Oikos

**OIK-00463**

Clauss, M., Dittmann, M. T., Müller, D. W. H., Meloro, C. and Codron, D. 2013. Bergmann's rule in mammals: a cross-species interspecific pattern. – Oikos 000: 000–000.

# Appendix 1

## Translation of several selected passages from Bergmann's original work (Bergmann 1848).

The work is freely available on the internet, e.g. via <www.bsb-muenchen-digital.de>. The text is written in the tradition of the time, with what would be received todays 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 (meaing '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 come to 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]

Bergmann, C. 1848. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Abgedruckt aus den Göttinger Studien 1847. – Vandenhoeck and Ruprecht.

James, F. C. 1970. Geographic size variation in birs and its relationship to climate. – Ecology 51: 365–390.

# Appendix 2

## 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 disctinction 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 |
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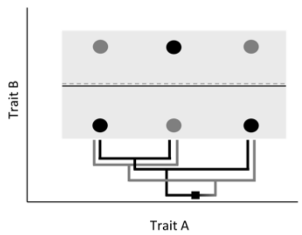
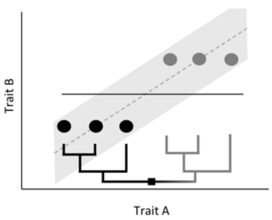
| **1** | OLS not significant<br>PGLS not significant |  | There is no significant relationship between A and B in the whole dataset or within a larger number of closely related taxonomic groups. This result does not exclude the existence of an A–B relationship at narrower taxonomic levels (e.g. in the 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<br>PGLS not significant |  | This is the typical example of a type 1 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 1 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 |

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| | | | 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. |

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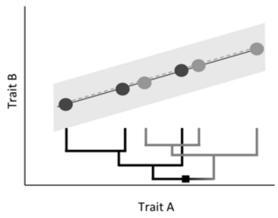
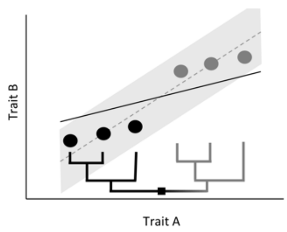
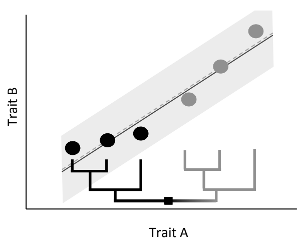
| **3 a** | |  | The same relationship that occurs at the basal node also occurs within more closely related taxa. At all levels, speciation appears to follow the A–B relationship. This may be evidence for convergence/homoplasy, or for a symplesiomorphy that cannot be modified by speciation events. Note that in this case, the SE (or the confidence interval) for the intercept and the slope should be similar in OLS and PGLS. |
| **3 b** | OLS significant<br>PGLS significant |  | 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 1 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. |
| **3 c** | |  | 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 repated 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. |

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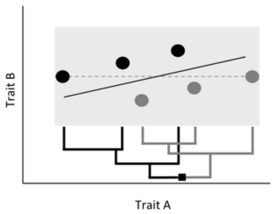
| **4** | OLS not significant<br>PGLS significant |  | This is the typical example for a type 2 error in statistical analyses using only OLS, because a significant result is not detected. This can also be considered a special case of example 3b, where a pattern is evident among closely related taxa, 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.<br>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. |