

The balance between predictions and evidence and the search for universal macroecological patterns: taking Bergmann's rule back to its endothermic origin

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Abstract Geographical variation in environmental temperatures is expected to impose clinal phenotypic selection that results in the expression of large-scale gradients of body mass variation within animal clades. Body size is predicted to increase with increasing latitude and elevation, and hence, with decreasing temperature, a pattern broadly known as Bergmann's rule. However, empirical observations are highly conflicting. Whilst most studies support this prediction in endotherms (birds and mammals), analyses conducted on ectotherms often fail to report this pattern. Does it reduce the validity of this macroecological rule? Since the original formulation of Bergmann's rule only involved endothermic organisms, I argue that the controversy is not a consequence of its predictive power, but a result of the later inclusion of ectotherms as part of the prediction. Here, I propose that the common conception of Bergmann's rule maintained for half a century is changed back to its original definition restricted to endotherms. This temperature–size relationship might therefore consolidate as a well-established macroecological rule if its original formulation is respected. Finally, I develop these claims on my initial suggestion that Bergmann's rule should be recognized as the evolutionary outcome of a general process with no phylogenetic scale distinction of species or populations, being equally applicable amongst and within species.

Keywords Bergmann's rule · James's rule · Temperature–size rule · Endotherms · Ectotherms · Body size

Introduction

Selection arising from environmental temperature has the potential to impose a major impact on several components of the phenotype, and is therefore regarded as a primary factor involved in the direction of adaptive evolution (Huey and Berrigan 2001; Angilletta 2009). At large spatial scales, this thermal selection is expected to result in the establishment of predictable patterns of phenotypic variation along environmental gradients, which has inspired the formulation of a number of macroecological hypotheses (Blackburn and Gaston 2003). One of the most emblematic such hypotheses suggests that patterns of variation in animal body size are influenced by variation in environmental temperatures. This hypothesis predicts that body size across phylogenetically related species increases in response to decreasing temperatures caused by higher latitudes and elevations (Blackburn et al. 1999; Blackburn and Ruggiero 2001; Cruz et al. 2005), a macroecological outcome broadly known as Bergmann's rule (Bergmann 1847; Mayr 1956; Blackburn et al. 1999; Meiri and Dayan 2003; Watt et al. 2010).

Bergmann's temperature–size prediction has persistently been investigated either amongst or within species for decades, which has resulted in a still unresolved debate. Although the original formulation of the rule focussed on interspecific body size gradients (Bergmann 1847; James 1970), Rensch (1938) and Mayr (1942) redefined the concept to refer to conspecific populations (see also Meiri and Thomas 2007; Watt et al. 2010, for additional detailed discussions). This distinction was taken into account by

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Blackburn et al. (1999), who suggested that the interspecific version should be recognized as the genuine Bergmann's rule, whilst the intraspecific version should be identified as a different process they termed James's rule. However, this separation has rarely been applied. One of the primary reasons might be that the distinction between these two versions is essentially a matter of phylogenetic (or taxonomic) scale at the lowest hierarchical levels of a phylogeny. Since species boundaries are often arbitrarily established (Coyne and Orr 2004), a series of phenotypically distinct populations distributed along a geographical gradient can be regarded as different species by some, or as a polymorphic group of conspecific populations by others (e.g. Meiri and Mace 2007). The asymmetrical criteria employed to taxonomically designate species and its potentially negative consequences for macroecological research have recently been illustrated by Isaac et al. (2004). These authors showed that even under the same species concept, different taxonomic criteria (the splitter–lumper balance) can be used to define species or infraspecies boundaries. For example, ant taxonomists tend to give full-species status to different morphological populations with restricted distributions (Wilson and Brown 1953), whilst butterfly specialists tend to place under a single specific name multiple polymorphic populations (Rothschild and Jordan 1906). Thus, whether the temperature–size rule involves variation between species or populations may heavily depend on a historical series of arbitrary taxonomic decisions. In addition, conspecific populations often experience adaptations to local selective conditions even in presence of gene exchange (i.e. Wright's multiple high-fitness combinations of genes), which indicates that fitness-related phenotypic traits differ not only between species, but also between conspecific populations subjected to different selective challenges (Smith et al. 1997; Gavrillets 2004). Therefore, it is difficult to perceive a strong theoretical reason to distinguish the evolutionary impact of thermal selection on body size variation when empirically comparing between phylogenetically related species or between conspecific populations. Indeed, results from interspecific and interpopulation tests of this prediction tend to show similar tendencies (Table 1). For these reasons, I suggest recognizing Bergmann's rule as a general rule of temperature–size association with no phylogenetic scale restrictions at the lowest hierarchical levels (i.e. species and populations), and hence, equally applicable to both comparisons between phylogenetically related species and conspecific populations. This view then opposes the recognition of James's rule as a different process. It is, finally, worth mentioning that an alternative view suggests that most Bergmann's rule studies regarded as interspecific tests should be recognized as assemblage level tests, as they involve several non-

closely related species belonging to major clades (e.g. birds in general). Therefore, only those tests involving closely related species of specific lineages (e.g. *Liolaemus* lizards, Pincheira-Donoso et al. 2007, 2008) would be comparable to intraspecific studies (Meiri and Thomas 2007).

Here, I reevaluate Bergmann's rule. I argue that both empirical evidence as well as the critical impact of thermal selection on body size evolution suggest that the originally formulated version of this rule has the power to describe patterns of body size variation amongst endotherms, as predicted by Bergmann (1847), whilst the later inclusion of ectotherm organisms as part of the prediction is the responsible factor behind the observation of conflicting findings. Hence, I conclude that Bergmann's rule should be returned to its endothermic origin. Finally, although most of my arguments focus on pattern (i.e. increasing body size with increasing latitude and elevation), my view does not ignore the mechanistic component behind the rule, as this view implies that the evolutionary responses of endothermic and ectothermic metabolisms are likely to follow different directions under similar environmental demands involving thermal selection (Pincheira-Donoso et al. 2008). Therefore, although I regard spatial variation in thermal regimes as a crucial factor shaping the direction of body size evolution in organisms in general, I question the generalized view that both endotherms and ectotherms experience similar responses to thermal selection.

Balancing predictions and evidence

For over a 150 years, Bergmann's rule has attracted substantial interest on both theoretical and empirical grounds, which has resulted in the publication of a large volume of research devoted to explore it from different angles (e.g. within and amongst species) (Mayr 1963; Blackburn et al. 1999; Meiri and Thomas 2007). However, unlike other longstanding ideas in biology, the universality of this rule has increasingly been questioned (Pincheira-Donoso et al. 2008; Thomas 2009). From a theoretical perspective, it is still unclear what factors would be responsible for the predicted inverse temperature–size relationship. Heat conservation requirements, life history tradeoffs, phylogenetic constraints, resistance to starvation, food availability and fecundity selection have been, amongst others, proposed as potential drivers (Atkinson 1994; Blackburn et al. 1999; Gaston and Blackburn 2000; Ashton and Feldman 2003; Cruz et al. 2005; Meiri et al. 2007; Adams and Church 2008; Wilson 2009; Watt et al. 2010). These body size clines might result from direct adaptation or from phenotypic plasticity (Van Voorhies 1996; Partridge and Coyne 1997). Although there is considerable disagreement, the original cause proposed by Bergmann (1847), the heat conservation benefit,

Table 1 Summary of empirical analyses of Bergmann's rule, detailing evidence supporting and rejecting the predicted temperature–size covariation, separately for endotherms and ectotherms

Group	Bergmann's rule prediction	
	Support	Reject
I. Endotherms		
Birds	Rensch (1938) ^a , James (1970) ^a , Blackburn and Gaston (1996) ^b , Gaston and Blackburn (1996) ^b , Ashton (2002b) ^a , Meiri and Dayan (2003) ^a , de Queiroz and Ashton (2004) ^a , Olson et al. (2009)	Zink and Remsen (1986)
Mammals	Rensch (1938) ^a , Tomilin (1946), Zaveloff and Boyce (1988), Ashton et al. (2000) ^a , Freckleton et al. (2003) ^{a,b} , Meiri and Dayan (2003) ^a , Blackburn and Hawkins (2004), de Queiroz and Ashton (2004) ^a , Rodríguez et al. (2006 ^g , 2008 ^g)	McNab (1971), Dayan et al. (1991), Medina et al. (2007)
II. Ectotherms		
In General	Ray (1960) ^a	–
Arthropods	Miller (1991a) ^f , Cushman et al. (1993), Kaspari and Vargo (1995), Poulin (1995) ^b , Poulin and Hamilton (1995) ^b	Miller (1991a), Barlow (1994), Hawkins (1995), Diniz-Filho and Fowler (1998), Porter and Hawkins (2001) ^b
Fish		
Freshwater	Lindsey (1966)	Belk and Houston (2002) ^a
Marine	Lindsey (1966), Wilson (2009) ^{b,c}	Wilson (2009) ^{b,d}
Amphibians		
Salamanders	Lindsey (1966), Ashton (2002a) ^a , de Queiroz and Ashton (2004) ^{a,b}	Feder et al. (1982), Adams and Church (2008) ^{b,e}
Anurans	Lindsey (1966), Ashton (2002a) ^a , de Queiroz and Ashton (2004) ^{a,b}	–
Reptiles		
Turtles ^c	Ashton and Feldman (2003) ^{a,b} , de Queiroz and Ashton (2004) ^{a,b}	Lindsey (1966)
Lizards	Cruz et al. (2005) ^b	Lindsey (1966), Ashton and Feldman (2003) ^{a,b} , de Queiroz and Ashton (2004) ^{a,b} , Pincheira-Donoso et al. (2007 ^b , 2008 ^b)
Snakes	Lindsey (1966)	Ashton and Feldman (2003) ^{a,b} , de Queiroz and Ashton (2004) ^{a,b}

Birds, mammals and arthropods are generalized. Only studies involving twenty or more species have been included, except for James (1970), which although based on 12 species, was kept in the summary given its significance for the problem of Bergmann's rule. Additional summaries of the voluminous literature on endotherms can be found in Ashton et al. (2000), Meiri et al. (2004), and Millien et al. (2006). Studies involving entire communities (e.g. based on grid cells) as units of analysis (e.g. Olalla-Tarraga et al. 2006; Olalla-Tarraga and Rodríguez 2007) have been excluded

^a Analysis between populations

^b Phylogenetic analysis

^c Among species of the genus *Syngnathus*

^d Among species of the genus *Hippocampus*

^e Both among populations and species

^f Only along altitudinal gradients

^g Under a 10.0–12.6°C thermal threshold

remains one of the most broadly accepted explanations. Thus, the problem of the mechanism behind this cline is in itself a considerable challenge. Blackburn et al.'s (1999) claim that the inclusion of a mechanistic component in the definition of Bergmann's rule is potentially unhelpful and inappropriate, as it would result in the falsification of a

largely demonstrated macroecological pattern (particularly in endotherms), seems at this time a rational position to adhere to. The recent Watt et al.'s (2010) review provides a summary of the different definitions of Bergmann's rule presented in some of the main studies published since Bergmann's (1847) original formulation of the idea.

From an empirical perspective, the controversy continues to grow with the publication of contradictory findings across several different animal groups. In general, however, these findings can be separated into two groups, those for endotherms and those for ectotherms. For endotherms (birds and mammals), there is a sustained tendency to report evidence supporting the pattern predicted by Bergmann's rule. In these organisms, body size often increases with decreasing environmental temperatures, as shown by a large number of studies conducted between species and populations, either using or not using phylogenetic methods (e.g. Rensch 1938; James 1970; Zaveloff and Boyce 1988; Blackburn and Gaston 1996; Gaston and Blackburn 1996; Ashton et al. 2000; Ashton 2002b; Freckleton et al. 2003; Meiri and Dayan 2003; de Queiroz and Ashton 2004; Olson et al. 2009; see Blackburn and Ruggiero 2001; Medina et al. 2007, for conflicting results) (Table 1). This trend has even been observed in whales, a highly migratory group of marine mammals (Tomilin 1946). Moreover, two of the only studies involving large numbers of endotherm species where Bergmann's rule has failed to be broadly supported (McNab 1971; Dayan et al. 1991) have been criticized on the basis of the analytical approaches employed to establish size–latitude relationships (Ashton et al. 2000; see also Zink and Remsen 1986, for a study on numerous bird species where Bergmann's rule is not supported either).

In strong contrast, analyses conducted on ectotherms (including both invertebrates and vertebrates) have consistently shown controversial results, often failing to support the expected negative temperature–size association, with several cases even conforming the converse to the rule (see Table 1 for details). Nevertheless, this situation was not evident since the beginning. Ray (1960) and Lindsey (1966) reported two of the first explicit analyses of Bergmann's rule conducted on ectotherms. These studies involved a large diversity of lineages that supported in at least 75% of the cases the negative temperature–size relationship predicted by Bergmann (1847), and which substantially exceeded the modest 50% threshold suggested by Mayr (1963) to consider that a rule is empirically proven. Similar evidence continued to be revealed by several other studies investigating this prediction in different groups of ectotherms (e.g. Tinkle 1961; Miller 1991b; Cushman et al. 1993; Kaspari and Vargo 1995; Ashton 2002a; Ashton and Feldman 2003; Angilletta et al. 2004; Cruz et al. 2005; Wilson 2009) (Table 1). Collectively, these observations have often stimulated the idea that ectotherms tend to follow Bergmann's rule. However, as shown by several other studies, Bergmann clines are far from being a generally supported rule in ectotherms. Indeed, even before Ray's (1960) and Lindsey's (1966) works appeared, some studies had already reported that this

temperature–size relationship was weak (Schuster 1950) or entirely unsupported in these organisms (Park 1949; it is also worth noting that this is the first analysis of Bergmann's rule in an ectotherm organism). After that, a great deal of research conducted both between populations (e.g. Hovanitz 1942; Masaki 1967; Guppy 1986; Brennan and Fairbairn 1995; Belk and Houston 2002; Ashton and Feldman 2003; Cvetkovic et al. 2009) and between species (e.g. Barlow 1994; Hawkins 1995; Porter and Hawkins 2001; Adams and Church 2008; Pincheira-Donoso et al. 2007, 2008; Wilson 2009) of several lineages has confirmed that this rule does not universally hold for ectotherms (see Blackburn et al. 1999; Watt et al. 2010, for reviews) (Table 1). Furthermore, conflicting findings have been revealed in several other studies where, within the same lineage, some ectotherm groups support this rule, whilst others do not (e.g. Hawkins and Lawton 1995; Blanckenhorn and Demont 2004; Sears and Angilletta 2004). As argued in previous studies (Ashton and Feldman 2003; Pincheira-Donoso et al. 2008), the inverse heating rate–body mass relationship of ectotherms would make larger body size physiologically (and hence ecologically) disadvantageous in colder environments for these organisms, causing the observed conflicting empirical scenario.

Do these conflicting results invalidate Bergmann's rule?

The universality of a rule relies on its power to predict the expression of a phenomenon within the frame of certain parameters. When empirical observations consistently match predictions under those parameters, the rule can be regarded as universal. In the case of Bergmann's rule, Bergmann (1847) established as two primary parameters to anticipate the negative temperature–size relationship (i) the decreasing environmental temperatures resulting from geographical gradients, and (ii) its impact on body size variation in endothermic thermoregulators. As stated above, a substantial stream of research at both the intraspecific and the interspecific levels has consistently demonstrated that the predicted inverse temperature–size pattern in general holds for endotherms (Table 1). The strong impact of thermal selection on body mass is even evident in cases where environmental factors other than temperature (e.g. topography, seasonality) significantly predict the direction of variation in body size (Rodríguez et al. 2006, 2008). For example, Rodríguez et al. (2008) observed that body size in Nearctic and Neotropical mammals follows the thermal-phenotypic relationship predicted by Bergmann's rule in areas where temperatures are lower than 10.9 and 12.6°C, respectively. Over these similar thresholds, body size is better predicted by topography. Remarkably, a very similar

situation had previously been observed for Palearctic mammals as well, on a 10.0°C threshold (Rodríguez et al. 2006). Collectively, these findings suggest that strong thermal selection arising from low environmental temperatures force mammals to optimize thermoregulatory adaptations. These optimizations are likely to be achieved through increasing body size with decreasing temperatures given their endothermic physiology, hence resulting in Bergmann's body mass clines (which are also expected to apply to birds, see Olson et al. 2009). This idea is consistent with Rodríguez et al.'s (2006, 2008) empirical observations and conclusions. In warmer environments (over the mentioned thresholds), in contrast, where the thermoregulatory phenotype is released from strong thermal selection (i.e. fitness is not heavily temperature-dependent), other selective pressures might exert a stronger impact on fitness. Therefore, the extent of temperature-based predictability on body size variation is reduced as a result of the higher predictability exerted by those other factors, which might be multiple (e.g. Brown and Sibly 2006). Consequently, if Bergmann's rule is regarded as the macroecological pattern resulting from thermal selection on body size, Rodríguez et al.'s studies provide support to this rule.

Nevertheless, when Ray (1960) suggested the formal inclusion of ectotherms into the original framework, one of these fundamental parameters (i.e. thermoregulatory physiology) was substantially altered, resulting in the formulation of a counterintuitive prediction. Therefore, whilst the rule as *originally formulated* has the empirical support to be recognized as a general macroecological rule for endotherms, the version extended to ectotherms is far from being universal.

The detrimental effects that the inclusion of ectotherms has had for the universality of Bergmann's rule suggests that Ray (1960) may have combined two different and largely incompatible phenomena (the adaptive response of body size to thermal selection in endotherms and in ectotherms) into a single prediction. Therefore, it seems reasonable to propose that the modern concept of this rule, maintained for half a century, is changed back to its original definition restricted to endotherms (Bergmann 1847). On the basis of these arguments and some previous discussions (e.g. Blackburn et al. 1999; Blackburn and Ruggiero 2001), I propose the following definition for this rule: '*Bergmann's rule is the tendency for interbreeding or reproductively isolated populations of endotherms within a monophyletic clade to evolve a negative covariation between body size and spatial (or temporal) gradients of environmental temperature*'. Populations are regarded in a broad-sense as either conspecific populations or species. Also, the above definition assumes that this body size gradient evolves adaptively in response to selection acting on body mass genes, or through the evolution of

phenotypic plasticity. Thus, although both evolutionary ways are clearly different, they converge into the adaptive origin of this cline (e.g. Partridge and Coyne 1997; Van Voorhies 1997; Pigliucci 2001). Given the same adaptive assumption, Bergmann clines should be expected to be detectable when the strength of this component of selection substantially varies along the distributional range of the populations under study. If the studied populations inhabit similar environments that only vary quantitatively in their thermal conditions, but not qualitatively (e.g. all restricted to a given tropical area), selection resulting from thermal variation might not impose a significant differential impact on fitness. Therefore, the impact of this specific selection component on body size might be eclipsed by other selective pressures with larger fitness effects (Pincheira-Donoso et al. 2008). Consequently, endotherm clades with larger geographical ranges might be more likely to exhibit Bergmann clines than geographically restricted clades (e.g. Blackburn and Ruggiero 2001; Meiri et al. 2007). In Conclusion, although body size and temperature are expected to negatively *covary*, temperature may not always directly influence adaptive change in body size.

Finally, it is worth noting that the main objective of this appeal is not exactly aimed to defend Bergmann's rule as an unbreakable law for endotherms, but rather, to suggest that comparative research on body size evolution in ectotherms should be conducted outside the context of this rule. This might contribute to stimulate ectotherm researchers to focus still more on the search for causes shaping the evolution of body size gradients in these organisms, rather than simply describing the observed patterns as an explicit test of Bergmann's rule. More information on the expression of patterns is, however, highly desired to evaluate how consistent (even in relation to the proportional availability of evidence for endotherms versus ectotherms) these tendencies are. As suggested by a number of authors (Blackburn et al. 1999; Angilletta and Dunham 2003; Walters and Hassall 2006; Meiri et al. 2007; Adams and Church 2008; Pincheira-Donoso et al. 2008; Thomas 2009), the establishment of such explanations is on its own a major challenge given the multiple factors that are potentially involved in the evolution of body size in organisms unable to thermoregulate through the metabolic generation of body heat. Determining and understanding those factors will need, however, a multidisciplinary perspective involving a combination of the principles of selection theory, evolutionary quantitative and population genetics, and macroecology. The use of model testing, with theory generating predictions followed by empirical data collected to test theory-driven predictions, appears as a promising way to proceed. This integrative framework would complement the increasing exploitation of statistical

instruments for phylogenetic analyses employed in macroecology, to potentially consolidate a formal research field of Evolutionary Macroecology.

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