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Oikos

Bergmann's rule in mammals: a cross-species interspecific pattern

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Summary

Although Bergmann's rule – stating that among closely related species, the bigger ones will inhabit the colder climates/higher latitudes – was formulated for inter-specific comparisons, most analyses that tested this pattern in mammals were on an intra-specific level. To date, no large-scale taxonomy-driven cross-species evaluation of the pattern predicted by Bergmann exists. Here we show, in a dataset comprising 3561 mammal species from 26 orders, that while there is no significant correlation between latitude and body mass using conventional methods, this correlation is highly significant when the phylogenetic structure of the dataset is accounted for, thus supporting Bergmann's claim that the rule only applies to closely related species. Analyses of different subsets indicate that the Bergmann's rule is evident across a variety of latitude ranges. In many taxonomic subsets, when analysed alone, there is no significant correlation between body mass and latitude. In combination with both the significant relationship in the overall dataset and with results of intra-specific analyses from the literature, this suggests that Bergmann's rule describes a fundamental principle within mammals, but that its expression has been modified by a variety of factors during mammalian diversification yet to be resolved.

Keywords: Body size; Latitude; Temperature; Convergence; Biogeography; Phylogeny; Comparative analysis

Introduction

Bergmann (1848) hypothesized that due to surface-volume ratios and the resulting effects on temperature regulation, animals of a ‘similar organisation’ should be of larger body size if they inhabit higher latitudes. Although there has been a historical debate whether the resulting rule, ‘Bergmann’s rule’, should apply intra-specifically or inter-specifically (Blackburn et al. 1999, Pincheira-Donoso 2010, Watt et al. 2010, Meiri 2011), the original text leaves no doubt that the author considered his mechanism to apply generally, i.e. both across and within species (see Appendix I for a translation of Bergmann’s original manuscript). The evidence Bergmann (1848) provided for his hypothesis, albeit qualitatively, is summarized by the author as the number of bird genera that showed the predicted size-latitude cline across their species.

In contrast to this inter-specific approach, the majority of work testing this pattern in mammals and birds focused on intra-specific comparisons; the decision on whether Bergmann’s rule applied or not is thus usually based on the number of species in which the pattern can be demonstrated intra-specifically (James 1970, Ashton et al. 2000, Ashton 2002, Meiri and Dayan 2003, de Queiroz and Ashton 2004, Meiri et al. 2004, Watt et al. 2010). Using the intra-specific relationship between latitude (or another environmental proxy) and body size as a species-specific characteristic, usually expressed as the correlation coefficient, inter-specific comparisons in mammals have tested for relationships of this correlation coefficient with body size (Freckleton et al. 2003, Diniz-Filho et al. 2007), geographical range (Meiri et al. 2007), or phylogeny (de Queiroz and Ashton 2004). Inter-specific comparisons that directly link a species body size to a single value that characterises its geographic or environmental habitat were mostly restricted to ectothermic organisms (Lindsey 1966, Kaspari and Vargo 1995, Adams and Church 2008, Pincheira-Donoso et al. 2008, Olalla-Tárraga et al. 2010, Watt et al. 2010), birds (Blackburn and Gaston 1996), or to assemblages of defined geographic ranges (Blackburn and Hawkins 2004, Rodríguez et al. 2006,

Rodríguez et al. 2008, Morales-Castilla et al. 2012) or global scale (Olson et al. 2009). In the assemblage approaches, it is not the variation within taxonomic lineages that is analysed primarily, but the variation in whole animal assemblages consisting of all taxa present at different geographical units. The only mammal groups in which an inter-specific pattern was to our knowledge investigated at higher taxonomic level, similar to the approach taken by Bergmann (1848) himself, are carnivores (Gittleman 1985, Diniz-Filho et al. 2007, Diniz-Filho et al. 2009), primates (Harcourt and Schreier 2009) and ruminants (Zerbe et al. 2012).

The work on carnivores and ruminants demonstrated two important restrictions in assessing the pattern in a large inter-specific dataset: a) the pattern only emerged when the phylogenetic structure of the dataset was accounted for, indicating that the rule is only evident, as Bergmann (1848) suggested, on the level of closely related species but not in the overall dataset; b) in ruminants, the pattern was only evident if African species were excluded, i.e. the majority of tropical species. Previous intra-specific analyses had shown that tropical species do not follow the expected pattern as often as temperate species (Meiri and Dayan 2003). Additionally, the fact that larger species (of a taxonomic unit) occur at all latitudes, whereas smaller ones occur mainly at lower latitudes (Harcourt and Schreier 2009) will contribute to this phenomenon.

Here, we tested the relationship between latitude and body mass (M) in a large dataset of mammal species. Our prediction was that whereas no significant relationship between M and latitude would be evident using an analysis that does not account for the phylogenetic structure of the dataset (here, Ordinary Least Squares, OLS), whereas such a relationship would be evident if that structure was accounted for (here, using Phylogenetic Generalized Least Squares, PGLS) – in other words, that the pattern predicted by Bergmann's rule can be demonstrated inter-specifically across mammal species. We expected the relationship to be more distinct if the maximum latitude rather than the median latitude for the species' distribution was used. We also tested whether the same pattern could be found in different

taxonomic subsets, to compare inter-specific patterns with those identified intra-specifically within different taxonomic groups (Meiri and Dayan 2003). Finally, because it has been suggested that the size-latitude cline, if related to Bergmann's original heat conservation hypothesis, should only occur in temperate to cold areas (e.g. Rodríguez et al. 2008), we analysed the dataset using a variety of latitude thresholds; we expected that the inclusion of more tropical species would dampen the pattern (Zerbe et al. 2012).

Methods

Data on body mass M and (absolute) median and maximum latitude of geographical distribution were taken from the PanTheria database (Jones et al. 2009) for all species for which this information was available, and then linked to a mammal supertree (Bininda-Emonds et al. 2007, Bininda-Emonds et al. 2008), resulting in a dataset of 3561 species from 26 orders (Fig. 1). We are aware that neither median latitude (corresponding to the 'midpoint approach' in Blackburn and Hawkins 2004, e.g. also used by Harcourt and Schreier 2009) nor maximum latitude optimally reflect a species' distribution range (Meiri and Thomas 2007, Olalla-Tárraga et al. 2010), but this approach is necessary in a broad-scale taxonomy-based comparison where one value for latitude and M are assigned per species (e.g. Gittleman 1985). As explained by Blackburn and Gaston (1996), geographical midpoints such as median latitude may be poor descriptors of the geographic range of large and widespread species. According to these authors, using midpoints will therefore make a detection of Bergmann's rule more difficult. This is because a species that occurs, for example, on both sides of the equator to latitudes of about 20° , will have a median latitude of 0° . For this reason, the median latitude approach, while the best compromise to describe a species actual geographical range in one datapoint, could be considered conservative with a comparatively restricted chance to confirm Bergmann's rule. In contrast, the maximum latitude approach might better describe the ecological potential of a species, and might hence be more suitable

to detect Bergmann's rule. Note that such limitations need not apply to either assemblage-based approaches where individual species can occur multiple times with their different respective M typical for the different geographical locations, or for intra-specific comparisons where, by definition, different M (or its proxies) are used for specimens originating from different geographical ranges.

We tested for a relationship between log-transformed M as the dependent, and absolute latitude as the independent variable in the whole dataset and in taxonomic subsets. Additionally, to test whether the exclusion of tropical or temperate species had an effect on the result, species occurring above or below (absolute) latitude thresholds were excluded in a stepwise procedure (excluding species whose latitude range lay outside of the chosen range that was modified in 1°-steps). This was done first using Generalized Least Squares as Ordinary Least Squares (OLS), i.e. without accounting for the phylogenetic structure of the dataset; subsequently, analyses were repeated using Phylogenetic Generalized Least Squares (PGLS) with a variance-covariance matrix of the data based on phylogeny. The influence of phylogeny on M -patterns in mammal lineages is well-documented (Smith et al. 2004). For PGLS, we set λ , the character describing the phylogenetic signal (Pagel 1999, Revell 2010), fixed at 1 (for the series of the analyses with shifting latitude thresholds), and we additionally calculated λ for the whole dataset and the various taxonomic subsets. λ is calculated by maximum likelihood in PGLS and can vary between 0 (no phylogenetic signal) and 1 (the observed pattern is predicted by the phylogeny; similarity among species scales in proportion to their shared evolutionary time, assuming a Brownian motion model of evolution) (Pagel 1999, Freckleton et al. 2002). As a caveat, it must be noted that Ornstein-Uhlenbeck and Early Burst models of evolution describe the distribution of M for several mammalian orders better than the Brownian motion model (Cooper and Purvis 2010). To test whether the use of PGLS was adequate, we compared the fit of OLS and PGLS approaches for the complete

dataset using their respective model log-likelihoods, and compared by the likelihood ratio test using a chi-square distribution (Pagel 1999, Freckleton et al. 2002).

Statistical tests were performed in *R* 2.15.0 (Team 2011) using the packages *ape* (Paradis et al. 2004), *caper* (Orme et al. 2010), *nlme* (Pinheiro et al. 2011) and *phytools* (Revell 2012). In contrast to a common recommendation (Freckleton 2009), we display results of both OLS and PGLS analyses. We do this because different combinations of results in OLS and PGLS require different interpretations (Appendix II). If OLS yields a significant result but PGLS does not, this does not necessarily refute the hypothesis in general, but can also indicate that in the taxonomic subset analysed, taxonomic diversification mirrored the pattern described by the rule under investigation. Only if taxa are included that diversified for other reasons will the rule then become evident in PGLS.

For a comparison with intra-specific analyses, we added the number of species of taxonomic subsets in which Bergmann's rule has been or has not been observed from Meiri and Dayan (2003) to our results.

Results

Despite of the high n in the overall dataset, OLS did not yield a significant result. In contrast, there was a significant positive relationship between both median and maximum latitude and M in PGLS in the overall dataset (Table 1). Pagel's λ was calculated at a value very close to 1.0, indicating that both M and latitude have a strong phylogenetic signal. The log-likelihoods in the default PGLS model with $\lambda=1$ and with actually calculated λ of 0.99 were both distinctively higher than the one for the OLS model (Table 1), and a chi-square comparison between the log-likelihoods of OLS and PGLS correspondingly indicated a highly significant difference ($p<0.0001$) in each case, corroborating that the PGLS models provided a better data fit. The analysis of the whole dataset thus represents a typical, rare example where statistical tests that account for the phylogenetic structure of the data (PGLS) detect a pattern,

but those not informed by phylogeny fail to support the biological hypothesis (cf. Fig. 1 on p. 147 in Baker 2002, Meloro and Raia 2010, Müller et al. 2011, Zerbe et al. 2012). Note that as expected based on theoretical considerations (Appendix II), the standard error (SE) of the intercept a is much larger in PGLS than in OLS, whereas the opposite is true for the regression slope b (Table 1).

The maximum latitude- M cline was significant in PGLS when tropical species were excluded, and became insignificant only when the lower latitude range was at 57°; in OLS, the cline was significant when the lower latitude range was between 12-21°, and from 35° onwards (Fig. 2a). When excluding species from higher latitudes, the cline was basically always significant in PGLS, with the only exception of an upper latitude range limit of 11°; in OLS, the cline was significant below an upper latitude range limit of 33° (Fig. 2b). While the finding in PGLS indicates the cline among closely related species in the sense of Bergmann's rule, the finding in OLS reflects on the one hand the fact that the lower body size threshold increases with increasing latitude, and on the other hand that species with an intermediate and high body mass become comparatively sparse at higher latitudes (Fig. 1).

In the individual analysis of orders and families, the analyses using median and maximum latitude yielded mostly similar results; yet, the latitude- M cline was more often significant if maximum rather than median latitude was used, corresponding to our reflections in the Methods section (Table 2). In particular, the cline followed Bergmann's rule in Artiodactyla and Carnivora if maximum latitude was used; in contrast, the cline was significant in Rodentia with median but not with maximum latitude (Table 2).

Of the 18 orders that were analysed individually, PGLS indicated a significant maximum latitude- M cline in 6 cases (Didelphimorphia, Dasyuromorphia, Primates, Artiodactyla, Chiroptera, Carnivora) (Table 2). For Rodents, there was a difference in the PGLS result depending on whether λ was fixed or not; when λ was calculated, the resulting relationship was not significant. In additional analyses of families (Table 2), there were cases where there

was no significant relationship in OLS but a significant or close to significant positive one in PGLS (e.g. Bovidae, Canidae), a significant positive relationship in OLS but no significance in PGLS (e.g. Cebidae, Cervidae, Emballonuridae), and significant positive (e.g. Cercopithecidae, Talpidae) and negative (Soricidae) relationships in both analyses.

When comparing the results on an order or family level to findings from intra-specific studies (last column in Table 2), existing data indicates similarity at inter-specific and intra-specific level particularly in Primates/Cercopithecidae, Chiroptera/Vespertilionidae and Carnivora/Canidae as examples where Bergmann's rule is followed. Interestingly, the Heteromyidae and the Mustelidae, in species of which the intra-specific pattern mostly or often does not follow Bergmann's rule, respectively, also did not show the pattern at inter-specific level. In many groups, especially in the Diprodontia and the Felidae, where a larger number of species was analysed intra-specifically, the intra-specific size-latitude cline was not found at the inter-specific level; the same difference was evident in the cervids, where in the inter-specific comparison the pattern was significant in OLS but not PGLS. In the Muridae, in which larger numbers of species both do and do not follow Bergmann's rule intra-specifically, results of the inter-specific analysis were particularly heterogenous with different results in OLS and PGLS with fixed and with calculated λ (Table 2).

Discussion

The results confirm that within the dataset, with its limitations due to the use of one M value and one latitude per species, the majority of closely related species statistically follows Bergmann's rule. However, a non-exhaustive variety of additional analyses performed here suggest that the pattern, while significant at various latitude thresholds, cannot be detected in many cases of lower-level taxonomic analyses. This has consequences for our interpretation of the universality and characteristic of Bergmann's rule, and for approaches investigating it.

A challenge to understand type II error situations in comparative analyses, especially with datasets as large as the one used here, is that it is difficult to represent the result in an easily accessible, graphical way. Examples for the graphic representation of data are given for hystricomorph rodents (Fig. 3) and artiodactyls (Fig. 4). Note that for the preparation of these graphs, taxonomic groups were selected that visually appear to follow Bergmann's rule; it would be just as easy to present examples in which this is not the case. Conceptually, a problem with the understanding of PGLS results is that one cannot fix the pattern to a certain taxonomic classification level such as 'Order' or 'Family'. The distinction of these taxonomic levels implies a (historical) arbitrariness anyhow, so that e.g. a 'Family' in one Order might rather correspond to a 'Genus' in another Order; for the same reason, simply counting the number of Orders in which a pattern can be detected is no test of the pattern itself. Even down to Genus level, the PGLS result will be determined by relationships that can, in their complexity, not be easily visualized in scatter plots.

de Queiroz and Ashton (2004) noted that the tendency to show a body size cline with latitude (that corresponds to Bergmann's rule) is by definition either a property of the species (if the rule is assessed intra-specifically) or of a taxonomic group (if the rule is assessed inter-specifically), rather than an organismal property; an organism itself cannot form a cline. This fact itself makes assessing Bergmann's rule different from other studies on convergence or symplesiomorphy in that the rule can only be detected if closely related species are included in the analysis. In intra-specific analyses, this condition is automatically met; in inter-specific analyses, this can only be guaranteed by the use of statistical procedures that account for the phylogenetic structure of the dataset, and by the inclusion of the highest number of species possible.

Convergence is investigated by comparing species or taxonomic groups from different phylogenetic lineages for the presence of a common characteristic expressed when living in similar niches or exposed to the same environmental conditions. In such studies, controlling

for phylogenetic relationships is usually employed to determine whether the common characteristic actually does occur in different phylogenetic lineages, or whether the finding is simply due to an uneven distribution of different phylogenetic groups in the dataset (Harvey and Pagel 1991). Therefore, the result that in different taxonomic lineages, larger body sizes are found at higher latitudes could indicate convergence among mammals in this respect. The finding that this effect is not found if only animals from very high (Fig. 2a) or extremely low latitudes (Fig. 2b) are investigated indicates that for the convergence to become evident, a certain range of latitudes needs to be included to yield sufficient resolution. In other words, Bergmann's rule would emerge as a convergence among animals exposed to a temperature or resource gradient that spans a certain range.

The interpretation of Bergmann's rule as a convergence is contrasted by the result that the size-latitude cline cannot be detected in many individual mammalian orders (Table 2). Actually, a characteristic that can be detected at the most basic level of a phylogenetic lineage (here, the whole mammal dataset) but not in all individual subsets could be considered a symplesiomorphy. Using the intra-specific approach to Bergmann's rule, de Queiroz and Ashton (2004) combined information on the presence and absence of the body size-latitude cline in individual species and a comprehensive phylogeny to show that the tendency to follow Bergmann's rule is ancestral for tetrapods. The question is, however, if the tendency to show the cline is really a heritable characteristic (as one would have to postulate, if one considered it either a convergence or a symplesiomorphy; cf. Stillwell 2010), or whether it is simply an indication for the presence of common selection pressures to which most species respond in the same way without being particularly (genetically) adapted to them. The absence of the cline in certain species or lineages similarly need not indicate the change of a genetically fixed adaptation, but simply (historical) modifications of the selective pressures as they apply to this species or lineage. In our view, a parsimonious interpretation of the results of this study, as combined with findings on intra-specific size-latitude clines, is that

Bergmann's rule represents a general selection pressure operating, in principle, on all mammals in general, but which is modified by a variety of other factors. In this sense, Bergmann's rule actually is an ecological rule and neither a convergence nor a symplesiomorphy; the effects of this putatively fundamental rule might be overwritten by various other modifications over evolutionary time, to the point that it can no longer be detected in particular datasets. Bergmann himself had already alluded to this possibility (see Appendix I). Another important possibility is that the quality of the data used here – for body mass, geographical range, or for phylogenetic relationships – is of sufficient resolution to detect Bergmann's rule at the level of a large dataset but not in smaller individual subsets where inaccuracies gain relatively more weight.

It is an important question what other factors operate and shape the overall pattern of mammal body size distribution, and at which taxonomic or geographic level. Such modifying effects for Bergmann's rule might originate from a variety of historical conditions, such as human impacts, changes in climate at different geographical scales, overall species richness, long distance dispersal events, or competition or replacement and extinctions of species from different lineages over time (Meiri and Thomas 2007, Diniz-Filho et al. 2009, Olson et al. 2009, Morales-Castilla et al. 2012). For example, McNab (2010) demonstrates how body size patterns in the large mammalian carnivore *Puma concolor* could be explained by the presence or absence of a competitor, *Panthera onca*. How this variety of historical conditions had different effects on the body size-latitude patterns in different taxonomic lineages mostly remains to be investigated.

The comparison of the inter- and the intra-specific results (Table 2) suggest that exploring such historical conditions may be particularly interesting in groups as the Diprodontia or the Felidae – groups in which the intra-specific size-latitude cline has been demonstrated, but who fail to display it at an inter-specific level. For groups where speciation appears to have followed a size-latitude cline (as indicated by a significant result in OLS but

not in PGLS, such as the Cebidae, Cervidae, the Emballonuridae), the validity of this scenario could in theory be corroborated using fossil taxa. Finally, the fact that in Mustelidae and especially in the Heteromyidae the size-latitude cline is neither present inter-specifically nor in most intra-specific cases suggests that these groups might be candidates to investigate if specific physiological or ecological adaptations can make lineages insensitive to the selective pressures summarized by Bergmann's rule.

Different mechanisms have been proposed to underlie patterns described by Bergmann's rule. Bergmann (1848) himself related it to the more efficient heat conservation in larger organisms – an argument supported by non-linear relationships between body size and temperature in assemblage analyses (Blackburn and Hawkins 2004, Rodríguez et al. 2008), indicating the relevance of including species from truly cold regions. Other authors have suggested fasting endurance, with larger animals able to withstand seasonal starvation better than smaller animals (Lindstedt and Boyce 1985), or resource availability, with body size following the productivity of the habitat (Rosenzweig 1968, Geist 1987, McNab 2010, Huston and Wolverton 2011), as more likely causes. Intra-specific patterns of decreasing size at very high latitudes (Geist 1987, Huston and Wolverton 2011), as well as our finding that the inter-specific size-latitude cline was not significant if only very high latitudes were considered (Fig. 2a), indicate that either both Bergmann's original concept or the fasting endurance concept do not apply, or that they are modified by additional constraints; evidently, resource availability might represent such a modifying constraint. Within latitudes, variations in temperature, altitude or humidity will have additional effects. Latitude itself – while convenient for a large-scale comparison that tests for the existence of the pattern – is not the covariable with which causes for the pattern can be explored (Hawkins and Diniz-Filho 2004); one should note, however, that other covariables such as temperature might also only represent a proxy for an unknown factor rather than the cause itself. Most importantly, because the differences in results at different taxonomic levels suggest historical influences,

correlations with any one set of recent measurements may not yield reliable insights. A perhaps astonishing result of this study was that even if only tropical species were considered, Bergmann's latitude-*M* cline could be demonstrated (Fig. 2b), in contrast to expectations voiced in the Introduction. This is also in contrast to the finding that in intra-specific comparisons, tropical species show the latitude-*M* cline less frequently than temperate species (Meiri and Dayan 2003). In the tropical latitude range, the relevance of temperature conservation, fasting endurance or resource availability has not been postulated so far. More detailed analyses of tropical species might therefore reveal additional factors relevant for the cline.

The results of our study demonstrate that Bergmann's rule is well-supported inter-specifically for mammals in general when phylogenetically-informed statistics are used. More detailed, parallel investigations into the body size distribution in various mammal groups, such as taxonomic lineages, extant and extinct or allochthon and autochthon species (Morales-Castilla et al. 2012), groups from distinct biogeographic origins (Holt et al. 2013), or groups of different physiological, ecological or life history characteristics, potentially also evaluating the species-specific latitude range rather than only a midpoint or maximum point (Felizola Diniz Filho et al. 2012), might elucidate which additional causes play a role in the origin of the pattern described by Bergmann's rule.

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References

Adams, D. C. and Church, J. O. 2008. Amphibians do not follow Bergmann's rule. - Evolution 62: 413-420.

353 Ashton, K. G. 2002. Patterns of within-species body size variation of birds: strong evidence
 354 for Bergmann's rule. - *Global Ecology and Biogeography* 11: 505–523.
 355 Ashton, K. G., Tracy, M. C. and de Queiroz, A. 2000. Is Bergmann's rule valid for mammals?
 356 - *American Naturalist* 156: 390–415.
 357 Baker, R. H. 2002. Comparative methods. - In: DeSalle, R., Giribet, G. and Wheeler, W.
 358 (eds.), *Techniques in molecular systematics and evolution*. Birkhäuser Verlag, pp. 146–161.
 359 Bergmann, C. 1848. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse.
 360 Abgedruckt aus den Göttinger Studien 1847. - Vandenhoeck & Ruprecht.
 361 Bininda-Emonds, O. R. P., Cardillo, M., Jones, K. E., MacPhee, R. D. E., Beck, R. M. D.,
 362 Grenyer, R., Price, S. A., Vos, R. A., Gittleman, J. L. and Purvis, A. 2007. The delayed rise of
 363 present-day mammals. - *Nature* 446: 507–512.
 364 Bininda-Emonds, O. R. P., Cardillo, M., Jones, K. E., MacPhee, R. D. E., Beck, R. M. D.,
 365 Grenyer, R., Price, S. A., Vos, R. A., Gittleman, J. L. and Purvis, A. 2008. Corrigendum: The
 366 delayed rise of present-day mammals. - *Nature* 456: 274.
 367 Blackburn, T. M. and Gaston, K. J. 1996. Spatial patterns in the body sizes of bird species in
 368 the New World. - *Oikos* 77: 436–446.
 369 Blackburn, T. M., Gaston, K. J. and Loder, N. 1999. Geographic gradients in body size: a
 370 clarification of Bergmann's rule. - *Diversity and Distributions* 5: 165–174.
 371 Blackburn, T. M. and Hawkins, B. A. 2004. Bergmann's rule and the mammal fauna of
 372 northern North America. - *Ecography* 27: 715–724.
 373 Cooper, N. and Purvis, A. 2010. Body size evolution in mammals: complexity in tempo and
 374 mode. - *American Naturalist* 175: 727–738.
 375 de Queiroz, A. and Ashton, K. G. 2004. The phylogeny of a species-level tendency: species
 376 heritability and possible deep origins of Bergmann's rule in tetrapods. - *Evolution* 58: 1674–
 377 1684.
 378 Diniz-Filho, J. A. F., Bini, L. M., Rodríguez, M. A., Rangel, T. F. L. V. B. and Hawkins, B.
 379 A. 2007. Seeing the forest for the trees: partitioning ecological and phylogenetic components
 380 of Bergmann's rule in European carnivora. - *Ecography* 30: 598–608.
 381 Diniz-Filho, J. A. F., Rodríguez, M. A., Bini, L. M., Olalla-Tarraga, M. A., Cardillo, M.,
 382 Nabout, J. C., Hortal, J. and Hawkins, B. A. 2009. Climate history, human impacts and global
 383 body size of Carnivora (Mammalia: Eutheria) at multiple evolutionary scales. - *Journal of*
 384 *Biogeography* 36: 2222–2236.
 385 Felizola Diniz Filho, J. A., Rangel, T. F., Santos, T. and Mauricio Bini, L. 2012. Exploring
 386 patterns of interspecific variation in quantitative traits using sequential phylogenetic
 387 eigenvector regressions. - *Evolution* 66: 1079–1090.
 388 Freckleton, R. P. 2009. The seven deadly sins of comparative analysis. - *Journal of*
 389 *Evolutionary Biology* 22: 1367–1375.
 390 Freckleton, R. P., Harvey, P. H. and Pagel, M. 2002. Phylogenetic analysis and comparative
 391 data: a test and review of evidence. - *American Naturalist* 160: 712–726.
 392 Freckleton, R. P., Harvey, P. H. and Pagel, M. 2003. Bergmann's rule and body size in
 393 mammals. - *American Naturalist* 161: 821–825.
 394 Geist, V. 1987. Bergmann's rule is invalid. - *Canadian Journal of Zoology* 65: 1035–1038.
 395 Gittleman, J. L. 1985. Carnivore body size: ecological and taxonomic correlates. - *Oecologia*
 396 67: 540–554.
 397 Harcourt, A. H. and Schreier, B. M. 2009. Diversity, body mass, and latitudinal gradients in
 398 primates. - *International Journal of Primatology* 30: 283–300.
 399 Harvey, P. H. and Pagel, M. D. 1991. *The comparative method in evolutionary biology*. -
 400 Oxford University Press.
 401 Hawkins, B. A. and Diniz-Filho, J. A. F. 2004. 'Latitude' and geographic patterns in species
 402 richness. - *Ecography* 27: 268–272.

403 Holt, B. G., Lessard, J.-P., Borregaard, M. K., Fritz, S. A., Araújo, M. B., Dimitrov, D.,
 404 Fabre, P.-H., Graham, C. H., Graves, G. R., Jönsson, K. A., Nogués-Bravo, D., Wang, Z.,
 405 Whittaker, R. J., Fjeldså, J. and Rahbek, C. 2013. An update of Wallace's zoogeographic
 406 regions of the world. - *Science* 339: 74-78.
 407 Huston, M. A. and Wolverton, S. 2011. Regulation of animal size by nNPP, Bergmann's rule,
 408 and related phenomena. - *Ecological Monographs* 81: 349-405.
 409 James, F. C. 1970. Geographic size variation in birds and its relationship to climate. - *Ecology*
 410 51: 365-390.
 411 Jones, K. E., Bielby, J., Cardillo, M., Fritz, S. A., O'Dell, J., Orme, C. D., Safi, K., Sechrest,
 412 W., Boakes, E. H., Carbone, C., Connolly, C., Cutts, M. J., Foster, J. K., Grenyer, R., Habib,
 413 M., Plaster, C. A., Price, S. A., Rigby, E. A., Rist, J., Teacher, A., Bininda-Emonds, O. R. P.,
 414 Gittleman, J. L., Mace, G. M. and Purvis, A. 2009. PanTHERIA: a species-level database of
 415 life history, ecology, and geography of extant and recently extinct mammals. - *Ecology* 90:
 416 2648 (Ecological Archives E090-184).
 417 Kamilar, J. M., Muldoon, K. M., Lehman, S. M. and Herrera, J. P. 2012. Testing Bergmann's
 418 rule and the resource seasonality hypothesis in Malagasy primates using GIS-based climate
 419 data. - *American Journal of Physical Anthropology* 147: 401-408.
 420 Kaspari, M. and Vargo, E. L. 1995. Colony size as a buffer against seasonality: Bergmann's
 421 Rule in social insects. - *American Naturalist* 145: 610-632.
 422 Lindsey, C. C. 1966. Body sizes of poikilotherm vertebrates at different latitudes. - *Evolution*
 423 20: 456-465.
 424 Lindstedt, S. L. and Boyce, M. S. 1985. Seasonality, fasting endurance, and body size in
 425 mammals. - *American Naturalist* 125: 873-878.
 426 McNab, B. K. 2010. Geographic and temporal correlations of mammalian size reconsidered: a
 427 resource rule. - *Oecologia* 164: 13-23.
 428 Meiri, S. 2011. Bergmann's Rule - what's in a name? - *Global Ecology and Biogeography* 20:
 429 203-207.
 430 Meiri, S. and Dayan, T. 2003. On the validity of Bergmann's rule. - *Journal of Biogeography*
 431 30: 331-351.
 432 Meiri, S., Dayan, T. and Simberloff, D. 2004. Carnivores, biases and Bergmann's rule. -
 433 *Biological Journal of the Linnean Society* 81: 579-588.
 434 Meiri, S. and Thomas, G. H. 2007. The geography of body size - challenges of the
 435 interspecific approach. - *Global Ecology and Biogeography* 16: 689-693.
 436 Meiri, S., Yom-Tov, Y. and Geffen, E. 2007. What determines conformity to Bergmann's
 437 rule? - *Global Ecology and Biogeography* 16: 788-794.
 438 Meloro, C. and Raia, P. 2010. Cats and dogs down the tree: the tempo and mode of evolution
 439 in the lower carnassial of fossil and living carnivora. - *Evolutionary Biology* 37: 177-186.
 440 Morales-Castilla, I., Olalla-Tárraga, M. A., Purvis, A., Hawkins, B. A. and Rodríguez, M. A.
 441 2012. The imprint of Cenozoic migrations and evolutionary history on the biogeographic
 442 gradient of body size in New World mammals. - *American Naturalist* 180: 246-256.
 443 Müller, D. W. H., Caton, J., Codron, D., Schwarm, A., Lentle, R., Streich, W. J., Hummel, J.
 444 and Clauss, M. 2011. Phylogenetic constraints on digesta separation: variation in fluid
 445 throughput in the digestive tract in mammalian herbivores. - *Comparative Biochemistry and*
 446 *Physiology A* 160: 207-220.
 447 Olalla-Tárraga, M. A., Bini, L. M., Diniz-Filho, J. A. F. and Rodríguez, M. A. 2010. Cross-
 448 species and assemblage-based approaches to Bergmann's rule and the biogeography of body
 449 size in *Plethodon* salamanders of eastern North America. - *Ecography* 33: 362-368.
 450 Olson, V. A., Davies, R. G., Orme, C. D. L., Thomas, G. H., Meiri, S., Blackburn, T. M.,
 451 Gaston, K. J. and Owens, I. P. F. 2009. Global biogeography and ecology of body size in
 452 birds. - *Ecology Letters* 12: 249-259.

Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S. and Isaac, N. 2010. Caper: comparative analyses of phylogenetics and evolution in R. - R package version 0.4/r71. See <http://www.R-Forge.R-project.org/projects/caper/>.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. - *Nature* 401: 877-884.

Paradis, E., Claude, J. and Strimmer, K. 2004. APE: analyses of phylogenetics and evolution in R language. - *Bioinformatics* 20: 289–290.

Pincheira-Donoso, D. 2010. The balance between predictions and evidence and the search for universal macroecological patterns: taking Bergmann's rule back to its endothermic origin. - *Theory in Biosciences* 129: 247-253.

Pincheira-Donoso, D., Hodgson, D. J. and 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.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and R Development Core Team. 2011. Nlme: linear and nonlinear mixed effects models. - R package version 3. 1–102. Available at <http://cran.rproject.org/web/packages/nlme/citation.html>.

Revell, L. J. 2010. Phylogenetic signal and linear regression on species data. - *Methods in Ecology and Evolution* 1: 319-329.

Revell, L. J. 2012. Phytools: an R package for phylogenetic comparative biology (and other things). - *Methods in Ecology and Evolution* 3: 217–223.

Rodríguez, M. Á., López-Sañudo, I. L. and Hawkins, B. A. 2006. The geographic distribution of mammal body size in Europe. - *Global Ecology and Biogeography* 15: 173–181.

Rodríguez, M. A., Olalla-Tárraga, M. A. and Hawkins, B. A. 2008. Bergmann's rule and the geography of mammal body size in the Western Hemisphere. - *Global Ecology and Biogeography* 17: 274–283.

Rosenzweig, M. L. 1968. The strategy of body size in mammalian carnivores. - *American Midland Naturalist* 80: 299-315.

Smith, F. A., Brown, J. H., Haskell, J. P., Lyons, S. K., Alroy, J., Charnov, E. L., Dayan, T., Enquist, B. J., Ernest, S. K. M., Hadly, E. A., Jones, K. E., Kaufman, D. M., Marquet, P. A., Maurer, B. A., Niklas, K. J., Porter, W. P., Tiffney, B. and Willig, M. R. 2004. Similarity of mammalian body size across the taxonomic hierarchy and across space and time. - *American Naturalist* 163: 672-691.

Stillwell, R. C. 2010. Are latitudinal clines in body size adaptive? - *Oikos* 119: 1387–1390.

Team, R. D. C. 2011. R: A language and environment for statistical computing. - R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.

Watt, C., Mitchell, S. and Salewski, V. 2010. Bergmann's rule; a concept cluster? - *Oikos* 119: 89-100.

Zerbe, P., Clauss, M., Codron, D., Bingaman Lackey, L., Rensch, E., Streich, W. J., Hatt, J.-M. and Müller, D. H. W. 2012. Reproductive seasonality in captive wild ruminants: implications for biogeographical adaptation, photoperiodic control, and life history. - *Biological Reviews* 87: 965-990.

497 Table 1. Model outputs for Ordinary Least Squares (OLS) and Phylogenetic Generalized Least Squares (PGLS) analysis of the relationship (log-
498 transformed) body mass = $a + b$ latitude for the complete dataset (n=3561 species from 26 orders).

Statistic	Intercept			Latitude			λ	logLik
	a ($\pm$ SE)	t	p	b ($\pm$ SE)	t	p		
Median latitude								
OLS	2.1960 ($\pm$ 0.0303)	72.407	<0.0001	-0.0012 ($\pm$ 0.0013)	-0.875	0.3814	(0)	-5523.768
PGLS	2.7858 ($\pm$ 0.5143)	5.417	<0.0001	0.0020 ($\pm$ 0.0004)	4.849	<0.0001	1.00	-890.945
PGLS	2.7940 ($\pm$ 0.4670)	5.983	<0.0001	0.0016 ($\pm$ 0.0005)	3.468	<0.0001	0.99*	-793.254
Maximum latitude								
OLS	2.1398 ($\pm$ 0.0358)	59.842	<0.0001	0.0014 ($\pm$ 0.0012)	1.177	0.2394	(0)	-5523.580
PGLS	2.7695 ($\pm$ 0.5137)	5.391	<0.0001	0.0019 ($\pm$ 0.0003)	5.690	<0.0001	1.00	-879.940
PGLS	2.7940 ($\pm$ 0.4668)	5.986	<0.0001	0.0016 ($\pm$ 0.0005)	3.464	<0.0001	0.99*	-786.625

499 *estimated by maximum likelihood

500

501 Table 2. p values of test for an association of latitude and body mass (M) in various mammalian orders using OLS and PGLS (with fixed λ and with
502 λ estimated by maximum likelihood). Asterix* indicates significant results that are opposite to Bergmann's rule (i.e. negative relationship).

Order	n	Median latitude			Maximum latitude			Bergmann's rule present/absent
Family		p			p			Number of species
		OLS	PGLS		OLS	PGLS		(Meiri and Dayan 2003)
		($\lambda=0$)	($\lambda=1$)	(λ estimated)	($\lambda=0$)	($\lambda=1$)	(λ estimated)	
Didelphimorphia	62	0.825	0.022	0.022 ($\lambda=1.00$)	0.002	0.044	0.044 ($\lambda=1.00$)	1/0
Dasyuromorphia	61	0.901	0.017	0.017 ($\lambda=1.00$)	0.819	0.013	0.013 ($\lambda=1.00$)	-
Peramelemorphia	17	0.964	0.269	0.964 ($\lambda=0.00$)	0.745	0.136	0.745 ($\lambda=0.00$)	0/1
Diprotodontia	107	0.595	0.129	0.347 ($\lambda=0.98$)	0.568	0.678	0.843 ($\lambda=0.98$)	6/0
Macropodidae	50	0.599	0.174	0.604 ($\lambda=0.89$)	0.130	0.890	0.454 ($\lambda=0.88$)	3/0
Macroscelidea	14	0.064*	0.221	0.221 ($\lambda=1.00$)	0.093*	0.569	0.569 ($\lambda=1.00$)	-
Afrosoricida	31	0.408	0.368	0.349 ($\lambda=0.86$)	0.577	0.367	0.444 ($\lambda=0.91$)	-
Pilosa	9	0.669	0.969	0.969 ($\lambda=1.00$)	0.569	0.891	0.891 ($\lambda=1.00$)	-
Cingulata	20	0.031*	0.100*	0.084* ($\lambda=0.92$)	0.535	0.850	0.840 ($\lambda=0.97$)	-
Scandentia	17	0.513	0.811	0.981 ($\lambda=0.91$)	0.588	0.525	0.525 ($\lambda=1.00$)	-
Primates	225	0.933	0.054	0.054 ($\lambda=1.00$) ^a	0.563	0.002	0.002 ($\lambda=1.00$) ^a	5/1
Callithrichidae	26	0.723	0.157	0.157 ($\lambda=1.00$) ^a	0.857	0.294	0.294 ($\lambda=1.00$) ^a	-
Cebidae	53	0.276	0.602	0.602 ($\lambda=1.00$) ^a	0.041	0.480	0.480 ($\lambda=1.00$) ^a	-
Cercopithecidae	81	0.001	0.010	0.008 ($\lambda=0.96$) ^a	0.000	0.000	0.000 ($\lambda=0.98$) ^a	4/0
Lemurs	30	0.814	0.710	0.602 ($\lambda=1.00$) ^b	0.386	0.706	0.706 ($\lambda=1.00$) ^b	-
Lagomorpha	72	0.033*	0.868	0.787 ($\lambda=0.97$)	0.166	0.317	0.354 ($\lambda=0.97$)	4/0
Rodentia	1390	0.001*	0.000	0.020 ($\lambda=0.99$)	0.029*	0.047	0.141 ($\lambda=0.99$)	20/30
Ctenomyidae	37	0.939	0.939	0.939 ($\lambda=0.50$)	0.708	0.708	0.708 ($\lambda=0.50$)	-
Echimyidae	56	0.223	0.083*	0.149 ($\lambda=0.50$)	0.346	0.595	0.388 ($\lambda=0.43$)	-
Geomyidae	30	0.000*	0.427	0.427 ($\lambda=1.00$)	0.000*	0.202	0.202 ($\lambda=1.00$)	1/0
Heteromyidae	52	0.004*	0.650	0.650 ($\lambda=1.00$)	0.000*	0.103	0.103 ($\lambda=1.00$)	1/16
Muridae	875	0.000*	0.000	0.680 ($\lambda=0.98$)	0.000*	0.308	0.591 ($\lambda=0.98$)	16/12

Scuiridae	214	0.026	0.065	0.021 ($\lambda=0.95$)	0.017	0.634	0.186 ($\lambda=0.95$)	2/2
Insectivora	206	0.306	0.533	0.548 ($\lambda=0.92$)	0.515	0.428	0.371 ($\lambda=0.92$)	4/3
Erinaceidae	20	0.074	0.148	0.126 ($\lambda=0.60$)	0.028	0.011	0.024 ($\lambda=0.75$)	-
Soricidae	158	0.002*	0.087*	0.083* ($\lambda=0.82$)	0.000*	0.035*	0.027* ($\lambda=0.79$)	2/2
Talpidae	26	0.004	0.010	0.012 ($\lambda=0.68$)	0.013	0.012	0.021 ($\lambda=0.75$)	2/1
Artiodactyla	190	0.214	0.196	0.092 ($\lambda=0.99$)	0.087	0.025	0.005 ($\lambda=0.99$)	7/0
Bovidae	119	0.155	0.007	0.007 ($\lambda=1.00$)	0.080	0.001	0.001 ($\lambda=1.00$)	3/0
Cervidae	40	0.021	0.913	0.913 ($\lambda=1.00$)	0.010	0.436	0.179 ($\lambda=0.99$)	3/0
Chiroptera	878	0.000*	0.072	0.110 ($\lambda=0.90$)	0.000*	0.013	0.046 ($\lambda=0.90$)	14/5
Emballonuridae	45	0.052	0.239	0.239 ($\lambda=1.00$)	0.033	0.349	0.349 ($\lambda=1.00$)	-
Molossidae	78	0.651	0.339	0.519 ($\lambda=0.74$)	0.216	0.159	0.277 ($\lambda=0.74$)	-
Phyllostomidae	137	0.652	0.754	0.922 ($\lambda=0.91$)	0.397	0.452	0.544 ($\lambda=0.92$)	3/2
Pteropodidae	154	0.010	0.474	0.251 ($\lambda=0.85$)	0.465	0.000	0.007 ($\lambda=0.87$)	1/0
Rhinolophidae	124	0.064*	0.766	0.345 ($\lambda=0.73$)	0.033*	0.028*	0.051* ($\lambda=0.74$)	-
Vespertilionidae	299	0.006	0.011	0.034 ($\lambda=0.93$)	0.000	0.001	0.022 ($\lambda=0.93$)	9/3
Perissodactyla	14	0.680	0.915	0.915 ($\lambda=1.00$)	0.690	0.922	0.922 ($\lambda=1.00$)	-
Pholidota	7	0.837	0.806	0.837 ($\lambda=0.00$)	0.641	0.562	0.641 ($\lambda=0.00$)	-
Carnivora	222	0.428 ^c	0.211	0.580 ($\lambda=0.98$)	0.027	0.001	0.008 ($\lambda=0.98$)	31/12
Canidae	32	0.305 ^c	0.051	0.064 ($\lambda=0.97$)	0.431	0.011	0.013 ($\lambda=0.98$)	10/3
Felidae	36	0.238 ^c	0.167	0.167 ($\lambda=1.00$)	0.404	0.479	0.479 ($\lambda=1.00$)	8/1
Herpestidae	35	0.092*	0.214	0.200 ($\lambda=0.85$)	0.850	0.464	0.684 ($\lambda=0.82$)	3/0
Mustelidae	58	0.099* ^c	0.990	0.963 ($\lambda=0.98$)	0.521	0.619	0.633 ($\lambda=0.98$)	6/7
Viverridae	34	0.540 ^c	0.442	0.441 ($\lambda=1.00$)	0.620	0.900	0.900 ($\lambda=1.00$)	-

^a similar result in Harcourt and Schreier (2009)

^b similar result in Kamilar et al. (2012)

^c similar result in Gittleman (1985)

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509 Figure 1. Body mass and maximum (absolute) latitude of the geographical range
510 on terrestrial mammals used in this study from PanTHERIA (Jones et al. 2009).
511

512 Figure 2. p values for the correlation between absolute maximum latitude and body mass (M)
 513 in mammal species, with a) stepwise exclusion of species *below* a latitude threshold, b)
 514 stepwise exclusion of species *above* a latitude threshold, analysed with Ordinary Least
 515 Squares (OLS), i.e. without accounting for the phylogenetic structure of the dataset, and with
 516 Phylogenetic Generalized Least Squares (PGLS with fixed $\lambda=1$), i.e. accounting for the
 517 phylogenetic structure; all significant correlations were positive. Grey dots indicate the
 518 sample size of the species set.

519 Figure 3. Example for visualising the data on the level of a) an order (Rodents), b) a suborder
 520 (Hystricomorpha), and c+d) different Families. Examples were specifically selected to
 521 visually fit to Bergmann's rule.

522 Figure 4. Example for visualising the data on the level of a) a (sub)order (Artiodactyla), b+c)
 523 different Families (Cervidae, Bovidae), and d) different Subfamilies. Note that examples were
 524 specifically selected to visually fit to Bergmann's rule.

Appendix I: Translation of several selected passages from Bergmann's original work (Bergmann 1848).

The work is freely available on the internet, e.g. via <http://www.bsb-muenchen-digital.de>. The text is written in the tradition of the time, with what would be received today as a lot of deviating narrative tracks. One of these customs was that a single author would use the word "we" when referring to himself (meaning "the reader and me"). A major proportion of the text deals with relationships between size and heat production/heat loss, which is not the focus here. The aim of this translation (which was not done by a professional translator) was only to highlight Bergmann's original approach to what has to be known as "Bergmann's Rule".

Words I (MC) added myself for clarity are marked by [brackets]. Other translations of Bergmann's original work are available in James (1970).

On the relationship of the heat economy of animals to their size

Carl Bergmann

Re-printed from the "Göttinger Studien 1847"
Göttingen, Vandenhoeck and Ruprecht 1848
(116 pages)

[In the beginning, Bergmann explains scaling differences of volume and surface in relation to body mass and how this should impact large and small homeotherms in relation to their susceptibility to cold climates]

Page 46:

We see the possibility of very different sizes of homeothermic animals in the same climate; this possibility is given by modifications of the factors of heat production and those of heat loss regardless of climate (climate we consider as given). The breadth of these modifications, which are given by the [organismal] organisation, will decrease the more similar animals are in their organisation. Such different sizes, as they are present in the extremes of different climates, especially in the tropics, require great differences in [organismal] organisation, as between colibri and elephant.

If we had two animal species, which were different only in terms of their size, then all these modifications would be ruled out: the relative geographic distribution of these two species would be determined by size. Whatever their absolute habitat, the smaller species would need a warmer, the larger species a colder climate.

A correctly identified zoological [phylogenetic] position of an animal represents the majority of similarities with closely related animals.

If there were genera, the species of which differed – as far as possible (a limitation of this option is further elaborated in the appendix) – only by size, then the smaller species would consistently require a warmer climate, in fact exactly according to the degree of their size difference.

Maybe such a degree of similarity does not exist or is rare. If the species differ, apart from their size, also in other characteristics of organisation and life style, which influence heat production and heat loss, and therefore influence the climate appropriate for this species, then the order of geographic distribution, which would occur without these characteristics, may be disturbed.

It is important to distinguish, in these possible disturbances (which stem from food, skin cover, life style), two cases. The differences in organisation, by which these are caused, can

- completely or partially be distributed in a manner, among the species of a genus, that is linked to body size
- or they can be completely independent of body size.

The first case could then have the effect that smaller species are all even yet more susceptible to cold than they would be (compared to larger species) due to their body size, or the opposite would be true (depending on whether the additional systematic effect that is linked to body size favours larger or smaller species).

In the second case, if these additional differences in organisation are not linked to body size, but are – with respect to body size – completely arbitrary, then according to the rules of probability, when assessing a larger number of cases, many cases of larger species should be more and smaller species less susceptible to cold than expected from their relative size, but in the same number of cases the opposite should occur, with larger species even less susceptible, and smaller species even more susceptible to cold than they would be anyhow because of their size. In other words: because, apart from chance factors, a constant factor (the relationship of cold susceptibility and size) is given, the smaller species should, on average, look for a warmer climate. This appears to be true, I think, in the following [I think this is a reference to a much later section where Bergmann actually delivers evidence for this pattern from many bird genera]. Yet it remains possible that what happens in nature is a mixture [of these cases], namely that some differences [in organismal organisation] are linked to size, and some are not. It is even conceivable that differences, which are linked to size, favour partly the larger and partly the smaller species, and thus compensate for their effect, so that only the effect of chance (apart from that of the constant factor of the volume-surface-relationship) remains detectable.

[The majority of text that follows now deals with evidence for these hypotheses, focussing on birds – information on which was taken mainly from one other textbook, from Naumann. This is then summarized:]

Page 90-91:

We did not take climate, but the [organismal, i.e. here phylogenetic] organisation as a fixed starting point, and found that animals of similar organisation [defined by phylogenetic relationship] reveal the influence of size insofar as, of all the different species of a genus, the smaller ones are more often more susceptible to cold than the larger ones and have warmer habitats.

Though it is impossible to use the complete, available material and use certain data for calculations, and though a finer mathematical approach of this matter would appear wasted effort [we, my co-authors and me, beg to differ], we nevertheless believe that our hypothesis can be confirmed sufficiently by the following remarks.

If we compare those genera, for which we only count two species, or where we can only compare the distribution of two species, then those cases are the majority where the smaller species lives more to the South, or where it proves more susceptible [to cold] based on its migration timing. A number of such genera we dismiss as questionable [now follows a list of these genera, and a short discussion of individual cases].

Genera with three species. The assessment is more complicated here [in a footnote, Bergmann here explains the alternative approach that one could sum up the results of all two-species comparisons one could do within genera of more than two species, and sum up the results of all these individual two-species comparisons – he evidently did this in several cases]. Only few cases are as simple as those just stated, i.e. so that the species of a genus form a series of habitats when ordered by their size. A part of these genera we call “mixed”; these are those where two species are as expected, but the third is not. One can distinguish the less abnormal cases, in which the intermediate-sized species does not show the expected pattern with respect

to one of the other two [he gives examples], and the more abnormal cases, in which the smallest or largest does not sort as expected when compared to the other two [he gives examples, and discusses several genera in detail].

Thus, already the genera with two or three species yield not unimportant evidence. Therefore, we can refrain from discussing the remaining material in depth, which would take a lot of space. The expected relationships are still also in the majority in genera with four and more species [he gives examples]. About the genera with more than five species, we think we can say with certainty that on average, the smaller species live in the more southern habitats.

[Bergmann finishes with a word of caution regarding his own use of his major source, the Naumann book]

Page 94:

Finally, a word on the correctness of reporting from Naumann's work. I [note that here where Bergmann describes an action that the reader could not participate in, he uses the word "I"] could not just refer the reader to that work, because the audience of this study is not the same as that of that worthy work, and because not everyone would be inclined to check the correctness of our statements in this way [by comparing against the original text]. I could also not have the whole of Naumann's reports on the home range of birds reprinted here. I could only, it seems to me, do no different than sum up in brief words what appeared to me the result of Naumann's reports. Now, this includes a danger. Even though I attempted to remain faithful [to the original text], and would have liked to use the author's own words always (as I have often done), I nevertheless need to admit the possibility that, dealing with the often ambiguous and complex data, my own prevailing viewpoint had an influence on my interpretations, so that I might have less heeded that which would have been an abnormality [not supporting the hypothesis], than those instances which were in favour of normal cases [supporting the hypothesis]. Therefore, any thorough re-testing must be welcome. By the way, I am firmly convinced that the result must always be, on the whole, as I found it, even if a case I thought normal [supporting the hypothesis] proves to be dubious, or if a case I thought dubious proves to be abnormal [contradicting the hypothesis].

[the text is finished with an appendix on other relationships of organismal organisation and body mass, in particular on characteristics of muscle fibres]

Appendix II: Potential combinations of results when applying statistical analyses without and with considering the phylogenetic structure of the sample, and relevant interpretations.

Note that for a full understanding of biological patterns, repeated analyses of the pattern in question should be performed at different phylogenetic levels, because patterns may differ depending on the number of speciose groups with closely related species. The shaded area represents the typical shape of the data cloud. The black and grey symbols represent species of two distinct taxonomic groups, linked by the phylogenetic tree with the basal node represented by the square. Interrupted regression line represents result from OLS, black regression line the result from PGLS. Note that in interpreting the results of comparative analyses, a formal distinction between convergence/homoplasy and homology/symplesiomorphy cannot be made based on the analytical results, but must be made based on the specific characteristics of the data in question.

Result combination of statistical analyses		Schematic data pattern	Interpretation
1	OLS not significant PGLS not significant		There is no significant relationship between A and B in the whole dataset or within a larger number of closely related taxonomic groups. This result does not exclude the existence of an A-B relationship at narrower taxonomic levels (e.g., in the two taxonomic groups represented by two data points each on the left-hand side of the graph, there is a positive A-B relationship in the black, and a negative A-B relationship in the grey group).
2	OLS significant PGLS not significant		This is the typical example of a type I error in statistical analyses using only OLS, because a significant result is given where there is, in reality, none. But just because this is a type I error, the result should not be dismissed directly. The relationship between A and B that leads to significance in OLS only occurs at the basal node. Within the more closely related taxa, the relationship does not exist and should therefore not be considered a general “rule” (not a symplesiomorphy, not an apomorphy, not a homoplasy). However, the fact that there is no significance in the PGLS analysis does not mean the question why this relationship occurs at the level of the basal node need not be answered. If possible, this pattern could be analysed by expanding the dataset so that multiple nodes on the level of the basal one in this dataset are included. Without such further analyses, the hypothesis that the pattern at the basal node is real must not be excluded. The pattern at the basal node may well represent a case of adaptation, the statistical significance of which cannot be demonstrated because of a lack of other taxonomic groups that share this pattern, yet it may still be functionally relevant. Note that in this example, the SE (or the confidence interval) for the intercept will be larger in PGLS than in OLS, whereas the opposite will be the case for the slope, suggesting that major diversification events are linked to a modification of the intercept.

3a			<p>The same relationship that occurs at the basal node also occurs within more closely related taxa. At all levels, speciation appears to follow the A-B relationship. This may be evidence for convergence/homoplasy, or for a symplesiomorphy that cannot be modified by speciation events. Note that in this case, the SE (or the confidence interval) for the intercept and the slope should be similar in OLS and PGLS.</p>
3b	<p>OLS significant PGLS significant</p>		<p>Although the A-B relationships at the basal node and within more closely related taxa are qualitatively similar, the two patterns differ, which will also lead to different mathematical equations derived from OLS and PGLS (in allometries, this would translate into different exponents, in this specific example with a shallower slope in PGLS than in OLS). When considering allometric exponents, therefore, this case could also be considered a special case of a type I error. The evident interpretation is that the A-B relationship does not follow a universal rule, but follows different rules at different levels of taxonomic organisation, indicating convergence/homoplasy or symplesiomorphy constrained by other effects of speciation. Note that analysing the A-B relationship in narrower taxonomic samples, such as the black species only, may turn the pattern into one as shown in examples 2 or 3a. Note that in this example, the SE (or the confidence interval) for the intercept will be larger in PGLS than in OLS, whereas the opposite may be the case for the slope, suggesting that major diversification events are linked to a modification of the intercept.</p>
3c			<p>Although the A-B relationships at the basal node and within more closely related taxa are qualitatively similar, the two patterns differ, but not, as in 3b, with a systematic difference in slope. In total, this might result in similar mathematical equations derived from OLS and PGLS (in allometries, this would translate into similar exponents, unless analyses are repeated at lower taxonomic levels). The evident interpretation is that the A-B relationship does not follow a universal rule, but follows different rules at different levels of taxonomic organisation, indicating convergence/homoplasy or symplesiomorphy modified by other effects of speciation. Note that analysing the A-B relationship in narrower taxonomic samples, such as the black species only, may turn the pattern into one as shown in examples 2 or 3a. Note that in this example, the SE (or the confidence interval) for the intercept will be larger in PGLS than in OLS, and a difference in this measure for the slope will be of similar magnitude between the analyses, suggesting that diversification events are linked to a modification of both intercept and slope.</p>

4	<p>OLS not significant PGLS significant</p>		<p>This is the typical example for a type II error in statistical analyses using only OLS, because a significant result is not detected. This can also be considered a special case of example 3b, where a pattern is evident among closely related taxa, but at more basal taxonomic levels, the pattern does not apply at all. This also represents evidence for convergence/homoplasy or a symplesiomorphy, but major speciation events need not follow the pattern. It indicates that large-scale variation in organismal organisation is not subject to the pattern, but that similarly-designed organisms are. Note that analysing the A-B relationship in narrower taxonomic samples, such as the black species only, may turn the pattern into one as shown in examples 2 or 3a.</p> <p>Note that in this example, the SE (or the confidence interval) for the intercept will be larger in PGLS than in OLS, whereas the opposite will be the case for the slope, suggesting that major diversification events are linked to a modification of the intercept.</p>
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