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

Felisa A. Smith,* Julio L. Betancourt, James H. Brown

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 paleomiddens 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 paleomiddens. 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 north-

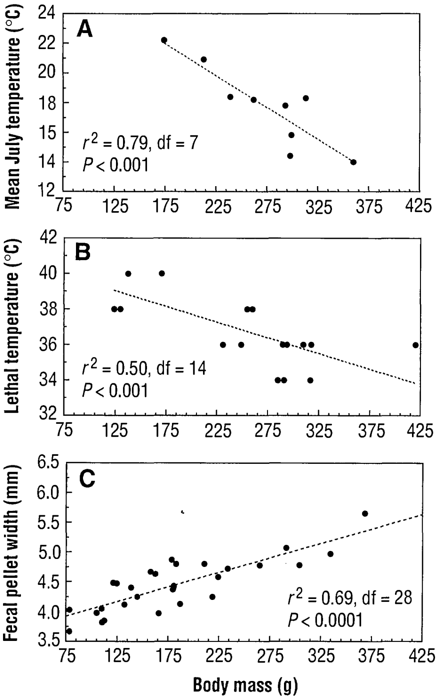

Fig. 1. Scatterplots and linear regression equations showing variation in characteristics of woodrats as a function of body mass. (**A**) Relation between adult body mass and average July temperature in nine contemporary populations of *N. cinerea* from western Northern America. Data are taken from museum 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. albigula*. A total of 30 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 ($y = 0.005x + 3.559$; $r^2 = 0.69$; $P < 0.0001$; 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, $P \gg 0.05$).

F. A. Smith and J. H. Brown, Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA.

J. L. Betancourt, U.S. Geological Survey Desert Laboratory, 1675 West Anklam Road, Tucson, AZ 85745, USA.

*To whom correspondence should be addressed.

ern Mexico (*9*). Deposition dates were determined by ^{14}C 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 ^{14}C-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-CCM0) (*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 dwarfing 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 Arizona 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

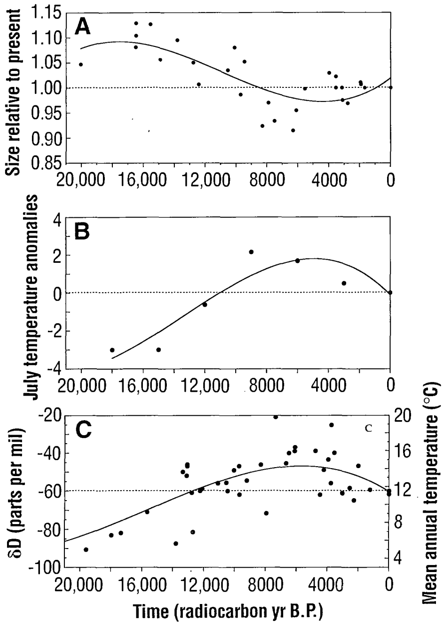

Fig. 3. Third-order regression equations (continuous curves) fitted to data (circles) for woodrat body size and environmental temperature over the past 20,000 years. (**A**) Mean size of fecal pellets from fossil middens plotted as a function of radiocarbon date and expressed relative to the size of 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 (R_s): δD (per mil) $= (R_x/R_s - 1)1000$, where R_x is the δH of the sample (*15*). All regression equations were constrained to give contemporary values (dotted line) at 0 yr B.P.

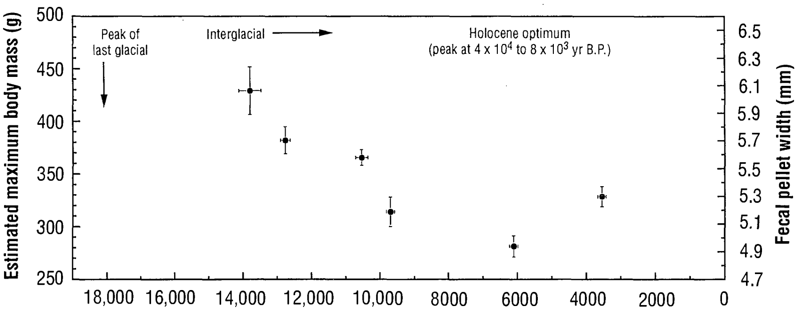

Fig. 2. Temporal variation in the body size of woodrats from Fishmouth Cave, Utah. Midden material was collected by J. L. Betancourt. Mean sizes of fecal pellets and resulting estimation of body size from Fig. 1C are plotted as a function of unadjusted radiocarbon date: Vertical and horizontal bars give 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.

highly heritable in rodents (*19*), and Brown (*20*) has shown that woodrats born and reared in the laboratory closely resemble their wild-caught parents in both body size and temperature tolerance. It is possible that some portion of the observed response reflects elevational 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

1. COHMAP Members, *Science* **241**, 1043 (1988); J. T. Houghton, G. J. Jenkins, J. J. Ephranms, Eds., *Climate Change: The IPCC Scientific Assessment* (Cambridge Univ. Press, Cambridge, 1990); H. E. Wright Jr. *et al.*, Eds., *Global Climates Since the Last Glacial Maximum* (Univ. of Minnesota Press, Minneapolis, MN, 1993).
2. M. B. Davis, in *Community Ecology*, J. Diamond and T. J. Case, Eds. (Harper and Row, New York, 1986), pp. 269–284; R. W. Graham, *ibid.*, pp. 300–313.
3. P. V. Wells and C. D. Jorgensen, *Science* **143**, 1171 (1964); P. V. Wells and R. Berger, *ibid.* **155**, 1640 (1967); T. R. Van Devender and W. G. Spaulding, *ibid.* **204**, 701 (1979); J. L. Betancourt and T. R. Van Devender, *ibid.* **214**, 656 (1981); J. L. Betancourt, T. R. Van Devender, P. S. Martin, Eds., *Packrat Middens: The Last 40,000 Years of Biotic Change* (Univ. of Arizona Press, Tucson, AZ, 1990).
4. C. Bergmann, *Göttinger Studien* **1**, 595 (1847); E. Mayr, *Evolution* **10**, 105 (1956); *Animal Species and Evolution* (Harvard Univ. Press, Cambridge, MA, 1963); W. P. Porter *et al.*, *Aust. J. Zool.* **42**, 125 (1994).
5. J. H. Brown and A. K. Lee, *Evolution* **23**, 329 (1969).
6. E. T. Hooper, *Univ. Calif. Publ. Zool.* **42**, 407 (1940).
7. F. B. Sumner, *Bibliogr. Genet.* **8**, 1 (1932); L. R. Dice and P. M. Blossom, *Carnegie Inst. Washington Publ.* **485**, 1 (1937); L. R. Dice, *Am. Nat.* **74**, 212 (1940); D. B. Thompson, *Evolution* **44**, 952 (1990).
8. R. H. Peters, *The Ecological Implications of Body Size* (Cambridge Univ. Press, Cambridge, 1983); W. A. Calder, *Size, Function, and Life History* (Harvard Univ. Press, Cambridge, MA, 1984); K. Schmidt-Nielsen, *Scaling: Why Is Animal Size So Important?* (Cambridge Univ. Press, Cambridge, 1984).
9. A. H. Harris, *Late Pleistocene Vertebrate Paleoecology of the West* (Univ. of Texas Press, Austin, TX, 1985).
10. P. K. Van de Water, S. W. Leavitt, J. L. Betancourt, *Science* **264**, 239 (1994).
11. S. O. Rogers and A. J. Bendich, *Plant Mol. Biol.* **5**, 69 (1985); B. D. Marino, M. B. McElroy, R. J. Salawitch, W. G. Spaulding, *Nature* **357**, 461 (1992).
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 Isotope Geochemistry (University of Arizona) from small aliquots of plant or fecal material. From very large unbiased samples of pellets, we selected and measured 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 sensitive to sampling method (as was the mean of the unbiased sample) and because the much larger size of *N. cinerea* made it possible to distinguish between it and other woodrat species.
13. Because dietary shifts could conceivably affect pellet morphology, we subjected the ability of the regression to predict the body mass of free-living woodrats eating varied natural diets to a blind independent test. Pellets were collected and measured from individuals of several species trapped in a wide variety of habitats during different seasons and 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 prediction error was quite large; consequently, no pellets below this threshold were used in the midden studies (this size corresponds to juvenile animals of about 80 g, which is below the adult body size range of woodrats).
14. J. J. Kutzbach and W. F. Ruddiman, in *Global Climates Since the Last Glacial Maximum*, H. E. Wright Jr., *et al.*, Eds. (Univ. of Minnesota Press, Minneapolis, MN, 1993), pp. 12–23; R. S. Thompson, C. Whitlock, P. J. Bartlein, S. P. Harrison, W. G. Spaulding, *ibid.*, pp. 468–513.
15. A. Long, L. A. Warneke, J. L. Betancourt, R. S. Thompson, in *Packrat Middens: The Last 40,000 Years of Biotic Change*, J. L. Betancourt, T. R. Van Devender, P. S. Martin, Eds. (Univ. of Arizona Press, Tucson, AZ, 1990), pp. 380–397.
16. Boundary conditions used in the CCM0 include the seasonal distribution of insolation calculated from orbital configurations and clocked in astronomical time, and land- and sea-surface boundary conditions (for example, sea-surface temperatures and the height of the Laurentide ice sheet) specified from paleoevidence dated in radiocarbon years. Radiocarbon years differ from calendar years because of cosmogenic production and carbon reservoir effects. Calibration of radiocarbon dates for body size and δD evidence to calendar years, based on the use of dendrochronology or U-Th dates on corals [M. Stuiver, A. Long R. Kra, Eds., *Radiocarbon* **35**, 1 (1993)] would not have resolved the mismatch between astronomical time and radiocarbon years inherent in the output of the CCM0. On the basis of paleoevidence, for example, the LGM occurred at 21,000 calendar years ago [18,000 radiocarbon years before the present (yr B.P.)], yet the orbital configurations used in the model are for 18,000 calendar years. Because the current model output for 3000-year "snapshots" offers a first approximation of temperature trends since the LGM, we opted not to correct radiocarbon years to calendar years. Corrected dates are available from the authors on request. Other sources of output error include oversimplified land- and sea-surface boundaries, coarse spatial resolution (4.4° latitude by 7.5° longitude), and unrealistic topography. The δD values were measured from cellulose of *Juniperus, Pinus, Picea*, and *Symphoricarpos* leaves and twigs preserved in woodrat middens from eastern Nevada, southeastern Utah, and northwestern New Mexico (*15*). We adjusted δD values to geographic location using δD from modern *Juniperus* populations sampled across a transect from west Texas to western Nevada. Linear regression of modern δD values and mean annual temperature at nearby meteorological stations accounted for 66% of the variance and was used to infer temperature variations from δD of the fossil plant remains (Fig. 3C).
17. Displacement of the lower limits of conifers along permanent streams on the Colorado Plateau suggests that LGM summers were 6° to 7°C cooler than during the Holocene (*3*). Other evidence also suggests greater temperature differentials than predicted by either the CCM0 or deuterium data. Stute *et al.* [*Quat. Res.* **43**, 209 (1995)], for example, estimate mean annual temperature differences of 5.4°C on the basis of concentrations of noble gases dissolved in ^{14}C-dated ground water of the San Juan Basin, northwestern New Mexico.
18. A. M. Lister, *Nature* **342**, 539 (1989); V. L. Roth, in *Body Size in Mammalian Paleobiology*, J. Damuth and B. J. MacFadden, Eds. (Cambridge Univ. Press, Cambridge, 1990), pp. 151–179; F. A. Smith, *Funct. Ecol.* **6**, 265 (1992).
19. J. J. Rutledge, E. J. Eisen, J. E. Legates, *Genetics* **75**, 709 (1973); L. Leamy, *Evolution* **42**, 42 (1988); but see J. L. Patton and P. V. Brylski, *Am. Nat.* **130**, 493 (1987).
20. J. H. Brown, *Misc. Publ. Mus. Zool. Univ. Mich.* **135**, 1 (1968).
21. We are currently investigating the genetic evolution of bushy-tailed woodrats from the Colorado Plateau, using ancient DNA extracted from midden materials.
22. C. B. Field, F. S. Chapin III, P. A. Matson, H. A. Mooney, *Annu. Rev. Ecol. Syst.* **23**, 201 (1992); D. D. Murphy and S. B. Weiss, in *Global Warming and Biological Diversity*, R. L. Peters and T. E. Lovejoy, Eds. (Yale Univ. Press, New Haven, CT, 1992), pp. 355–358; T. Webb III and P. J. Bartlein, *Annu. Rev. Ecol. Syst.* **23**, 141 (1992); P. M. Vitousek, *ibid.*, p. 1; P. M. Kareiva, J. G. Kingsolver, R. B. Huey, Eds., *Biotic Interactions and Global Change* (Sinauer, Sunderland, MA, 1993); P. M. Vitousek, *Ecology* **75**, 1861 (1994).
23. F. A. Smith, J. L. Betancourt, J. H. Brown, data not shown.
24. J. H. Brown, unpublished data from a study in the 1960s dealing with physiological adaptations to environmental temperature (*20*). Metabolic rates of several subspecies of *N. cinerea* were measured while ambient temperature was increased in 2°C increments until the animals died of heat stress.
24. We thank J. Mead, P. Koehler, and S. Sharpe (Northern Arizona University) for the loan of midden samples; B. Stein and J. L. Patton (University of California, Berkeley), and W. Gannon and C. Ramick (University of New Mexico) for access to museum collections. P. Rodriguez-Moran and S. Simpson assisted with data collection; K. Aasen-Rylander at the U.S. Geological Survey Desert Laboratory was responsible for much of the midden processing. P. A. Kelly and J. S. Millar provided unpublished data on *N. cinerea*. S. M. Elliott, P. S. Martin, J. A. Wolfe, and two anonymous reviewers made helpful comments on the manuscript, and E. A. Elliott Smith helped to prepare illustrations. Supported by an NSF postdoctoral fellowship (F.A.S.), NSF grants DEB-9221238 and DEB-9318096 (J.H.B.), and the U.S. Geological Survey Global Change Program (J.L.B.).

9 June 1995; accepted 19 September 1995