

Vallecillo, S., Brotons, L. & Osborne, P. E. (under review) Geographical variation in ecological constraints on species distributions along a gradient of population aggregation.

Vallecillo, S., Brotons, L. & Thuiller, W. (2009) Dangers of predicting bird species distributions in response to land-cover changes. *Ecological Applications*, 19, 538–549.

Vallecillo, S., Brotons, L. & Possingham, H. (to be submitted) Minimizing future threats when setting conservation targets for bird species with different response to fire disturbance.

Edited by Núria Roura-Pascual

thesis abstract

On the biogeography of vertebrate body size: ecological and evolutionary insights from assemblage-level patterns

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Biogeographers, evolutionary biologists and ecologists have suggested a number of ecogeographical and evolutionary “rules” to describe general trends in the variation of biological attributes across broad spatial and temporal scales. This includes the latitudinal gradient in species richness, as well as Gloger’s, Bergmann’s, Allen’s, Cope’s, Jordan’s, Foster’s and Rapoport’s rules (see Lomolino et al. 2006 or Gaston et al. 2008 for details). Nonetheless, many of these “rules” were originally proposed with insufficient empirical evidence and have reiteratively been called into question. Recent investigations have found exceptions to the proposed patterns and suggested that most of the “rules” are invalid or would need to be reconsidered (see e.g. Ashton 2001).

Under this historical framework, the study of Bergmann’s rule is a paradigmatic example. In 1847, Karl Bergmann suggested that body size plays a major role in determining the geographic distribution of mammals and birds; large-bodied species are favoured in colder climates because of their better heat conservation (lower surface-to-volume ratio). As with the rest of ecological and evolutionary “rules”, both the original pattern and mechanism have not been exempt from criticism. Interestingly, however, after more than 160 years and despite controversies around its validity, Bergmann’s rule still attracts special attention among scientists (Blackburn et al. 1999, Ashton et al. 2000, Meiri & Dayan 2003, Blackburn & Haw-

kins 2004, Rodríguez et al. 2006). This stands in contrast to some other “rules” (e.g. Gloger’s, Allen’s or Jordan’s), whose interest largely remains historic or anecdotic. Such longstanding fascination with Bergmann’s rule is undoubtedly related to the importance of organismal body size in determining physiological, ecological and evolutionary processes.

Along these lines, the debate around the generality of Bergmann’s rule has long been fostered by Ray’s (1960) and Lindsey’s (1966) pioneering observations that some ectothermic organisms also displayed intra- and interspecific body size clines as a response to environmental gradients. Apparently, these findings required alternative explanations to the ones offered for endotherms (Cushman et al. 1993). Since then, researchers have tried to identify ecological or evolutionary mechanisms accounting for geographic body size gradients in ectotherms. A critical step before searching for underlying mechanisms is indeed examining what the patterns look like in nature. Because Bergmann’s rule was originally formulated for endothermic vertebrates, numerous studies have reported the existence of body size gradients in mammals and birds (e.g. Blackburn et al. 1999, Ashton et al. 2000, Meiri & Dayan 2003 and references therein), whereas the geographical variation of body size for many ectothermic organisms remains mostly unknown (but see below).

Gaston et al. (2008) recently identified three approaches to studying spatial patterns in biological traits in general and Bergmann's rule in particular: intraspecific, interspecific ("cross-species") and assemblage-based. Although Bergmann's rule was conceived as an interspecific pattern, this version of the rule has received limited attention since Rensch (1938) and Mayr (1956) (cited in Blackburn et al. 1999) reformulated the original hypothesis at the intraspecific level. Beyond the contribution to the autoecology of species provided by classic intraspecific studies, the search for geographic patterns in interspecific body size can generate insights into the evolutionary and ecological mechanisms structuring faunal assemblages.

In this PhD thesis we applied an assemblage-based approach to document biogeographic patterns of body size in regional faunas (Western Palearctic, Nearctic and Neotropics) for different vertebrate groups (mammals, amphibians and reptiles). Also, we evaluated the support for several hypotheses proposed to explain Bergmann's rule so far, namely: heat conservation, migration ability, primary productivity, seasonality, habitat availability, size-dependence and water availability (see Olalla-Tárraga et al. 2006, 2009, 2010, Olalla-Tárraga & Rodríguez 2007 and Rodríguez et al. 2008 for details). Aimed at generating insights into the energetic and physiological mechanisms, we specially focused the analyses on two ectothermic vertebrate groups: amphibians and reptiles.

Overall, we used a novel methodological approach to the study of broad-scale body size gradients. Interspecific analyses have traditionally adopted a "cross-species" approach by treating each species as an independent datum and using bivariate scatter-plots to examine covariation of body size and latitude (or occasionally temperature) across species. This method has also been termed the "midpoint approach" (Blackburn & Hawkins 2004) since it involves obtaining a single spatial descriptor to characterize the distribution of each species (usually the latitudinal midpoint of its geographic range) and then plotting these midpoints against species' body sizes. In contrast, the

assemblage-based approach adopted in this thesis has explored geographical patterns within grids covering the study regions and combined the species' presences/absences in the cells with their body sizes to obtain cell-mean body size values (usually log-transformed geometric means) (see also Ruggiero & Hawkins 2006). Blackburn and Hawkins (2004) named this the "community approach", because such investigations examine the spatial distribution of summary statistics for body size across faunal assemblages (grid cells) of a particular biogeographic region. Accordingly, the units of analysis in cross-species approaches are single species, whereas in assemblage-based methods they are measures of average body size of all the species occurring within grid-cells. Bearing in mind that the distinction between cross-species and assemblage-based analyses may not be trivial in terms of interpreting patterns and processes, we paid special attention to discussing the implications and methodological disparities between methods (Olalla-Tárraga et al. 2010). Because cross-species approaches ignore the geographical structure in the data by reducing the multidimensional nature of geographic ranges to single values, we suggested examining interspecific body size gradients using spatially explicit assemblage approaches (i.e. using complete geographic information). Cross-species and assemblage-based methods may converge to similar results only when distribution ranges for the whole set of analysed species within the clade are either extremely restricted or mostly unknown, but that is not the case when species ranges are well known and comprise enough environmental variation (Olalla-Tárraga et al. 2010).

Our assemblage-based analyses involved compiling biological and distributional information of species and subsequently using multivariate analysis techniques complemented with spatial statistic methods to evaluate the spatial autocorrelation structure. We used AIC-based model selection procedures to evaluate the relative support for each of the hypotheses that have been suggested to account for broad-scale body size gradients. The use of model selection approaches based on information theory is rapidly gaining

support in ecology and biogeography as an alternative to hypothesis testing and model simplification methods such as stepwise regression (Stephens et al. 2007). Additionally, we incorporated a Phylogenetic eigenVector Regression (PVR) method (Diniz-Filho et al. 1998) to estimate the phylogenetic signal in the data and partition the phylogenetic and ecological components of the interspecific variation in body size. Thus, we controlled for two potential sources of pseudoreplication in the data (spatial and phylogenetic), while simultaneously considering the distribution of species in a geographic and phylogenetic framework (Diniz-Filho et al. 2007, see below). Notably, jointly dealing with spatially and phylogenetically structured units of analysis is an issue of increasing concern in biogeographic publications (e.g., Freckleton & Jetz 2009, Kühn et al. 2009).

We found that the geographical distribution of body size is markedly idiosyncratic and Bergmann's physiological mechanism cannot explain the observed size clines everywhere. For mammals in the northern Nearctic region, we detected clear body size gradients and a negative relationship between mean body size and environmental temperature variation (Rodríguez et al. 2008). However, the strong association between size and temperature is weaker and eventually disappears as we move towards southern latitudes in the Nearctic and Neotropical regions. Interestingly, our analyses for the whole non-volant mammal fauna in the Western Hemisphere distinguished an environmental temperature threshold around 11°C, above which patterns consistent with Bergmann's rule are no longer evident. The heat conservation mechanism was found to be an explanation solely for body size patterns below this temperature threshold, whereas the habitat availability hypothesis, through the interaction between topography and macroclimate, became more important in tropical regions (Rodríguez et al. 2008).

Environmental energy availability, linked to the heat conservation hypothesis, also played a leading role in determining the geographic distribution of body size in ectothermic vertebrates. Geographic body size gradients of squamate reptile assemblages in the Nearctic and, especially, in

the Western Palearctic displayed a clear correlation with potential evapotranspiration (PET), a joint measure of temperature and solar radiation in the environment (Olalla-Tárraga et al. 2006). Interestingly, this pattern was conflicting for lizards and snakes as lizards increased in size northwards whereas snakes decreased in size. We concluded that Bergmann's physiological mechanism is insufficient to explain body size patterns in animals whose heat balance does not only rely on heat conservation, but more importantly on heat gain. We suggested that large thermoregulating ectothermic vertebrates (e.g. snakes) might not be able to warm their bodies rapidly enough to meet their needs in the narrow activity windows available in cold environments. In other words, large snake species would be limited by a combination of both intrinsic (i.e. reduced heating rates) and extrinsic (i.e. lower environmental energy availability) factors in colder climates. As a result, the detection of body size–temperature relationships in thermoregulating ectotherms would be conditioned by a trade-off between heat gain and heat conservation that largely depends on relative organismal size. Our findings also identified the importance of the behavioural control on thermal interactions when analysing body size trends in ectotherms (Olalla-Tárraga et al. 2006).

On the basis of our findings for squamate reptiles, we proposed the heat balance hypothesis as a general explanation to account for the patterns exhibited by both thermoregulators (i.e. animals with good thermoregulating abilities) and thermoconformers (animals whose body temperatures fluctuates more closely to ambient temperature) (Olalla-Tárraga & Rodríguez 2007). For thermoregulators, this hypothesis coincides with the heat conservation mechanism proposed by Bergmann for endotherms, and can also be extended to ectotherms that are able to control body temperature effectively through physiological and/or behavioural adjustments. Among thermoregulating ectotherms, the relative size of an organism also plays a role in determining the occurrence of patterns consistent with Bergmann's rule (Olalla-Tárraga et al. 2006). Conversely, among thermoconformers, smaller organisms would be favoured

in cold areas because their greater surface-to-volume ratios allow them to have shorter heating times. Using data for amphibian faunas in the Nearctic and Western Palearctic, we tested the heat balance hypothesis along with five other hypotheses that have a possible influence on body size gradients (Olalla-Tárraga & Rodríguez 2007). While anurans are able to achieve some control over heat exchange with the environment, urodeles are thermoconformers and their body temperatures closely parallel variations in the thermal environment. Hence, according to the heat balance hypothesis, we expected size increases towards colder areas in anurans and size decreases towards warm territories in urodeles. We found consistent body size gradients across both biogeographic regions and confirmed the predictions of the heat balance hypothesis, i.e. anurans followed a marked Bergmann's rule gradient and urodeles exhibited the reverse trend. Moreover, PET was the strongest predictor of mean body size in both regions and each group responded differently to ambient energy as expected from the heat balance hypothesis. These results suggest that the thermoregulatory abilities of anurans would allow them to reach larger sizes in colder climates by optimizing the trade-off between heating and cooling rates, whereas a lack of such strategies among urodele faunas would explain why these organisms tend to be smaller in cooler areas (Olalla-Tárraga & Rodríguez 2007).

Because our studies of amphibians and reptiles had been restricted to the Holarctic, which may limit an extension of their conclusions to warmer tropical climates, we investigated body size gradients of anurans in a Neotropical biome to test the validity of previous generalizations. We addressed this question using data from the most extensive woodland-savanna in South America: the Brazilian Cerrado (Olalla-Tárraga et al. 2009). Anurans in this biome showed clear body size patterns, with the smallest mean sizes in the Southwest bordering the Pantanal, a wetland biome, and the largest sizes in the drier areas of the Northeast, near the limits of the Caatinga semi-arid region. Water deficit was the best predictor of this gradient and the relationship remained

consistent even in the presence of a strong phylogenetic signal in body size variation. That is, species larger than expected by their phylogenetic relatedness were more frequently found in drier environments, whereas species smaller than expected were mostly distributed in low-water-deficit areas. This suggests a selective advantage for larger anurans under high water deficit conditions in tropical regions. The seasonal climate of the Cerrado is characterized by a six-month period of dry and hot conditions, which imposes serious hydric constraints on its anuran fauna. Amphibians have little resistance to cutaneous evaporative water loss and are particularly sensitive to long droughts. Since water loss is positively correlated with surface-to-volume ratios in anurans, a simple mechanism to reduce desiccation is decreasing the surface-to-volume ratio by increasing body size. Our results were consistent with the water availability hypothesis which, coupled with previous findings, suggests that the major determinant of interspecific body size variation in anurans switches from energy to water towards the equator. In a context of latitudinal variation in the relative importance of energy and water from temperate to tropical regions, anuran body size gradients may reflect effects of reduced surface-to-volume ratios in larger species to control both heat and water balance (Olalla-Tárraga et al. 2009).

In sum, this PhD thesis shows how the assemblage approach, complemented with a phylogenetic comparative method, can be useful for exploring both ecological and evolutionary mechanisms associated with Bergmann's rule in a spatially explicit context. We have detected remarkable broad-scale body size gradients for both endothermic and ectothermic terrestrial vertebrates and contributed to generate insights into potential underlying processes. Bergmann's physiological mechanism cannot explain geographic body size variation everywhere and in every taxon. Alternatively, we have proposed a complementary explanation that may be able to account for assemblage-level patterns of body size in both endotherms and ectothermic organisms with limited capabilities for internal heat production. Even so,

a general explanation for Bergmann's rule still remains elusive. We emphasize the need for a pluralistic search for mechanisms that contributes to avoid the traditional conflation between pattern (increasing body size towards colder regions) and mechanism (heat conservation) that is traditionally associated with the study of Bergmann's rule.

Acknowledgements

I am very grateful to Prof. Miguel Á. Rodríguez for his continuous support and for injecting such a level of enthusiasm and motivation to my PhD thesis. I also specially appreciate the valuable contributions of Professors Luis M. Bini, Jose A.F. Diniz-Filho and Bradford A. Hawkins to this thesis.

References

- Ashton, K.G., Tracy, M.C., & de Queiroz, A. (2000) Is Bergmann's rule valid for mammals? *American Naturalist*, 156, 390-415.
- Ashton, K.G. (2001) Are ecological and evolutionary rules being dismissed prematurely? *Diversity and Distributions*, 7, 289-295.
- 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.
- Blackburn, T.M., & Hawkins, B.A. (2004) Bergmann's rule and the mammal fauna of northern North America. *Ecography*, 27, 715-724.
- Cushman, J.H., Lawton J.H., & Manly B.F.J. (1993) Latitudinal patterns in European ant assemblages: variation in species richness and body size. *Oecologia*, 95, 30-37.
- Diniz-Filho, J.A.F., Ramos de Sant'Ana, C.E., & Bini, L.M. (1998) An eigenvector method for estimating phylogenetic inertia. *Evolution*, 52, 1247-1262.
- Diniz-Filho, J.A.F., Bini, L.M., Rodríguez, M.Á., Rangel T.F.L.V.B., & 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.
- Freckleton, R.P., & Jetz, W. (2009) Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. *Proceedings of the Royal Society B*, 276, 269-278.
- Gaston, K.J., Chown, S., & Evans, K.L. (2008) Ecogeographical rules: elements of a synthesis. *Journal of Biogeography*, 35, 483-500.
- Kühn, I., Nobis, M.P., & Durka, W. (2009) Combining spatial and phylogenetic eigenvector filtering in trait analysis. *Global Ecology and Biogeography*, 18, 745-758.
- Lomolino, M.V., Sax, D.F., Riddle, B.R., & Brown, J.H. (2006) The island rule and a research agenda for studying ecogeographic patterns. *Journal of Biogeography*, 33, 1503-1510.
- Lindsey, C.C. (1966) Body sizes of poikilotherm vertebrates at different latitudes. *Evolution*, 20, 456-465.
- Meiri, S., & Dayan, T. (2003) On the validity of Bergmann's rule. *Journal of Biogeography*, 30, 331-351.
- Olalla-Tárraga, M.Á., Rodríguez, M.Á., & Hawkins, B.A. (2006) Broad-scale body size patterns in squamate reptiles of Europe and North America. *Journal of Biogeography*, 33, 781-793.
- Olalla-Tárraga, M.Á., & Rodríguez, M.Á. (2007) Energy and interspecific body size patterns of amphibian faunas in Europe and North America: anurans follow Bergmann's rule, urodeles its converse. *Global Ecology and Biogeography*, 16, 606-617.
- Olalla-Tárraga, M.Á., Diniz-Filho, J.A.F., Bastos, R.P., & Rodríguez M.Á. (2009) Geographic body size gradients in tropical regions: Water deficit and anuran body size in the Brazilian Cerrado. *Ecography*, 32, 581-590.
- Olalla-Tárraga, M.Á., Bini, L.M., Diniz-Filho, J.A.F., & Rodríguez, M.Á. (2010) Cross-species and assemblage-based approaches to Bergmann's rule and the biogeography of body size in *Plethodon* salamanders of Eastern North America. *Ecography*, 33, doi:10.1111/j.1600-0587.2010.06244.x
- Ray, C. (1960) The application of Bergmann's and Allen's rules to the poikilotherms. *Journal of Morphology*, 106, 85-108.
- Rodríguez, M.Á., Olalla-Tárraga, M.Á., & 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.
- Ruggiero, A., & Hawkins, B.A. (2006) Mapping macroecology. *Global Ecology and Biogeography*, 15, 433-437.
- Stephens, P.A., Buskirk, S.W., & Martínez del Rio, C. (2007) Inference in ecology and evolution. *Trends in Ecology and Evolution*, 22, 192-197.

Edited by Camilla Fløjgaard