic and vegetative shifts is clearly crucial to an understanding of the effects of global warming on terrestrial ecosystems, yet it requires a more thorough understanding of life history and ecosystem function than is often available.

Increasingly, paleoecologists are recognizing that temperature fluctuations during the late Quaternary may have occurred at higher frequencies than previously thought (Betancourt, 1996). The Greenland ice core record, for example, suggests at least 20 abrupt warming events during the last glacial period (Dansgaard et al., 1993; Bond and Lotti,

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* Corresponding author. Fax: +1-505-277-6725.
E-mail address: fasmith@unm.edu (F.A. Smith).

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1995). High-resolution cores of lake sediments suggest even more oscillations in temperature and hydrology (i.e., Benson et al., 2002). Further, these events may have occurred very rapidly, perhaps within the order of decades or centuries. Dendroclimatic reconstructions of the last millennium also suggest that this period was characterized by low-amplitude, high-frequency climate shifts (Biondi et al., 1999). Although the magnitude of most annual climate shifts was of 1°C or less relative to modern temperature, approximately 5% exceeded 2°C, and a few approached 3°C (Biondi et al., 1999, from Fig. 4). Such rapid and dramatic temperature fluctuations exerted substantial selection pressures on organisms (e.g., Grayson 2000a, 2000b) — effects that were likely most pronounced at the range boundaries of species. Consequently, the past few thousand years are arguably the best proxy we have for investigating the response of individual species to environmental change (Cronin and Schneider, 1990; Graham and Grimm, 1990).

All woodrat (*Neotoma*) species are profoundly sensitive to environmental temperature (Lee, 1963; Brown, 1968; Brown and Lee, 1969). Not only does body size vary with latitude in accordance with Bergmann's rule (Rameaux and Sarrus, 1838; Bergmann, 1847; Brown and Lee, 1969), but lethal temperatures are also a function of body mass (Smith et al., 1995). Further, previous work has demonstrated that woodrats adapt to climate change by altering body size (Smith et al., 1995; Smith et al., 1998; Smith and Betancourt, 1998). The response is robust and in the direction predicted by Bergmann's Rule; animals are larger during cold intervals, and smaller during warmer episodes.

Here, we examine the influence of mid- to late Holocene climatic fluctuations on the ecology and evolution of woodrats at five locations within south central Idaho and northwestern Utah (Fig. 1). A number of studies indicate that the middle Holocene in the Great Basin and surrounding area was much warmer and drier than today leading to marked effects on the flora and fauna (e.g., Betancourt, 1990; Grayson, 1993; Thompson et al., 1993; Grayson 2000a, 2000b; Benson et al., 2002). Today, the region encompasses the ecotone between two very different woodrat species: *Neotoma cinerea* (the bushy-tailed woodrat), a large forest or woodland adapted species, and *Neotoma lepida* (the desert woodrat), a much smaller animal inhabiting desert and semi-desert environments (Finley, 1958; Smith, 1997). Southern Idaho represents the modern northern limit of *N. lepida* (Hall, 1981; Fig. 1); currently, there is no evidence that the range extended any further north even during the arid and warmer conditions of the Altithermal (e.g. FAUNMAP). *Neotoma cinerea,* however, is found in mountainous regions as far south as northern New Mexico (Hall, 1981; Smith, 1997) and ranged even further south during the Pleistocene (Harris, 1984, 1985, 1993). Although these two species may be sympatric elsewhere in their ranges, they are allopatric in southern Idaho; *N. cinerea* is found in higher elevation montane habitats, and *N. lepida* is restricted to low-elevation desert shrub.

We focus on the relationship between woodrat body size, temperature and position in the geographic range. Body size is estimated by measuring fossil fecal pellets, an abundant component of paleomiddens—which in turn are a ubiquitous feature of cave and crevices across much of the western United States (Betancourt et al., 1990). In general, phenotypic changes in body size should reflect temperature shifts across this region. Lower-elevation sites, however, are marginal habitats for bushy-tailed woodrats today (Finley, 1958; Grayson et al., 1996; Smith, 1997). Thus, we expect that local extirpations may have occurred during the mid- to late Holocene. We examine contemporary patterns of body size and environmental temperature for both woodrat species across their entire geographic range to determine the thermal thresholds at which extirpation and/or species replacements were likely. Our aim is to determine the extent to which woodrats are capable of evolving in response to climatic and vegetative shifts, and when such shifts exceed their adaptive capability.

Materials and methods

Study sites

Three of the five limestone caves were located in the Snake River Plain of central Idaho; the other two were in southeastern Idaho, and northern Utah, respectively (Fig. 1, Table 1). All are within the modern distribution of *Neotoma cinerea,* the bushy-tailed woodrat (Hall, 1981). This species is not only the largest member of the genus in the Southwest, but the only one adapted to montane or boreal habitat (Finley, 1958; Smith, 1997). Only one study location (Homestead Cave) is included within the contemporary range of other woodrat species. This relatively low-elevation cave (1406 m) in the northern Bonneville Basin is unusual in that two very different species of woodrat coexist in close proximity there today. *Neotoma lepida* (the desert woodrat) is found near the mouth of the cave and on the arid valley floor, and *N. cinerea* occupies the mesic recesses of the cave itself (Grayson et al., 1996; Grayson and Madsen, 2000; Madsen, 2000). Although fossil evidence indicates that *N. cinerea* inhabited Homestead Cave in the Pleistocene and early Holocene, its current presence may actually represent a recolonization sometime during the last millennium (Grayson and Madsen, 2000). During the full glacial, *N. cinerea* was much more widespread at lower elevations (Harris, 1984, 1985, 1993); *N. lepida* were probably restricted to the more southerly portions and/or lower elevations of their extant range (FAUNMAP data).

Modern temperatures for each study location were determined by extracting data for the nearest weather station from the Western Regional Climate Center (Desert Research Institute; www.wrcc.dri.edu). January and July averages were used to represent the minimum and maximum yearly temperatures; in the Western Hemi-

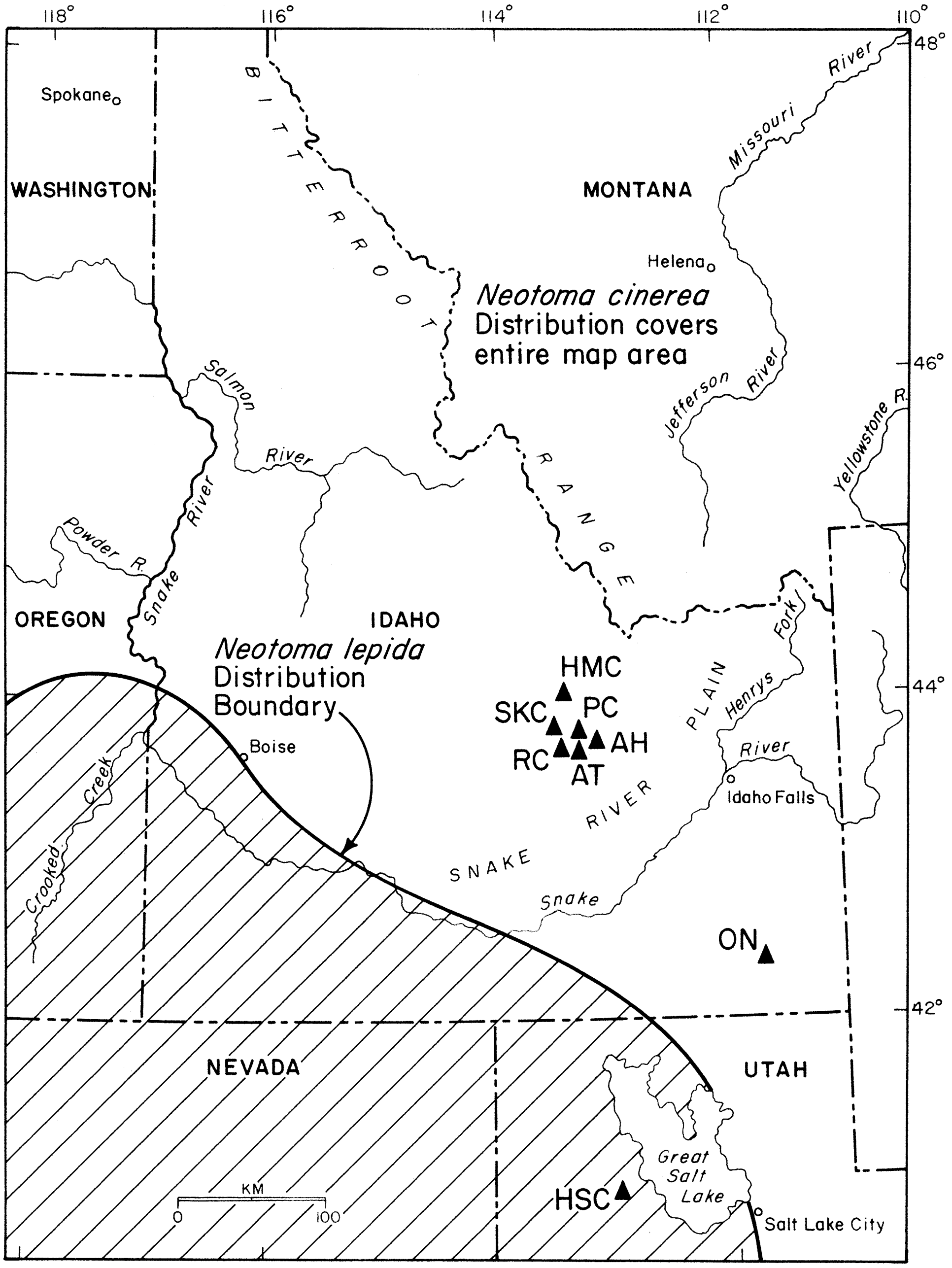

Fig. 1. Contemporary distribution of *Neotoma lepida* and *N. cinerea* in Idaho and surrounding areas and location of limestone caves from which paleomiddens were collected. Legend as follows: AH = Arco Hills, HMC = Hidden Mouth Cave, HSC = Homestead Cave (stratigraphic sample), ON = Oneida Narrows, PC = Pictograph Cave, RC = Rocky Canyon. For further information about cave sites, see Table 1.

sphere these represent the coolest and warmest months, respectively. Climatic records generally represent a 50 to 100 year average. They were adjusted for elevational differences as necessary, using a warm-month lapse rate of 5.31 ± 0.50°C/km ($r = -0.939$, $P < 0.001$) and cold-month lapse rate of 5.02 ± 0.64°C/km ($r = -0.897$, $P < 0.001$) for Idaho, and a warm-month lapse rate of 8.19 ± 1.03°C/km ($r = -0.905$, $P < 0.001$) and cold-month lapse rate of 4.77 ± 1.46°C/km ($r = -0.658$, $P < 0.006$) for Utah (Meyer, 1992).

Midden processing and pellet measurements

Woodrat (sometimes called “packrat”) middens in Idaho were collected from recessed rock shelters or caves within limestone formations by J.L. Betancourt and colleagues. Each cave contained 2–18 separate indurated woodrat middens, each of which was independently radiocarbon dated. Each indurated midden was disassociated by soaking in water for several days, dried and sieved; fecal pellets were separated from other materials (Spaulding et al. 1990).

Table 1
Information about cave sites used in study

	Arco Hills	Hidden Mouth Cave	Homestead Cave	Oneida Narrows	Pictograph Cave	Rocky Canyon
Symbol	AH	HMC	HSC	ON	PC	RC
Elevation (m)	1920	2255	1406	1550	1800	1800
Longitude	113°08′	113°26′	113°	111°50′	113°20′	113°25′
Latitude	43°39′	43°57′	41°	42°15′	43°41′	43°42′
State	ID	ID	UT	ID	ID	ID
Number of paleomiddens or strata available	3	3	7	2	2	12
Age range (^{14}C yr B.P.)	2,400 to 3,880	3,160 to 3,985	1,020 to 11,168	2,315 to 3,185	3,970 to 4,050	455 to 3,925
Aspect	NW	N	—	S	S-SE	N
Nearest weather station & elevation (m)	Arco 1640	Arco 1640	Knolls 1305	Preston 1469	Arco 1640	Craters of the Moon 1818
Modern mean[a] January temperature (°C)	−10.1	−11.9	−3.5	−5.9	−10.0	−6.7
Modern mean July temperature (°C)	17.8	16.0	24.1	20.0	17.9	20.2

Note. More middens were collected from Arco Hills, Hidden Mouth Cave, and Rocky Canyon than are shown here. They were excluded from the study because an aliquot from these was removed for radiocarbon dating before they could be measured.

[a] Weather data corrected for elevational differences between weather station and cave site (see text for details). Note by comparison with Figs. 3 and 4 that today only Homestead Cave is within the temperature thresholds for *N. lepida.*

When processed in this manner, pellets maintain structural integrity and appear little affected by taphonomy. In contrast, samples from Homestead Cave were the result of a stratigraphic excavation led by D.B. Madsen (Grayson 2000a, 2000b; Grayson and Madsen, 2000; Madsen 2000). The floor of the cave was a matrix of organic material including both raptor deposits (primarily owls) and loose woodrat middens. Materials removed from a 1 m by 1 m column sample were identified as belonging to 1 of 18 separate strata; 21 radiocarbon dates were later determined on representative samples (for procedural details at this site see Grayson 2000a, 2000b; Grayson and Madsen, 2000; Madsen 2000). Because of the coarse stratigraphic resolution, there are much larger uncertainties in the radiocarbon dates for these woodrat pellets. Further, pellets from the various Homestead Cave strata were loose; all pellets were noticeably more desiccated than those from indurated middens.

For all samples, the width of the largest ~200 pellets (or ~20% of those available, whatever was greater) was measured to the nearest 0.1 mm using digital calipers. Previous work has shown that pellet width is significantly related to body mass; this relationship is not appreciably affected by diet, gender or species (Smith et al. 1995). Further, measuring 10–20% of the sample is sufficient to characterize the largest animals: above this threshold maximum size does not vary with sample size (Smith and Betancourt, 1998). When fewer than 200 pellets were present, all were measured. Radiocarbon dates were determined either from associated plant macrofossils or directly from previously measured fecal pellets by Geochron Laboratories; values reported are uncorrected ^{14}C ages.

Pellets with widths less than 4.0 mm (~90 g) were discarded because of a large increase in measurement error that arose at these size classes (e.g., Smith et al. 1995; Smith and Betancourt, 1998), and because of the difficulty in excluding juvenile woodrats or even large deer mice (*Peromyscus* spp.). The mean, standard deviation, and 95% confidence interval of the 20 largest pellets was calculated and used to estimate body mass with the linear regression equation provided by Smith et al. (1995; $y = 0.005x + 3.559$). To examine body size fluctuations at each cave site, we plotted the mass estimate *versus* the uncorrected radiocarbon date for each sample.

Modern body size and temperature

We examined thermal tolerances and characteristic body mass for a number of contemporary populations of both *N. cinerea* and *N. lepida.* These spanned the distributional range currently occupied by these species, and so represented the thermal extremes the animals are likely to encounter. Measurements of body size (length exclusive of tail and mass, if provided) were obtained from museum specimens housed at the National Museum of Natural History (Smithsonian), Museum of Vertebrate Zoology (University of California Berkeley), Museum of Southwestern Biology (University of New Mexico), San Diego Natural History Museum, Burke Museum of Natural History and Culture (University of Washington), United States Biological Survey Collection (University of New Mexico), and from field notes (F.A. Smith, unpublished). Collecting localities were identified and data aggregated into local populations consisting of ~15 to >100 individuals; maximum size was computed as the mean of the largest 2 males and females for each population. Analyses used both mean and maximum size, although the latter is preferred because it can be compared directly with the paleomidden data and because other work suggests that mean body size underestimates the effect of temperature on size (Smith and Betancourt, 1998). By

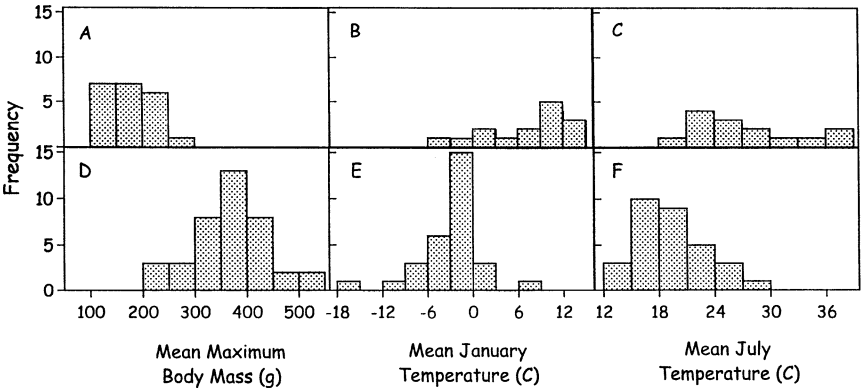

Fig. 2. Histograms of mean maximum body mass and January and July mean temperatures for various populations of *N. lepida* and *N. cinerea.* The top row represents 21 populations of *N. lepida;* the bottom row contains data for 39 populations of *N. cinerea.* In both cases, locations were chosen that span the approximate distributional range of the species. Data derived from museum specimens and the Western Regional Climatic Center (see text for details). Note that *N. cinerea* can tolerate much colder temperatures than *N. lepida,* but rarely occupies habitat where July temperatures exceed ~24–25 °C. There is overlap in maximum body mass between ~250–300 g.

utilizing maximum size we include only mature animals that have experienced multiple episodes of thermal (both hot and cold) selection. Climatic data for the nearest weather station were obtained from the Western Regional Climate Center, and corrected for elevational differences as discussed earlier. We compared population body sizes with mean January and July temperatures; these represent the coolest and warmest months in the Western Hemisphere, respectively. All statistical analyses were conducted using SPSS v6.1.1 for the Power Macintosh.

Results

Modern body size and temperature

As expected, we found clear differences not only in the body mass ranges of *N. cinerea* and *N. lepida* populations, but also in the thermal characteristics of the environments they inhabited (Fig. 2). Note that because efforts were concentrated at the geographic range boundaries, histograms are not normally distributed. Although there was some overlap between the largest *N. lepida* and the smallest *N. cinerea* at ~250–300 g (Figs. 2A, 2D), animals of this size were unlikely to co-occur. Body size variation in *N. cinerea* showed a strong latitudinal gradient, with the body size of populations larger in the north and smaller in the south. In contrast, body size variation in *N. lepida* was largely east to west, reflecting the underlying thermal gradient. The largest bodied populations were along the coastal portions of upper and lower California; the smallest in the interior deserts (Smith and Charnov, 2001). The lack of a North–South gradient for *N. lepida* was largely driven by the fairly restricted latitudinal extent occupied. While the distributional range of *N. cinerea* encompasses >31° of latitude and extends well into Canada, that of *N. lepida* occupies <15°, and barely extends as far north as Idaho (Hall, 1981). Environmental temperature thresholds are quite different for the two species: *N. lepida* are not found where mean January temperature drops below ~−5°C, and *N. cinerea* are not found where mean July temperatures rise above ~25°C (Fig. 2).

Regressions of both mean and mean maximum body mass against ambient July temperature yielded highly significant relationships for both species (Fig. 3; Table 2). Analysis of covariance revealed a strong species effect ($P < 0.0001$, df = 43), suggesting that *N. cinerea* and *N. lepida* responded differently to warm temperature. For *N. lepida,* the range of body size possible *increased* as mean July temperatures *decreased* (Fig. 3). The largest populations (~225 g), for example, were found in environments with mean July temperatures ranging from 19 to 26°C, but the range of possible body sizes was much more tightly con-

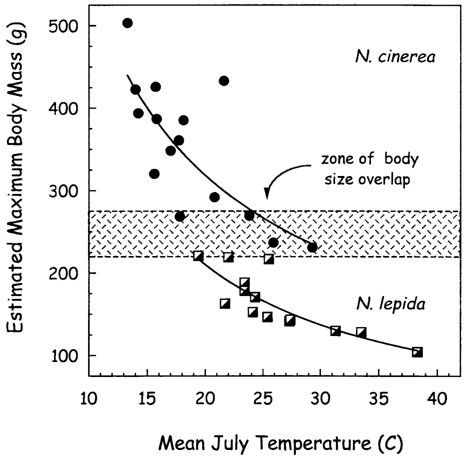

Fig. 3. Mean maximum body mass of *N. lepida* and *N. cinerea* as a function of mean July temperature. Regression equations: $y = 4901.3x^{-1.051}$, $r = 0.857$, df = 19; $y = 3470.6x^{-0.798}$, $r = 0.786$, df = 13. Not all populations shown in Figure 2 were used because of incomplete climate information. Note the higher variance at the tails of the regressions.

Table 2
Results from regressions of mean population body mass against various thermal characteristics of the environment

Regression	Species	Equation	*r* value	*P* value
Mean body mass vs mean July temperature	*N. lepida*	$y = 2766.69x^{-0.943}$	0.900	<0.0001
	N. cinerea	$y = 2850.96x^{-0.815}$	0.763	<0.001
	Combined regression	$y = 14{,}450.47x^{-1.403}$	0.853	<0.001
Mean maximum body mass vs mean July temperature	*N. lepida*	$y = 4901.30x^{-1.051}$	0.857	<0.001
	N. cinerea	$y = 3470.60x^{-0.798}$	0.786	<0.001
	Combined regression	$y = 19{,}718.78x^{-1.429}$	0.829	<0.001
Mean body mass vs mean January temperature	*N. lepida*	—	—	n.s.
	N. cinerea	$y = 0.063x^2 - 6.45x + 252.13$	0.614	<0.05
Mean maximum body mass vs mean January temperature	*N. lepida*	—	—	n.s.
	N. cinerea	$y = 0.156x^2 - 7.30x + 322.19$	0.647	<0.05

Note. Note that body mass is the dependent variable; this is a deliberate comment on the evolutionary process on our part, since we believe that environmental temperature has been selected for particular body masses. Although body size estimates were available for 21 populations of *N. lepida* and 39 populations of *N. cinerea*, lack of temperature stations for some locations and exclusion of peninsular forms restricted the analysis to 15 populations of the latter. For further details see text.

strained at warmer temperatures. This may reflect more intense thermal selection resulting from a more extreme environment. The smallest *Neotoma lepida* population (~88 g) was at Death Valley, where July temperatures exceed 41°C and maximums exceeding 50°C are not uncommon (Smith and Charnov, 2001). Conversely, there was no relationship between January temperature and *N. lepida* body size, perhaps because minimum temperature in the habitats occupied was always fairly mild (e.g., Fig. 2). There was, however, a significant relationship between both mean and maximum *N. cinerea* body mass and mean or minimum January temperatures (Table 2), confirming relationships reported in earlier work (e.g., Smith et al., 1995; Smith and Betancourt, 1998).

Chronosequences

Considerable fluctuations in body mass were seen at all sites across the middle Holocene (Fig. 4, Table 3). These presumably reflected underlying climatic shifts, with larger body size found during colder conditions, and smaller size during warmer conditions. Higher elevation sites (i.e., Hidden Mouth Cave and Pictograph Cave) exhibited less variability in body mass than other locations (Fig. 4a), but whether this was a result of less variable climate or an artifact of fewer middens was unclear. There were clear differences in the characteristic body size at each location, reflecting an underlying latitudinal and elevational gradient. Note, for example, that paleomiddens dating to ~4000 ^{14}C yr B.P. were recovered from almost every site. Even a cursory examination of Fig. 4 (the panels are oriented from highest to lowest elevation, and from north to south) clearly demonstrates the important influence of varying elevation and latitude on body size.

The highest resolution chronosequence was collected at Rocky Canyon Cave (Fig. 4b). The 12 paleomiddens recovered provide a detailed record of the past 4000 years. The variation seen in body size suggested considerable fluctuations in temperature, with markedly cooler periods around 3200 and 650 ^{14}C yr B.P. (Fig. 4b, Table 3). Using data from Fig. 3, we estimated that summer temperatures were ~3°C warmer during portions of the Holocene (Table 3; Fig. 5). Comparison of body size fluctuations over the past millennium with well-characterized temperature records yielded good correspondence. The most reliable estimates of July temperature in the region are from an 858-yr tree-ring chronology collected ~100 km northwest of Rocky Canyon Cave (Biondi et al. 1999; see also Perkins and Swetnam 1996). This chronology indicated multi-decadal periods of extreme cooling centered around AD 1300, 1340, 1460, and after AD 1600, interrupted by warm spells in the early 1400s, late 1500s, and in the 1930s (Biondi et al., 1999). The maximum body size at Rocky Canyon Cave occurs at ~650 ^{14}C yr B.P., roughly coincident with 14th-century cold spells evident in the tree-ring record. Because of inadequate sample depth, the first century of this tree-ring record is probably not as reliable as the rest of the chronology. Hence, we cannot ascertain if the marked reduction in body size at 795 ^{14}C yr B.P. corresponded to a warm spell in the early 12th century. The reduction in body size at 455 ^{14}C yr B.P. roughly coincided with warming in the late 16th century. Clearly, however, considerable variability was illustrated by both the tree ring record and woodrat body size over this period. The abrupt reversal of about 5°C seen around 3300 ^{14}C yr B.P. although considerable, is consistent with recent evidence from cores of lake sediments in Nevada (Benson et al., 2002). Benson and his colleagues reported temperature reversals of ~5–7°C for this same period in the middle Holocene.

The oldest pellets recovered were from the stratigraphic samples at Homestead Cave dating to 11,168 and 10,255 ^{14}C yr B.P., respectively (Table 3, Fig. 4d). Based on body size, we estimated July temperatures were ~5°C cooler than modern. This may be a slight underestimate. Temperature

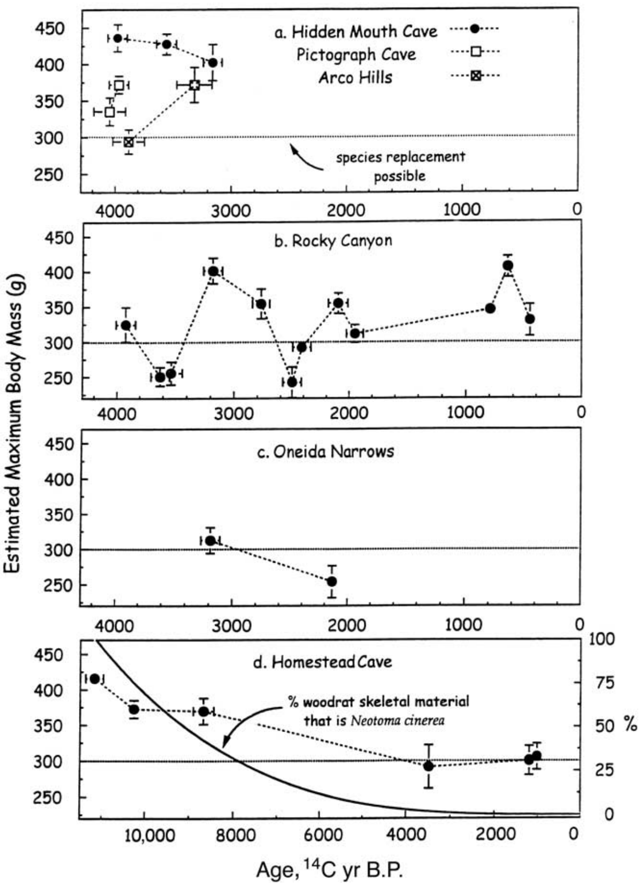

Fig. 4. Chronosequences of estimated maximum body size from limestone caves in Idaho and Utah plotted against uncorrected radiocarbon age. Results have been plotted as body size estimates rather than the actual measured pellet width for ease of interpretation. Bars around values represent the 95% confidence interval; if none are indicated, the uncertainty in the estimate was less than the size of the symbol. Deposition date was determined by radiocarbon dating the pellets and/or plant macrofossils contained within the paleomidden. For each panel, the dotted line indicates the body mass threshold at which a species replacement is possible. Panels are arranged from North to South, and in decreasing order of elevation (see Fig. 1, Table 1). A) Sequences from Hidden Mouth Cave (2255 m), Arco Hills (~1900 m) and Pictograph Cave (~1900 m), in the Lost River Range. B) Sequence from Rocky Canyon (1798 m), a xeric south facing site from Appendicitus Hill. C) Sequence from Oneida Narrows (1550m) situated in the western foothills of the Bear River Range. D) Sequence from Homestead Cave (1406 m) in northwestern Utah. This cave site was once on the shore of the Pleistocene Lake Bonneville. The curve indicates as a function of time the percentage of woodrat skeletal material recovered from this cave that was identified as *N. cinerea.* Note that by 4000 ^{14}C yr B.P., virtually all the woodrat skeletal material found was *N. lepida,* and further, that the body mass estimates for the population are ≤~300 g. Data derived from Grayson (2000).

based on woodrat body size reflected the localized mesic microclimate of the cave itself, whereas the modern temperature estimates are from Knolls weather station. Although these were corrected for the slight elevation gradient between the cave site and weather station, we did not correct for slope aspect or microhabitat differences. Although this was true for other localities as well, the differences were exacerbated at this very low elevation xeric site (e.g., Table 1). Note that the transition from the large body size characteristic of the early Holocene to the smaller body size evident at around 4000 ^{14}C yr B.P. is undocumented because so few woodrat fecal pellets were recovered from the intervening strata (Fig. 4d). Our findings of large body size persisting to ~8000 ^{14}C yr B.P., however, corroborate Grayson's (2000) conclusion that the early Holocene was relatively cool and moist in the northern Great Basin; a finding at odds with some climatic models (e.g., Thompson et al., 1993).

Only 100 km separated Hidden Mouth and Rocky Canyon Caves (Fig. 1, Table 1). Nonetheless, the small difference in latitude was compounded by a >400-m difference in elevation, leading to very different body mass and a different response to temperature change. Whereas warming between 3000 and 4000 ^{14}C years ago led to a decrease in body size for the Hidden Mouth Cave population, it appears to have led instead to a species replacement in the Rocky Canyon population (mean body mass dropped precipitously to ~225–250 g; Figs. 4a, 4b). Because the much larger *N. cinerea* are behaviorally dominant over *N. lepida,* such a range expansion was only possible if *N. cinerea* went locally extinct. Species replacements may have also occurred at Oneida Narrows and Homestead Cave during the middle Holocene (Figs. 4c, 4d; Table 3). Mean body mass at several time periods dropped to <250–300 g, within the range of species replacements by the smaller *N. lepida.* For Homestead Cave, at least, fossil evidence supported this interpretation. Virtually all skeletal fragments found within the mid-Holocene were those of *Neotoma lepida* although older strata yielded primarily bones of *N. cinerea* (Fig. 4d; Grayson 2000a, 2000b; Grayson and Madsen, 2000). Today, both woodrats are found in close proximity near the cave, although *N. cinerea* occupies the much cooler microhabitat within the cave (and surrounding higher elevation sites), and *N. lepida* is restricted to the arid desert floor (Grayson 2000a, 2000b; Grayson and Madsen, 2000). The recolonization of Homestead Cave by *N. cinerea* apparently occurred around 1000 ^{14}C yr B.P. (stratum XVII), concomitant with the reappearance of other taxa characteristic of cooler conditions (e.g., *Lemmiscus curtatus, Reithrodontomys megalotis,* etc.; Grayson 2000b).

Discussion

Organisms respond to climate change either by adapting to altered environmental conditions or, more commonly, by shifts in abundance and distribution (Betancourt, 1984; Dawson, 1992; Field et al., 1992; Tracy, 1992; Webb and Bartlein, 1992; Nowak et al., 1994; Grayson 2000a, 2000b). Responses are likely to be individualistic because of organisms' differing physiological tolerances to temperature or precipitation changes (Graham, 1986; Graham and Grimm, 1990). Here, we provide examples of both types of responses, and estimate the thermal threshold at which a

Table 3
Summary data for middens collected in Idaho and stratigraphic samples from Utah

Midden	Age (^{14}C yr B.P.)	Age CI	*N*	Pellet width (mm)	Std dev	Body mass estimate (g)	95% CI	July temperature estimated from *N. cinerea* (°C)	Deviation from modern July temperature	July temperature estimated from combined data (°C)	Deviation from modern July temperature
AH 1H	3880	140	56	4.99	0.183	294.2	16.4	22.0	4.2	19.0	1.2
AH 1G	3315	150	105	5.37	0.267	371.7	24.0	16.4	−1.4	16.1	−1.7
HMC 10	3985	85	218	5.68	0.207	435.7	18.5	13.5	−2.5	14.4	−1.6
HMC 8	3555	85	210	5.64	0.158	427.4	14.2	13.8	−2.2	14.6	−1.4
HMC 9	3160	80	315	5.52	0.273	402.3	24.5	14.9	−1.1	15.2	−0.8
ON 2	3185	80	53	5.08	0.140	312.6	18.05	20.4	0.4	18.2	−1.8
ON 1	2135	70	80	4.67	0.190	228.2	17.2	30.3	10.3	22.7	2.7
PC 1B	4050	140	86	5.19	0.210	335.2	18.8	18.7	0.8	17.3	−0.6
PC 1A	3970	85	116	5.37	0.130	371.7	11.8	16.4	−1.5	16.1	−1.8
RC 7D	3925	85	118	5.14	0.272	324.9	24.5	19.5	−0.7	17.7	−2.5
RC 7C	3625	80	77	4.78	0.149	250.7	13.3	26.9	6.7	21.2	1.0
RC 5	3535	95	85	4.80	0.180	255.6	16.3	26.3	6.1	20.9	0.7
RC 8C-2	3225	80	55	4.64	0.205	222.9	18.4	31.2	11.0	23.0	2.8
RC 8B	3180	80	276	5.51	0.189	401.0	17.0	14.9	−5.3	15.3	−4.9
RC 7B	2770	75	137	5.28	0.235	353.9	21.1	17.5	−2.7	16.7	−3.5
RC 7A	2500	80	137	4.74	0.239	242.4	21.5	28.1	7.9	21.7	1.5
RC 9	2415	80	88	4.98	0.212	292.0	19.0	22.2	2.0	19.1	−1.1
RC 4B	2100	85	200	5.29	0.150	354.5	14.3	17.4	−2.8	16.6	−3.6
RC 4A	1950	75	148	5.07	0.140	311.1	12.6	20.5	0.3	18.2	−2.0
RC 1A	795	65	233	5.24	0.100	345.2	8.6	18.0	−2.2	17.0	−3.2
RC 3	645	65	206	5.54	0.170	405.8	14.9	14.7	−5.5	15.1	−5.1
RC 8D	455	70	225	5.17	0.251	330.0	22.6	19.1	−1.1	17.5	−2.7
RC 1B			283	4.98	0.190	292.2	16.8	22.2	2.0	19.1	−1.1
RC 2B			179	5.07	0.190	309.5	17.0	20.7	0.5	18.3	−1.9
HSC93/94	11168	208	209	5.59	0.056	416.0	11.5	14.3	−9.8	14.9	−9.2
HSC95/92	10255	180	238	5.38	0.061	372.7	12.5	16.4	−7.7	16.1	−8.0
HSC62	8675	235	156	5.36	0.090	369.7	18.5	16.5	−7.6	16.2	−7.9
HSC49	3480	40	60	4.98	0.147	291.5	30.1	22.3	−1.8	19.1	−5.0
HSC48	2850	50	47	4.53	0.089	199.5	18.1	35.8	11.7	24.9	0.8
HSC37	2025	775	188	5.31	0.135	358.5	27.7	17.2	−6.9	16.5	−7.6
HSC34	1200	50	71	5.02	0.097	300.4	19.9	21.5	−2.6	18.7	−5.4
HSC33	1020	40	132	5.05	0.088	305.8	18.1	21.0	−3.1	18.5	−5.6

Note. Midden ages were determined by tandem mass accelerator and are given in unadjusted radiocarbon years before present. *N* is the total number of pellets measured. Pellet width (in mm) represents the mean of the largest 20 pellets; body mass was estimated from these (Smith et al. 1995; see text). July temperature was estimated from body size using regression equations presented in Table 2. See Fig. 1 and Table 1 for details about midden locations.

switch from one strategy to the other takes place. By altering body size, woodrats are able to adapt to changing environmental conditions. Numerous studies with both contemporary and paleo woodrat populations have demonstrated a robust phenotypic response to climate change (i.e. Smith et al., 1995; Smith and Betancourt, 1998; Smith et al., 1998). As in these earlier studies, we find considerable fluctuation in woodrat body size during the middle to late Holocene (Fig. 4). The size shifts are amazingly rapid in some instances, presumably reflecting intense selection pressure. Earlier work suggested that the mechanism involved might be heat stress; woodrats are particularly sensitive to temperature (Lee, 1963; Brown, 1968; Brown and Lee, 1969). Do the phenotypic adaptations at least partially reflect underlying genetic change? We suspect so; body size is highly heritable for most mammals (e.g. Rutledge et al., 1973; Leamy, 1988). A preliminary sib-sib analysis conducted on 12 woodrat litters yielded a broad sense heritability for body size of ~0.9 (Smith, unpublished). Although we do not have an estimate of the actual additive genetic component (narrow sense heritability), it is probably substantial.

Regardless of the degree to which the body size changes are genetically based, however, the life history consequences are profound. Many fundamental physiological and ecological factors scale allometrically with an organism's size, including fecundity, energetic requirements, diet, territory and home range size, longevity and even extinction rates (e.g. Peters, 1983; Calder, 1984; Schmidt-Nielson, 1984). Recent work on other species of *Neotoma*, for example, suggests that intense thermal selection can even cause profound changes in basic reproductive strategies, including a shift from interoparity to semelparity (Smith and Charnov, 2001). Using allometric equations presented in Peters (1983), we estimated population density, home range, fecundity, metabolic rate, and several other life history characteristics for woodrats occupying Rocky Canyon Cave over the Holocene (Table 4). The equations are drawn

Table 4
Predicted differences in life history characteristics for selected middens recovered at Rocky Canyon Cave

Factor	Equation	Midden								
		RC7d	RC7c	RC8b	RC7b	RC7a	RC4b	RC4a	RC3	RC8d
Age (^{14}C yr B.P.)		3925	3625	3180	2770	2500	2099	1950	645	455
Body mass (g)		325	251	401	354	242	355	311	406	330
Metabolic rate (J s^{-1})	$y = 3.28M^{0.756}$	1.40	1.15	1.64	1.50	1.12	1.50	1.36	1.66	1.42
Locomotion (m s^{-1})	$y = 10.4M^{0.38}$	6.78	6.15	7.3	7.0	6.1	7.0	6.7	7.4	6.8
Density (km^{-2})	$y = 55M^{0.90}$	151	191	125	140	197	140	157	124	149
Home range (ha)	$y = 3.1M^{0.63}$	1.52	1.30	1.74	1.61	1.27	1.61	1.49	1.76	1.54
Litter mass (g)	$y = 159M^{0.82}$	63.3	51.2	75.2	67.9	49.7	68.0	61.0	75.9	64.1
Average life span (d)	$y = 2040M^{0.27}$	1685	1613	1746	1710	1603	1711	1176	1750	1690
Mean size of predators (kg)	$M = 0.735y^{1.24}$	3.31	2.7	3.9	3.6	2.6	3.6	3.2	4.0	3.4

Note. Allometeric equations are taken from Peters (1983, and references therein) and are derived from interspecific regressions; actual intraspecific relationships are probably somewhat different.

from interspecific comparisons spanning many orders of magnitude and are used here mostly for illustrative purposes. Clearly, differences in body size translate into profound differences in life history (Table 4). Population density, for example, is highly related to body mass. Changes in density influence not only the woodrat population, but also the plants they feed on, the animals they compete with, and the predators (e.g., owls, snakes, coyotes, ringtails, etc.) that feed upon them. These in turn have substantial impacts on other components of the ecosystem, which themselves may be directly impacted by temperature shifts.

Our analysis also indicated that climatic warming apparently exceeded thermal tolerances in several instances, leading to local extirpation and subsequent invasion by a differently sized, but closely related animal. We conclude that the drastic body size reductions seen at lower elevation sites in the mid-Holocene (Fig. 4b–d) are due to species turnover and not the result of particularly rapid phenotypic responses for a variety of reasons. First, very few populations of *Neotoma cinerea* are this small today (Fig. 2d), and all display substantial pelage modifications beyond that resultant from their decreased body size (Hooper, 1940; Smith, 1997), a combination of phenotypic changes that might entail a longer response time than that observed (e.g., Fig. 4b). Second, a body size of ~250 g for *N. cinerea* implies a January temperature above 10°C (Table 2). Yet, modern January temperatures at suspect cave sites range from −3.5 to −6.7°C (Table 1), and it seems implausible that winter temperatures warmed by >13–16°C during the late Holocene. Third, the skeletal material from Homestead Cave (Fig. 4d) indicates a complete lack of *N. cinerea* at this site during the middle to late Holocene, despite its presence earlier (and today). Virtually all *Neotoma* bones found from roughly 8000 years and later are those of *N. lepida* (Grayson 2000a, 2000b). The sizes of the fossil fecal pellets recovered during this time indicate a maximum body mass of ~280–300 g (Fig. 4d). If the absence of *N. cinerea* bones indicates their absence from the cave, as seems likely given their abundance prior to this time, this suggests that the pellets were deposited by *N. lepida.* Note that January temperature for this cave is well within the thermal tolerance of desert woodrats (Table 1, Fig. 2). Although no skeletal material was recovered at Rocky Canyon Cave, pellets from this more northern site (Fig. 1) indicate an even smaller maximum size (~240 g) at several periods during the late Holocene (Fig. 4b). Although modern January temperature is at the thermal threshold for *N. lepida* (Table 1, Fig. 2), it was likely somewhat warmer during the altithermal (e.g., Elias, 1996; Smith and Betancourt, 1998). Finally, we note that at all times, the body size of woodrats occupying nearby high elevation sites remained well within the size range of *N. cinerea* (Fig. 4a).

All woodrat species are highly territorial, excluding even conspecifics from their den (Finley, 1958; Cameron, 1971; Escherich, 1981; Carraway and Verts, 1991; Smith, 1996, 1997). Such intolerance precludes the possibility of two species coexisting within a single cave site. Given that *N. cinerea* is behaviorally and physically dominant over other woodrat species (e.g., Finley, 1958; Smith, 1997), a species replacement must then necessarily first involve its local extirpation. If the proximate causal mechanism is indeed temperature, we can estimate the threshold at which species turnovers occurred. For *N. cinerea* to be replaced by the smaller, more heat tolerant *N. lepida,* suggests that average July temperature probably exceeded ~25°C, and further, that January temperatures were above ~−5°C (Fig. 2). Recolonization by *N. cinerea* was possible when summer temperatures fell below ~24–25°C. The only site approximating these conditions today is Homestead Cave, where both woodrat species are found in close proximity (Grayson 2000a, 2000b; Grayson and Madsen, 2000; Madsen, 2000). Other locations all have milder summer conditions and more extreme winters (Table 1) and consequently fall outside the thermal tolerances and modern geographic range of *N. lepida* (Figs. 1, 2). That neither Hidden Mouth Cave nor Pictograph Cave provides any indication of species turnovers suggests that they remained outside the expanded distribution of *N. lepida* within the middle to late Holocene (Fig. 4a).

The picture that arises from our analysis is the concept of a very dynamic range boundary that fluctuates with chang-

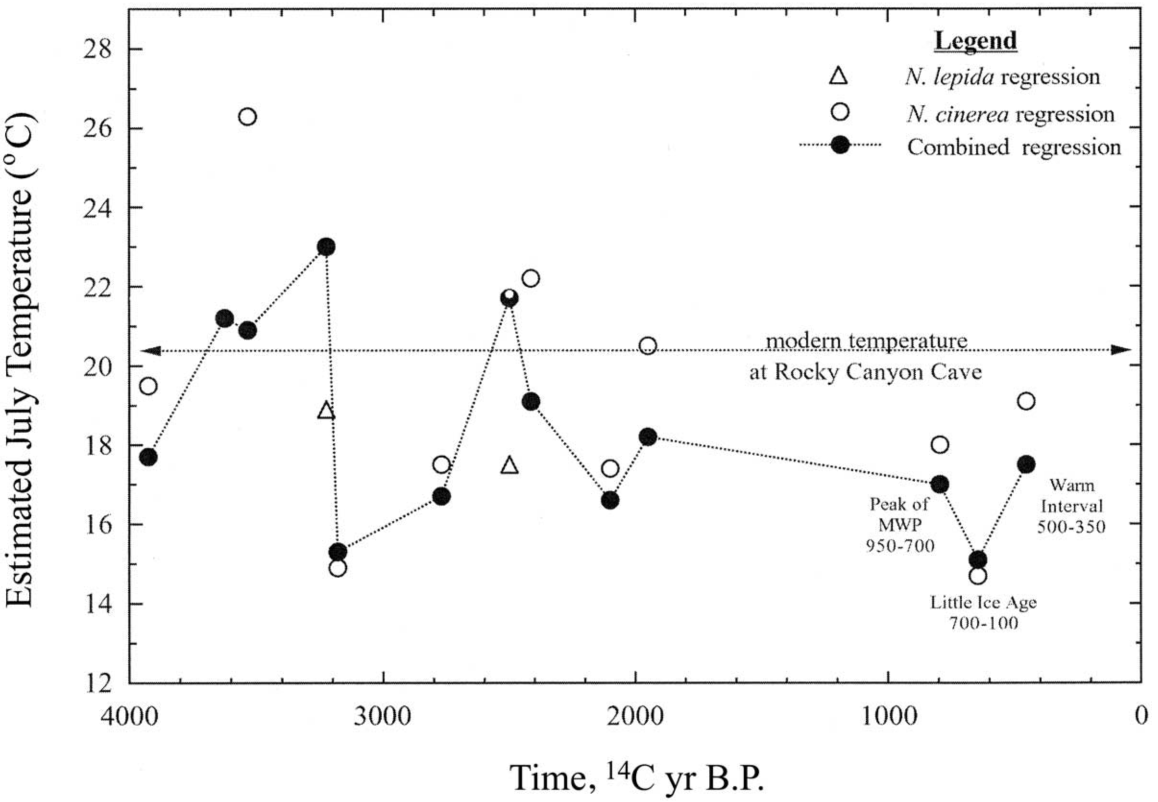

Fig. 5. July temperature over the past 4000 years reconstructed from the body size of woodrats at Rocky Canyon Cave. Temperature estimates are derived from the combined regression provided in Table 2. The combined regression was used because of the large uncertainites in the tails of the regressions for the individual woodrat species; these overlapped at approximately 250–300 g (Fig. 3). The dashed line between values does not imply a temperature reconstruction but is only present to help orient the graph. Modern July temperature is indicated by the dotted line. Several postulated climatic episodes are indicated for comparative purposes (Porter, 1986; Jones and Bradley, 1992; Hughes and Diaz, 1994), although the tree-ring chronology of Biondi et al. (1999) is a more appropriate comparison (see text).

ing climatic conditions. Recently, a variety of unpublished records for bushy-tailed woodrats in low-elevation xeric settings have been reported (Grayson et al., 1996). Given the very robust response to ambient and lethal temperature repeatedly demonstrated for this species in particular (e.g., Lee, 1963; Brown, 1968; Brown and Lee, 1969; Smith et al., 1995; Smith, 1997; Smith and Betancourt, 1998; Smith et al., 1998; Smith and Charnov, 2001), we believe these may reflect opportunistic range expansions during favorable climatic conditions. Although adult woodrats are fairly sedentary, juveniles have been reported dispersing as far as 5 km over a short period (Escherich, 1981). Further, over much of their range there is considerable topographic relief (Fig. 1), so that responses to climate fluctuations can include elevational movements. Conversely, local extinctions may occur in thermally marginal habitats during unfavorable climatic conditions. Because caves provide particularly good den sites, and dens are a limiting resource (e.g., Cameron, 1971; Escherich, 1981; Smith, 1996, 1997), an unoccupied cave serves as a magnet to any other woodrat (or woodrat species) in the vicinity. Smith (1996), for example, not only found a significant relationship between woodrat survivorship and den type, with the oldest animals occupying rock crevices or caves, but also found that the "best dens" were virtually continually occupied by series of woodrats.

Finally, we note that woodrat body size over the Holocene provides a unique paleothermometer, which operates over relatively small temporal and spatial scales. Using the regressions presented in Fig. 3 and Table 2, we translated middle to late Holocene body sizes into estimates of local temperature fluctuations (Smith and Betancourt, 1998; Fig. 5). The patterns correspond well with those derived from tree-ring chronologies (Biondi et al., 1999) and with recent high-resolution cores of lake sediments (Benson et al., 2002). Not only do we observe considerable climate fluctuations during the middle and late Holocene, but many of these temperature reversals were abrupt and of considerable magnitude (i.e., Fig. 5). Again, our conclusions are concordant with other studies that suggest temperature and/or hydrology reversals of comparable magnitude occurring at centennial or even decadal scales (Biondi et al., 1999; Benson et al., 2002).

Clearly, the resolution of a woodrat body sized based climate proxy is limited by the number of middens available from any location, and by uncertainties in the radiocarbon dating. Yet, identifying climate reversals on the order of 10 to 100 years in other unglaciated records has been difficult because of the coarse spatial and temporal resolution of most paleodatasets (Kneller and Peteet, 1999); even detailed ice-core records can be difficult to interpret for mid-latitude climates. Analysis of lake sediment cores are hampered by the availability of suitable sites and interpretation can be complicated by erosion, the reworking or resuspension of older sediments, bioturbation, and other factors. Dendroclimatic reconstructions, although providing annually resolved climatic data, are largely limited to the last few centuries (but see Biondi et al., 1999). The strong response of woodrat body size to temperature, coupled with the ubiquity of woodrat paleomiddens across southwestern North America, suggests they may be invaluable in reconstructing detailed local temperature records over much of the late Quaternary.

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