



Original Investigation

Association between climate and body size in rodents: A phylogenetic test of Bergmann's rule

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ABSTRACT

The pattern of increased body size in colder climates, or Bergmann's rule, is common in endotherms. However, empirical support has been mixed among clades, and it varies among taxonomic levels. Taking advantage of greatly improved phylogenetic resolution among rodents, we tested Bergmann's rule using 19 bioclimatic variables, and body mass data, for 1315 species on a recent supermatrix phylogeny. We did not find the predicted negative relationship between body mass and temperature. Instead, phylogenetic generalized least squares (PGLS) analysis indicated that precipitation variables (especially variables associated with primary productivity) had a positive correlation with body mass, suggesting that rodent species tend to be larger in more productive regions. Multivariate regression between body mass and overall climate (based on 19 bioclimatic variables) found a significant relationship, that was robust to phylogenetic correction. Bergmann's rule was not detected in smaller and surface-dwelling rodents (despite their greater exposure to external climate), any more than in larger and subterranean rodents. We suggest that food availability, and not heat conservation, is the more important mechanism driving body size variation across rodent species at the order level.

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Introduction

Bergmann's rule (1847) is a widely studied zoogeographic, eco-geographic trend of increased body size in cooler climates. It, along with others (e.g. Allen's rule [1877]), are empirical generalizations of the observed correlation between variation in the environment and morphology (Mayr, 1963). In its original formulation, Bergmann's rule states that, within a broadly distributed endothermic vertebrate genus, species inhabiting colder regions have greater body mass than those from warmer regions (Mayr, 1956).

Bergmann's rule has been subsequently expanded to include intraspecific variation, with populations living in colder regions tending to be larger than those living in warmer regions (Rensch, 1938; Mayr, 1963). The trend of increasing body size in cooler climates has even been documented in ectothermic vertebrates and invertebrates (e.g. Lindsey, 1966; Cushman et al., 1993; Atkinson, 1994; Ashton, 2002a,b). Moreover, Bergmann's rule, along with other ecogeographic trends, has been expanded to broader taxonomic scales than genera (Blackburn et al., 1999; Millien et al.,

2006; Adams et al., 2008). This rule has also been tested using various proxies for body size, other than body mass, that may be influenced by other selective forces, such as competition manifested in teeth size (Dayan et al., 1989; Meiri and Dayan, 2003).

Bergmann's rule has been observed in most studied mammal (Ashton et al., 2000; Meiri and Dayan, 2003; Blackburn and Hawkins, 2004; but see McNab, 1971) and bird species (Ashton, 2002a,b; Meiri and Dayan, 2003). The most common explanation for the negative relationship between body size and environmental temperature in endotherms is adaptation to reduce heat dissipation in cold regions (Bergmann, 1847; Walters and Hassall, 2006). In endotherms, heat generation is proportional to their volume, whereas heat loss is proportional to their surface; because surface area to volume ratio decreases with increasing body size, proportional heat loss is also reduced, an advantage in cold regions (Mayr, 1963; Meiri and Dayan, 2003).

In absolute terms, larger animals lose a greater amount of heat to the environment than smaller animals, leading some to reject the thermal-conservation explanation for Bergmann's rule (e.g. McNab, 1971), in favor of other, taxon-specific, explanations for body size variation, such as prey size in carnivores, and character displacement in granivores. Moreover, James (1970) proposed that in some taxa, geographic body size variation is not related to temperature alone, but rather to a combination of climatic factors, that

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include both temperature and humidity. Several subsequent studies showed that in some taxa, temperature and/or humidity seem to better explain geographic clines in body size than temperature alone (e.g. Burnett, 1983; Wigginton and Dobson, 1999).

An adaptive explanation for the association between environmental moisture with body size is the increased need for water conservation in warm, arid environments, where a smaller body size leads to a lower evaporative water loss, due to the reduction in surface area (Burnett, 1983). Moreover, increased plant primary productivity (and consequently food availability) in wetter environments may also account for the positive relationship between body size and humidity (Rosenzweig, 1968; Kolb, 1978; Burnett, 1983; Yom-Tov and Nix, 1986; Geist, 1987; Medina et al., 2007). Since Bergmann's rule is often tested using latitude as a proxy for temperature (Ashton et al., 2000), the thermal explanation for Bergmann's rule is often conflated with other mechanisms. This occurs because latitude is also correlated with precipitation, primary productivity, and environmental predictability, which could all contribute to differential survival rates for species of different size (Boyce, 1978, 1979; Lindstedt and Boyce, 1985; Wigginton and Dobson, 1999).

Other than increased body size, mammals can mitigate heat loss by improved insulation via pelage modification, which empirical data and biophysical modeling indicates is more important in larger mammals, which attain greater heat conservation via pelage modification when compared with further increased body size (Scholander, 1955, 1956; Irving, 1957; Searcy, 1980; Porter et al., 1994; Steudel et al., 1994). Thus, when compared with larger mammals, smaller mammals attain a greater increase heat conservation via increased body size (relative to pelage modification), and therefore smaller mammals are expected to follow Bergmann's rule (via the original thermal mechanism) more strongly than larger mammals (Ashton et al., 2000).

Bergmann's rule predicts an association between body size and the climate actually experienced by the animal. Therefore, a stronger correlation is expected in animals that live above-ground, than that those that live below-ground (i.e. subterranean). The pattern is expected to be weaker or absent in the latter (Medina et al., 2007; Feldman and Meiri, 2014) because species that live underground are shielded from the external climate; temperature and humidity also tend to be more stable and constant in their burrows (Mayr, 1963; Nevo, 1999; Whitaker and Shine, 2002). The subterranean rodent genus *Ctenomys*, which consists of around 60 species, have been shown to follow a trend in interspecific body size variation that is opposite to that of Bergmann's rule (Medina et al., 2007). However, a weak Bergmannian trend was observed in fossorial Australian snakes, but this relationship disappeared when correcting for phylogeny (Feldman and Meiri, 2014).

Rodents are an ideal model system to test the association between body size and climate. They are the most diverse order of mammals, with around 2277 extant species in 481 genera (Musser and Carleton, 2005). Their adult body mass ranges over four orders of magnitude, from 7 grams in pygmy jerboas (Gromov and Eszhanov, 2004) to 50 kilograms in capybaras (Barbella, 1987). Moreover, they are found on all continents and all major land-masses, except for Antarctica and New Zealand (Fabre et al., 2012), and they inhabit all terrestrial ecosystems (Kay and Hoekstra, 2008). Rodents also have very diverse ecologies, ranging from arboreal to subterranean, the latter defined as those that spend the majority of their lifetimes in burrows that they construct themselves (Nowak, 1999; Begall et al., 2007).

Our primary goal is to test the overall association between body size and climate in rodents at the ordinal level (species within the order). We test the association between body mass and temperature (Bergmann's original formulation) as well as the association between body mass and various climatic variables that incorporate

information on both temperature and precipitation. We test both these associations with, and without phylogenetic correction, in order to determine whether the potential significance might be an artifact of phylogenetic relatedness.

A secondary goal is to test the hypothesis that Bergmann's rule, or other associations between body size and climate, are more evident in: (1) small species when compared with large species and (2) surface-dwelling species when compared with subterranean species. Compliance to both these predictions would be expected if heat conservation is the principal mechanism responsible for the body size trend. However, our extensive climatic dataset would also enable us to explore other potential mechanisms that may be responsible for the predicted trend in body size, by isolating the climatic variables that covary most strongly with it. For example, if primary production (and by extension food availability) is more important in determining body size than temperature, then a positive relationship between precipitation and body mass is expected.

Material and methods

Data collection

Body mass data was obtained for all the available rodent species in the PanTHERIA database (Jones et al., 2009). For each species, 19 bioclimatic variables (BIO1–19; see below) were extracted from the WorldClim database (www.worldclim.org; Hijmans et al., 2005) at a spatial resolution of 2.5 min, using DIVA-GIS 7.5 (Hijmans et al., 2012). Averages for each variable were calculated across the range of each species, as designated in the International Union for Conservation of Nature Red List (IUCN, 2015), following Alhajeri et al. (2015). In order to meet the assumptions of normality of subsequent statistical analyses, body mass, BIO4, BIO7, and BIO12–19 were log-transformed; the remaining bioclimatic variables were not transformed. A few species had a value of zero for BIO14, BIO17, and BIO18—zeros were replaced by a small value (0.000001) prior to log transformation.

The final dataset includes all rodent species with body mass data available in PanTHERIA except: (1) species with no range data in IUCN; (2) species with extremely wide distribution (resulting in high variance within species); and (3) species absent from the most comprehensive available phylogeny of rodents (Fabre et al., 2012). The resulting dataset includes 58% of rodent species (1315 out of 2261), 78% of genera (371 out of 474), and 91% of families (30 out of 33) recognized in Wilson and Reeder (2005). All three unsampled families (Platacanthomyidae, Heptaxodontidae, and Myocastoridae) consist of a few species belonging to few genera, and failed one or more criteria listed above. The final data matrix appears in Table S1.

Comparative analyses

Because of the large taxonomic scale examined in this study, correlations among variables due to phylogenetic relatedness may override any other patterns in the data. Therefore, we apply phylogenetic correction in all our comparative analyses using PGLS (Harvey and Pagel, 1991). Phylogenetically-corrected analyses were conducted using the chronogram estimated by Fabre et al. (2012) from a compartmentalized supermatrix analysis (Fig. S1). A visual inspection suggests that the sampled species are not clustered on a particular region on their phylogeny. Species with no body mass data were pruned from the tree prior to subsequent comparative analyses. In this resulting tree, 75.7% of the nodes were resolved. Since PGLS requires a fully bifurcating tree, the remaining 24.3% of the nodes (polytomies) were randomly resolved (with internal branches of length zero) prior to subsequent analyses. The

Table 1

Summary of linear regressions between body mass and mean annual temperature (BIO1) in the five datasets described in the Methods. TIPs analyses do not correct for phylogenetic relationship. b = coefficient estimate; R^2_{adj} = adjusted R -squared value. Significant P -values are in bold.

Dataset	Conventional (TIPs) analysis				Phylogenetic (PGLS) analysis			
	b	F -stat	R^2_{adj}	P -value	b	F -stat	R^2_{adj}	P -value
All species	0.0205	14.9308	0.0105	0.0001	0.0046	2.4519	0.0011	0.1176
Large species	−0.0036	0.2915	−0.0015	0.5895	0.0049	0.9522	−0.0001	0.3297
Small species	0.0079	5.6363	0.0054	0.0178	0.0024	0.7620	−0.0003	0.3829
Subterranean species	0.0360	9.7039	0.0452	0.0021	0.0134	3.7318	0.0146	0.0549
Aboveground species	0.0193	10.2771	0.0082	0.0014	0.0034	1.0947	0.0001	0.2957

comparative analyses were repeated on 10 trees, having different topologies yielded from the random resolution of the polytomies, which resulted in identical results, indicating that the results were insensitive to the topological uncertainty resulting from the random resolution method. PGLS was conducted in the Caper library (Orme et al., 2013), and random resolution in the Ape library (Paradis et al., 2004); both in R (R Development Core Team, 2015). We also conduct standard (non-phylogenetic, or “TIPs”) analyses to compare the results with the phylogenetic analyses, and in order to make our results more comparable to the majority of studies in the literature, that do not apply phylogenetic correction.

Supplementary Fig. S1 related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2015.12.001>.

We tested Bergmann's rule by determining whether there was a significant negative relationship between body mass and mean annual temperature (BIO1). We also tested for a relationship between body mass and overall climate (based on BIO1–19) using multiple PGLS analysis (and non-phylogenetic multiple regression); this test was used to determine if body mass is correlated with overall climate.

Because many environmental variables are correlated, we also tested the relationship between body mass and overall climate (BIO1–19) by conducting a PGLS on individual principal components (PCs) of BIO1–19 (see below). The Principal Component Analyses (PCA) was conducted to extract independent factors and reduce the dimensionality of the climate data, and thus describe major trends in climate variation. Only the first two PCs had eigenvalues greater than values generated by the broken stick model (Legendre and Legendre, 1998) as implemented in the Vegan library (Oksanen et al., 2015) in R. Therefore, only the first two PCs were retained for subsequent analyses. In order to improve the interpretation of these components, they were rotated using the VARIMAX criterion (Kaiser, 1958) as implemented in the Psych library (Revelle, 2015) in R. For the purpose of interpretation, we designated a conservative, but arbitrary, cut-off loading value of 0.8, to indicate which variables were most associated with each PC axis. Thus, PGLS was conducted on individual PCs to determine the correlation between body mass and the major trends in climate.

In addition to analyses on the full data set of 1315 species, we also ran analyses on several partitions (see Introduction): (1) species belonging to the ‘large’ size class (463 species); (2) species belonging to the ‘small’ size class (852 species); (3) subterranean species (185 species); and (4) ‘aboveground’ species (1130 species), as indicated in Table S1.

Supplementary Table S1 related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2015.12.001>.

The literature does not provide a biological basis for splitting species into size classes. Thus, size classes were determined objectively using Jenks natural breaks optimization, as implemented in the Classint library (Bivand et al., 2015) in R. Jenk's method is the one-dimensional equivalent of the widely used K-means clustering method, that groups values into a preselected number of classes by minimizing the variance within classes and maximizing variance between classes (Jenks, 1967). The natural breakpoint detected in the log body mass data occurred between 4.91 and 4.92 (=136 g and 138 g respectively). Therefore, species with a log body mass ≤ 4.91 were designated as ‘small’ and those with log body mass ≥ 4.92 were designated as ‘large.’

Species belonging to subterranean genera were determined following the list compiled by Begall et al. (2007). All others were designated as ‘aboveground’ (or surface-dwelling).

Results

Body mass vs. mean annual temperature

We found no support for an interspecific Bergmann's rule pattern in rodents. In the TIPs analysis, there was a weak, but significant, positive relationship between body mass and mean annual temperature ($b=0.0205$, $R^2_{adj}=0.0105$, $P=0.0001$)—after correcting for phylogeny (using PGLS), this relationship disappears ($P=0.1176$; Table 1, Fig. 1a).

When the data were partitioned into large, small, subterranean, and aboveground species, similar patterns were observed. A weak, but significant, positive relationship was observed between body mass and mean annual temperature in small, subterranean, and

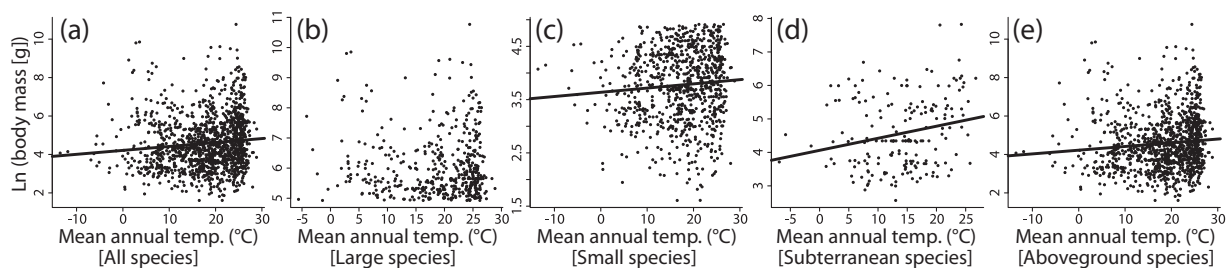


Fig. 1. Linear regressions between the log body mass and mean annual temperature (BIO1): (a) all species, (b) ‘large’ species, (c) ‘small’ species, (d) subterranean species, and (e) ‘aboveground’ species. A best-fit line is shown only for significant regressions based on the TIPs analysis. Full output of statistical analyses is in Table 1.

Table 2
Summary of multiple linear regressions between body mass and overall climate (BIO1–19) in the five datasets described in the Methods. TIPs analyses do not correct for phylogenetic relationship. R^2_{adj} = adjusted R -squared value. All P -values are significant.

Dataset	Conventional (TIPs) analysis			Phylogenetic (PGLS) analysis		
	F -stat	R^2_{adj}	P -value	F -stat	R^2_{adj}	P -value
All species	4.3440	0.0461	<0.0001	4.4040	0.0469	<0.0001
Large species	2.5970	0.0616	0.0003	1.7440	0.0297	0.0270
Small species	3.2140	0.0471	<0.0001	4.8840	0.0798	<0.0001
Subterranean species	1.8660	0.0821	0.0198	2.2660	0.1156	0.0031
Aboveground species	4.5560	0.0565	<0.0001	4.5190	0.0559	<0.0001

Table 3
PCA of the bioclimatic variables. High loadings (≥ 0.8) are indicated in bold. Although the ≥ 0.8 cut-off is arbitrary, it is more conservative than the more commonly used ≥ 0.5 cut-off, which would include many more variables than could be intelligibly discussed. All temperature variables are in $^{\circ}\text{C}$ and all precipitation variables are in millimeters.

	PC1	PC2
BIO1 (Average annual temperature)	0.19	0.98
BIO2 (Average diurnal range in temperature)	−0.71	−0.12
BIO3 (Isothermality)	0.60	0.55
BIO4 (Temperature seasonality)	−0.71	−0.50
BIO5 (Maximum temperature of the warmest month)	−0.38	0.76
BIO6 (Minimum temperature of coldest month)	0.44	0.88
BIO7 (Annual range in temperature)	−0.75	−0.53
BIO8 (Average temperature of the wettest quarter)	0.12	0.83
BIO9 (Average temperature of the driest quarter)	0.17	0.88
BIO10 (Average temperature of the warmest quarter)	−0.16	0.86
BIO11 (Average temperature of the coldest quarter)	0.35	0.91
BIO12 (Annual precipitation)	0.92	0.26
BIO13 (Precipitation of the wettest month)	0.80	0.38
BIO14 (Precipitation of the driest month)	0.79	−0.14
BIO15 (Seasonality of precipitation)	−0.60	0.28
BIO16 (Precipitation of wettest quarter)	0.82	0.35
BIO17 (Precipitation of driest quarter)	0.91	−0.08
BIO18 (Precipitation of warmest quarter)	0.75	0.13
BIO19 (Precipitation of coldest quarter)	0.79	0.06
Exp. variance	40.1%	34.8%

aboveground species in the TIPs analysis ($b = 0.008$ – 0.036 , $R^2_{adj} = 0.005$ – 0.045 , all $P < 0.018$) but that was not sustained after correcting for phylogeny using PGLS (all $P > 0.05$; Table 1, Fig. 1c–e). In large species, there was no significant relationship between body mass and mean annual temperature, in either the TIPs or PGLS analysis (both $P > 0.3$; Table 1, Fig. 1b).

Body mass vs. overall climate

There was a significant relationship between body mass and overall climate based on the multiple linear regression analysis, in both the TIPs and the PGLS analysis, in both the full dataset (all rodents), and in all four data partitions (large, small,

Table 4
Summary of linear regressions between body mass and the first two PCs of climate (BIO1–19) in the five datasets described in the Methods. Units and descriptions of BIO1–19 appear in Table 3. Loadings and explained variance for the PCs appear in Table 3. TIPs analyses do not correct for phylogenetic relationship. b = coefficient estimate; R^2_{adj} = adjusted R -squared value. Significant P -values are in bold.

Dataset		Conventional (TIPs) analysis				Phylogenetic (PGLS) analysis			
		b	F -stat	R^2_{adj}	P -value	b	F -stat	R^2_{adj}	P -value
PC1	All species	0.2259	36.9941	0.0267	< 0.0001	0.0456	4.5924	0.0027	0.0323
PC1	Large species	0.1570	9.5312	0.0181	0.0021	0.0985	7.0111	0.0128	0.0084
PC1	Small species	0.0998	20.0107	0.0219	< 0.0001	0.0338	3.1848	0.0026	0.0747
PC1	Subterranean species	−0.1834	3.0103	0.0108	0.0844	0.1171	4.1899	0.0170	0.0421
PC1	Aboveground species	0.2588	42.4965	0.0355	< 0.0001	0.0349	2.3288	0.0012	0.1273
PC2	All species	0.1030	7.5240	0.0049	0.0062	0.0165	0.7365	−0.0002	0.3909
PC2	Large species	−0.0567	1.3444	0.0007	0.2469	0.0043	0.0149	−0.0021	0.9029
PC2	Small species	0.0409	3.1499	0.0025	0.0763	0.0088	0.2619	−0.0009	0.6090
PC2	Subterranean species	0.2673	11.2133	0.0526	0.0010	0.0697	1.9593	0.0052	0.1633
PC2	Aboveground species	0.0835	3.7962	0.0025	0.0516	0.0110	0.2795	−0.0006	0.5971

subterranean, and aboveground species) ($R^2_{adj} = 0.012$ – 0.03 , all $P < 0.027$; Table 2).

The first two VARIMAX rotated PCs of overall climate (BIO1–19) explained 74.9% of the variation (40.1% and 34.8% for PC1 and PC2 respectively; Table 3). Precipitation variables (annual precipitation, precipitation of the wettest month, precipitation of wettest quarter, and precipitation of driest quarter) loaded most strongly (all in the positive direction) on PC1 (all loadings ≥ 0.8 ; Table 3). Temperature variables (average annual temperature, minimum temperature of coldest month, average temperature of the wettest quarter, average temperature of the driest quarter, average temperature of the warmest quarter, and average temperature of the coldest quarter) loaded most strongly (all in the positive direction) on PC2 (all loadings ≥ 0.8 ; Table 3).

A weak, but significant, positive relationship was observed between body mass and PC1 of climate (associated with increased precipitation), in the full rodent dataset, in the PGLS analysis ($b = 0.0456$, $R^2_{adj} = 0.0027$, $P = 0.0323$) as well as the TIPs analysis ($b = 0.2259$, $R^2_{adj} = 0.0267$, $P < 0.0001$; Table 4, Fig. 2a). Similarly, in the partitioned dataset that includes only large species, there was a weak, but significant, positive relationship between body mass and PC1 of climate, in both the PGLS analysis ($b = 0.0985$, $R^2_{adj} = 0.0128$, $P = 0.0084$) and the TIPs analysis ($b = 0.1570$, $R^2_{adj} = 0.0181$, $P = 0.0021$; Table 4, Fig. 2b). There was no significant relationship between body mass and PC1 of climate in either the small size or aboveground partitions in the PGLS analysis (both $P > 0.074$; Table 4, Fig. 2c, e). There was a weak significant positive relationship between them in the TIPs analyses ($b = 0.0998$, $R^2_{adj} = 0.0219$, $P < 0.0001$ and $b = 0.2588$, $R^2_{adj} = 0.0355$, $P < 0.0001$, respectively). In contrast, there was a weak significant positive relationship between body mass and PC1 of climate in the PGLS analysis for subterranean species ($b = 0.1171$, $R^2_{adj} = 0.0170$, $P = 0.0421$; Table 4, Fig. 2d) whereas there was none in the TIPs analysis ($P = 0.0844$). Out of all five datasets, only the full and the subterranean rodent datasets exhibited a significant relationship between body mass and PC2 of climate (associated with increased temperature; both weak and in the positive, not the predicted negative, direction)

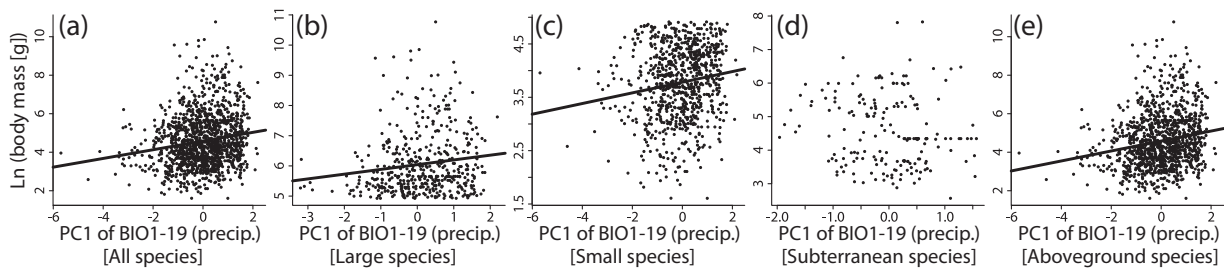


Fig. 2. Regressions between log body mass and the PC1 of climate variables: (a) all species, (b) 'large' species, (c) 'small' species, (d) subterranean species, and (e) 'aboveground' species. Bioclimatic variables associated with precipitation load strongly on PC1. A best-fit line is shown only for significant regressions based on the TIPs analysis. Full output of statistical analyses is in Table 4. Units and descriptions of BIO1-19 appear in Table 3. Loadings and explained variance for the PCs also appear in Table 3.

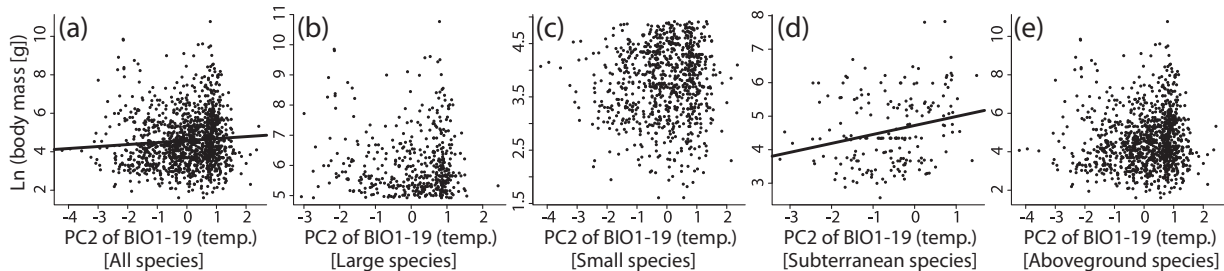


Fig. 3. Regressions between log body mass and the PC2 of climate: (a) all species, (b) 'large' species, (c) 'small' species, (d) subterranean species, and (e) 'aboveground' species. Bioclimatic variables associated with temperature load strongly on PC2. A best-fit line is shown only for significant regressions based on the TIPs analysis. Full output of statistical analyses is in Table 4. Loadings and explained variance for the PCs appear in Table 3.

in the TIPs analysis (full: $b = 0.1030$, $R^2_{adj} = 0.0049$, $P = 0.0062$; subterranean: $b = 0.2673$, $R^2_{adj} = 0.0526$, $P = 0.0010$; Table 4, Fig. 3a, d). After phylogenetic correction using PGLS, body mass and PC2 of climate are no longer correlated in any of the five datasets ($P > 0.1633$; Table 4, Fig. 3).

Discussion

A trend of increased body size in colder climates, or Bergmann's rule, is very common in mammal and bird clades (Blackburn et al., 1999; Ashton et al., 2000; Ashton, 2002a,b; Meiri and Dayan, 2003). However, empirical support is not universal, and the cline is absent in some examined taxa, such as Australian snakes (Feldman and Meiri, 2014) and amphibians in general (Adams et al., 2008), and other clades even exhibit a reverse trend (increased body mass in warmer regions) as occurs in *Ctenomys* (Medina et al., 2007).

This trend has been examined at various taxonomic scales, including within species, as well as between species, at the genus, order, and class levels (Blackburn et al., 1999; Millien et al., 2006; Adams et al., 2008). The applicability of Bergmann's rule at different taxonomic scales is still debated, along with whether mechanisms that operate at one taxonomic scale are the same as those that operate at others; particularly, whether there is a qualitative difference between intra- and interspecific trends (Blackburn et al., 1999; Ashton et al., 2000; Bidau et al., 2011). While Bergman originally formulated an interspecific pattern within genera, by far, most studies, including meta-analyses, test Bergmann's rule at the intraspecific level; relatively few studies conduct comparative analyses across species. Because many adaptive hypotheses have been proposed to explain geographic variation in body size, and because many mechanisms have been proposed to explain it at different taxonomic levels, Bergmann's rule has been described as a "concept cluster" (Peet, 1974; Lawton, 1999; Watt et al., 2010; Bidau et al., 2011).

Other mechanisms potentially influencing geographic body size variation, that may operate either independently or in synchrony,

include adaptation to environmental seasonality in food availability, competition, prey size and frequency, predation risk, and selection on life-history traits correlated with body size (Millar and Hickling, 1990; Ashton et al., 2000; Medina et al., 2007).

In most studies that use both TIPs and PGLS (or phylogenetic independent contrasts) analyses, correlations go from being significant in the TIPs analysis to insignificant with phylogenetic methods (Garland et al., 1999; Ashton et al., 2000), indicating that some reported support for Bergman's rule is an artifact arising from the correlations of both temperature and size with phylogenetic distance. We observe a similar pattern among rodents. Because phylogenetic analyses are preferred statistically, we focus on them below.

We found no support for Bergmann's rule in rodents. In contrast, we did find a weak but significant positive relationship between body size and precipitation variables. We therefore conclude that Bergmann's rule does not apply broadly to rodents at the order level. This result runs counter to most recent studies that find Bergmann's rule to be a valid generalization for mammals; however, these studies tend to examine intraspecific variation (Ashton et al., 2000; Meiri and Dayan, 2003; Blackburn and Hawkins, 2004; but see McNab, 1971). Our results are in agreement with a recent meta-analysis by Meiri and Dayan (2003) of intraspecific studies; they found that out of all the mammalian orders examined, only Rodentia and the monotypic Peramelemorphia (bandicoots) did not conform to Bergmann's rule.

Our results indicate that, at the order level, decreased environmental temperature does not explain increased body size in rodent species. The PCA analyses on the full bioclimatic dataset further corroborated this conclusion, because PC2, which was exclusively associated with temperature variables, was not correlated with body mass in the PGLS analysis. Support for Bergmann's rule is expected to decrease with increased taxonomic scale. At the order level, increased body size may be explained by various unexamined climatic and non-climatic factors, such as adaptation for food acquisition, as species tend to be widely differentiated in their niches, leading among-clade differences to greatly overwhelm

within-species variation. Thus, unlike populations of a single species, which tend to exploit similar resources across their geographic range, species within an order can exploit very different resources, which are consequently associated with different body sizes. A Bergmannian trend in body size should be more strongly observed at the intraspecific level because it is one of few modifications available to respond to the stress imposed by decreased temperature, whereas more elaborate changes, when they occur in geographically isolated populations, may lead to speciation.

Thus, our results do not rule out the possibility that Bergmann's rule may operate at individual rodent genera or species, as various other studies demonstrate (Ashton et al., 2000; Meiri and Dayan, 2003). Moreover, unique life histories of individual clades may determine whether Bergmann's rule is followed. While increased body size may be an adaptive response for heat conservation in some rodent clades, others may have alternative mechanisms to conserve heat, such as improved insulation, via pelage modification, as suggested for larger mammals (Scholander, 1955, 1956; Irving, 1957; McNab, 1971; Searcy, 1980; Geist, 1987; Porter et al., 1994; Steudel et al., 1994). Increased pelage length conserves heat in cold environments, and some rodent species show a pattern of increased hair density at higher elevations, while maintaining a similar body mass (Wasserman and Nash, 1979). However, some have argued that this strategy is less effective, and even maladaptive, in small animals, because it would inhibit their locomotion (Porter et al., 1994; Steudel et al., 1994).

We found a significant relationship between body mass and overall climate, consistent with James' (1970) claim that body size variation is better explained by a combination of climatic factors, that include temperature and humidity. However, after phylogenetic correction, climate only explains ~5% of the interspecific body size variation in rodents, which indicates that the other ~95% of the variation may be explained by other species-specific niche parameters.

Furthermore, increased body mass was significantly correlated with increased precipitation variables (as indexed by PC1), even after correcting for phylogeny. PC1 is directly associated with primary productivity and food availability, because it represents both the annual trend in precipitation (annual precipitation), as well as limiting environmental factors (precipitation of the wettest month, wettest quarter, and driest quarter) but not seasonality (e.g. annual range in precipitation). The relationship between increased body mass and increased precipitation (and increased primary productivity) have been observed in various mammals (Rosenzweig, 1968; Kolb, 1978; Burnett, 1983; Yom-Tov and Nix, 1986; Geist, 1987). Assuming that precipitation is correlated with primary productivity, our result may point to the importance of food availability in determining the body size of rodents. This result is consistent with Medina et al. (2007), where they hypothesized that body size variation may be a response to differential food availability in *Ctenomys*. However, the association between precipitation and primary productivity is not clear cut—rainfall tends to be more limiting to the primary productivity of arid, but not mesic, regions (Yom-Tov and Geffen, 2006).

Partitioning the dataset into large vs. small species, and subterranean vs. surface-dwelling species, did not change the direction of the significant results. However, in the PGLS regressions between body mass and PC1 of climate (habitat productivity), the relationships (based on the R^2 values) were stronger in the large and subterranean data partitions, than in the unpartitioned dataset (and absent in the small and aboveground data partitions). This result is unexpected, and contra our prediction that climate more strongly impacts small and aboveground species than large and subterranean species, because these two species categories have different exposures to external environmental temperature and overall climate (Feldman and Meiri, 2014).

A possible explanation for why the aforementioned relationship might be present in large species (and absent in small species) is that relatively small species may more easily find microhabitats with sufficient food resources in various regions; whereas relatively large species are more dependent on regional productivity. Similarly, the reason why subterranean (but not aboveground) species show the pattern of increased body size in more productive regions is that aboveground species (due to their relatively increased freedom of movement) may more easily find sufficient food resources within their range; whereas subterranean species are more limited by the regional productivity. This result is consistent with Medina et al. (2007), that similarly showed that the body size of *Ctenomys* species increases in more productive regions. However, both these explanations need to be verified by testing the association between body size and more direct indices of overall habitat productivity (e.g. a vegetation index).

In conclusion, our results indicate that Bergmann's rule does not operate in the broad taxonomic scale of the order Rodentia, and thus temperature does not seem to influence body size in rodents at this level, in contrast to many studies in other mammals, conducted at scales that are more limited. Instead, we do find a significant relationship between increased size and climatic variables associated with increased primary productivity. This result does lend some support to James's (1970) modification of Bergmann's rule to include precipitation. The primary productivity hypothesis appears to be a better predictor of body size variation in rodents than temperature. For this hypothesis to be confirmed, the relationship between body size and a more direct index of primary productivity (such as a vegetation index) need to be tested—this association will be explored in a subsequent study. It also seems that specific life-history attributes may be more important in heat conservation than increased body size among species of rodents. However, our results do not rule out the potential applicability of this rule to narrower taxonomic scales (e.g. within species).

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