Mammalian Biology 81 (2016) 219–225

Contents lists available at ScienceDirect

Mammalian Biology

journal homepage: www.elsevier.com/locate/mambio

Original Investigation

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

Bader H. Alhajeri[a,*], Scott J. Steppan[b]

[a] *Department of Biological Sciences, Kuwait University, Safat 13060, Kuwait*
[b] *Department of Biological Science, Florida State University, Tallahassee, FL 32306, USA*

ARTICLE INFO

Article history:
Received 15 October 2015
Accepted 8 December 2015
Handled by Vera Weisbecker
Available online 15 December 2015

Keywords:
Adaptation
Body mass
Primary productivity
Rodentia
Temperature

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.

Introduction

Bergmann's rule (1847) is a widely studied zoogeographic, ecogeographic 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 for 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

---

* Corresponding author.
E-mail address: bader.alhajeri@ku.edu.kw (B.H. Alhajeri).

http://dx.doi.org/10.1016/j.mambio.2015.12.001
1616-5047/

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 landmasses, 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