



Melting climates shrink North American small mammals

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Mammals play important ecological roles in terrestrial ecosystems, with their particular niches and their impacts on energy flow and nutrient cycling being strongly influenced by one of their most fundamental traits—their body size. Body size influences nearly all of the physiological, behavioral, and ecological traits of mammals, and thus, shifts in body size often serve as key mechanisms of adaptation to variation in environmental conditions over space and time. Along with shifts in phenology and distributions, declining body size has been purported to be one of the three universal responses to anthropogenic climate change, yet few studies have been conducted at the spatial and temporal scales appropriate to test this claim. Here, we report that in response to warming of terrestrial ecosystems across North America over the past century, small mammals are decreasing in body size. We further estimate that by 2100 (when global temperatures may have risen some 2.5 to 5.5 °C since 1880), the total anthropogenic decline in body mass of these ecologically and economically important species may range from 10 to 21%. Such shifts in body size of the great multitudes of small mammal populations are, in turn, likely to have major impacts on the structural and functional diversity of terrestrial assemblages across the globe.

climate change | mammals | body size | North America

Global climate change has become the most pervasive and formidable threat to conserving biological diversity at all levels; these threats are only predicted to intensify over the coming decades (1). In their attempts to predict and possibly mitigate the impacts of increasing temperatures on native wildlife, conservation biologists often draw on broad-scale lessons and natural experiments from the field of biogeography. In response to past, natural shifts in climatic regimes, species survived by one or two means: either they dispersed and shifted in their distributions to track their optimal climate regimes or they remained and adapted in their native ranges (2). The latter adaptations included a diverse suite of adjustments of physiological, behavioral, and ecological traits (3–6)—most if not all of these strongly correlated with body size. Heart rates, blood perfusion, respiration, overall metabolic rates, diets, along with a diversity of traits influencing intra- and interspecific interactions among individuals and species all scale with body size of the organisms (7–13).

One salient result of these scaling relationships across broad geographic dimensions is the ecogeographic pattern referred to as Bergmann's rule—first articulated in 1847 by Carl Bergmann (14). Mammals and a variety of other vertebrates often tend to exhibit a trend toward increased body size along latitudinal and elevational gradients [i.e., their body size increases as we move toward regions of colder climates (15–24)]. Paleocologists have detected this to be an ancient pattern in some mammals, with some notable research reporting a temporal (time-for-space) corollary of the rule, where body size of particular species of mammals decreased as temperatures warmed during previous periods of natural climate change (e.g., during the Paleocene-Eocene Thermal Maximum (PETM) and the Eocene Thermal Maximum 2 (ETM2) (25, 26) and more recently during climatic cycles of the Pleistocene Epoch and during the Early Holocene (3, 27). This has led neo-ecologists and conservation biologists to predict that contemporary and future populations of mammals may be adapting or at least responding to the ongoing and impending increases in global temperatures by decreasing in body size (28, 29). Hypothesized physiological advantages of smaller size in a warming world include reduced total metabolism, energy and water requirements, increased abilities to find underground and other refugia during periods of intense heat or extended droughts, and abilities to enter torpor more rapidly and conserve water and energy during those periods (12).

Here, we investigate the above hypothesis by testing the predicted time-for-space corollary of Bergmann's rule. We focus on nonvolant, small (<1.4 kg) terrestrial mammals of North America, capitalizing on over a century of specimen collections now stored in natural history museums. Our approach was to identify locations where at least two specimen series of the same species were collected over periods of 3 to 89 y apart, with at least 10 specimens collected during each period. We then visited museums with these collections

Significance

The three postulated “universal” responses of animals to climate change include shifts in geographic ranges, in phenology, and in body size. Because the latter influences nearly all ecological traits of animals, its impacts on ecological communities may be pervasive, yet this phenomenon—body size reduction in response to warming climates—has yet to be clearly demonstrated. Here, we investigate body size shifts of North American small mammals during the past century, and we find that these species are indeed shrinking. We estimate that by 2100, the total anthropogenic reduction in body size may range from 10 to 21%, morphological shifts that are likely to have cascading impacts on the structure and functioning of terrestrial communities across the globe.

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and took a series of measurements on each adult specimen, including skull size (condylobasal length, breadth of braincase, depth of braincase, and mandibular length); total body length, inclusive of tail; tail length; body length, exclusive of tail; foot length; ear length; and body mass. We measured a total of 1,121 specimens from 23 species of small mammals, including 8 sciurids, 5 cricetids, 4 heteromyids, 3 geomyids, 1 zaptodid, and 2 soricids. We included collections from 29 sites across North America, ranging from 30 to 48°N in latitude, 90 to 120°W in longitude, and 150 to 3,150 m in elevation, with collection periods ranging from 1902 to 2008. In order to combine data across species, we first standardized each of the measured shifts in body size over time by dividing observed differences in size between periods by the mean body size of that species during the first collection period. We also collected climate data for each of the sites and periods of specimen collection to allow us to test whether the above morphological measures shifted with changes in local climatic conditions (the latter including mean annual temperatures and total annual precipitation measured during the previous 1- or 5-y periods prior to each collection period and Net Primary Productivity (NPP) calculated from these indices of temperature and precipitation). These sites experienced climatic conditions ranging from those that warmed up to 11.8 °C since the first collection period to others that cooled by as much as 7.2 °C (based on annual mean temperatures for 1-y period prior to collection of specimens). Our independent variables also included latitude, longitude, and elevation of sites, along with two species traits including whether or not they undergo torpor (including hibernation or daily torpor) and whether they are fossorial. Given the complex, likely nonlinear and contextual nature of potential morphological responses to these independent (environmental, geographic, and species) variables, we utilized Regression Tree Analyses (RTA) to test the time-for-space prediction of Bergmann's rule—that body size of species of mammals we studied decreased as local temperatures increased. We conducted a total of 30 RTAs; 10 on measures of body size (dependent variables), each repeated in three separate sets of analyses—one where independent variables included just the geographic variables (without climate variables and species traits), one with climatic variables measured over the 1-y window prior to periods of specimen collection, and one for climate variables measured over the 5-y window prior to specimen collection.

Results and Discussion

Climatic and Geographic Factors Associated with Body Size Shifts. RTAs revealed that morphological shifts of the North American mammals we studied were most strongly influenced by concurrent shifts in mean annual temperatures (Table 1 and Fig. 1). RTAs generally had high explanatory power, with R-squared values ranging from 37.6 to 74.4% (mean = 60.8%) and MAPEs all less than 8% (mean = 1.7%).

Consistent with the time-for-space corollary of Bergmann's rule, shifts in mean annual temperatures were by far the most common primary (first-level) splitting variable in RTAs, with 11 out of 12 of these indicating that body size measurements decreased as temperatures increased. The relative slopes of the size-temperature relationships (Fig. 1 *A* and *B*) accord with the differences in dimensionality of body size metrics, with mass—being a cubed function of linear measurements—decreasing much more rapidly with shifts in local temperatures than the linear measures of size. Mann–Whitney–Wilcoxon tests confirmed that RTAs split body mass responses of mammals into two distinct groups, with those experiencing warmer temperatures exhibiting significantly more pronounced declines in body mass; $W_{8,9} = 94.5$ and $W_{6,11} = 74.0$ ($P = 0.017$ and $= 0.025$)

for mass shifts in response to 1-y and 5-y shifts in mean temperatures, respectively.

Ear size also exhibited a highly labile relationship with shifts in local temperature, again decreasing with increased temperature, but much more rapidly than other linear measures of body size (Fig. 1*B*). Tail length was the only size measure determined by RTA to increase as local temperatures increased (Fig. 1*A*), possibly reflecting another thermoregulatory-based adaptation known as Allen's rule (31–39) where the length of appendages tends to increase—facilitating heat dissipation in warmer climates. Although ear length increases in warmer climates in larger mammals such as leporids (38, 39), we failed to observe this phenomenon in the small mammals we studied, and, instead, ear length shifted consistent with other body size metrics (i.e., allometrically and consistent with Bergmann's rule). These results are entirely consistent with the results of a global study of Allen's rule (covering 86% of all rodent species), which found that while the tail length of rodents did vary consistent with Allen's rule, ear length did not (40).

NPP was the second most common primary splitting variable in RTAs (Table 1), with body size declining as NPP increased (i.e., as local climates became warmer and/or more mesic; six out of seven trials). Although only three of the 30 RTAs identified latitude as the primary splitting variable, its relationship to shifts in body size over time was, like that of temperature, also consistent with Bergmann's rule, with populations from higher latitudes (colder regions) exhibiting more pronounced shifts toward larger body size (Table 1 and Fig. 1*C*). In contrast, annual precipitation and the capacity of a species to enter torpor or hibernation were not detected as primary splitting variables in any of the 30 RTAs [the latter inference being consistent with McCain and King's (41) meta-analysis and conclusion that hibernation and heterothermy did not influence species responses to climate change].

Synthesis and Cascading Impacts of Impending Climate-Body Size Dynamics. Over the past century, body size of the 23 species (1,121 specimens, representing populations from two different time periods at 29 sites) of small mammals studied shifted with the dynamics of climatic conditions, with 22 of 30 RTAs indicating that temperature, NPP (a function of temperature and precipitation) and latitude (a correlate of temperature) were the primary factors influencing shifts in body size. These results were not only consistent with patterns of or associated with Bergmann's rule, where mammalian body size is expected to decrease in a warming world, but they also allow estimates of the degree to which body size of these and similar mammals should decrease in the future.

The slopes of the size–temperature relationships in Fig. 1 *A* and *B* enable predictions of the magnitude of body size declines that may be expected under various scenarios of impending climate change. For example, IPCC (Intergovernmental Panel on Climate Change) scenarios for 2081 to 2100 predict average global temperature increases of 1.4 °C under scenarios of low greenhouse gas emissions and 4.4 °C for scenarios of very high greenhouse gas emissions (1). Under these scenarios and noting that global temperatures have already risen approximately 1.1 °C since 1880 (42), the total anthropogenic rise in average global temperatures by 2100 may range from 2.5 to 5.5 °C (again, under low- and very high greenhouse gas scenarios, respectively). Applying our calculation of the slope of the relationship between body mass and temperature changes (3.864% decline in mass per °C increase; Fig. 1*A*), we estimate the total anthropogenic decline in body mass of small mammals by 2100 to range from 9.7 to 21.3%. To be conservative, we have assumed a linear response to temperature shifts but, as one anonymous reviewer observed, we might predict more pronounced shifts in body size as

Table 1. Results of RTA on the factors influencing morphological shifts of small mammals of North America

Primary splitting variable	Relative importance (%) [*]	Body size measure	No. of populations included	Nature of relationship	R-squared (%)	MAPE (%) [†]
Average annual temperature—5 y	100	CBL	35	Negative	66.0	0.7
Average annual temperature—5 y	100	BB	35	Negative	64.3	1.1
Average annual temperature—5 y	100	ML	35	Negative	74.4	1.4
Average annual temperature—5 y	100	Total	33	Negative	71.0	4.0
Average annual temperature—1 y	100	Total	33	Negative	62.1	2.3
Average annual temperature—5 y	100	Tail	33	Positive	65.1	1.1
Average annual temperature—5 y	100	BL	33	Negative	67.5	0.8
Average annual temperature—1 y	100	BL	33	Negative	59.5	0.7
Average annual temperature—5 y	100	Ear	27	Negative	67.8	2.9
Average annual temperature—1 y	100	Ear	27	Negative	61.5	2.9
Average annual temperature—1 y	100	Mass	17	Negative	53.0	0.7
Average annual temperature—5 y	81.9 (NPP)	Mass	17	Negative	65.9	0.5
NPP—1 y	100	CBL	35	Negative	57.8	1.1
NPP—1 y	100	ML	35	Negative	70.4	1.1
NPP—5 y	59 (Temperature)	DBC	35	Negative	46.9	2.3
NPP—1 y	100	DBC	35	Negative	45.2	2.7
NPP—1 y	100	Tail	33	Positive	62.7	1.1
NPP—5 y	60 (Precipitation)	Foot	33	Negative	62.8	1.8
NPP—1 y	100	Foot	33	Negative	68.8	2.3
Latitude	100	CBL	35	Positive	63.7	0.0
Latitude	100	Tail	33	Positive	57.6	0.9
Latitude	50 (Longitude)	BL	33	Positive	61.8	0.8
Elevation	100	ML	35	Negative	60.4	1.3
Elevation	100	BB	35	Negative	73.4	0.9
Elevation	100	Foot	33	Positive	60.2	1.6
Elevational difference (Time 2–Time 1)	93 (Longitude)	DBC	35	Negative	37.6	1.8
Elevational difference (Time 2–Time 1)	32 (Latitude)	Total	33	Positive	56.8	2.8
Elevational difference (Time 2–Time 1)	100	Ear	27	Positive	52.0	7.9
Longitude	100	Mass	17	Positive	51.1	0.9
Fossoriality—1 y	24 (Temperature)	BB	35	Negative	57.0	0.0

^{*}When the primary splitting variable was not the most important overall for the tree, that variable is listed in parentheses. Importance values are based on the effect of each variable on unexplained errors across the entire tree and, thus, may differ from the primary splitting variable which is only based on its effect determined on the first branching of the dataset.

[†]A value of MAPE < 10 is considered highly accurate (30).

Explanatory factors include dynamics in climatic conditions, differences in geographic variables, and differences in the ability of species of small mammals to undergo torpor or exploit fossorial refugia on body size shifts over time and space. Relative importance is a measure of the influence of this variable in comparison to (as % of) that of the most important variable in each of the 30 RTAs. Codes for body size measures: CBL = condylobasal length; BB = breadth of braincase; DBC = depth of braincase; ML = mandibular length; Total = total body length, inclusive of tail; Tail = tail length; BL = body length, exclusive of tail; Foot = foot length; Ear = ear length; Mass = body mass. R-squared is an estimate of the proportion of temporal shifts in the dependent variable (body size measurement) explained by the independent variables; MAPE is a measure of prediction accuracy = $100/n \times \text{SUM}i = 1 \text{ to } n(A-P)/A$, where A and P = the actual and predicted values of the dependent variable and n is the number of predictions. RTAs conducted in MiniTab using Least squared error node splitting, and Maximum R-squared optimal tree methods (detailed results of each of the 30 RTAs presented in *SI Appendix*).

temperatures approach thermoregulatory limits of the focal species. Our estimated response of small mammals to anthropogenic climate warming (~4% mass decline per °C) is comparable to that reported

for North American bison (*Bos bison*) during a period of natural climate warming during the past 40,000 y (estimated at 6% decline in mass/°C increase) (43). Dwarfing in response to earlier periods

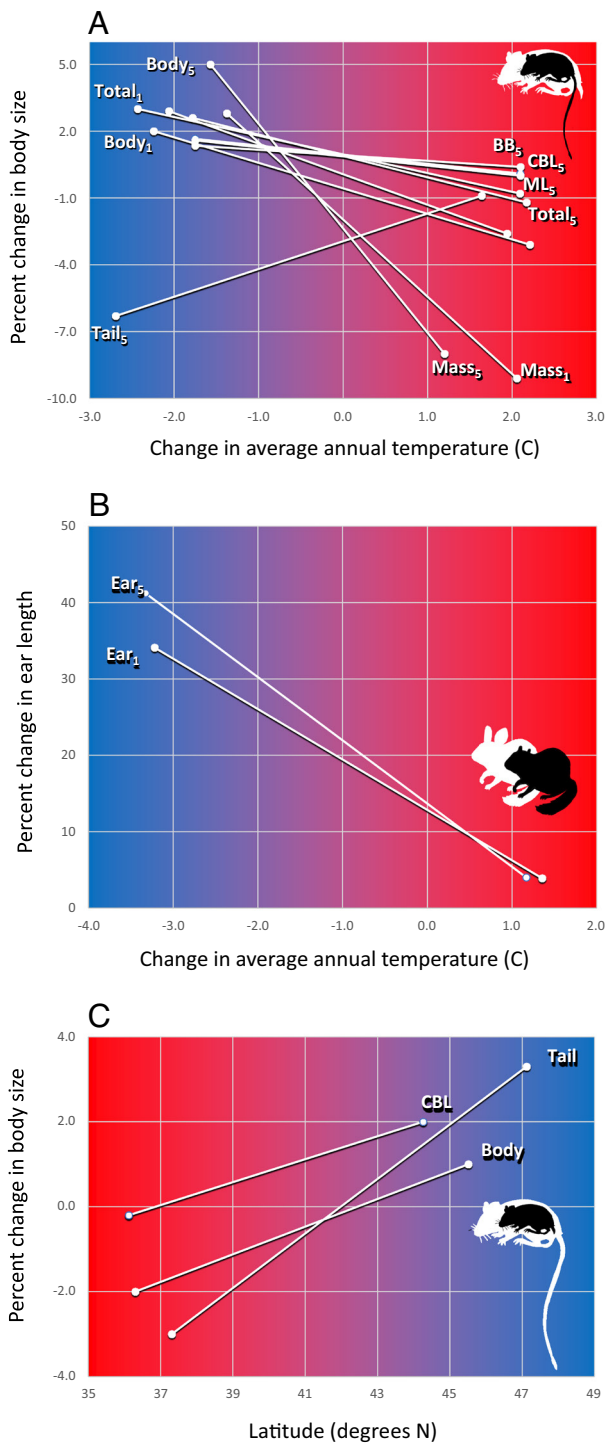


Fig. 1. Shifts in body size of small mammals of North America during the past century. (A and B) Temporal dynamics in the morphology of these nonvolant, terrestrial mammals vary with shifts in mean annual temperatures, exhibiting the expected negative relationship (decreasing size as temperatures increased) consistent with the time-for-space prediction of Bergmann's rule. The one exception—tail length increasing in regions that experienced increased temperatures, presumably facilitating heat dissipation—is consistent with another thermoregulatory-based ecogeographic pattern, Allen's rule. (C) The observed tendency for these small mammals to exhibit more pronounced increases in body size in the higher latitudes is also consistent with Bergmann's rule. Codes for body size measurements labeled here are described in Table 1; subscripts for the labels in these charts indicate whether the climate data were that for the 1-y or 5-y windows prior to specimen collection [chart background reflects temperature gradient from climates that became cooler (blue) to those that warmed (red) between collection periods]. Silhouettes were adapted from "phylopic" (<https://www.phylopic.org/>) and indicate changes in morphology along the temperature gradient from climates that became cooler (white) to those that warmed (black).

of global warming has also been reported in other large mammals, including equids and even-toed ungulates during the Eocene Thermal Maximum (25, 26).

Our study has the strengths of being based on natural experiments conducted across multiple (≈ 23) species and at scales most appropriate to assess the long-term (decadal to century) and broad-scale (local to regional and continental) impacts of climate change on native assemblages of mammals. Despite the logistical limits of opportunistic studies conducted at these broad scales of time, space, and biological diversity, our inferences are consistent with a growing body of research, including that from both paleo- and neo-ecologists. Historical records provide some of the most compelling demonstrations of the influence of climate change on the body size of small mammals. Analyses of shifts in size of preserved fecal pellets of woodrats (*Neotoma* spp.) over the past 25,000 y revealed that the body size of these species was tightly (and inversely) correlated with ambient temperature (3, 44). Pocket gophers (*Thomomys talpoides*) from Yellowstone National Park exhibited a similar correlation of shifts in body size and ambient temperatures, in this case over the past 3,000 y (27).

Additionally, several studies have demonstrated a relationship between body size shifts in mammals and climate change in more recent periods (29). For example, over a 25-y period spanning the turn of the century, mean body size of wood mice (*Apodemus sylvaticus*) in a Spanish national park declined by 30% during a period of increased temperatures (by ~ 0.7 °C) and declining rainfall (by $\sim 25\%$) (45). In another contemporary study, woodrats (*Neotoma albigula*) at the Sevilleta National Wildlife Refuge in the Southwestern United States declined in body mass by approximately 17% in less than a decade during a period marked by a 2 to 3 °C rise in mean minimum temperatures (44). Multispecies reviews and meta-analyses of this phenomenon have attempted to assess both the generality and causality of the pattern, but with equivocal results (11, 19, 46–49). We, therefore, echo the calls of others for large-scale, multispecies comparative studies to rigorously evaluate the claim that declining body size, along with shifts in phenology and distributions, is one of the three universal responses to anthropogenic climate change (28). Studies utilizing the immense trove of museum specimens and data from long-term field studies and adopting approaches similar to that we used here for small mammals of North America will go a long way toward testing the above claim and developing accurate projections on the morphological and associated ecological impacts of anthropogenic climate change on native wildlife [e.g., in birds (50)].

Small mammals such as those studied here play important ecological roles in terrestrial ecosystems. Given their diversity and the magnitudes of their populations, they strongly influence energy flow and nutrient cycling through all ecological communities across the terrestrial realm, serving as key herbivores, insectivores, prey species, and dispersal agents for parasites and disease, as well as providing beneficial roles in dispersing plant seeds and fungi essential to productivity, decomposition, and nutrient cycling (51–55). Given the complexity of these interactions among the many integral components of all natural ecosystems, and the myriad effects of body size on the physiological, behavioral, and ecological traits of all species (7, 8, 10, 13), it is far beyond the scope of this research article to offer detailed predictions on the wholesale impacts of climate-driven body size dynamics of small mammals on other components of animal and plant communities. Yet the evidence is strong that humanity has affected global climates (1) and, in those regions where temperatures have and will continue to increase, our research predicts that body size of small mammals will continue to decline—strongly impacting the structural and functional diversity of native terrestrial ecosystems across the globe.

Materials and Methods

Data Collection. Suitable collections were identified by searching multiple institution museum databases [MANIS (56) and Arctos (57)] and by contacting museum curators and collection managers. Museum records were then examined to determine the number of specimens collected at each site and for each time period in order to identify specimen series collected in the same sites or those of close geographic proximity (<50 km apart) and between 3 and 89 y apart. Prior to measurement of specimens, we visually inspected them to verify that they were structurally intact and that they were not juveniles by confirming closure of cranial (interfrontal and sagittal) sutures. We also screened specimens to identify and exclude juveniles by inspecting CBL measurements and identifying outliers of small size using the interquartile range method, excluding from our analyses any specimens whose CBL measurement fell below the “lower fence” ($Q1 - (1.5 * IQR)$) for that collection series.

We then took a series of measurements on each specimen with digital calipers (Mitutoyo 500–196–20, 15 cm, accurate to the nearest 0.01 mm) (SI Appendix, Fig. S1 and Dataset S1); these included measurements of skull size including condylobasal length (CBL); breadth of braincase (BB); depth of braincase (DBC); and mandibular length (ML); measurements of skins, including total length (TOTAL), inclusive of tail; tail length (TL); body length (BL), exclusive of tail; foot length (FL); ear length (EAR); and we also recorded body mass (MASS) measurements from specimen records. If more than 30 individuals were available from one location and collection year, we used a random number generator to select the 30 individuals to be included in our study. To avoid measurement error and bias from multiple observers, K.B.S. was the only one to take specimen measurements (Dataset S1).

We collected climate data for each location and each time period from PRISM (58) (Parameter-elevation Regressions on Independent Slopes Model). We then obtained mean annual temperature and annual precipitation data for the two time periods immediately prior to collections; here including the two alternative temporal windows of 5-y and 1-y periods prior to specimen collection (Dataset S1).

We calculated NPP using the Miami Method, which is based on temperature (NPP_T) or precipitation (NPP_P), whichever is the most likely limiting factor (59, 60). NPP for each site and time period was calculated using the following formulas:

$$NPP = \min(NPP_T, NPP_P),$$

$$NPP_T = 3000(1 + \exp(1.315 - 119 * \bar{T}))^{-1},$$

$$NPP_P = 3000(1 - \exp(-0.000664 * \bar{P})),$$

where \bar{T} and \bar{P} = mean annual temperature and precipitation, respectively.

We then compared these data for the two collection periods (i.e., most recent minus the earliest) to calculate the shifts in climate conditions (temperature, precipitation, and NPP), again repeating this for the 5-y and 1-y climate windows.

Data Analyses and Visualizations. Given the opportunistic nature of these natural experiments in body size dynamics, and the likelihood that measures of body size, climatic and geographic variables and their interactions are non-normal, nonlinear and contextual, we tested the predicted relationships among body size measures and the independent variables using RTA (in Minitab—node splitting method = Least squared error; optimal tree determined using the Maximum R-squared method). As Olden et al. (61) summarized, RTA is a nonparametric method that is distribution-free and thus, does not require transformations. It can handle categorical, interval, and continuous variables, is able to deal efficiently with missing variables and with high dimensionality, and is not affected by outliers. It also provides readily interpretable descriptions of the relationships between predictor and response variables even when complex, contextual relationships exist [i.e., when the relationships between these variables varies among subgroups of the data (e.g., a positive relationship within one region or one family of mammals but negative relationship in another)].

RTA produces a recursively branching tree that describes the direct, interactive, and contextual relationships between the response variable (here temporal shifts in standardized body size for all 23 species, combined) and predictor/

independent variables. The first split or branch in RTA is determined by first sorting the entire dataset by the values of each predictor variable and then determining which of those variables is best at splitting the data into two subgroups that are most homogeneous with respect to values of the response variable. One advantage of this and other machine-learning methods is that they do not assume data independence, thus alleviating the need for phylogenetic controls of such data (62–65).

We conducted 30 RTAs—10 measures of body size as the dependent variable and three sets of independent variables, one including only geographic variables (latitude, longitude, and elevation), and two sets including species-level traits [whether or not they undergo torpor (hibernation or daily torpor), and whether they are fossorial] and temporal shifts in three climate variables (mean annual temperature, total annual precipitation, NPP) either for the 1-y or the 5-y window prior to each period of specimen collection. As indicated above, in order to combine data across species, we first standardized each of the measured shifts in body size over time by dividing observed differences (Time 2–Time 1) in mean body size between periods by the mean body size of that species at the time of the first collection (Time 1).

To test the predictions associated with Bergmann’s rule and assess the relationships between temporal shifts in body size, geographic variables, species traits, and temporal shifts in climatic conditions, we recorded the following from the results of each of the 30 RTAs and we report them in Table 1: N, the number of species populations included in the RTA; the particular measure of body size (the dependent variable) used in each RTA; the primary splitting variable and its relative importance (where the primary splitting variable was not the most important variable over the entire tree, we also noted that and report that in Table 1 as well); the nature of the relationship (positive or negative) between temporal shifts in the body size measure and the independent variable (e.g., whether body size increased or decreased as temperatures increased); the R-squared value; and the Mean Absolute Percent Error (MAPE). To confirm the efficacy of RTA results, we used Mann–Whitney–Wilcoxon tests to determine whether RTAs where mean temperatures (both 1-y and 5-y windows) were the primary splitting variables separated mammals shifting in body mass into two significantly distinct groups (those exposed to warmer temperatures experiencing more pronounced declines in body mass; thus, performing a one-tailed test of the time-for-space corollary of Bergmann’s rule). Detailed results of each of the 30 RTAs are included in Supplementary Material.

To visualize (creating the charts in Fig. 1) and estimate the slopes of the relationship between shifts in body size and shifts in temperature, we focused on the RTAs where temperature and latitude were the primary splitting variables. We then noted which observations were in each side of the primary split, calculated the means for their dependent (body size shifts = y) and independent variables (temperature shifts or difference in latitude = x), and then used the resultant two pairs of means as coordinates (x and y values) to construct the lines describing the per °C or degree latitude shifts for each body size measurement and generate the plots of Fig. 1. Results consistent with Bergmann’s rule would be those with a negative slope of temporal shifts in body size as a function of temperature and a positive slope for temporal shifts in body size as a function of latitude. The slopes of the lines between the pairs of points in Fig. 1 can then be used to estimate how much each particular measure of body size should shift per °C increase in temperature.

Data, Materials, and Software Availability. All study data are included in the article and/or supporting information.

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1. IPCC, "Climate change 2021: The physical science basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change", V. Masson-Delmotte *et al.*, Eds. (Cambridge University Press, 2021), 10.1017/9781009157896.
2. M. V. Lomolino, B. R. Riddle, R. J. Whittaker, *Biogeography: Biological Diversity Across Space and Time* (Sinauer Associates, Sunderland, MA, ed. 5, 2017), (April 25, 2023).
3. F. A. Smith, J. L. Betancourt, J. H. Brown, Evolution of body size in the woodrat over the past 25,000 years of climate change. *Science* **270**, 2012–2014 (1995).
4. R. W. Graham *et al.*, Spatial response of mammals to late quaternary environmental fluctuations. *Science* **272**, 1601–1606 (1996).
5. S. K. Lyons, A quantitative assessment of the range shifts of Pleistocene mammals. *J. Mammal.* **84**, 385–402 (2003).
6. A. Feurdean *et al.*, Tree migration-rates: Narrowing the gap between inferred post-glacial rates and projected rates. *Plos One* **8**, e71797 (2013).
7. J. H. Brown, P. A. Marquet, M. L. Taper, Evolution of body size: Consequences of an energetic definition of fitness. *Am. Nat.* **142**, 573–584 (1993).
8. W. A. Calder, *Size, Function, and Life History* (Harvard University Press, 1984).
9. J. B. S. Haldane, On being the right size. *Harper's Magazine*, (March 1926), pp. 424–427.
10. B. K. McNab, *The Physiological Ecology of Vertebrates: A View from Energetics* (Cornell University Press, 2002).
11. B. K. McNab, Geographic and temporal correlations of mammalian size reconsidered: A resource rule. *Oecologia* **164**, 13–23 (2010).
12. B. K. McNab, *Extreme Measures: The Ecological Energetics of Birds and Mammals* (University of Chicago Press, 2012).
13. F. A. Smith, S. K. Lyons, *Animal Body Size: Linking Pattern and Process across Space, Time, and Taxonomic Group* (University of Chicago Press, 2013), (April 25, 2023).
14. C. Bergmann, Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Größe. *Göttinger Studien* **1**, 595–708 (1847).
15. J. H. Brown, A. K. Lee, Bergmann's rule and climatic adaptation in woodrats (Neotoma). *Evolution* **23**, 329–338 (1969).
16. K. G. Ashton, M. C. Tracy, A. de Queiroz, Is Bergmann's rule valid for mammals? *Am. Nat.* **156**, 390–415 (2000).
17. K. G. Ashton, Patterns of within-species body size variation of birds: Strong evidence for Bergmann's rule. *Glob. Ecol. Biogeogr.* **11**, 505–523 (2002).
18. K. G. Ashton, C. R. Feldman, Bergmann's rule in nonavian reptiles: Turtles follow it, lizards and snakes reverse it. *Evolution* **57**, 1151–1163 (2003).
19. Y. Yom-Tov, J. Yom-Tov, Global warming, Bergmann's Rule and body size in the masked Shrew *Sorex cinereus* Kerr in Alaska. *J. Anim. Ecol.* **74**, 803–808 (2005).
20. M. Á. Rodríguez, M. Á. Olalla-Tárraga, B. A. Hawkins, Bergmann's rule and the geography of mammal body size in the Western Hemisphere. *Glob. Ecol. Biogeogr.* **17**, 274–283 (2008).
21. S. K. Berke, D. Jablonski, A. Z. Krug, K. Roy, A. Tomasovych, Beyond Bergmann's rule: Size–latitude relationships in marine Bivalvia world-wide. *Glob. Ecol. Biogeogr.* **22**, 173–183 (2013).
22. S. Meiri, T. Dayan, On the validity of Bergmann's rule. *J. Biogeogr.* **30**, 331–351 (2003).
23. C. Teplitsky, V. Millien, Climate warming and Bergmann's rule through time: Is there any evidence? *Evol. Appl.* **7**, 156–168 (2014).
24. B. H. Alhajer, S. J. Stepan, Association between climate and body size in rodents: A phylogenetic test of Bergmann's rule. *Mamm. Biol.* **81**, 219–225 (2016).
25. A. R. D'Ambrosia, W. C. Clyde, H. C. Fricke, P. D. Gingerich, H. A. Abels, Repetitive mammalian dwarfing during ancient greenhouse warming events. *Sci. Adv.* **3**, e1601430 (2017).
26. R. Secord *et al.*, Evolution of the earliest horses driven by climate change in the paleocene-eocene thermal maximum. *Science* **335**, 959–962 (2012).
27. E. A. Hadly, Evolutionary and ecological response of pocket gophers (*Thomomys talpoides*) to late-Holocene climatic change. *Biol. J. Linn. Soc. Lond.* **60**, 277–296 (1997).
28. J. L. Gardner, A. Peters, M. R. Kearney, L. Joseph, R. Heinsohn, Declining body size: A third universal response to warming? *TREE* **26**, 285–291 (2011).
29. J. A. Sheridan, D. Bickford, Shrinking body size as an ecological response to climate change. *Nat. Clim. Change* **1**, 401–406 (2011).
30. C. D. Lewis, *Industrial and Business Forecasting Methods: A Practical Guide to Exponential Smoothing and Curve Fitting* (Butterworth Scientific, 1982).
31. J. A. Allen, The influence of physical conditions in the genesis of species. *Radic. Rev.* **1**, 108–140 (1877).
32. J. H. Brown, R. C. Lasiewski, Metabolism of weasels: The cost of being long and thin. *Ecology* **53**, 939–943 (1972).
33. R. L. Nudds, S. A. Oswald, An interspecific test of Allen's rule: Evolutionary implications for endothermic species. *Evolution* **61**, 2839–2848 (2007).
34. W. P. Porter, M. Kearney, Size, shape, and the thermal niche of endotherms. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 19666–19672 (2009).
35. J. Alroy, Small mammals have big tails in the tropics. *Glob. Ecol. Biogeogr.* **28**, 1042–1050 (2019).
36. S. Ryding, M. Klaassen, G. J. Tattersall, J. L. Gardner, M. R. E. Symonds, Shape-shifting: Changing animal morphologies as a response to climatic warming. *TREE* **36**, 1036–1048 (2021).
37. M. A. Ballinger, M. W. Nachman, The contribution of genetic and environmental effects to Bergmann's rule and Allen's rule in house mice. *Am. Nat.* **199**, 691–704 (2022).
38. R. D. Stevenson, Allen's rule in North American rabbits (*Sylvilagus*) and Hares (*Lepus*) is an exception, not a rule. *J. Mammal.* **67**, 312–316 (1986).
39. C. K. Williams, R. J. Moore, Phenotypic adaptation and natural selection in the wild rabbit, *Oryctolagus cuniculus*, Australia. *J. Anim. Ecol.* **58**, 495–507 (1989).
40. B. H. Alhajer, Y. Fourcade, N. S. Upham, H. Alhaddad, A global test of Allen's rule in rodents. *Glob. Ecol. Biogeogr.* **29**, 2248–2260 (2020).
41. C. M. McCain, S. R. B. King, Body size and activity times mediate mammalian responses to climate change. *Global Chang. Biol.* **20**, 1760–1769 (2014).
42. J. Hansen, R. Ruedy, M. Sato, K. Lo, Global surface temperature change. *Rev. Geophys.* **48**, 1–29 (2010).
43. J. M. Martin, J. I. Mead, P. S. Barboza, Bison body size and climate change. *Ecol. Evol.* **8**, 4564–4574 (2018).
44. F. A. Smith, H. Browning, U. L. Shepherd, The influence of climate change on the body mass of woodrats neotoma in an arid region of New Mexico, USA. *Ecography* **21**, 140–148 (1998).
45. M. Docampo, S. Moreno, S. Santoro, Marked reduction in body size of a wood mouse population in less than 30 years. *Mamm. Biol.* **95**, 127–134 (2019).
46. C. H. Willar, D. E. Naya, Climate change and temporal trends in body size: The case of rodents. *Oikos* **127**, 1186–1194 (2018).
47. C. Moritz *et al.*, Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* **322**, 261–264 (2008).
48. Y. Yom-Tov, E. Geffen, Recent spatial and temporal changes in body size of terrestrial vertebrates: Probable causes and pitfalls. *Biol. Rev. Camb. Philos. Soc.* **86**, 531–541 (2010).
49. B. C. Weeks *et al.*, Shared morphological consequences of global warming in North American migratory birds. *Ecol. Lett.* **23**, 316–325 (2020).
50. V. Jirinec *et al.*, Morphological consequences of climate change for resident birds in intact Amazonian rainforest. *Sci. Adv.* **7**, eabk1743 (2021).
51. C. R. Dickman, C. P. Doncaster, The ecology of small mammals in urban habitats. I. Populations in a patchy environment. *J. Anim. Ecol.* **56**, 629–640 (1987).
52. C. N. Johnson, Interactions between mammals and ectomycorrhizal fungi. *TREE* **11**, 503–507 (1996).
53. G. W. Barrett, J. D. Peles, *Landscape Ecology of Small Mammals* (Springer, 1999), 10.1007/978-0-387-21622-5 (April 25, 2023).
54. C. G. Curtin, D. A. Kelt, T. C. Frey, J. H. Brown, On the role of small mammals in mediating climatically driven vegetation change. *Ecol. Lett.* **3**, 309–317 (2000).
55. D. M. Stoddart, *Ecology of Small Mammals* (Springer, Netherlands, 1979), 10.1007/978-94-009-5772-5 (April 25, 2023).
56. B. R. Stein, J. R. Wieczorek, Mammals of the World: MaNIS as an example of data integration in a distributed network environment. *Biodivers. Inform.* **1**, 14–22 (2004).
57. U. of C. Museum of Vertebrate Zoology, Arctos collaborative collection management solution. <https://arctosdb.org/>. Accessed 26 May 2023.
58. O. S. U. PRISM Climate Group, PRISM: Parameter-elevation regressions on independent slopes model. <https://prism.oregonstate.edu/>. Accessed 1 June 2015.
59. J. Grieser, R. Gommers, M. Bernardi, "The Miami model of climatic net primary production of biomass" (The Agromet Group, SDRN, FAO of the UN, Viale delle Terme di Caracalla, 00100 Rome, Italy, 2006).
60. H. Lieth, "Modeling the primary productivity of the world" in *Primary Productivity of the Biosphere, Ecological Studies*, H. Lieth, R. H. Whittaker, Eds. (Springer, 1975), pp. 237–263.
61. J. D. Olden, J. J. Lawler, N. L. Poff, Machine learning methods without tears: A primer for ecologists. *Q. Rev. Biol.* **83**, 171–193 (2008).
62. M. Westoby, M. Leishman, J. Lord, Further remarks on phylogenetic correction. *J. Ecol.* **83**, 727 (1995).
63. J. F. Bell, "Tree-based methods" in *Machine Learning Methods for Ecological Applications*, A. H. Fielding, Ed. (Springer, US, 1999), pp. 89–105.
64. A. D. Davidson, M. J. Hamilton, A. G. Boyer, J. H. Brown, G. Ceballos, Multiple ecological pathways to extinction in mammals. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 10702–10705 (2009).
65. A. S. Melo, T. F. L. V. B. Rangel, J. A. F. Diniz-Filho, Environmental drivers of beta-diversity patterns in new-world birds and mammals. *Ecography* **32**, 226–236 (2009).