Evolution of Body Size in the Woodrat over the Past 25,000 Years of Climate Change

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Microevolutionary changes in the body size of the bushy-tailed woodrat (Neotoma cinerea) since the last glacial maximum were estimated from measurements of fecal pellets preserved in paleo middens from the Great Basin and Colorado Plateau of the United States. The changes closely track regional temperature fluctuations simulated by the Community Climate Model of the National Center for Atmospheric Research and also those estimated from deuterium isotope ratios of plant cellulose recovered from paleo middens. Body size decreased during periods of climatic warming, as predicted from Bergmann’s rule and from physiological responses to temperature stress. Fossil woodrat middens, by providing detailed temporal sequences of body sizes from many locations, permit precise quantification of responses to climatic change that have occurred in the past and may occur in the future.

The past 2 million years of Earth history have been characterized by large fluctuations in atmospheric chemistry and global climate—the glacial-interglacial cycles of the Pleistocene. The past 25,000 years have seen a general warming trend, beginning with the last glacial maximum (LGM) about 21,000 years ago, accelerating with deglaciation between 15,000 and 12,000 years ago, and increasing in the past several decades probably as a result of anthropogenic loading of atmospheric greenhouse gases (1). Associated with such climatic variation have been major changes in vegetation and in the composition of plant and animal communities (2, 3). Presumably these changes represent the effects of environmental temperature and other conditions on both the performance of individual organisms and the ecology of populations and ecosystems. A major question is whether plants and animals have remained essentially unchanged but have dramatically altered their distributions in response to climate fluctuations, or have remained in place and adapted to the varying environment by some combination of phenotypic plasticity and evolutionary change.

Contemporary populations of North American rodents exhibit extensive geographic variation in body size and coat color (4–6). Classical studies have shown that this variation reflects genetic adaptation to local and regional environmental conditions (7). An example of such adaptation is Bergmann’s rule, a positive relation between body size and latitude that reflects the advantages of large size as a way of conserving heat and of small size as a way of dissipating heat (4). Woodrats of the genus Neotoma conform to Bergmann’s rule (5). They are smaller in warmer regions (Fig. 1A), presumably reflecting the capacity of smaller individuals to dissipate heat and hence to survive the stress of high ambient temperatures (Fig. 1B). An animal’s size affects such fundamental physiological and ecological factors as metabolic rate, fecundity, longevity, home range, and even extinction rates (8). Thus, the identification of factors that influence body size is crucial to understanding the basic ecology and evolution of a species, as well as for predicting responses to changing environmental conditions.

Woodrats are ideal for investigation of the influences of past climate fluctuations on mammalian body size. These herbivorous rodents produce middens containing plant fragments, copious fecal pellets, and other materials embedded in crystallized urine (“amberat”); sheltered in caves and rock crevices, these deposits persist for tens of thousands of years. The preservation of plant and animal remains in the deposits is excellent, allowing reconstruction of former distributions (3, 9) and diverse morphological, geochemical, and even genetic analyses (10, 11). Because fecal pellet width and woodrat body size are closely correlated (Fig. 1C), the numerous fecal pellets in these middens provide a record of body size variations over time. If local populations have adapted to large swings in temperature, as expected from Bergmann’s rule, we predict that woodrats in the western United States should have become smaller during the last deglaciation. In general, we predict a strong inverse correlation between body size and past temperature estimates.

We measured the sizes of fecal pellets in middens collected at several locations in the southwestern United States (12). To avoid the potential complication of changes in woodrat species, we examined only sites inhabited at present and in the past by N. cinerea, the largest and most cold-tolerant species of woodrat. This species currently ranges from southern Canada to the mountains of northern New Mexico and Arizona, but in the Pleistocene it was found at much lower elevations and as far south as northern California.

**Fig. 1.** Scatterplots and linear regression equations showing variation in characteristics of woodrats as a function of body mass. (A) Relation between adult body mass and average July temperature in nine contemporary populations of N. cinerea from western Northern America. Data are taken from museum specimens and from unpublished field notes. Values represent location means of a minimum of 20 individuals. Weather data were taken from the U.S. Historical Climatology Network and generally represent a minimum of a 50-year average. We used a terrestrial lapse rate of −0.5°C per 100 m to correct for elevational differences between collection sites of locations in Northern California and the nearest weather station. Only a weak relation was observed between body mass and average January temperatures (23). (B) Relation between body mass and upper lethal temperature for 16 individual N. cinerea representing several populations; data were taken from (24). (C) Relation between body mass and the average width of fecal pellets for three woodrat species: N. cinerea, N. lepida, and N. albigena. A total of 50 field-trapped animals (10 per species) were housed in the laboratory under a constant temperature and light regime (20°C; 12 hours light, 12 hours dark) and fed a diet of 40% fiber. Fecal pellets were collected, dried, and later measured in a blind study. A linear model provides the best fit (r² = 0.69, P < 0.0001; partial F test). The size of a fecal pellet can be used to estimate adult body mass with a prediction error of only 21%; diet does not appreciably alter the relation (13). Little of the variation is attributable to species or gender (analysis of covariance, P > 0.05).
ern Mexico (9). Deposition dates were determined by ¹⁴C dating of pellets or of associated plant macrofossils (or both) and in most instances were established to within 50 to 100 years. We investigated the potential influence of diet on the relation between fecal pellet width and body size by conducting a blind test with field-trapped individuals (13); the prediction error was only 21% for pellets wider than 4 mm.

For each sample, we estimated body size using the regression equation in the legend of Fig. 1C and plotted it as a function of radiocarbon date. Results for one locality, Fishmouth Cave in southeastern Utah, are given in Fig. 2. The population not only shows the overall predicted trend of decreasing size from the last glacial to the present but also appears to have responded quite precisely to past temperature fluctuations. Thus, size decreased at the onset of the interglacial as local and global temperatures increased. Similarly, body size showed a further decrease between 9000 and 6000 years ago, corresponding to elevated temperatures during the Altithermal interval (1). The paleomidden sequences for other localities yielded similar results, but the resolution for any given site was limited by the number of ¹⁴C-dated samples available.

To overcome this limitation and to quantify the response of body size to climate change throughout the region, we wished to pool samples from all localities. The sites span a range of latitudes and elevations so that they differ in their present and presumably in their past environmental temperatures. Because body size varies geographically in accordance with Bergmann’s rule, it was necessary to account for this variation. We accomplished this by computing relative size: the average pellet width for each paleomidden divided by the mean pellet width of a modern sample from the same location. The index enabled us to combine data from all of the localities. A pattern of change in body size resulted that is similar to that obtained for Fishmouth Cave (Fig. 3A). Despite the geographic dispersion of the sites, there is only a small amount of scatter in the data, and the data are best fit by a third-order polynomial.

We compared changes in body size with past temperature fluctuations in the intermountain west estimated from two sources: departures from mean July temperature simulated by the Community Climate Model of the National Center for Atmospheric Research (NCAR-CCM3) (14) (Fig. 3B) and mean annual temperature inferred from the deuterium isotope ratios (δD) of plant cellulose from woodrat middens (10, 15) (Fig. 3C). Neither time series can be considered a precise paleothermometer (16), but they do provide two independent estimates of relative temperature variations during the past 25,000 years. Estimates from other empirical evidence indicate a somewhat larger difference between the LGM and the Holocene (17). We analyzed the CCM0 and δD time series by fitting a third-order polynomial, as was done for body size. The resulting temperature curves closely resemble one another and are approximately mirror images of the curve fitted to the size data. A conservative estimate of the influence of temperature on the evolution of body size can be obtained by regression of the relative size calculated from fecal pellets (the individual data points in Fig. 3A) against paleotemperatures estimated from the regression equations (the fitted curves in Fig. 3, B and C). The paleotemperatures derived from the CCM0 and δD accounted for 65 and 49%, respectively, of the variation in body size. These estimates are conservative because the methods used to obtain and fit the data on regional paleotemperature fluctuations necessarily obscure the details of the local climate changes at each midden site.

The precision with which the body size of woodrats tracked changes in environmental temperature is striking. The high rates of evolution implied are similar to the rapid shifts in body size of many insular mammal populations after isolation by rising sea levels at the end of the last glacial (18). The mechanisms responsible for causing size change on islands are uncertain. The size changes of woodrats documented here, however, are inferred to represent adaptations to environmental temperature. All populations exhibited a consistent decrease in body size in response to each episode of increasing environmental temperature. A conservative estimate of the dwarving that occurred within populations from the height of the last glacial to the mid-Holocene is about 20% in mass (Fig. 3A). This figure is more than a quarter of the entire body size variation seen within the current geographic range of N. cinerea (Fig. 1A), a range that extends from northern Mexico to Canada. Although it is likely that some component of the overall response reflects phenotypic plasticity, most can probably be attributed to genetic changes. Body size has been found to be

![Fig. 2. Temporal variation in the body size of woodrats from Fishmouth Cave, Utah. Midden material was collected by J. L. Betancourt. Mean sizes of fecal pellets and resulting estimation of body size from Fig. 1C are plotted as a function of unadjusted radiocarbon date: Vertical and horizontal bars give 95% confidence intervals. Times of the coldest period (peak of the last glacial), most rapid warming (glacial-interglacial interval), and warmest period (the Altithermal or Holocene optimum) are indicated.](image)

![Fig. 3. Third-order regression equations (continuous curves) fitted to data (circles) for woodrat body size and environmental temperature over the past 20,000 years. (A) Mean size of fecal pellets from fossil middens plotted as a function of radiocarbon date and expressed relative to the size of pellets from modern middens at the same localities. (B) Simulated July temperature anomalies expressed as deviations from modern temperatures from the NCAR-CCM0 (14). (C) Mean annual temperature estimated from deuterium isotope ratios. Stable isotope ratios (δD) are expressed as parts per thousand difference from the standard mean ocean water reference standard (δD): δD (per mil) = (Rsample/Rstandard – 1)1000, where R is the δH of the sample (15). All regression equations were constrained to give contemporary values (dotted line) at 0 yr B.P.](image)
highly heritable in rodents (19), and Brown (20) has shown that woodrats born and reared in the laboratory closely resemble their wild relatives in both body size and temperature tolerance. It is possible that some portion of the observed response reflects evolutionary or latitudinal migration of woodrats (as opposed to in situ evolution), although this too presumably reflects underlying selection acting on body size. The evolutionary outcome is the same in both instances, although the mechanisms operating are quite different. Because woodrats are relatively sedentary and because in some instances dramatic size changes occurred very rapidly, we favor the latter explanation. Resolution of this issue, however, must await genetic analyses (21).

Additional global warming resulting from human activities is predicted to occur within the next century, and the magnitude of the warming is likely to equal that occurring at the Pleistocene-Holocene boundary (1, 22). Our results suggest that, in addition to any potential distributional shifts, environmental changes are likely to cause substantial microevolutionary responses in woodrats and potentially in other organisms.

REFERENCES AND NOTES


9. A. H. Harris, Late Pleistocene Vertebrale Paleoecol- ogy of the West (Univ. of Texas Press, Austin, TX, 1985).


12. Pellets were isolated from discrete samples of midden material weighing 0.2 to 2 kg. Radiocarbon dates were determined by Krueger Enterprises (Geochron Laboratories) or the Laboratory of Iso- tope Geochemistry (University of Arizona) from small aliquots of plant or fossil material. From very large unbiassed samples of pellets, we selected and mea- sured a biased sample of the largest 200 to 300, using digital calipers; of these, the mean of the largest 20 was used to characterize maximum size. Maximum size was chosen because it was not sen- sitive to sampling method (as was the mean of the unbiased sample) and because the much larger size of high camera midden distinguished it from the other woodrat species.

13. Because dietary shifts could conceivably affect pellet morphology, we subjected the ability of the regression analysis to detect the size of free-living woodrats eating varied natural diets to a blind independent test. Pellets were collected and measured from indi- viduals of several species trapped in a wide variety of habitats during different years. The difference between actual mass and that predicted by the width-mass regression was calculated: The overall value for pellets wider than 4 mm was only 21%. Below 4 mm the error was quite large; consequently, no pellets below this threshold were used in the midden studies (this size corre- sponds to juvenile animals of about 60 g, which is below the adult body size range of woodrats).


16. Boundary conditions used in the CCM0 include the sea-land distribution, when calculated from orbital configurations and clocked in astronomical time, and land- and sea-surface boundary condi- tions (for example, sea-surface temperatures and the height of the oceans). The Earth's orbital configuration was used from palaeo evidenced dates in radiocarbon years. Radiocarbon years differ from calendar years because of cosmic-ray production and carbon reservoir ef- fects. Calibrated year, or radiocarbon error, is defined and used for the purpose of this study.

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