

CORRESPONDENCE



**Bergmann's Rule – what's in a name?**

**ABSTRACT**

Despite the great interest it generates, the definition of Bergmann's Rule is vague and often contested. Debate focuses on whether the rule should be described in terms of pattern or process, what taxa it should apply to and what taxonomic level it should be associated with. Here I review the historical development of studies of Bergmann's Rule. I suggest that Bergmann thought that his rule should be strongest at the intra-specific level, rather than between closely related species as is usually thought. I argue that the rule is a pattern that can be studied regardless of mechanism in any taxon and at any taxonomic level.

**Keywords**

**Assemblage level, Bergmann's Rule, interspecific, intraspecific, latitude, pattern, process, temperature.**

One of the earliest and best known ecological generalizations is that large homeotherms are found at higher latitudes, or in colder climates than closely related smaller ones (Bergmann, 1847). Bergmann suggested this is the result of better heat retention in large animals because of their lower surface to volume ratio. This generalization, which I suggest is the one to which the name 'Bergmann's Rule' should apply, has enjoyed continued interest for many decades. Since the works of Rensch (e.g. Rensch, 1924, 1938) and Mayr (1942, 1956), the rule has mostly been studied at the intra-specific level, and correlates size variation to temperature, latitude or altitude. Rosenzweig (1968), James (1970) and Calder (1974; see also Lindsey, 1966) have suggested alternative mechanisms for latitudinal size clines, driven by primary productivity, heat load and environmental predictability, respectively.

Lindsey (1966) identified latitudinal size clines between assemblages (often, somewhat misleadingly, termed 'inter-specific level'). Lately this assemblage approach has gained much popularity, and has been used in the study of size clines of multiple groups of homeotherms, poikilotherm vertebrates and invertebrates (e.g. Olalla-Tárraga *et al.*, 2006; Diniz-Filho *et al.*, 2007; Entling *et al.*, 2010). In such studies, all species in a taxon are analysed regardless of phylogenetic affinities within it. Each species is either counted once, in the middle of its range and its size, or in all the grid cells or latitudinal bands in which it appears. In the first approach each datum represents one species and one climatic value. In the second approach some measure of central tendency of body size is calculated across all species within grid cells or across latitudinal bands (e.g. mean body size across all mammal species present in a 1° × 1° grid cell) and is regressed against the cell climate or latitude. Intra-specific size variation is ignored in both approaches.

Although Bergmann's thermoregulatory mechanism should theoretically apply to homeotherms only, size clines in poikilotherms have been routinely studied ever since Park (1949), Ray (1960) and Lindsey (1966). There is, however, much debate regarding whether one should expect to find similar patterns in poikilotherms and homeotherms, and whether the former should be expected to show any patterns at all (cf. Olalla-Tárraga *et al.*, 2006; Pincheira-Donoso *et al.*, 2008). There seems therefore to be much confusion and disagreement regarding the taxonomic levels, taxa and mechanisms relating to Bergmann's Rule.

Karl Georg Lucas Christian Bergmann formulated 'Bergmann's Rule' in 1847. Unfortunately, his work has three attributes that discourage modern scholars from reading it (I never have): (1) it is very difficult to obtain; (2) it is 114 pages long; (3) it is in German and has never been translated. James (1970) provided an English translation of about a page's worth of Bergmann's (1847) paper. Watt *et al.* (2010) criticized the scientific community for not reading the original, and criticized the translation in James (1970) for

lacking 'the full context of the paper'. Then, excitingly, they announced that they provide one, writing: 'a direct translation is provided': 'The goal is to improve clarity regarding Bergmann's Rule by providing direct translations from Bergmann's manuscript'; and 'we provide a translation of Bergmann's Rule'. Unfortunately, they translated fewer parts than James did and these mostly overlap James's translations. The only new insight one would gain into Bergmann's work by reading Watt *et al.* is that he 'tested the rule intraspecifically, among races of domestic animals'. That these failed to show the rule is already mentioned by James (1970). Watt *et al.* (2010) argue that 'some prevalent problems in ecology, and science as a whole . . . arise from misinterpretations and by not going back to the original source of information'. I disagree. I doubt many physicists read Einstein (1905, 1917; also in German), but would be surprised if this hampers their understanding of relativity. Many of us try hard to find reasons to quote Darwin (1859), but cannot claim that not reading 'the Origin' (or Darwin & Wallace, 1858) hinders a clear understanding of evolutionary theory. While I agree that we should strive to, and will often greatly benefit from, reading the original works on a certain topic, this is by no means a prerequisite for writing insightful works. It is possible to conduct brilliant evolutionary studies without even reading the works by the formulators of the modern synthesis in evolutionary biology: our science has advanced since the days of Darwin and Bergmann.

Because Bergmann's Rule has continued to generate much interest, research effort and debate for over 160 years, and because Bergmann's paper is seldom read, the meaning of the term is somewhat obscure, and hotly contested (Blackburn *et al.*, 1999; Watt *et al.*, 2010). The debate has mainly focused on three aspects: (1) Is Bergmann's Rule a pattern or a process? (2) Which taxa should it, or should it not, be applied to, and what is the correct taxonomic level in which it should apply? (3) Do we need different names for different mechanisms, patterns, taxa and taxonomic levels?

Here I first I argue that Bergmann's Rule is a pattern, and that while it probably applies most to homeotherms at the intra-specific level, studies of this pattern at the inter-specific and assemblage levels and in all taxa qualify as studies of the same rule.

### **ECOLOGICAL RULES ARE EMPIRICAL GENERALIZATIONS AND ARE INDEPENDENT OF MECHANISMS**

Many critiques of Bergmann's Rule, ever since Scholander (1955), doubted Bergmann's heat retention mechanism. While attempts to establish adaptive explanations for observed phenomena is at the heart of evolutionary science I argue, with Mayr (1956), that even if a suggested mechanistic hypothesis is wrong it is not an argument against an ecological rule.

Ecological and evolutionary 'rules' – Bergmann's, Cope's, Allen's, Gloger's, Rapoport's, the Island Rule, the latitudinal diversity gradient, the species–area relationship, etc. – are all descriptions of patterns (Mayr, 1956). The latitudinal diversity gradient for example has many proposed non-mutually exclusive explanations, yet this does not detract from its value as a pattern. Describing the Island Rule, Van Valen (1973) explicitly expressed ignorance regarding its causes. Later explanations always presented several mechanisms (Case, 1978; Heaney, 1978), some contradictory (Dayan & Simberloff, 1998). Whether this rule is valid or not (cf. Meiri, 2007; Meiri *et al.*, 2008; Lomolino, 2010) tells us little about the proposed mechanisms. In fact, some mechanisms may be operating and a rule may still be invalid (Raia & Meiri, 2006). Lamarck (1809) was right that species evolve, despite his explanation being wrong. Similarly an observation that a species is larger in colder environments than in warmer ones is consistent with Bergmann's Rule regardless of what brought this pattern about.

### **SHOULD THE STUDY OF BERGMANN'S RULE BE CONFINED TO HOMEOTHERMS? IS IT AN INTRA-SPECIFIC, INTER-SPECIFIC OR AN ASSEMBLAGE-LEVEL PHENOMENON?**

While Bergmann (1847) formulated his rule for homeotherms, finding similar latitudinal or temperature-related size clines in poikilotherms is consistent with the rule. If

Bergmann's Rule is a pattern, than the physiological attributes of the taxa showing this pattern are irrelevant for establishing support for it, even though they are of the utmost importance for deciphering the underlying processes.

Some of those now studying the rule at the assemblage level argue that Bergmann (1847) formulated the rule for species within genera, and that the shift to variation within species was influenced by Rensch (1938) and Mayr (1956). Thus some argue that the inter-specific level is the correct way to study Bergmann's Rule. Interestingly, James (1970) and Watt *et al.* (2010) hint that Bergmann thought his rule would work within species, writing that 'It seems paradoxical that the effects of the same rule in races of animals are not very apparent. Is it not to be expected that races which should be more similar to each other in their organization than the species of a genus, should be more dependent on their size ratios in their distribution than the latter? This sounds obvious.' (Bergmann, 1847, in James, 1970). Watt *et al.* (2010) write that 'Although Bergmann (1847, p.677) believed the rule would be more apparent within species he was surprised that the pattern was not found in domestic animals'. Thus it seems that Bergmann's own inferred focus on interspecific patterns was based not on mechanism, but on what he found empirical support for.

What most of the adherents of an inter-specific approach to Bergmann's Rule seem not to accord sufficient importance to, is that the shift towards intra-specific studies was advocated by Rensch and Mayr as a part of a new view on taxonomy. This 'new taxonomy' (Mayr, 1942) involved the lumping of many formerly named species into much fewer, polytypic species or Rassenkreise, reducing bird numbers, for example, from 19,000 species to 8500 despite describing 8000 additional forms (Mayr, 1942). This new taxonomy and the notion of the polytypic species were key to bringing systematics into the embrace of the modern synthesis in evolutionary biology. To Rensch (e.g. Rensch, 1924, 1938; the 1938 paper being the only one in a series of papers on Bergmann's Rule by Rensch written in English is the only one usually cited) and Mayr (1942), the fact that different populations show Bergmannian size clines was key in deciding that they belonged to the same species. Size clines were, to them, evidence that within these biological species, different populations are under different selection regimes promoting the evolution of differ-

ent sizes. This is because one would expect size differences to evolve in response to climate, everything else being equal, but between different species, size differences may evolve for unrelated reasons. Thus what were, in Bergmann's time, considered distinct species would later be considered populations within a species, and thus the shift in focus from inter- to intra-specific studies is more apparent than real (Mayr, 1956; Meiri & Thomas, 2007). Mayr (1942) recognized, however, that, 'What we consider as new systematics . . . may, indeed, be very old systematics fifty years hence'. The mode in taxonomic studies seems to shift back towards splitting rather than to lumping species (e.g. Agapow *et al.*, 2004; Chaitra *et al.*, 2004; Meiri & Mace, 2007; Sangster, 2009). Bergmann's Rule would be expected to manifest itself between 'species' that have been split, and between 'populations' within lumped species, if only because substantial climatic variation within a range is needed for size clines to evolve (Meiri *et al.*, 2004, 2007).

Be that as it may, Bergmann (1847, in James, 1970) seems to have thought his rule would apply to closely related taxa, writing 'If there are genera in which the species differ only in size, the smaller species would demand a warmer climate'. While he wrote 'Although it is not clear as we would like, it is obvious that on the whole the larger species live farther north and the smaller ones farther south', the context for this sentence is lacking in James (1970), and it is thus unclear whether Bergmann believed his rule should work for assemblages, e.g. when all mammals are viewed simultaneously. Interestingly, even though extending the well-supported patterns found within species to inter-specific studies of closely related species seems an obvious avenue for research (Meiri & Thomas, 2007), this approach is rarely taken (but see Diniz-Filho *et al.*, 2007, 2009; Pincheira-Donoso *et al.*, 2007, 2008). A far more common method is to examine patterns at the assemblage level within an inclusive taxon (e.g. Lindsey, 1966; Hawkins & Lawton, 1995; Olalla-Tárraga *et al.*, 2006; Entling *et al.*, 2010). Given that within inclusive assemblages size patterns may manifest taxon replacement rather than selection on size per se (Meiri & Thomas, 2007), I recommend that such studies be carried out in a phylogenetic framework. If a species-level phylogeny is lacking, then examining relationships between patterns shown at nested taxonomic levels within the assemblage may prove illuminating (Olson *et al.*, 2009).

## WHAT NAMES SHOULD WE USE?

If ecological 'rules' are patterns, one needs to define what pattern is related to a given rule. I suggest that the term 'Bergmann's Rule' be applied to studies of size variation with temperature or latitude in any taxon. Studies of size variation with productivity (Rosenzweig, 1968), precipitation (Dunbar, 1990) or seasonality (Calder, 1974) clearly examine distinct phenomena and should therefore not be classified as studies of Bergmann's Rule. Studies of heat load or wet-bulb temperatures (Hamilton, 1961; James, 1970) are clearly modifications of temperature studies; they probably should be seen as studies of Bergmann's Rule.

Associating size with temperature is apparently contradictory to the assertion that Bergmann's Rule is a pattern, because it seems to suggest that Bergmann's thermoregulatory mechanism, rather than, for example, Rosenzweig's productivity hypothesis, drives size evolution. Even if the rule is a pattern, however, it should be related to some aspect of the environment, but not to others: we would not, for example, call size increase with longitude, or with habitat heterogeneity, or with distance from the range centroid of a species 'Bergmann's Rule'. While a temperature–size relationship may conceivably arise because of a third factor that affects size, and happens to be correlated with temperature (e.g. productivity), this would simply mean we study the wrong variable.

A solution to this conundrum is that a temperature–size relationship is a pattern, not a mechanism. The mechanism may be heat retention, as suggested by Bergmann, or some other temperature-related mechanism. For example, it may be argued that because of the positive environmental temperature–metabolic rate relationship (e.g. Lovegrove, 2003; Clarke *et al.*, 2010), a Bergmannian cline is a manifestation of the lower activity levels of warm-climate animals that result in them obtaining less food. Such a pattern may also arise because lower temperatures are often associated with longer growth periods enabling animals to attain larger sizes. Thus a size–temperature correlation is a pattern that may be explained by any one of several potential mechanisms, Bergmann's thermoregulatory explanation being just one of them.

Blackburn *et al.* (1999) suggested that Bergmann's 'clear intention was that it should be interpreted interspecifically'. They rely on Rensch's (1938) assertion that the

shift from inter- to intra-specific studies was his own invention, and on James (1970) who used a definition of Bergmann's Rule by Mayr (1963). James suggested calling Mayr's (1963; although actually present at least as early as Mayr, 1942) formulation the 'neo-Bergmannian Rule'. Blackburn *et al.* (1999) thus suggested retaining the name 'Bergmann's Rule' to inter-specific (actually referring to assemblage level) studies such as those of Hawkins & Lawton (1995) and Blackburn & Gaston (1996). They suggested calling intra-specific patterns 'James's Rule'.

I am uncomfortable with James's and Blackburn *et al.*'s interpretation and terms. As evident both from James's (1970) translation and Watt *et al.*'s (2010) assertion, it seems that Bergmann thought his rule would apply at the intra-specific level, and was surprised that it did not. Rensch's assertion that he shifted the focus from inter- to intra-specific studies may thus be somewhat too strong. Mayr (1956) states that 'Bergmann and other authors applied these rules equally to species and races, but it must be admitted that most of their 'species' are considered races by modern authors'. That an analysis fails to support a rule is not reason enough to change its name. Furthermore it seems that Bergmann thought his rule would work for species contrasts (i.e. the smaller of two closely related species will occur in warmer areas), rather than for mean size within assemblages. That Bergmann's 'species' were Rensch and Mayr's 'races', as recognized by Blackburn *et al.* (1999), further makes the taxonomic distinction redundant. Naming intra-specific patterns 'James's Rule' does, I think, little justice to James, who forcefully advocated (James, 1970, preceded by Hamilton, 1961) a change of focus from temperature to wet-bulb temperature. If one insists on a different name for intra-specific studies I suggest we use 'Mayr's Rule', as 'Rensch's Rule' is already taken. Many studies were conducted at the intra-specific level before James (1970) (reviewed in Meiri & Dayan, 2003), and thus calling it 'James's Rule' is a misnomer. However, I propose that the name Bergmann's Rule is retained for intra- and inter-specific studies, as well as for assemblage-level ones. Should one insist on a different name for the assemblage level, I suggest 'Lindsey's Rule' be used.

The question of utility, I think, is of great importance. Biogeographers, evolutionary biologists and macroecologists know that Bergmann's Rule associates large size with cold temperatures and high latitudes and small size with low latitudes and warm temperatures. Partitioning the name according to

mechanism, taxa and taxonomic rank seems to me of little value, and likely to add confusion rather than clarity. There is no need for a separate name for every taxonomic level, every mechanism, every taxon and their numerous interactions: 'Bergmann's Rule' will do.

I suggest that Bergmann's Rule is simply defined as 'a tendency of organisms to be smaller at high temperatures and low latitudes and larger at low temperatures and high latitudes'. I predict that this rule would prove stronger in homeotherms than in poikilotherms, because of Bergmann's proposed mechanism. I further predict – and think this accords with the writings of Bergmann (1847), Rensch (1938) and Mayr (1942, 1956, 1963) – that patterns would generally be stronger at the population level than between closely related species, where, in turn, they would be stronger than at the assemblage level. The mechanisms driving Bergmann's Rule and the selective forces governing size evolution in general are still obscure, despite decades of research. For over 160 years Bergmann's thermoregulatory hypothesis has been key to studying the evolution of size. Recently the study of the pattern named 'Bergmann's Rule' has generated some intriguing new hypotheses and new findings. I suggest future attempts will probably benefit from a macroecological approach involving an integration of intra- and inter-specific size variation studied in an explicitly phylogenetic context, combined with a meta-analysis of detailed autecological case studies.

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## REFERENCES

- Agapow, P.M., Bininda-Emonds, O.R.P., Crandall, K.A., Gittleman, J.L., Mace, G.M., Marshall, J.C. & Purvis, A. (2004)

- The impact of species concept on biodiversity studies. *Quarterly Review of Biology*, **79**, 161–179.
- Bergmann, K.G.L.C. (1847) Über die Verhältnisse der wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien*, **3**, 595–708.
- Blackburn, T.M. & Gaston, K.J. (1996) Spatial patterns in the body sizes of bird species in the New World. *Oikos*, **77**, 436–446.
- Blackburn, T.M., Gaston, K.J. & Loder, N. (1999) Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions*, **5**, 165–174.
- Calder, W.A. (1974) Consequences of body size for avian energetics. *Avian energetics* (ed. by R.A. Paynter Jr), pp. 86–151. Nuttall Ornithological Club, Cambridge, MA.
- Case, T.J. (1978) A general explanation for insular body size trends in terrestrial vertebrates. *Ecology*, **59**, 1–18.
- Chaitra, M.S., Vasudevan, K. & Shanker, K. (2004) The biodiversity bandwagon: the splitters have it. *Current Science*, **86**, 897–899.
- Clarke, A., Rothery, P.R. & Isaac, N.J.B. (2010) Scaling of basal metabolic rate with body mass and temperature in mammals. *Journal of Animal Ecology*, **79**, 610–619.
- Darwin, C.R. (1859) *On the origin of species by means of natural selection*. John Murray, London.
- Darwin, C. & Wallace, A.R. (1858) On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection. *Journal of the Proceedings of the Linnean Society, Zoology*, **3**, 45–62.
- Dayan, T. & Simberloff, D. (1998) Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. *Mammal Review*, **28**, 99–124.
- Diniz-Filho, J.A.F., Bini, L.M.B., Rodríguez, M.Á., Rangel, T.F.L.V. & Hawkins, B.A. (2007) Seeing the forest for the trees: partitioning ecological and phylogenetic components of Bergmann's rule in European Carnivora. *Ecography*, **30**, 598–608.
- Diniz-Filho, J.A.F., Rodríguez, M.Á., Bini, L.M., Olalla-Tárraga, M.Á., Cardillo, M., Nabout, J.C., Hortal, J. & Hawkins, B. (2009) Climate history, human impacts and global body size of Carnivora (Mammalia: Eutheria) at multiple evolutionary scales. *Journal of Biogeography*, **36**, 2222–2236.
- Dunbar, R.I.M. (1990) Environmental determinants of intraspecific variation in body weight in baboons (*Papio* spp.). *Journal of Zoology*, **220**, 157–169.
- Einstein, A. (1905) Zur Elektrodynamik bewegter Körper. *Annalen der Physik*, **17**, 891–921.
- Einstein, A. (1917) Kosmologische Betrachtungen zur allgemeinen Relativitätstheorie. *Königlich Preussische Akademie der Wissenschaften Sitzungsberichte*, 142–152.
- Entling, W., Martin, H., Schmidt-Entling, M.H., Bacher, S., Brandl, R. & Nentwig, W. (2010) Body size–climate relationships of European spiders. *Journal of Biogeography*, **37**, 477–485.
- Hamilton, T.H. (1961) The adaptive significance of intraspecific trends of variation in wing length and body size among bird species. *Evolution*, **15**, 180–195.
- Hawkins, B.A. & Lawton, J.H. (1995) Latitudinal gradients in butterfly body sizes: is there a general pattern? *Oecologia*, **102**, 31–36.
- Heaney, L.R. (1978) Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. *Evolution*, **32**, 29–44.
- James, F.C. (1970) Geographic size variation in birds and its relationship to climate. *Ecology*, **51**, 365–390.
- Lamarck, J.P.B. (1809) *Philosophie zoologique*. Dentu, Paris.
- Lindsey, C.C. (1966) Body sizes of poikilotherm vertebrates at different latitudes. *Evolution*, **20**, 456–465.
- Lomolino, M.V. (2010) Four Darwinian themes on the origin, evolution and preservation of island life. *Journal of Biogeography*, **37**, 985–994.
- Lovegrove, B.G. (2003) The influence of climate on the basal metabolic rate of small mammals: a slow-fast metabolic continuum. *Journal of Comparative Physiology B*, **173**, 87–112.
- Mayr, E. (1942) *Systematics and the origin of species*. Columbia University Press, New York.
- Mayr, E. (1956) Geographical character gradients and climatic adaptation. *Evolution*, **10**, 105–108.
- Mayr, E. (1963) *Animal species and evolution*. Belknap Press, Cambridge, MA.
- Meiri, S. (2007) Size evolution in island lizards. *Global Ecology and Biogeography*, **16**, 702–708.
- Meiri, S. & Dayan, T. (2003) On the validity of Bergmann's rule. *Journal of Biogeography*, **30**, 331–351.
- Meiri, S. & Mace, G.M. (2007) New taxonomy and the origin of species. *PLoS Biology*, **5**, 1385–1386.
- Meiri, S. & Thomas, G.H. (2007) The geography of body size – challenges of the interspecific approach. *Global Ecology and Biogeography*, **16**, 689–693.
- Meiri, S., Dayan, T. & Simberloff, D. (2004) Carnivores, biases and Bergmann's rule. *Biological Journal of the Linnean Society*, **81**, 579–588.
- Meiri, S., Yom-Tov, Y. & Geffen, E. (2007) What determines conformity to Bergmann's rule? *Global Ecology and Biogeography*, **16**, 788–794.
- Meiri, S., Cooper, N. & Purvis, A. (2008) The island rule: made to be broken? *Proceedings of the Royal Society B: Biological Sciences*, **275**, 141–148.
- Olalla-Tárraga, M.A., Rodríguez, M.A. & Hawkins, B.A. (2006) Broad-scale patterns of body size in squamate reptiles of Europe and North America. *Journal of Biogeography*, **33**, 781–793.
- Olson, V., Davies, R.G., Orme, C.D.L., Thomas, G.H., Meiri, S., Blackburn, T.M., Gaston, K.J., Owens, I.P.F. & Bennett, P.M. (2009) Global biogeography and ecology of body size in birds. *Ecology Letters*, **12**, 249–259.
- Park, O. (1949) Application of the converse Bergmann principle to the carabid beetle, *Dicaelus purpuratus*. *Physiological Zoology*, **22**, 359–372.
- Pincheira-Donoso, D., Tregenza, T. & Hodgson, D.J. (2007) Body size evolution in South American *Liolaemus* lizards of the *boulengeri* clade: a contrasting reassessment. *Journal of Evolutionary Biology*, **20**, 2067–2071.
- Pincheira-Donoso, D., Hodgson, D.J. & Tregenza, T. (2008) The evolution of body size under environmental gradients in ectotherms: why should Bergmann's rule apply to lizards? *BMC Evolutionary Biology*, **8**, 68.
- Raia, P. & Meiri, S. (2006) The island rule in large mammals: paleontology meets ecology. *Evolution*, **60**, 1731–1742.
- Ray, C. (1960) The application of Bergmann's and Allen's rules to the poikilotherms. *Journal of Morphology*, **106**, 85–108.
- Rensch, B. (1924) Das Deperetsche Gesetz und die Regel von der Kleinheit der Inselformen als Specialfall des Bergmannschen Gesetzes und ein Erklärungsversuch desselben: eine Hypothese. *Zeitschrift für Induktive Abstammungs- und Vererbungslehre*, **35**, 139–155.
- Rensch, B. (1938) Some problems of geographical variation and species formation.

- Proceedings of the Linnean Society of London*, **150**, 275–285.
- Rosenzweig, M.L. (1968) The strategy of body size in mammalian carnivores. *American Midland Naturalist*, **80**, 299–315.
- Sangster, G. (2009) Increasing numbers of bird species result from taxonomic progress, not taxonomic inflation. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 3185–3191.
- Scholander, P.F. (1955) Evolution of climatic adaptation in homeotherms. *Evolution*, **9**, 15–26.
- Van Valen, L.M. (1973) Body size and numbers of plants and animals. *Evolution*, **27**, 27–35.
- Watt, C., Mitchell, S. & Salewski, V. (2010) Bergmann's rule; a concept cluster? *Oikos*, **119**, 89–100.

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