



Predicting woodrat (*Neotoma*) responses to anthropogenic warming from studies of the palaeomidden record

Felisa A. Smith^{1*} and Julio L. Betancourt²

¹Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA and

²US Geological Survey, 1675 W. Anklam Road, Tucson, AZ 85745, USA

ABSTRACT

Aim The influence of anthropogenic climate change on organisms is an area of great scientific concern. Increasingly there is recognition that abrupt climate transitions have occurred over the late Quaternary; studies of these shifts may yield insights into likely biotic responses to contemporary warming. Here, we review research undertaken over the past decade investigating the response of *Neotoma* (woodrats) body size and distribution to climate change over the late Quaternary (the last 40,000 years). By integrating information from woodrat palaeomiddens, historical museum specimens and field studies of modern populations, we identify potential evolutionary responses to climate change occurring over a variety of temporal and spatial scales. Specifically, we characterize climatic thresholds in the past that led to local species extirpation and/or range alterations rather than *in situ* adaptation, and apply them to anticipate potential biotic responses to anthropogenic climate change.

Location Middens were collected at about 55 sites scattered across the western United States, ranging from about 34 to 46° N and about 104 to 116° W, respectively. Data for modern populations were drawn from studies conducted in Death Valley, California, Missoula, Montana and the Sevilleta LTER site in central New Mexico.

Methods We analysed faecal pellets from midden series collected at numerous cave sites across the western United States. From these we estimated body mass using techniques validated in earlier studies. We compared body size fluctuations at different elevations in different regions and integrated these results with studies investigating temperature–body size tradeoffs in modern animals. We also quantify the rapidity of the size changes over the late Quaternary to estimate the evolutionary capacity of woodrats to deal with predicted rates of anthropogenic climate change over the next century.

Results We find remarkable similarities across the geographical range to late Quaternary climate change. In the middle of the geographical range woodrats respond in accordance to Bergmann's rule: colder climatic conditions select for larger body size and warmer conditions select for smaller body size. Patterns are more complicated at range boundaries, and local environmental conditions influence the observed response. In general, woodrat body size fluctuates with approximately the same amplitude and frequency as climate; there is a significant and positive correlation between woodrat body size and generalized climate proxies (such as ice core records). Woodrats have achieved evolutionary rates of change equal to or greater than those needed to adapt *in situ* to anthropogenic climate change.

Main conclusions *In situ* body size evolution is a likely outcome of climate change, and such shifts are part of a normal spectrum of adaptation. Woodrats

*Correspondence: Felisa A. Smith, Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA.
E-mail: fasmith@unm.edu

appear to be subject to ongoing body size selection in response to fluctuating environmental conditions. Allometric considerations suggest that these shifts in body size lead to substantial changes in the physiology, life history and ecology of woodrats, and on their direct and indirect interactions with other organisms in the ecosystem. Our work highlights the importance of a finely resolved and long-term record in understanding biotic responses to climatic shifts.

Keywords

Adaptation, body size, darwins, evolutionary change, global climate change, late Quaternary, temperature, western North America, woodrat middens.

INTRODUCTION

Climate change is a natural part of the earth system. Over the 2.8 Myr of the Late Pliocene and Pleistocene epochs, for example, some 20 glacial–interglacial oscillations occurred, each profoundly influencing the abundance, distribution and evolution of species. Numerous studies have documented the influence of late Quaternary climate fluctuations on phylogeographical patterns, patterns of morphological change, speciation and extinction rates, spatial use and distribution shifts and faunal structure and dynamics (e.g. Davis, 1977, 1981; Graham, 1986; Cronin & Schneider, 1990; Goodwin, 1993; Roy *et al.*, 1995; Smith *et al.*, 1995; Graham *et al.*, 1996; Grayson, 2000; Jackson & Overpeck, 2000; Davis & Shaw, 2001; Schmidt *et al.*, 2003; Davis *et al.*, 2005; National Research Council, Committee on the Geological Record of Biosphere Dynamics, 2005).

Unlike earlier fluctuations in climate, anthropogenic warming poses unique challenges to organisms because of the rapid rate and magnitude of the expected temperature and precipitation shifts (Holt, 1990; Houghton *et al.*, 2001; Thomas *et al.*, 2004; Davis *et al.*, 2005). Recent projections, for example, suggest temperature increases of 2.8 to 5.4°C within the next 100 years with higher frequencies of extreme weather events (Houghton *et al.*, 2001). Studies clearly indicate that changes in climate over the past few decades have already affected physical and biological systems in many parts of the world (Hughes, 2000; Parmesan & Yohe, 2003 and references therein). Yet because the rate of change is likely to accelerate, the magnitude, timing and nature of future responses remain unclear.

Here, we review results from studies conducted over the past decade to investigate how a group of small mammalian herbivores have responded to climate shifts over the past 25,000 years. Our work on woodrats (*Neotoma*) has been conducted at a variety of spatial and temporal scales, drawing from *c.* 55 sites scattered throughout the western United States (Fig. 1). We integrate the palaeorecord with investigations conducted on extant populations to examine *in situ* adaptation and to characterize climatic thresholds leading to local species extirpation and/or range contraction/expansions. To date, most studies of biotic responses to climatic

fluctuations have been analysed in the context of the Pleistocene/Holocene transition with little attention paid to changes during the current interglacial substage. This is largely because short-term oscillations in climate occur at rates close to the resolution limits of most palaeoecological records. The documentary quality of our study system is considerably higher than most, with virtually no spatial and limited temporal averaging. With the exception of the pollen record, which can yield detailed information about regional responses to past climate change, there is no other comparable terrestrial record.

Most of the responses to late Quaternary climate fluctuations we discuss here involve changes in woodrat body size. Temperature has long been known to influence organism body size; the pattern is common enough to have led to the formation of ‘Bergmann’s rule’. Bergmann’s rule states that there is a positive relationship between body size and latitude, with populations (or species) in the colder portions of the distribution larger than populations (or species) occurring in warmer regions (Rensch, 1938; Mayr, 1956, 1963). Bergmann’s rule is often attributed to the selective advantage of a higher body surface to volume ratio in warm areas, or conversely, to the reduced heat loss that accompanies a lowered surface to volume ratio in cooler climates (Bergmann, 1847; Mayr, 1956, 1963). This pattern is among the oldest and most robustly supported ecogeographical rules, with more than 65% of mammals and 72% of bird species demonstrating adherence (e.g. Ashton *et al.*, 2000; Meiri & Dayan, 2003; Millien *et al.*, 2006). More recently it has been documented over historical and geological time (Davis, 1977, 1981; Purdue, 1980; Smith *et al.*, 1995, 1998; Yom-Tov *et al.*, 2006). Although Bergmann’s rule is generally considered to reflect a direct response to environmental temperatures, for some organisms it may actually reflect a correlated response to other factors that scale with temperature (e.g. productivity, moisture index, metabolic rate; Rosenzweig, 1968; McNab, 1971; Calder, 1984; Schmidt-Nielsen, 1984; Yom-Tov & Nix, 1986).

Because any number of fundamental physiological and ecological factors scale allometrically with organism size, including fecundity, energetic requirements, diet, territory and home range size (e.g. Peters, 1983; Calder, 1984; Schmidt-

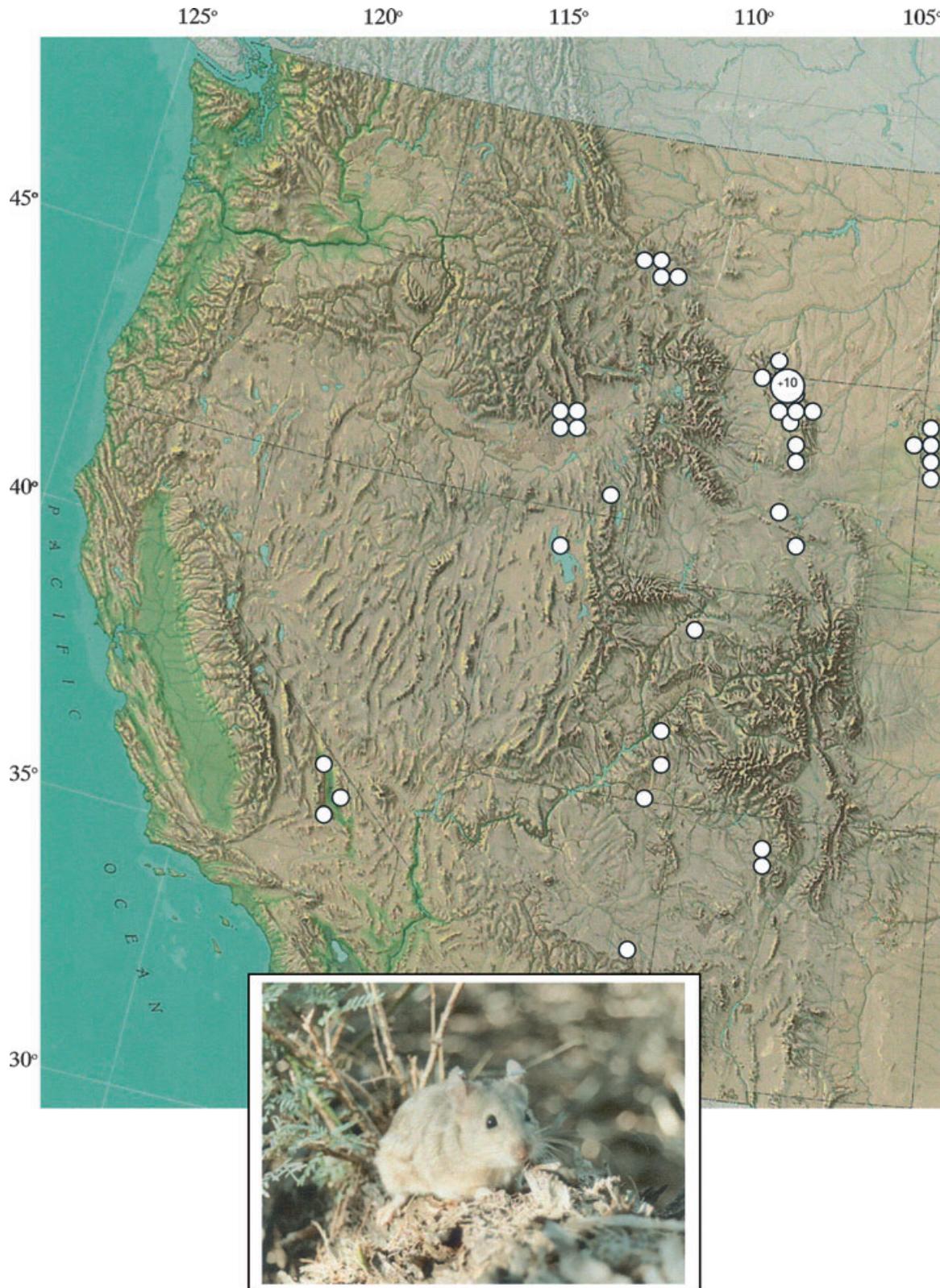


Figure 1 Geographical extent of current midden sites (*c.* 55) across the western United States. Sites are located in rocky crevices, caves or shelters and may contain several to dozens of discretely radiocarbon-dated palaeomiddens. The best sites contain a chonosequence spanning 20,000 years or more. We currently have *c.* 375 individual radiocarbon-dated middens from these locations. Each palaeomidden contains hundreds to thousands of faecal pellets; because pellet width is related to body size we can construct histograms of body size of populations over time. Inset: *N. lepida* (desert woodrat), one of the smallest-bodied species in the genus responsible for most of the middens in the Mojave Desert.

Nielsen, 1984), changes in body size can in turn profoundly influence the life history, ecology and evolution of organisms. Thus, understanding the responses of mammalian body size to past temperature fluctuations may be of considerable importance in evaluating how organisms may respond to future climate shifts.

RESEARCH SYSTEM

Woodrats (or packrats; Fig. 1 inset) are small herbivorous mammals found throughout much of North and Central America, which reach their greatest diversity in the southwestern United States (Hall, 1981). The studies we discuss here involve two species of *Neotoma* differing significantly in size and habitat requirements. *Neotoma lepida* is a small (c. 85–200 g) desert-adapted species found in low-elevation xeric sites throughout much of California, Nevada and Utah, that reaches its northern range limits at the very southern edge of Idaho (Hall, 1981). Current thought is that *N. lepida* expanded into the northern and eastern portions of its range mostly during the late Pleistocene (Patton & Álvarez-Castañeda, 2004). In contrast, *Neotoma cinerea* is a large woodrat (it can exceed 600 g) found in forested habitat as far north as the Yukon Territory. It ranges throughout much of the West, including Idaho, Wyoming and high-elevation portions of Utah, and reaches its southern limits in northern New Mexico and Arizona, and the Sierra Nevada of California (Hall, 1981; Smith, 1997). Fossil evidence suggests that it was found as far south as northern Mexico during the full glacial period (Harris, 1984, 1985, 1993; see also FAUNMAP at <http://www.museum.state.il.us/research/faunMap>). The two species are sympatric in parts of their ranges, although considerable ecological separation is evident. Body size variation in *N. cinerea* demonstrates a strong latitudinal gradient, with populations larger in the north and smaller in the south. In contrast, body size variation in *N. lepida* is largely east to west. The largest populations lie along the coast of upper and lower California; the smallest in the hot interior deserts (Smith, 1992; Smith & Betancourt, 2003). In addition to differences in size, environmental thresholds are quite different: *Neotoma lepida* does not occur where mean January temperature drops below c. -5°C , and *N. cinerea* does not occur where mean July temperatures rise above c. 25°C (Smith & Betancourt, 2003).

Previous studies have shown that woodrats are particularly sensitive to environmental temperature (Lee, 1963; Brown, 1968; Brown & Lee, 1969; Smith *et al.*, 1995, 1998; Smith & Betancourt, 1998, 2003). A strong correlation exists between mean adult body mass and ambient temperature across populations in the western United States (Fig. 2 & Table 1), with smaller adults found in hotter environments. Such relationships are found for all species studied. The underlying mechanism is probably physiological; lethal temperature is also an inverse function of body mass (Brown, 1968; Smith *et al.*, 1995). There is a species-specific response to temperature; at any given ambient temperature there is a significant difference in characteristic body mass (Table 1). The empirically derived

upper critical temperature for the smallest woodrat species (*N. lepida*) is about 42°C (Lee, 1963; Brown & Lee, 1969), fairly low for a desert animal (e.g. Tracy & Walsberg, 2002). Larger boreal species, such as *N. cinerea*, have even lower upper critical temperatures (c. 38°C).

These low temperature thresholds for woodrats are due, at least partially, to their inability to concentrate urine (MacMillen, 1964) and lack of specialized physiological adaptations to heat (e.g. inability to aestivate or utilize evaporative cooling, lack of specialized nasal passages to conserve water) typical of other desert rodents (Tracy & Walsberg, 2002). A recent molecular phylogeographical study suggests that expansion into arid and warm interior deserts may be a fairly recent event (Patton & Álvarez-Castañeda, 2004); desert woodrats apparently speciated in the more moderate conditions of coastal California and only radiated into deserts within the last 100,000 to 50,000 years (Patton, personal communication). Thus, the lack of specialized adaptations to heat and the sensitivity of body size to temperature may be a result of a relatively recent occupation of hot and arid habitats.

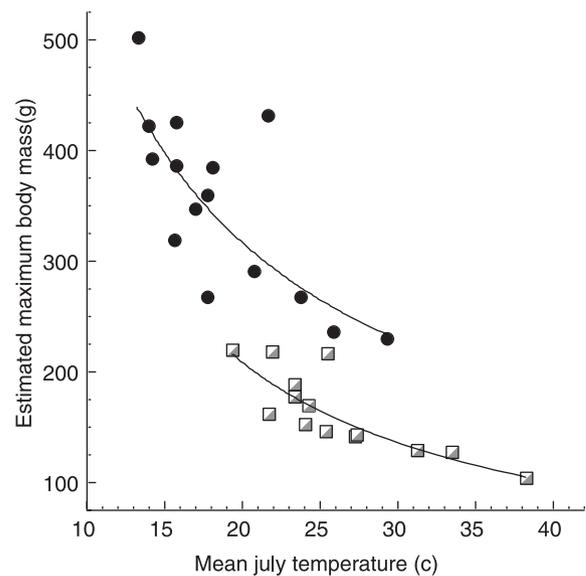


Figure 2 Relationship between population body mass and ambient temperature of the habitat. Plotted here is mean maximum body mass vs. July mean temperature for various populations of *N. lepida* (shaded squares) and *N. cinerea* (bushy-tailed woodrat, filled circles). Each population estimate is derived from a minimum of 20 individuals (up to > 200), and temperature represents an average for 50 yr+. Body size data from museum specimens and field notes; weather data from the Western Regional Climatic Center. Locations were chosen that bracket the approximate distributional edges. Note that *N. cinerea* can tolerate much colder temperatures than *N. lepida*, but rarely occupies habitat where July temperatures exceed c. 25°C . The two large populations of *N. lepida* represent peninsular forms occupying mesic and mild environments. Such relationships are seen for all woodrat species, although they differ in their thermal tolerances. See Table 1 for regression equations and significance values. Redrawn after Smith & Charnov (2001).

Table 1 Results from separate and combined regressions of mean and maximum population body mass of *N. lepida* and *N. cinerea*, vs. minimum and maximum mean temperatures of their habitat. In the Northern Hemisphere, January and July temperatures represent the minimum and maximum that animals are exposed to. Regressions are based on 15 populations of each species chosen to provide a thorough representation of the temperature extremes found within the modern geographical range. Analysis of covariance reveals a strong species effect ($P < 0.0001$), suggesting that *N. cinerea* and *N. lepida* respond differently to temperature

Regression	Species	Equation	<i>r</i> value	<i>P</i> value
Mean body mass vs. mean July temperature	<i>N. lepida</i>	$y = 2766.69x^{-0.943}$	0.900	< 0.0001
	<i>N. cinerea</i>	$y = 2850.96x^{-0.815}$	0.763	< 0.001
	Combined regression	$y = 14450.47x^{-1.403}$	0.853	< 0.001
Mean maximum body mass vs. mean July temperature	<i>N. lepida</i>	$y = 4901.30x^{-1.051}$	0.857	< 0.001
	<i>N. cinerea</i>	$y = 3470.60x^{-0.798}$	0.786	< 0.001
	Combined regression	$y = 19718.78^{-1.429}$	0.829	< 0.001
Mean body mass vs. mean January temperature	<i>N. lepida</i>	–	–	n.s.
	<i>N. cinerea</i>	$y = 0.063x^2 - 6.45x + 252.13$	0.614	< 0.05
Mean maximum body mass vs. mean January temperature	<i>N. lepida</i>	–	–	n.s.
	<i>N. cinerea</i>	$y = 0.156x^2 - 7.30x + 322.19$	0.647	< 0.05

Woodrats construct elaborate houses or dens around cacti, trees, in rock outcrops/crevices or in vacated human buildings. Houses are probably largely responsible for their successful existence under thermally stressful conditions; depending on the substrate, dens ameliorate ambient temperature by up to 5°C (Lee, 1963; Brown, 1968) and reduce predation intensities (Smith, 1996). In addition to nest chambers and food caches, houses contain middens, or debris piles, composed of plant fragments, copious faecal pellets and other materials. In arid environments, these materials commonly become embedded in crystallized urine (called ‘amberat’) to form an indurated midden that can persist for thousands of years. Such palaeomiddens provide a unique and rich historical and evolutionary record of the past.

Woodrat middens have permitted reconstruction of the late Quaternary vegetation history of western North America and have supported an impressive array of related applications (see reviews by Van Devender & Spaulding, 1979; Van Devender *et al.*, 1987; Betancourt *et al.*, 1990; Thompson *et al.*, 1993; Rhode, 2001; Betancourt, 2004). We are, however, at present the only researchers using the midden record to study the evolutionary responses of the woodrats themselves to climate change. Hence our review of this study system will necessarily largely focus on our own work.

Although palaeomiddens contain plant macrofossils, rocks and sometimes even archaeological artefacts, by far the most abundant constituent is faecal pellets. In earlier work, we demonstrated that there is robust relationship between pellet *width* and body mass, which is not influenced appreciably by gender, species or diet (Smith *et al.*, 1995; Fig. 3a). Because each discretely radiocarbon dated midden may contain hundreds to thousands of pellets, and a cave complex may yield several to dozens of distinct middens, it is thus possible to examine changes in body size of woodrats from single locations over long temporal spans. Such midden sequences can be compared across sites and regions to obtain a larger geographical perspective of responses to past climatic change.

METHODS

Sampling and processing methods for middens are generally similar among researchers (Spaulding *et al.*, 1990), though there can be important variations. In particular, the temporal resolution and integrity of a single midden sample (the actual indurated mass that is dissolved in a bucket of water) is subject to many factors, including subjective decisions made by the researcher in the field and the laboratory. Midden deposition can be slow or fast, as well as episodic. The exact duration of the depositional episode cannot be resolved within a century even with multiple dates of individual fragments from the same midden. An important underlying assumption on our part is that pellets in individual midden samples represent deposition by multiple generations (*c.* 20–100 generations; Betancourt *et al.*, 1990); this assumption has been tested indirectly through studies of modern midden composition and distribution (Figs 3 & 4).

In the laboratory, middens are weighed, vouchers removed and the remaining material disassociated by soaking in water for several days. Samples are strained, wet sieved and then dried in a forced-air oven. After drying, plant and faecal pellets are separated from other materials using a series of soil sieves (Spaulding *et al.*, 1990). Identification of plant macrofossils is made visually under a stereoscope using a reference collection established for the area, and relative frequencies of each plant type recorded. For the past 50 years, radiocarbon dating of plant macrofossils, or less frequently of pellet aliquots, has been conducted by gas proportional counting, liquid scintillation counting and most recently by accelerator mass spectrometry (AMS). The bulk methods yield average dates for midden assemblages, whereas AMS can date an individual plant fragment to test for contemporaneity in the assemblage.

After midden processing, pellets are sorted by size. The width of the *largest* 200+ (or *c.* 50% of the sample, whatever is greater) pellets is measured to the nearest 0.1 mm using digital callipers. Measurements are conducted blind; that is, without knowledge of the radiocarbon age of the pellets. The

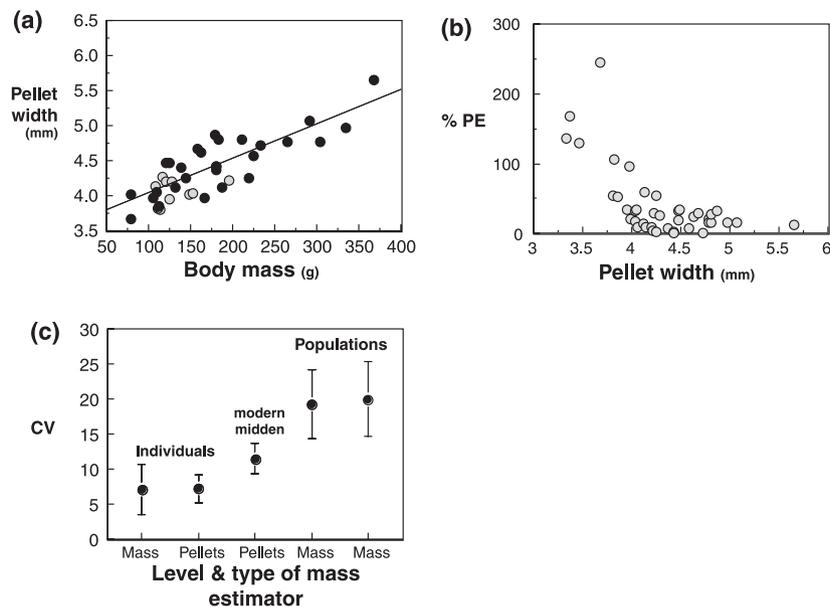


Figure 3 The relationship between pellet width and body size. (a) Body mass and mean pellet width for three species of woodrat: *N. cinerea*, *N. lepida* and *N. albigula*. A total of 30 field-trapped animals were housed in the laboratory (20°C, 12-h light/12-h dark cycle) and fed a 40% fibre diet. Pellets were collected, dried and measured in a blind study. A partial *F* test confirmed that a linear model is the best fit ($y = 0.005x + 3.559$; $r^2 = 0.69$; $P < 0.0001$). The relationship was not affected by gender or species (two-way ANCOVA, $P \gg 0.05$). The grey symbols indicate a new test of the relationship conducted in 2003; results were identical with the previous study (some symbols overlap). (b) Percentage predicted error (%PE, ratio of predicted minus observed mass divided by predicted mass) vs. pellet width. Validation studies were conducted in both 1995 and 2003 with field-collected animals not used to derive the original regression. Pellets were collected and measured blind, and then compared with the actual mass of the animal. Results indicated that %PE is $< 21\%$ at widths greater than 4 mm. This value is considerably less than in many palaeoecological studies (e.g. Van Valkenburgh, 1990), suggesting that pellet width is a better estimator of mass than long bones or teeth. (c) Coefficient of variation of body mass at different levels (individuals and populations) as estimated by live trapping or by inferring from faecal pellets. The magnitude of variation in body mass over an individual's life is $c. 7.2\%$, irregardless of gender, species, diet, habitat quality or differences in reproductive output. Body mass as estimated by pellet width varies $c. 7.3\%$ in magnitude, suggesting that width is a good proxy for size. The magnitude of variation in body mass of modern middens (those collected during a single season at a single den locality) is about twice that of individuals ($c. 11\%$), reflecting the contribution of multiple animals to the sample. The magnitude of body size variation within a species, and between different species (the last value) is about three times that seen in individuals over their lifetime ($c. 20\%$). These values were invariant across different species of woodrat (*N. lepida*, *N. albigula*, *N. cinerea* and *Neotoma fuscipes*).

mean, standard deviation and 95% confidence interval of the 10, 20 and 50 largest pellets, respectively, are calculated. Here, we use the mean of the largest 10 (mean₁₀) to represent body size instead of the grand mean because: (1) it is not sensitive to sample size, (2) it avoids the confounding effects of ontogeny by excluding juveniles, (3) it excludes pellets of other den commensals (i.e. large-bodied *Peromyscus*), and (4) it allows us to differentiate between middens constructed by *N. cinerea* and other species; no other woodrat within the western US overlaps in maximum body mass, and even subadult *N. cinerea* are usually larger than the largest individuals of other co-existing species. Measurements are converted to body size estimates using the regression shown (Fig. 3a). Although we routinely use mean₁₀ body size, results are qualitatively similar with other measures (grand mean, mean₂₀, etc.). To date, we have measured $> 50,000$ fossil pellets (Table 2).

In several validation studies with modern woodrats, we have examined the possible confounding effects of diet,

habitat quality and other environmental influences on the pellet width–body size relationship (Smith *et al.*, 1995; Fig. 3). For example, pellets from field-trapped animals of several species collected in different habitats, at different seasons and in multiple locations were measured in several blind studies. Values were converted to mass estimates and then compared to actual field mass. We calculated percentage predicted error (%PE; the difference between the predicted and actual mass divided by the predicted mass) and obtained values $< 21\%$ for pellets ≥ 4 mm (Fig. 3b). The %PE is a comparative index of predictive accuracy; typical values in the palaeoliterature range from 18% to 55% for molar and bone measures (Van Valkenburgh, 1990). Thus, despite differences in habitat quality, thermal regimes and diet, there was no significant effect on the pellet width–body mass relationship for pellets > 4 mm (ANCOVA, $P > 0.05$). Note, however, that %PE increases sharply for pellets < 4 mm (< 80 g body mass). We attribute this largely to an increase in measurement error.

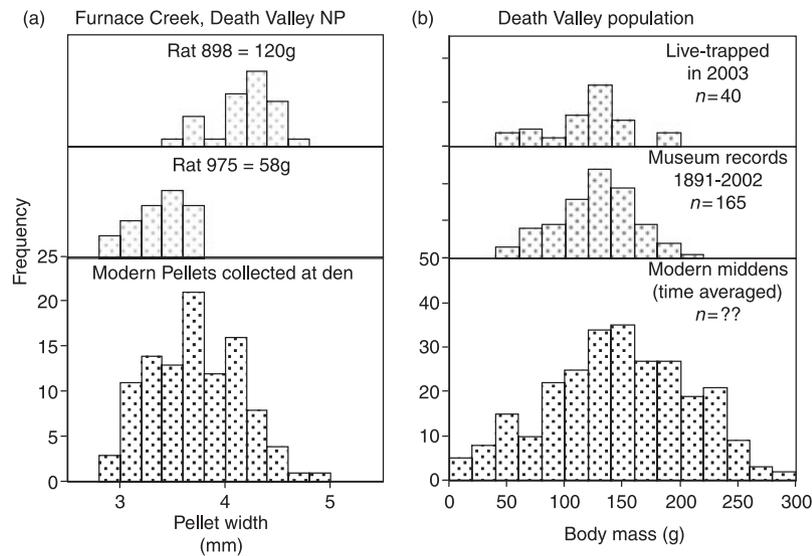


Figure 4 Body size variation at different scales. (a) Frequency distributions of pellet widths for individual animals and for a collection of pellets collected at a single den. The scale and axes are the same in all panels. We have been examining individual variation in pellet widths as a function of ontogeny and seasonality (over 30 animals were analysed in this fashion). The top panel represents the pellet variation from an animal live trapped during 2003, and whose body mass varied over the course of the study from 112 to 120 g. The second panel represents a juvenile live trapped in 2003, weighing 58 g when last trapped. The bottom panel illustrates the widths found in a loose collection of pellets gathered directly from the runways at this den location. Because these pellets were exposed, they represent at most a season's worth of animal deposition. Masses estimated from these pellets indicate animals varying from *c.* 40 to 150 g, the slight hump to the left probably indicates the impact of the juvenile on the sample. (b) Body mass range of woodrats at Furnace Creek at different temporal scales. Top panel: animals live trapped at Furnace Creek during 2003. Middle panel: range in mass from museum records of animals collected from 1891 to 2002. Bottom panel: body mass range estimated from a 'modern' midden. This modern midden was sampled from a large protected debris pile and was only loosely indurated. These results suggest the time span for modern midden deposition is greater than that represented by the museum records (> 100 years). Note the considerably greater range of body masses represented in the bottom panel. Note also that in this instance, all samples yielded the same approximate average body mass for the population, suggesting that climate has been approximately constant during these intervals. These results were consistent across different species and for different locations. Based on analyses like this, we estimate that palaeomiddens probably contain samples from about 100 animals.

A question that underlies many morphological studies is whether patterns reflect plastic physiological responses, or whether there is an underlying evolutionary basis. We suspect that a large component may be genetically based. For most mammals (pocket gophers are a notable exception), body size is generally considered to be highly heritable (Falconer, 1953, 1973; Rutledge *et al.*, 1973; Leamy, 1988). The small coefficient of variation of body size for woodrats caught repeatedly in the field, for example, suggests that body size does not fluctuate widely in adult animals (Figs 3c & 4).

We were able to directly estimate broad-sense heritability using data provided by O. Schwartz. For a study on growth rates, he captured 13 pregnant white-throated and desert woodrats (*Neotoma albigula* and *N. lepida*) and brought them into the laboratory where they were fed *ad libitum*. After parturition, the offspring were weighed every few days until they reached maturity. We used these data to conduct a heritability analysis. We regressed average offspring mass against maternal mass (no paternal mass was available), and sibling masses against each other. Both regressions employing the laboratory raised offspring yielded a broad sense heritability estimate of > 0.8 (Fig. 5b), with no species

effects. Because paternal data were lacking, we are unable to estimate the magnitude of maternal effects to obtain a narrow sense heritability estimate. Nonetheless, our calculations suggest a substantial genetic component. It should be noted, however, that such laboratory estimates might be of questionable value when extrapolated for populations that existed 20,000 years ago. Our emphasis on phenotypic evolution is true of most palaeoecological studies because of the difficulty in determining heritabilities for fossil materials and/or traits.

RESULTS AND DISCUSSION

Response of woodrats to late Quaternary climate change

We find remarkable congruence across the geographical range to late Quaternary climate change. Midden sequences plotted for each location consistently demonstrate that woodrats respond as predicted from Bergmann's rule: colder climatic conditions select for larger body size and warmer conditions select for smaller body size (Figs 6 & 7). Thus, body size

Table 2 Characteristics of palaeomiddens used in the study

Midden sequence	ID	Middens collected*	Age range (^{14}C years)	State	Elevation range (m)	N Latitude	W Longitude	Region
Lyman Lake	LL	8	1690–16,480	AZ	1880	34.50	109.50	White Mountains
Atlatl Cave	ATC	7	0–10,080	NM	1910	36.05	107.59	Chaco Canyon NP
Titus Canyon	TiC	77	Not yet known	CA	200–1700	36.27	116.53	Grapevines, Death Valley NP
Fishmouth Cave	FMC	6	3550–13,800	UT	1585	37.25	109.39	Comb Ridge
Allen Canyon	AC	2	10,030–11,310	UT	2195	37.47	109.35	
Bison Alcove	BA	13	50–20,050	UT	1317	38.44	109.30	Arches NP
Sand Canyon	SC	7	Not yet known	UT	1920	40.20	109.01	
Dutch John Mountain	DJM	50	0–35,170	WY	2000–2092	40.57	109.00	Flaming Gorge
Homestead Cave†	HSC	10	0–11,168	UT	1406	41.00	113.00	Pluvial lake Bonneville
Oneida Narrows	ON	2	2135–3185	ID	1550	42.15	111.50	
Fremont Canyon	FC	16	165–8930	WY	1772–1889	42.31	106.46	North Platte River
Tweaver pass	TP	5	1025–4,450	WY	1870	42.42	108.33	Wind River Mountains
Bird's Eye Canyon	BEC	3	80–3110	WY	1673	43.23	108.05	
Wind River Canyon	WRC	13	375–3590	WY	1378–1428	43.34	108.12	Wind River Mountains
Mahogany Butte	MB	14	0–7650	WY	1650	43.38	107.21	
Arco Hills	AH	3	2400–3880	ID	1926	43.39	113.08	
T Hill	Thill	2	18,190–18,300	WY	1440	43.39	108.12	
Pictograph Cave	PC	2	3970–4050	ID	1900	43.41	113.20	
Rocky Canyon	RC	20	455–3925	ID	1800	43.42	113.25	
Hidden Mouth Cave	HMC	3	3160–3987	ID	2255	43.57	113.26	
Outlaw Cave Campground	OCC	3	209–2227	WY	1994–2006	43.57	106.96	East Bighorns
Cook's Canyon	CC	6	500–4620	WY	1723–1969	43.59	107.14	
Redbird Canyon	RBC	7	0–3554	SD	1471–1560	43.81	104.00	Black Hills
Slip Road	SR	6	2091–4942	WY	1994–2095	43.83	106.88	East Bighorns
Black Canyon	BC	5	1145–4441	WY	1852–1975	44.02	107.29	West Bighorns
10 Sleep Canyon	10S	10		WY	1858	44.05	107.18	
South Fork Brokenback	SFB	16	612–9602	WY	1520–1769	44.13	107.39	West Bighorns
Brokenback Narrows	BBN	6	921–2401	WY	2129–2209	44.15	107.36	West Bighorns
Medicine Lodge Canyon	ML	12	1450–7840	WY	1538–1600	44.19	107.32	
MC Creeks	MC	10	139–2907	WY	1754–1846	44.21	107.43	West Bighorns
Meyer Spring Draw	MSD	6	225–4630	WY	1883–1895	44.22	107.33	
Spearfish Canyon	SPFC	3	109–135	SD	1538	44.30	103.90	Black Hills
Inyan Kara Drainage	IKD	1	153	SD	1280	44.49	104.79	Black Hills
Miller Creek	MC	1	795	SD	1538	44.50	104.70	Black Hills
Southern Big Horn Mtns, eastern Pryor Mtns	SBH-EP	37	450–23,860	WY	1286–1606	45.02	108.15	Bighorn Mountains
Pryor Mountains	PM	22	490–9980	WY	1514–1662	45.08	108.38	Pryor Mountains
Spring Creek Canyon	SCC	5	368–2223	MT	1585	46.55	110.45	Little Belt Mountains
Beaver Creek Canyon	BCC	5	192–7039	MT	1169	46.79	111.87	Big Belt Mountains
Judith River	JR	7	309–5105	MT	1588–1637	46.83	110.28	Little Belt Mountains
Coyote Hills	CH	2	10,635–13,830	NM				
Lakota Ridge	LR	5	0–2760	WY	1732			
Lower Canyon Creek	LCC	7	615–1880	WY	1582	44.02	107.20	
Twin Creek	TC	9	99–1930	WY	1860–1920	42.40	108.30	

*Not all collected middens are submitted for radiocarbon dating, nor do all yield sufficient samples for estimates of population body size.

†This site is an excavation containing woodrat pellets in distinct layers; taphonomy is different from that of indurated palaeomiddens.

decreased during the Pleistocene/Holocene transition, increased during the Younger Dryas cold episode, decreased during the warm conditions of the middle Holocene (also referred to as the Altithermal or Hypsithermal in North America and Europe, respectively), and was greater during the Little Ice Age (Figs 6 & 7; note that sites vary in the time span represented). That changes in climate were the proximate

driving force behind these changes has been demonstrated in earlier work (i.e. Smith *et al.*, 1995, 1998; Smith & Betancourt, 1998, 2003; Smith & Charnov, 2001).

We attribute the observed patterns primarily to *in situ* evolution as opposed to large-scale migration events, for several reasons. First, the magnitude and rate of change of body size fluctuations at many cave localities far exceeds that

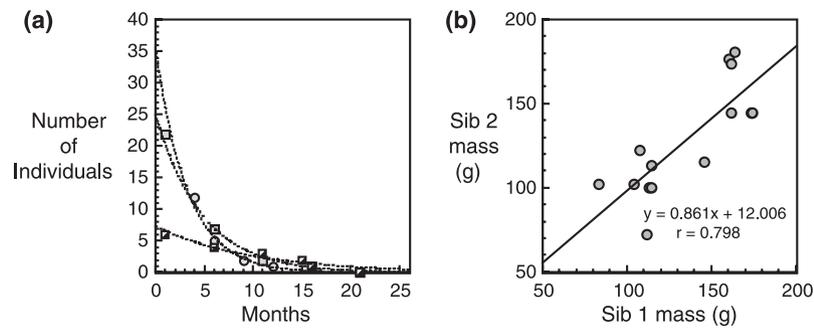


Figure 5 Survivorship and heritability of body mass. (a) Survivorship of three cohorts of desert woodrats studied at the Granite Mountain reserve in the Mojave Desert in the late 1980s (Smith, 1996). Although a few individuals persist for 2 or 3 years, average life expectancy is around 6 months; these results are consistent with survivorship curves constructed for other species of woodrats (e.g. Linsdale & Tevis, 1951). (b) Sib–sib plot of body size for laboratory reared offspring of wild woodrats. Pregnant white-throated (*N. albigula*) and desert woodrats (*N. lepida*) were captured and allowed to give birth in the laboratory. Offspring were measured at regular intervals until mature. These estimates are based on mass at 101 days; these unpublished data were kindly supplied by O. Schwartz. The slope is an estimate of broad sense heritability. Regression equation: $y = 0.861x + 12.0$, $r = 0.798$, d.f. = 11.

possible given the relatively short generational dispersal distances recorded in the genus (Smith, 1995). In some instances, for example, body size shifts of 25% or more are seen over less than a century. Elevational body size gradients can account for very little of this variation in size. Moreover, maximum recorded dispersal distances for the very largest species are considerably less than 10 km, and most dispersal occurs over much shorter spatial scales (Smith, 1995). Second, other studies on small mammals have demonstrated that morphological changes over the late Holocene in response to climate shifts were paralleled by significant genetic changes (Hadly *et al.*, 1998, 2004). These authors attribute such results to *in situ* evolutionary change. These factors combined with the robust physiological relationships observed between body size and both ambient and lethal temperature (e.g. Smith *et al.*, 1995; Smith & Charnov, 2001) strongly suggest that in this genus alterations in body size appear to be the most parsimonious way to deal with changing climatic regimes.

As might be expected, the more proximate the sites are, the greater the concordance in observed patterns. The four cave sites in Wyoming shown in Fig. 6b (Brokenback Narrows, Southfork Brokenback Narrows, Lower Canyon Creek and Medicine Lodge) exemplify this pattern. Although varying somewhat in elevation (c. 1600–2000 m), they all demonstrate comparable responses to temperature change over the past 2500 years. Palaeomiddens dating to the same age yield indistinguishable and completely overlapping body mass estimates (Fig. 6b). Although there are differences among the sites in topography, microclimate and vegetation, the correspondence in body size suggests they responded similarly to the climatic challenges of the late Holocene. These results highlight the repeatability of our unique study system.

A major feature of the midden sequences is that the finer the resolution (i.e. the more palaeomiddens collected at a site), the more fluctuations in body size we detect (see, for example, Figs 6a & 7a). The body size of woodrat populations did not

remain static over time, but instead fluctuated substantially. We attribute these size shifts to a response to low-amplitude, but high-frequency, climatic flickers; such temperature fluctuations have become evident in recent years as annually resolved ice cores spanning the late Pleistocene and Holocene have become available (Allen & Anderson, 1993; Dansgaard *et al.*, 1993; Severinghaus *et al.*, 1998; Indermühle *et al.*, 1999; Grootes *et al.*, 2001; Martrat *et al.*, 2004; Rial, 2004). There are some interesting trends evident in these data. For example, virtually all sites (representing some 10+ degrees of latitude) demonstrate an abrupt decrease in body mass at c. 2100–2200 yr BP. Examination of a highly resolved Greenland ice core (Indermühle *et al.*, 1999) that includes this time period indicates an abrupt and sharp change in temperature not previously documented in proxy records. Similarly, there is an abrupt and dramatic decrease in size at c. 3300 yr BP (Figs 6a & 7a).

The absence of palaeomiddens for some sites during the mid-Holocene is also interesting and has been noted in other locations in western North America (Webb & Betancourt, 1990; Spaulding, 1991). Because Pleistocene middens are surprisingly common, the scarcity of mid-Holocene ones cannot be attributed to exponential decay of the midden record with time. It has been ascribed instead to reduced woodrat abundance and/or midden deposition during warmer and drier times with lower ecosystem productivity (Webb & Betancourt, 1990). In some instances, especially those in marginal habitats, the absence of mid-Holocene palaeomiddens might well reflect local extirpation of the *N. cinerea* population. Animals may have colonized sites during colder periods when environmental conditions were favourable, but the warming of climate during the Altithermal (when the temperature may have been 2–3°C higher than today) may have exceeded their adaptive capability.

In locations at the southern part of the range, particularly in Idaho and Utah where *N. lepida* is found in sympatry,

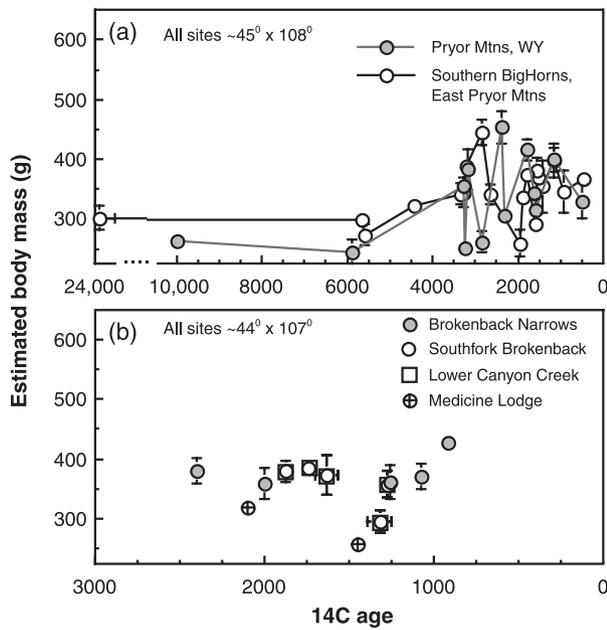


Figure 6 Chronosequences of palaeomiddens collected at various locations in Wyoming. All pellet measures were translated into body size estimates. Error bars indicate 95% confidence intervals for the estimates; if not shown, the error is less than the size of the datum. (a) Two northern locations overlaid. The Pryor Mountain and Southern Big Horns sites straddle northern Wyoming and southern Montana. These represent some of the most northern palaeomiddens recovered ($> 45^\circ \text{N}$), and are near the southern limits of the ice sheet during the last glacial. Note the long gap between the first records (three middens collected $> 24 \text{ ka}$) and the early Holocene. In radiocarbon years, the peak of the last glacial was at approximately 18 ka. Note also the considerable fluctuations in body size over the mid to late Holocene. (b) Four sites all located at about 44° latitude by 107° longitude. Note the close concordance of body mass for middens overlapping in age. All indicate a reduction in population body size at around 1.3 to 1.5 ka. Note that many of the symbols overlap completely indicating identical body size estimates for a time period. These sequences all yielded fairly young dates (3 ka to modern).

we have evidence of mid-Holocene species replacements due to climate warming (Smith & Betancourt, 2003). At several low-elevation sites, the larger-bodied but heat-sensitive *N. cinerea* were extirpated and the much smaller-bodied and more heat-tolerant *N. lepida* quickly colonized the den location. Examination of bioclimatic envelopes for modern populations suggests that such species replacements are likely in locations where summer temperatures exceed 25°C and winter temperatures are greater than -5°C (Smith & Betancourt, 2003); conditions that were likely to have been met at this time. These results are consistent with other studies that demonstrate local extirpations of *N. cinerea* at low-elevation sites during the mid-Holocene, and a subsequent recolonization during the cooler conditions of the late Holocene (e.g. Grayson & Madsen, 2000; Grayson, 2000).

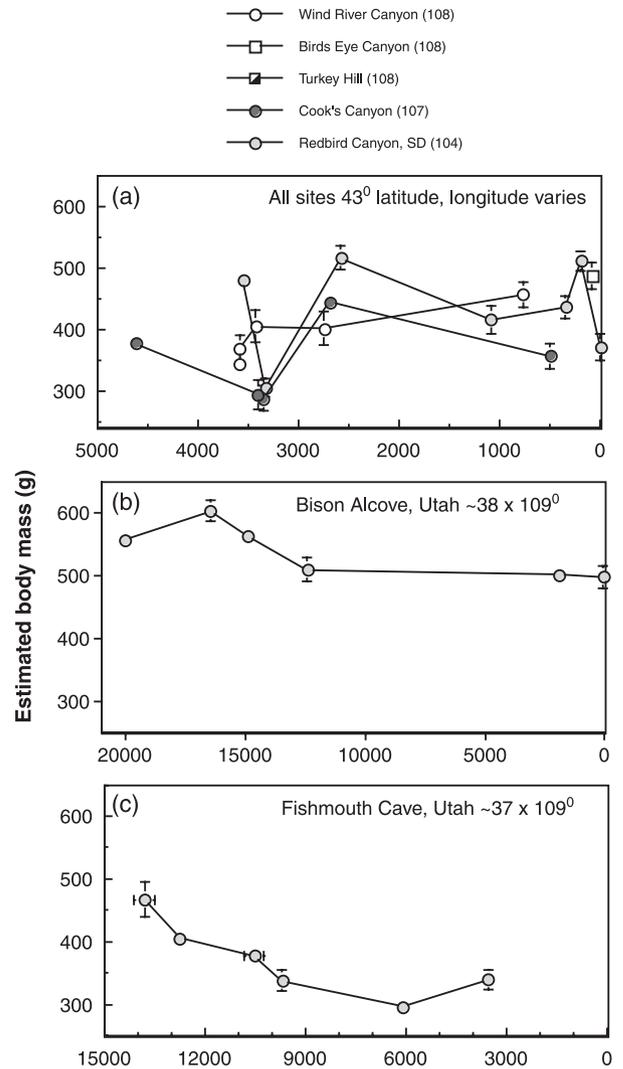


Figure 7 Chronosequences of selected palaeomiddens collected at various locations in South Dakota, Wyoming and Utah. All pellet measures were translated into body size estimates. Error bars indicate 95% confidence intervals for the estimates; if not shown, the error is less than the size of the datum. (a) Five cave locations at about 43°N ; longitude and elevation vary between these sites. Note the rapidity of some of the body size shifts. In several instances the average mass of the population changes by $> 25\%$ within less than a few hundred years. Longitude is shown in parentheses after name in the legend. (b) Sequence from Bison Alcove, at Arches National Park. It is not clear whether the large gap in the record reflects local extirpation during the warmer conditions of the mid-Holocene or an absence of data; an additional eight middens were recovered from this cave and have yet to be dated. Based on the mass estimates from these, we anticipate that several at least will date to this period. (c) Sequence from Fishmouth Cave in south-east Utah. Parts (b) and (c) redrawn from Smith & Betancourt (1998).

A question we can address with our unique study system is whether woodrats have sufficient evolutionary plasticity to adapt to the predicted rapid rate of anthropogenic warming. The Intergovernmental Panel on Climate Change (IPCC)

recently issued a revised update predicting temperature increases of up to 5.8°C within 100 years. The spatial relationship between body size and temperature for modern animals (Fig. 2, Table 1), suggests that this differential represents the difference between a population averaging 350 and 275 g. If woodrats are able to adapt *in situ*, the phenotypic change required translates into a phenomenal rate of 2412 darwins. Can rates of this magnitude be detected in our midden sequences?

To address this question we calculated the evolutionary rate of change of body size for midden sequences containing two or more samples. Evolutionary rates were computed using darwins (d):

$$d = \frac{\ln(x_1/x_2)}{D_t}$$

where x_1 and x_2 represent the character state (in this case pellet width) at two different time intervals, and D_t is the difference in time, in Myr. The use of darwins as a metric allowed us to deal with differences in proportions caused by the different sizes represented in our data. We were able to largely circumvent biases caused by differences in the measurement interval because the time spans represented in our data mostly ranged from hundreds to thousands of years (Haldane, 1949; Gingerich, 1983; Gould, 1984).

Our results suggested that most body size changes over the Holocene were relatively small shifts, but that a few did reach rates of over 2000 d (Fig. 8a; Smith and Betancourt, in preparation), suggesting that under some circumstances woodrats might be able to adapt *in situ* to severe climatic

fluctuations. However, it is not clear if the paucity of high-amplitude shifts is due to a lack of evolutionary plasticity or simply because of a lack of climatic variability of this magnitude.

To compare the rate and magnitude of body size changes with those of climate, we compared our results to several climate proxies. We obtained data from the Summit ice cores in central Greenland – GISP2 (Greenland Ice Sheet Project Two), GRIP (Greenland Ice Core Project) and NGRIP (North Greenland Ice Core Project) – which provide highly resolved and generally concordant palaeoenvironmental records for the Northern Hemisphere over the past 100,000+ years (Taylor *et al.*, 1997; Dahl-Jensen *et al.*, 1998; North Greenland Ice Core Project Members, 2004).

We chose to use ice cores because of their high resolution and long temporal span; admittedly there are substantial differences in location and local climate regimes between Greenland and western North America. However, our main interest was in the relative rates of change over different time periods, not the absolute temperature shifts. Thus, we took reported temperature estimates derived from $\delta^{18}\text{O}$ values and/or the $\delta^{18}\text{O}$ values themselves and converted them to a rate of change in darwins as described above.

Our results indicated that the rate at which climate changed was highly variable, although most rates were relatively low (Fig. 8b,c). Only a few intervals experienced rates exceeding 200 d, and many of these were concentrated at *c.* 13,000–11,000 yr BP and again in the late Holocene. Comparison with body size changes seen in woodrats over the Holocene again suggests that the size shifts seen do largely reflect underlying

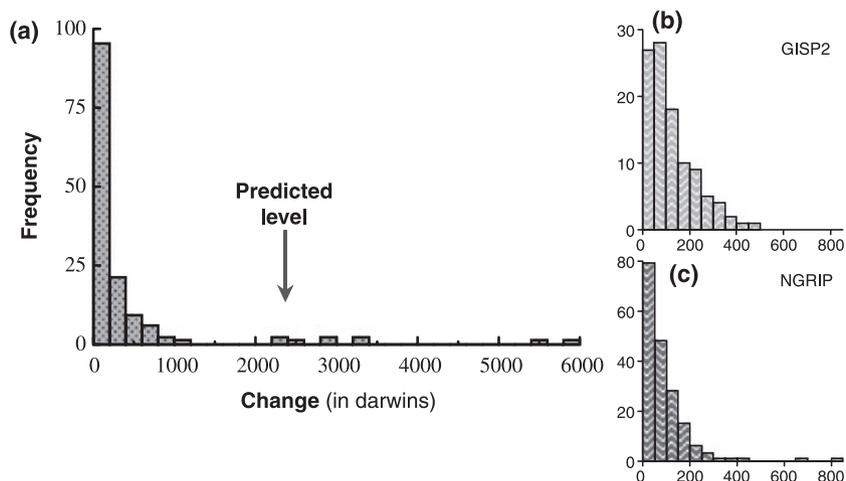


Figure 8 Histograms of rates of change over the late Quaternary. The axes are the same in all panels. (a) Histogram of evolutionary rates of body size achieved by woodrats (as measured in darwins) over the late Quaternary. Data are aggregated from across their range. Note that most changes are low-magnitude events, but that woodrats have occasionally demonstrated extremely fast evolutionary rates exceeding those needed to adapt *in situ* to predicted anthropogenic climate change. (b) Histogram of changes in oxygen isotope ($\delta^{18}\text{O}$) levels as determined from the GISP2 ice core from central Greenland. (c) Histogram of changes in oxygen isotope levels as determined from the NGRIP ice core from Greenland. Oxygen isotope levels are an excellent proxy for climate, with higher levels indicating warmer temperatures. Note that most shifts in temperature over the Holocene involved small changes, but a few were larger in magnitude; the overall pattern is quite similar to that seen for woodrat body size in (a).

temperature change. Note that large climate shifts (and corresponding body size shifts) were particularly common over the past 3000 years, with some of the highest rates of change exceeding those evident during the rest of the Holocene. This suggests that the past 2000–3000 years have posed considerable challenges to the adaptive capability of animals. The concordance between woodrat body size and oxygen isotope records is remarkable because of the substantial differences in the resolution of the two: woodrat palaeomiddens provide a highly resolved record primarily for the interior western United States, while the GISP2 and GRIP cores yield information at a much broader and much coarser climatic scales. Nonetheless, our results suggest that woodrats did occasionally achieve evolutionary rates exceeding 2000 d over the late Quaternary, and that, moreover, the infrequency of these rates perfectly reflects the infrequency of large climate shifts.

That body size changes were in response to temperature and not due to other causal mechanisms can be inferred from several observations. First, body mass fluctuations are highly correlated with a number of palaeotemperature proxies (Smith *et al.*, 1995). In previous work, we have used several independent proxies of temperature, including deuterium isotope ratios derived from fossil plants and modelling output from general circulation models (GCMs) to establish a strong correlative relationship between these factors and the body mass of woodrats over the past 20,000 years (Smith *et al.*, 1995). Indeed, even the magnitude of body mass fluctuations is highly correlated with the magnitude of temperature fluctuations (Fig. 8). Second, recall the robust relationships established for modern animals between the body size of a population and ambient temperature (Fig. 2, Table 1) and between the body size of individuals or populations and lethal temperature (Fig. 3d); these strongly suggest that temperature is an underlying causal mechanism (Smith & Charnov, 2001). The response of woodrat body size to temperature is so predictable across time and space that we have used the fluctuations to reconstruct temperature at local to regional sites (e.g. Smith & Betancourt, 2003). There is a major effort under way by governmental and geoscience agencies to develop climate proxies that will aid in the characterization and interpretation of late Quaternary environments (e.g. <http://gcmd.gsfc.nasa.gov/>). Few proxies provide the level of resolution that we can obtain by analysis of woodrat body size trajectories.

Implications for anthropogenic climate change

Our work with well-resolved palaeomiddens strongly suggests that a likely outcome of anthropogenic climate change includes shifts in the body size of woodrat populations. Such shifts will certainly influence important life history and ecological strategies. For example, the ability to digest plant fibre (a key component of the diet of woodrats) has been demonstrated to significantly decrease with decreasing body mass (Justice & Smith, 1992; Smith, 1995). Thus, smaller body size will dictate a shift to higher-quality food sources, and if these are not

readily available may negatively influence reproductive abilities and population dynamics.

Given how sensitive woodrat body mass is to temperature, a reasonable question is not *if* anthropogenic climate change will influence population dynamics, but whether we can *already* detect such change. Numerous studies have indicated that anthropogenic warming is already detectable in many systems (e.g. Hughes, 2000; Parmesan & Yohe, 2003). Examples of such observed changes include the thawing of permafrost and shrinkage of glaciers, the lengthening of mid- to high-latitude growing seasons, significant poleward and elevational shifts of both plant and animal species, declines in abundance and changes in morphology and phenology (i.e. earlier egg laying by birds, flowering of trees, changes in body size of mammals and insect emergence; Parmesan & Yohe, 2003; Schwartz, 2003; Thomas *et al.*, 2004; Root *et al.*, 2005; and references therein).

In recent work, we examined the body size of white-throated woodrats (*N. albigula*) at the Sevilleta LTER site in New Mexico over an 8-year period from 1989 to 1996 (Smith *et al.*, 1998). We asked whether climate had deviated significantly over this period of time relative to a long-term average and whether this had resulted in any change in the average body mass of the woodrat population. Our results confirmed both a significant shift in regional climate and in the body size of woodrats (Fig. 9). Overall, the mean body size of the woodrat population was about 20–25 g smaller in 1997 than it had been in 1988. These body size changes were highly correlated with fluctuations in both average cold and warm temperature. Because most of the woodrat data came from animals permanently removed from the trapping grids, the differences we saw represented turnover in the population, presumably caused by smaller-bodied animals successfully over-wintering and driving down the average body size of the population. Each c. 1°C increase in temperature had led to approximately a 10 g reduction in the average body mass of the woodrat population at the Sevilleta LTER site (Fig. 9; Smith *et al.*, 1998). Moreover, these changes were not correlated with reproductive status, vegetation abundance or other abiotic variables, such as precipitation.

Our research programme focuses on a synoptic examination of the responses of a single mammalian genus to late Quaternary climate change, with the aim of achieving a better understanding of how anthropogenic warming may influence organisms. Of course, other researchers are also conducting similar studies at different temporal, hierarchical or spatial scales. Hadly and her colleagues, for example, have focused on in-depth understanding of community level responses to mid and late Holocene climate at several well characterized cave sites in western North America (e.g. Hadly, 1996; Hadly *et al.*, 1998, 2004; van Tuinen *et al.*, 2004). Their work incorporates morphological change with changes in the abundance and genetics of several different species of small mammals. Similarly, Grayson and his colleagues have examined the effects of mid-Holocene climate change on the diversity and abundance of small mammals in the Great Basin using a rich

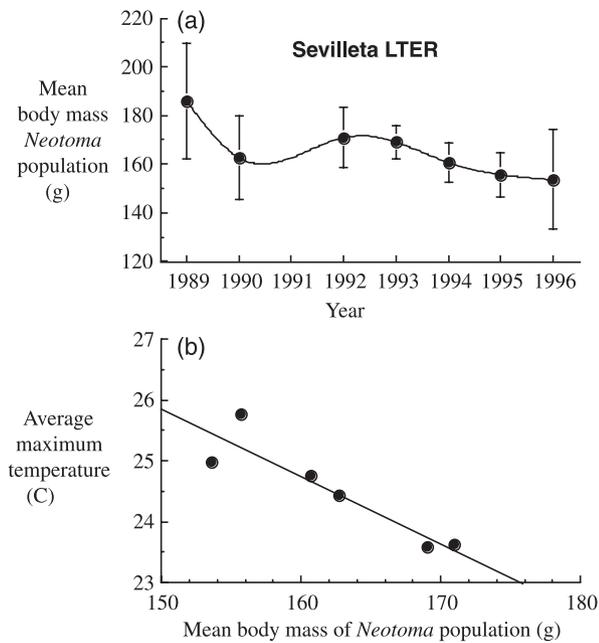


Figure 9 Results from study of white-throated woodrats (*N. albigula*) at the Sevilleta LTER site in central New Mexico. (a) Mean body mass of the population over time. Bars indicate 95% confidence intervals. Note the shift in overall body size that occurred over the 8 years studied. (b) Average maximum (July) temperature over the 8 years plotted against the mean body mass of the population. This was a highly significant relationship ($y = -0.111x + 42.46$, $r^2 = 0.839$, $P < 0.010$, d.f. = 6), as was the relationship with cold (January) temperature ($y = -0.203x + 37.42$, $r^2 = 0.766$, $P < 0.022$, d.f. = 6). Redrawn after Smith *et al.* (1998).

and stratified cave site near the eastern edge of the Bonneville Salt Flats (Grayson, 1998, 2000; Grayson & Madsen, 2000). Over longer time-scales, Barnosky and his colleagues have focused on the interaction between the physical environment (i.e. climate and physiogeological change) and the evolution of mammal species and abundance and diversity patterns (e.g. Barnosky, 1994, 2004; Barnosky & Bell, 2003; Barnosky *et al.*, 2003). The integration of these different studies will ultimately yield a comprehensive view of mammalian adaptation and evolution.

Finally, we note that woodrats are but one component of an ecosystem. Anthropogenic warming will also have direct and indirect influences on other species in the ecosystem. Our emphasis on woodrats reflects a unique ability to examine in a rigorous and fine-grained manner the influence of temperature on the ecology and evolution of a species over space and time. Such studies are increasingly important to scientists and politicians alike as we attempt to understand the magnitude and implications of anthropogenic warming on the earth's biota.

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BIOSKETCHES

Felisa Smith is an Associate Professor of Biology at the University of New Mexico. Her research investigates evolutionary and ecological consequences of climate change across a variety of spatial and temporal scales. Current studies range from field investigations of physiological tradeoffs to stressful environments to macroevolutionary patterns of mammalian body size across the Cenozoic and across different continents.

Julio Betancourt is a Research Hydrologist with the US Geological Survey. He is interested in how climate variability affects physical and biological systems on time-scales from years to millennia. He has employed a battery of morphological, geochemical and genetic analyses of fossil plant and animal material to test long-standing hypotheses about responses to changes in atmospheric CO₂ levels and climate.

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