

ZOOGEOGRAPHY: AN ECOLOGICAL PERSPECTIVE

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Summary

Zoogeography studies distribution patterns of animal species and processes. This chapter presents some of the main topics covered by ecological zoogeography, involving analysis of the specific ecology of organisms on relatively small spatial and temporal scales. It begins by examining some of the most intriguing zoogeographical patterns concerning animal body size, for which Bergmann and Allen formulated two famous “ecogeographical rules” which, despite being heavily criticized, are now being re-evaluated; and also cover Rapoport’s rule, stating that that species’ latitudinal ranges are generally smaller at lower than at higher latitudes. It then highlights that understanding the observed distribution of animal species is a key task for

zoogeographers. Species conceptualization and delimitation are vital to reach that goal. Recent advances in DNA studies have revealed previously undetected species, profoundly changing our view of animal distribution. Some species (endemisms) have narrow ranges, others are widespread. Factors such as biogeographical corridors, isolation history, glacial or postglacial events, abiotic and biotic ecological factors and also human impact all influence distribution patterns. Active movement of organisms over short temporal scales also influences the composition of animal assemblages. Migration, one of the most striking phenomena in the animal world, implies a seasonal change in species occurrence in many regions of the world. Science is gradually making important steps forward in identifying the factors that trigger and control migration and orientation. Not only is zoogeography intellectually exciting, it also has important conservation applications because it is vital to understand species ranges for biodiversity management. Besides recording species distribution, state-of-the-art modeling techniques can help predict species range even when little observational information is available, thus aiding species management and conservation. We conclude the chapter by summarizing the biogeographical implications of the massive species extinction occurring on Earth, and discuss global warming as one of the main factors impacting biodiversity and altering species occurrence and distribution. Finally, we use the case of Lessepsian colonization, i.e. the colonization of the Mediterranean Sea by tropical species following the opening of the Suez Canal, as a striking example of human influence on zoogeographical patterns.

1. What Is Ecological Zoogeography

Biogeography studies the patterns of distribution of biological systems, processes or characteristics at several spatial and temporal scales. Spatial scales under analysis span over a wide range, including genes, organisms or groups of organisms and ecosystems or biomes.

Likewise, temporal scales examined in biogeography also vary greatly. Temporal patterns relevant for biogeographical studies span from million years to seasonal movements.

Large-scale phenomena such as continental drifts, today explained by modern plate tectonics, have had undoubtedly a huge effect on biodiversity patterns and species distributions, both those currently observed and those occurred in the past and inferred from fossils. Macroevolutionary patterns, mass extinctions or adaptive radiations leading to many taxonomical groups can only be interpreted when a long temporal scale is considered.

Today we also know that evolutionary processes can be much faster than previously thought; besides, on smaller scales distributional patterns of organisms are often influenced by changes occurred in historical times (such as e.g. land use change, or current human-driven climate change), or natural cycles covering short times such as seasonal or daily migrations.

Classically, biogeography is split into two main branches, historical biogeography and ecological biogeography (Cox and Moore, 2010).

Historical biogeography examines long-term processes, taking place over evolutionary or geological times, in often large geographical areas, concerning large taxonomical groups or taxa that are now extinct. The historical factors leading to the current distribution of a certain taxon, its history of radiation and colonization, the identification of the taxon's closest relatives and the analysis of their occurrence all form aspects analyzed by historical biogeographers. In most cases their interpretation would be impossible if long-term processes such as continental drift or the alternation of glacial and interglacial phases were not taken into account.

The scale of analysis of ecological biogeography, instead, is generally smaller in time and space. It often looks at species, or populations, rather than larger taxonomical units, and is more concerned with shorter times and intracontinental, landscape or habitat scales. Ecological biogeography looks at how abiotic and biotic forces can shape, or influence, a species' range, species replacements along altitudinal or latitudinal gradients, species richness in different habitats, etc.

Both historical and ecological biogeography take into account forces, events and processes which as a whole determine micro- and macroevolutionary changes: we might say that biogeography is the discipline analyzing the effect of space on evolutionary processes.

Zoogeography is the branch of biogeography dealing with distributional patterns of animals. In the past, animals have been often considered in historical analyses, whereas ecological biogeography has focused more on plants, though of course today this distinction has completely disappeared. As Cox and Moore (2010) put it, plants are static and their life traits more explicitly linked with the ecological features of the place where they live, a fact that helps ecological analyses. On the other hand, plants leave fossils more rarely than do animals, because the latter often possess bones (vertebrates), exoskeletons or other hard parts (from foraminifera to mollusks, crustaceans, insects, echinoderms, etc.) that are more likely to fossilize. The analysis of fossils has been a major approach to the study of historical biogeography.

The history of zoogeography includes the most prominent scientists of the last two-three centuries, scholars who gave an immense contribution to modern biology and ecology. Although no space is available here to even briefly review their work, it is important to remind the reader that modern zoogeography builds upon the outstanding work of people such as Alexander von Humboldt, Philip Sclater, Charles Darwin, George Simpson and Philip Darlington, to mention some; but it is Alfred Russel Wallace, the author in 1876 of *“The Geographical Distribution of Animals, With a Study of the Relations of Living and Extinct Faunas As Elucidating the Past Changes of the Earth's Surface”*, who deserves to be regarded as the “father” of zoogeography.

In this chapter we will focus on ecological zoogeography. The subject is so wide that it would be impossible to cover it thoroughly and a selection of topics is inevitable. Therefore, we will only focus on the main phenomena and processes regarding distributional patterns of animals based on the analysis scale typical of ecological zoogeography; among them, we will look at those that mostly contribute to the current scientific debate.

We will start our review by examining three of the best known “ecogeographical rules”. Although, as we will see, most of them are poorly supported by sufficient scientific data or remain largely controversial, the impact they have had on classical zoogeography is considerable. Particularly, the first two cases we will briefly cover are of special interest for the ecological zoogeographer because they look at the relationships between an animal’s size and the place where it occurs, i.e. the climatic constraints it faces.

2. Ecogeographical “Rules”

One of the most intriguing aspects of biogeography is represented by the recurrence of patterns concerning animal distribution or morphology which may be linked with factors such as latitude, altitude or climate. The fact that such patterns are found in a range of different organisms has often been interpreted as a general law, leading to the formulation of “rules”. However, when such rules were first proposed they relied on little empirical evidence, so that over time they have been questioned, corrected or revisited in the light of more robust, quantitative datasets and more effective analytical approaches (Olalla-Tàrraga, 2010). Several of these “rules” still remain anecdotal, rely on little evidence, or are at best largely controversial. Two of those that still attract the attention of many researchers concern the relationship between climate and body size, or size of certain body parts of animals, respectively Bergmann’s and Allen’s rules. We will also mention Rapoport’s rule, at least because it has had the merit to stimulate much research on species’ distributional patterns.

2.1. Bergmann’s Rule

This is a famous ecogeographical rule first formulated by Bergmann (1847): it originally stated that in cold climates endothermic species with a large body size are more frequent than in warmer areas (Figure 1). Note that the original formulation concerned species assemblages and was confined to endotherms. Studies on ectotherms have often failed to report this pattern. Pincheira-Donoso (2010) argues that this does not diminish the rule’s predictive power as far as the latter is only tested on endothermic organisms, i.e. according to its original formulation. Further reformulations soon shifted the scale of interest of this rule from interspecific to intraspecific variation, so that more evidence is now available for patterns of size variation observed within species, but studies verifying its validity for species groups (e.g. birds, mammals) also exist.

Imagine, for simplicity, a spherical animal. The area of its surface is calculated as $A = 4\pi r^2$ whereas its volume as $V = \frac{4}{3}\pi r^3$, r being the sphere’s radius. When the radius increases, the A/V ratio will decrease because A grows according to a quadratic exponential, V according to a cubic one. Animals dwelling cold climates vitally need to preserve as much heat as possible. Reducing the A/V ratio means reducing the surface available for heat loss per volume unit. Besides, larger animals also show thicker insulation layers (Blackburn et al., 1999). Logically, within a certain species the populations made of larger individuals should occur at higher latitudes / altitudes, i.e. in colder climates, whereas smaller-sized individuals should be found in lower latitudes or elevations.

Quite often this variation does not show abrupt changes in an animal's size, but rather a continuous pattern, called a cline.

The phenomenon is especially evident for some endothermic species. Grey wolves inhabiting northern latitudes, for example, such as arctic tundra populations, are clearly larger in size than those found at lower latitudes, e.g. in Mexico or the Mediterranean.



Figure 1. A comparison between skulls of white tailed deer, *Odocoileus virginianus*, respectively from Mexico (up) and Canada (bottom). The clear difference in size can be explained in terms of Bergmann's rule. Image courtesy of Terra Nova Genomics Inc – Dr Steven Carr.

Patterns apparently contradicting Bergmann's rule are found even among endotherms, however. Palearctic shrews follow the converse to the rule, i.e. size decreases at higher latitudes (Ochocińska and Taylor, 2003; Yom-Tov and Yom-Tov, 2005), possibly because of other dominating effects such as character displacement or food availability.

Although more studies have addressed intraspecific variation (e.g. Ray, 1960; Ashton *et al.*, 2000; Meiri *et al.*, 2004), patterns occurring across species have also been analyzed (e.g. Blackburn and Gaston, 1996; Gaston and Blackburn, 2000; Rodríguez *et al.* 2006). More recent research showed the existence of non-linear relationships between body size and temperature. In mammals, for instance, gradients of body size are more influenced by temperature in colder climates than those in warmer because the selective pressure posed by conserving heat is only significant in the former (Rodríguez *et al.*

2006; 2008). In the warmer areas of southern Nearctic and the Neotropics, both local and broad-scale patterns of variation in the body size of mammals are influenced by climatic gradients occurring in mountainous areas, possibly because the extent of habitat in mountains is limited and counters the occurrence of species of a larger size (Rodríguez *et al.* 2008).

2.2. Allen's Rule

This rule (Allen, 1877) states that in endotherms protruding body parts, such as tail, ears, bill, extremities, and so forth, are relatively shorter in the cooler parts of the range of a species than in the warmer parts. The rule follows the same logic as Bergmann's, because shorter protruding parts minimize the A/V ratio of an animal's body, thus countering heat loss. Although widely mentioned in textbooks, the available evidence is limited to few validations for single species. Again, the rule is often extended to ectotherms, with no significant supporting evidence, which in thermally heterogeneous habitats would benefit by slowing down changes in body temperature thus improving their performance. Few studies have verified this rule across species. One studies focused on seabirds (Nudds and Oswald, 2007) whereas a recent one (Symonds and Tattersall, 2010) comprised birds from several taxonomic groups and showed that direct association between beak length and temperature occurs in parrots, galliforms, penguins and gulls, whereas support for the rule in leg element lengths was weak (i.e. beaks would be more constrained by temperature).

There is scientific evidence (Serrat *et al.* 2008) that mammal limbs and ears may grow longer under warmer ambient temperature, as seen in mice in lab conditions, because the latter would prompt cartilage proliferation. This might explain Allen's patterns in terms of phenotypic plasticity rather than by advocating strict genetic control for the development of appendages in different climates, but prudence is needed before drawing conclusions from a single case study.

2.3. Rapoport's Rule

Rapoport's rule states that organisms living at lower latitudes show narrower latitudinal ranges than those occurring at higher latitudes; the rule would also apply to elevation (organisms at higher elevation would have narrower altitudinal ranges). The rule was first enunciated by Stevens (1989) and is named after E.H. Rapoport who provided the first evidence for the phenomenon. It has been employed as a possible explanation for tropical species diversity (narrower ranges granting coexistence to more species).

There is little consensus on the rule's validity – in fact studies confuting it are more numerous than those supporting it. Clearly, species that have evolved recently in the tropics may show narrower ranges because they have not yet had the time to spread, vice versa for species with a longer evolutionary history (Rohde, 1998).

3. Distribution of Animals: Patterns and Causal Factors

3.1. Species Conceptualization and Delimitation: Their Importance for Zoogeography

The analysis of animal species distribution, with the identification of its proximate and remote causes, is a central issue in zoogeography. Clearly, understanding (and agreeing on) what a given species actually is constitutes a fundamental condition for analyzing its geographical range. Although this may seem obvious, the ever growing number of species recognized by scientists, often resulting from the splitting of taxa previously described as valid “species”, may make the task anything but easy. Besides describing new species, scientists often revise taxonomy, and this complicates biogeographical analyses even further.

In fact, the concept of species itself is a widely debated issue, raised in a wealth of scientific literature and leading to almost 30 different definitions. As De Queiroz (2007) puts it, in all the different concepts, species is recognized as a separately evolving metapopulation lineage, but the concepts differ as to which properties manifest divergence. However, a discussion of the various species concepts goes well beyond the scope of this chapter, and the interested reader is invited to consult the numerous sources covering this important topic.

Species conceptualization and delimitation are actually separate problems, although they are frequently confused. The latter task is linked to which operational procedure is adopted to recognize species, and certainly complicated by the fuzzy nature of species boundaries (De Queiroz, 2007). In their review, Sites and Marshall (2004) show how virtually no method can effectively delimit species boundaries *in all cases* and that conflicting results can derive from the adoption of different approaches. Moreover, some qualitative judgment is inevitable whatever method is adopted. Overall, a degree of prudence should always be adopted in species delimitation. It should be noted that far from being a sophisticated intellectual activity, describing new species has important practical consequences, first of all from the conservation point of view. To manage a species effectively we have to be able to delimit it unambiguously. One attempt to overcome the problem is the formulation of “Evolutionary Significant Units” (ESUs), namely a set of populations that are morphologically and genetically distinct from others and show a distinct evolutionary history (Ryder, 1986).

Since the 1990s, the advances in DNA analysis have revealed the existence of a lot of previously unsuspected species whose morphology is so similar as to make separation based on the assessment of external characters difficult or impossible. Such species, known as cryptic species, may in many cases be recognized only from molecular analysis. Morphological stasis in speciation – i.e. the process in which external morphology remains stable during species evolution – appears to be a common phenomenon in animals, for it is estimated that up to 30% of all existing animal species are cryptic. The discovery of cryptic species typically consists of splitting a previously described taxon into two or more “good” (i.e. scientifically valid) species. Clearly, once a taxon is split, its formerly described distribution has little meaning, being a “mixture” of the geographical ranges covered by the newly separated species. Recent studies suggest that cryptic species occur evenly among animal groups and biogeographical regions (Pfenninger and Schwenk, 2007).

An interesting example is provided by a butterfly in the HesperIIDae family occurring in Costa Rica, *Astraptēs fulgerator*. According to molecular studies, it is in fact a complex

of at least 10 largely sympatric cryptic species (Hebert *et al.*, 2004). Although all these species feed on different plants and have different caterpillars and ecological requirements, adult morphology is of little help in separating them effectively. In the European bat fauna, it was only in the 1990's that zoologists realized that one of the commonest bats found throughout the continent, the common pipistrelle (formerly known as *Pipistrellus pipistrellus*) actually consists of two species, one of which retained the former name *P. pipistrellus* while the other was named *P. pygmaeus*. In this case the molecular validation only occurred after a lot of evidence had been gathered on the two separate species, including echolocation (the maximum energy frequency of *P. pygmaeus* calls is ca. 10 kHz higher than those of *P. pipistrellus*), social call structure, morphological details, and ecology.



Figure 2. Left: parapatric distribution of the two sibling salamanders, northern spectacled salamander, *Salamandrina perspicillata* (northern range) and spectacled salamander *S. terdigitata* (southern range). Right: *S. perspicillata*. Image courtesy of Luca Cistrone

The two pipistrelles largely occur in sympatry, but in other cases, cryptic species may occur on separate territories. For example, in Italy salamanders in the genus *Salamandrina* were until recently regarded as a single monotypic endemic species, *S. terdigitata*, the spectacled salamander (Zuffi, 1999). DNA analysis has shown that the taxon actually consists of two cryptic entities, *S. perspicillata* (northern spectacled salamander) and *S. terdigitata*, whose speciation dates back to 4.5-10 Ma). The two species occur in the Italian Apennines and hilly areas and occupy adjoining geographical ranges (i.e. they are parapatric; Figure 2), *S. terdigitata* replacing *S. perspicillata* south of the Volturno River, in Southern Italy. Noticeably, where the two species ranges come into contact, hybridization does occur (Hauswaldt *et al.*, 2011). There must still be many undiscovered cryptic taxa, meaning that the biological diversity of many animal groups, and their inter-relationships in ecosystems, is still largely underestimated, and this certainly affects the appropriateness of conservation strategies. From what has been said so far, it should be clear that biogeographers are waiting for taxonomists to identify actual distributional ranges and analyze the causal factors which have delimited them.

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Bibliography

Alerstam T. (2009). Flight by night or day? Optimal daily timing of bird migration. *Journal of Theoretical Biology* 258: 530-536. [This study explains from a theoretical perspective the reason for migrating birds to fly more often at night]

Allen Joel Asaph (1877). The influence of physical conditions in the genesis of species. *Radical Review* 1: 108–140. [The classical paper by Allen where his famous ecogeographical rule is first reported]

Ashton K.G., Tracy M.C. and de Queiroz A. (2000). Is Bergmann's rule valid for mammals? *American Naturalist*: 156390-156415. [This study offers support for Bergmann's rule as a general trend for mammals but not for heat conservation as the explanation.]

Barnosky A.D., Matzke N., Tomiya S., Wogan G.O., Swartz B., Quental T.B., Marshall C., McGuire J.L., Lindsey E.L., Maguire K.C., Mersey B. and Ferrer E.A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature* 471: 51-57. [A state-of-art assessment of extinction rate addressing the question of whether we are facing the sixth mass extinction and showing current extinction rates to be higher than would be expected from fossil record]

Bergmann C (1847). Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien* 3: 595–708. [The classical presentation of Bergmann's ecogeographical rule]

Berthold P. (1996). *Control of bird migration*. London: Chapman & Hall. [A thorough analysis of the phenomenon of bird migration]

Beyer, H.L., Merrill E.H., Varley N., and Boyce M.S. (2007). Willow on Yellowstone's Northern Range: Evidence for a trophic cascade? *Ecological Applications* 17: 1563–1571. [A study providing evidence for a behaviorally mediated trophic cascade triggered by wolf reintroduction in the Yellowstone area leading to a drop in elk browsing and consequent willow regrowth]

Blackburn T.M. and Gaston K.J. (1996). A sideways look at patterns in species richness, or why there are so few species outside the tropics. *Biodiversity Letters* 3: 44–53. [An interesting analysis of the interactions between spatial richness patterns and factors such as energy flowing into a region, individual and species body size and density]

Blackburn T.M., Gaston K.J. and Loder N. (1999). Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions* 5: 165–174. [An analysis of the controversial Bergmann's rule providing a practical definition retaining the essential features of the original formulation]

Blondel J. and Aronson J. (1999). *Biology and Wildlife of the Mediterranean Region*. Oxford: Oxford University Press. [A comprehensive analysis of biodiversity and ecology of the Mediterranean Region]

Blondel J., Catzeflis F. and Perret P. (1996). Molecular phylogeny and the historical biogeography of the warblers of the genus *Sylvia* (Aves). *Journal of Evolutionary Biology* 9: 871-891. [An analysis of phylogeography of birds in the *Sylvia* genus]

Bøhn T., Amundsen P.-A. and Sparrow A. (2008). Competitive exclusion after invasion? *Biological Invasions* 10: 359–368. [A study demonstrating how the introduction of an alien fish in a sub-Arctic river has led to a massive displacement of a native species]

Boles L.C. and Lohmann K.J. (2003). True navigation and magnetic maps in spiny lobsters. *Nature* 421: 60–63. [Lobsters may navigate relying on the Earth's magnetic field for orientation]

Both C. and Visser M.E. (2001). Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*. 411, 296–298. [Long-distance migrant birds, whose migration is linked with photoperiod rather than temperature, run the risk of missing food peak at their breeding quarters, because food peaks earlier as an effect of climate warming]

Brown J.H. (1971). Mechanisms of competitive exclusion between two species of chipmunks. *Ecology* 52:305-311. [Two species of chipmunks tend to exclude each other and the competition winner is decided by tree density – an observational albeit interesting study on how behavior, species ecology and habitat structure may interact]

Cain S.D., Boles L.C., Wang J.H. and Lohmann K.J. (2005). Magnetic orientation and navigation in marine turtles, lobsters, and molluscs: concepts and conundrums. *Integrative and Comparative Biology* 45: 539–546. [An analysis of how several animal taxa rely on Earth's magnetic field for orientation]

Christman M.C., Culver D.C., Madden M.K. and White D. (2005). Patterns of endemism of the eastern North American cave fauna. *Journal of Biogeography* 32:1441–1452. [An analysis of diversity patterns of endemic cave-dwelling organisms in eastern US reveals that both a non-spatial (association of high levels of single-cave endemism with areas of high diversity of non-endemics) and spatial component help explain the pattern of single-cave endemism.]

Cockrum E.L. (1969) Migration in the guano bat, *Tadarida brasiliensis*. *Miscellaneous Publications, The University of Kansas Museum of Natural History* 51: 303–336. [An account of migratory behavior in this charismatic American bat]

Cox C.B. and Moore P.D. (2010). *Biogeography: An Ecological and Evolutionary Approach*. 8th edition. Wiley, USA. [an excellent biogeography textbook]

Creel S. and Christianson D. (2009). Wolf presence and increased willow consumption by Yellowstone elk: implications for trophic cascades. *Ecology* 90:2454 –2466. [A study questioning the behavioral impact on individual elk of wolves reintroduced in Yellowstone as the factor causing a decline in willow consumption. Trophic cascade would more likely be due to a reduction in elk density caused by increased predation]

de Queiroz K (2007). Species concepts and species delimitation. *Systematic Biology*, 56: 879-886. [On the crucial importance of unifying species concept in biology and its implications for species delimitation]

Drake V.A. and Gatehouse A.G. (eds.). (1995). *Insect migration: Tracking Resources through Space and Time*. 1995. 478 pp. Cambridge University Press, Cambridge. ISBN 0521 44000 9. [A reference work on insect migration]

Dunn R.R. (2005). Modern insect extinctions, the neglected majority. *Conservation Biology* 19:1030–1036. [Small species such as insects disappear at an alarming pace but their extinction is largely overlooked]

Elmes G.W. and Thomas J. A. (1992). Complexity of species conservation in managed habitats: interaction between *Maculinea* butterflies and their ant hosts. *Biodiversity and Conservation* 1: 155-169. [*Maculinea* butterflies depend on the presence of species-specific hosts, ants representing food for the butterfly's late larval stage. Managing habitat to protect the ants is crucial to preserve the butterfly]

Fischer S., Poschold P. and Beinlich B. (1996). Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. *Journal of Applied Ecology* 33: 1206–1222. [Sheep may act as important dispersers of certain organisms such as e.g. snails]

Fransson T., Jakobsson S., Johansson P., Kullberg C., Lind J. and Vallin A. (2001). Bird migration: magnetic cues trigger extensive refuelling. *Nature* 414: 35–36. [A study showing that magnetic cues enable inexperienced migratory birds (thrush nightingales) to recognize areas where they need to replenish their body fat. Magnetic cues can be used to confront major ecological barriers]

Fransson T., Jakobsson S. and Kullberg C. (2005). Non-random distribution of ring recoveries from trans-Saharan migrants indicates species-specific stopover sites. *Journal of Avian Biology* 36: 6–11. [Identification of stop-over sites for trans-Saharan migratory birds based on ring recoveries datasets]

- Fransson T., Jakobsson S., Kullberg C., Mellroth R. and Pettersson T. (2006). Fuelling in front of the Sahara desert in autumn – an overview of Swedish field studies of migratory birds in the eastern Mediterranean. *Ornis Svecica* 16: 74-83. [A synthesis of research on migratory birds in Eastern Mediterranean done by Swedish researchers]
- Gaston K.J. and Blackburn T.M. (2000). *Pattern and Processes in Macroecology*. Oxford: Blackwell Scientific. [A comprehensive piece of work on patterns and processes observed on a large scale, forming the subject of the ecology's subfield called macroecology]
- Gause G.F. (1934). *The Struggle for Existence*. Baltimore, MD: Williams & Wilkins. [The classical formulation of Gause's competitive exclusion mechanism]
- Giannini N.P. and Simmons N.P. (2003). A phylogeny of megachiropteran bats (Mammalia: Chiroptera: Pteropodidae) based on direct optimization analysis of one nuclear and four mitochondrial genes. *Cladistics* 19: 496–511. [A molecular phylogeny of fruit bats 1) showing them to be monophyletic, 2) finding that nectarivory and cave-roosting appeared several times, but echolocation only once, and 3) identifying south-east Asia-Melanesia as the possible origin area for the group, which later colonized Africa at least four times]
- Golani D. (2000). First record of the bluespotted cornetfish from the Mediterranean Sea. *Journal of Fish Biology* 56: 1545–1547. [Title is self-explaining, the fish in question is a Lessepsian invader that has crossed Suez canal and is now spreading in the Mediterranean]
- Goodenough A.E., Hart A.G. and Elliot S.L. (2010). What prevents phenological adjustment to climate change in migrant bird species? Evidence against the "arrival constraint" hypothesis. *International Journal of Biometeorology*. 55:97–102. [Unlike other migratory birds and despite apparently strong selection for early laying, pied flycatcher breeding in the UK do not show any anticipation in egg laying as would be needed to counter the mismatch with food availability caused by global warming]
- Guisan A. and Zimmermann N.E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147–186. [An analysis of predictive habitat distribution models and corresponding methods for testing their accuracy]
- Habel J.C., Schmitt T., Meyer M., Finger A., Rodder D., Assmann T. e Zachos F.E. (2010). Biogeography meets conservation: the genetic structure of the endangered lycaenid butterfly *Lycaena helle* (Denis & Schiffmüller, 1775). *Biological Journal of the Linnean Society* 101:155–168. [An analysis of temporal changes in allele frequencies and their link with habitat isolation in an endangered butterfly over a 15-year timescale]
- Hahn S., Bauer S. and Liechti F. (2009). The natural link between Europe and Africa – 2.1 billion birds on migration. *Oikos* 118: 624–626. [A reassessment of the magnitude of bird mass migration between Europe and Africa]
- Hall S. and Fransson T. (2001). Wing moult in relation to autumn migration in adult Common Whitethroats *Sylvia communis communis*. *Ibis* 143: 580–586. [The effects of late breeding on moult timing in the long-distance migrating common whitethroat]
- Hauswaldt J.S., Angelini C., Pollok A., and Steinfartz S. (2011). Hybridization of two ancient salamander lineages: molecular evidence for endemic spectacled salamanders on the Apennine peninsula. *Journal of Zoology, London* 284: 248–256. [Two parapatric cryptic salamanders show high levels of hybridization where their ranges overlap]
- Heatwole H.F. (1965). Some aspects of association of cattle egrets with cattle. *Animal Behaviour* 13: 79–83. [An observational study reporting on facultative mutualism between cattle and egrets]
- Hebert P.D.N., Penton E.H., Burns J.M., Janzen D.H. and Hallwachs W. (2004). Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. *Proceeding of the National Academy of Sciences of the United States of America* 101: 14812-14817. [A DNA barcoding analysis showing an outstanding number of cryptic species as revealed by previously thought to be one butterfly species only]
- Heupel M. (2007). *Exiting Terra Ceia Bay: examination of cues stimulating migration from a summer nursery area*. Pp. 265– 280 in: Bethesda M.D. (ed.). Shark Nursery Grounds of the Gulf of Mexico and

the East Coast Waters of the United States. American Fisheries Society [Assessing factors that influence migration timing in sharks]

Hirzel A.H., Hausser J., Chessel D. and Perrin N. (2002). Ecological-niche factor analysis: How to compute habitat- suitability maps without absence data? *Ecology* 83: 2027–2036. [The reference paper for ENFA – a habitat distribution modeling approach]

Hoegh-Guldberg O., Hughes L., McIntyre S., Lindenmayer D.B., Parmesan C., Possingham H.P. and Thomas C.D. (2008). Assisted colonization and rapid climate change. *Science* 321: 345–346. [Assisted migration, or colonization, has been proposed as a strategy to counter the effect of climate change and help species move northwards across fragmented landscapes]

Huntley B. (1988). *European post-glacial vegetation history: a new perspective*. Pp. 1061–1077 in: Ouellet, H. (ed.). Acta XIX Congressus Internationalis Ornithologici, Vol. 1. National Museum of Natural Sciences, Ottawa: IUCN. [An interpretation of vegetational changes occurred in Europe after the last Ice Age]

Kullberg C., Jakobsson S. and Fransson T. (2000). High migratory fuel loads impair predator evasion in sedge warblers. *Auk* 117: 1034 –1038. [Fat load may affect bird’s ability to evade predators]

Lawton J.H. and May R.M. (1995) *Extinction Rates*. Oxford: Oxford University Press [An authoritative book examining patterns of extinction and their rates]

Leggett W.C. (1977). The ecology of fish migrations. *Annual Review of Ecology and Systematics* 8: 285 – 308. [A comprehensive review on the ecology of migration in fishes]

Leslie P.H., Park T. and Mertz D. B. (1968). The effect of varying the initial numbers on the outcome of competition between two *Tribolium* species. *Journal of Animal Ecology* 37: 9 –23. [A classical study on competitive exclusion showing the effect of initial numbers of individuals from competing species]

Lomolino M.V., Sax D.F., Riddle B.R. and Brown J.H. (2006). The island rule and a research agenda for studying ecogeographical patterns. *Journal of Biogeography* 33:1503 –1510. [A paper highlighting the importance of looking at different clines in morphology, geographical ranges and diversity as related phenomena within the general resurgence of interest for ecogeographical “rules”]

McLusky D.S. (1968). Some effects of salinity on the distribution and abundance of *Corophium volutator* in the Ythan estuary. *Journal of the Marine Biological Association of the United Kingdom* 48: 443-454. [A study of the effects of salinity on the distribution and abundance of the amphipod *Corophium volutator* (Pallas)]

McNaughton S.J. (1990). Mineral nutrition and seasonal movements of African migratory ungulates. *Nature* 334: 343–345. [Evidence is presented that seasonal movements of migratory grazers in the Serengeti, East Africa, are also related to grass mineral content]

Means D.B. (1975). Competitive exclusion along a habitat gradient between two species of salamanders (*Desmognathus*) in western Florida. *Journal of Biogeography* 2: 253–263. [A study suggesting that competitive exclusion occurs between two *Desmognathus* salamanders: the smaller *D. fuscus* would displace *D. auriculatus* from headwater habitats wherever the former species enters a drainage already occupied by the latter]

Meiri S., Dayan T. and Simberloff D. (2004). Carnivores, biases T and Bergmann’s rule. *Biological Journal of the Linnean Society* 81: 579–588. [This study highlights that a significant number of carnivore species do not follow Bergmann’s rule and argues that studies so far published are biased towards species that follow the pattern]

Meyer C.G., Holland K.N. and Papastamatiou Y.P. (2004). Sharks can detect changes in the geomagnetic field. *Journal of the Royal Society Interface* 2: 129–130. [Sharks may use the Earth’s magnetic field to navigate]

Moreau R.E. (1972). *The Palaearctic African Bird Migration Systems*. Academic Press. [A monograph on the mass migration of birds between Europe and Africa]

Muirhead J. and Wroe S. (1998). A new genus and species, *Badjcinus turnbulli* (Thylacinidae: Marsupialia), from the late Oligocene of Riversleigh, northern Australia, and an investigation of

thylacinid phylogeny. *Journal of Vertebrate Paleontology* 18: 612–626. [A paper describing a new thylacinid genus and offering an overview of this marsupial family's evolution]

Newton I. and Dale L.C. (1996). Relationship between migration and latitude among west European birds. *Journal of Animal Ecology* 65:137–146. [Patterns of migration, including number of winter or summer visiting species or resident depend on latitude, i.e. climate. This study describes a general pattern for this phenomenon]

Nudds R.L. and Oswald S.A. (2007). An interspecific test of Allen's rule: evolutionary implications for endothermic species. *Evolution* 61: 2839–2848. [A study on seabirds showing for the first time that Allen's rule holds for closely related endothermic species]

Ochocińska D. and Taylor J.R.E. (2003). Bergmann's rule in shrews: geographical variation of body size in Palearctic *Sorex* species. *Biological Journal of the Linnean Society* 78: 365–8. [A study questioning the general validity of Bergmann's rule showing that shrews follow the converse to it]

Ogutu-Ohwayo R. (1990). The decline in the native fishes of Lakes Victoria and Kyoga (East Africa) and the impact of the introduced species, especially the Nile perch, *Lates niloticus* and Nile tilapia, *Oreochromis niloticus*. *Environmental Biology of Fishes* 27:81–96. [The impact of invasive introduced predatory fish species on native fish assemblages in the East African Lakes]

Olalla-Tárraga M.Á (2010). On the biogeography of vertebrate body size: ecological and evolutionary insights from assemblage-level patterns. *Frontiers of Biogeography* 2: 13–17. [A PhD thesis abstract illustrating that the assemblage approach, complemented with a phylogenetic comparison, can be useful to explore both ecological and evolutionary processes linked with Bergmann's rule in a spatially explicit context.]

Pais A., Merella P., Follesa M.C. and Garippa G. (2007). Westward range expansion of the Lessepsian migrant *Fistularia commersonii* (Fistulariidae) in the Mediterranean Sea, with notes on its parasites. *Journal of Fish Biology* 70: 269–277. [A study addressing the spread of a Lessepsian colonizer fish in west Mediterranean]

Papastamatiou Y.P., Cartamil D.P., Lowe C.G., Meyer C.G., Wetherbee B.M. and Holland K.M.(2011). Scales of orientation, directed walks and movement path structure in sharks. *Journal of Animal Ecology*, doi: 10.1111/j.1365-2656.2011.01815.x. [This study first showed that sharks perform directed walks over large spatial scales; scales of movements reflect site fidelity and home range size.]

Pérez T., Albornoz J. and Domínguez A. (2002). Phylogeography of chamois (*Rupicapra* spp.) inferred from microsatellites. *Molecular Phylogenetics and Evolution* 25: 524–534. [A microsatellite-based phylogeographic reconstruction of chamois group]

Petretti F. (2003). *Gestione della Fauna*. Edagricole, Bologna. [A general textbook on wildlife management – in Italian]

Pfenninger M. and Schwenk K. (2007). Cryptic animal species are homogeneously distributed among taxa and biogeographical regions. *BMC Evolutionary Biology* 7: 21. [A large-scale analysis showing the occurrence of homogenous distribution of cryptic entities across taxa and biogeographical regions]

Phillips S.J. and Dudík M. (2008). Modelling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31: 161–175. [A paper implementing the use of MaxEnt software for distribution modeling]

Phillips S. J., Anderson R. P. and Schapire R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231–259. [The reference paper introducing maximum entropy modeling of species distributions]

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. [A paper arguing that when applied within its original formulation – i.e. to endotherms – Bergmann's rule holds valid]

Prop J., Black J.M. and Shimmings P. (2003). Travel schedules to the high-Arctic: barnacle geese trade-off the timing of migration with accumulation of fat deposits. *Oikos* 103: 403–414. [A study relating timing and patterns of fat storing in barnacle geese in relation to breeding success when they stage on islands off the coast of Norway on the way to breeding quarters]

- Pullin A.S. (2002). *Conservation Biology*. Cambridge University Press. [An excellent conservation biology textbook]
- Putman N.F., Endres C.S., Lohmann C.M.F. and Lohmann K.J. (2011). Longitude perception and bicoordinate magnetic maps in sea turtles. *Current Biology* doi:10.1016/j.cub.2011.01.057. [Sea turtles can amazingly determine longitude besides latitude thanks to their ability to detect the Earth's magnetic field]
- Ray C. (1960). The application of Bergmann's and Allen's rules to poikilotherms. *Journal of Morphology* 106: 85–108. [An old study extending ecogeographical rules to ectotherms]
- Ripple W. J. and Beschta R.L. (2004). Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of Southwestern Montana, USA. *Forest Ecology and Management* 200:161–181. [A study assessing the effects of wolf return on herbivory by elk and willow regrowth]
- Ripple W. J. and Beschta R. L. (2007). Restoring Yellowstone's aspen with wolves. *Biological Conservation* 138: 514–519. [The trophic cascade following wolf reintroduction in the Yellowstone Nat. Park is analyzed here]
- 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: 185–193. [A large-scale analysis of body size patterns of mammals across Europe]
- Rodríguez M.A., Olalla-Tárraga M.A., 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. [A study analyzing body size patterns in mammals in Nearctic and the Neotropics, confirming Bergmann's trends in cold macroclimates but not in warmer areas.]
- Rohde K. (1998). Latitudinal gradients in species diversity. Area matters, but how much? *Oikos* 82: 184–190. [an opinion paper addressing global gradients in species richness and emphasizing the implications of species' evolutionary history on latitudinal range size]
- Root T.L., Price J.T., Hall R.K., Schneider S.H., Rosenzweig C. and Pounds J.A. (2003). Fingerprints of global warming on wild animals and plants. *Nature* 421: 57–60. [Evidence of biological effects of global warming on living organisms – an important reference study]
- Russo D., Cistrone L. and Garonna A. (2011). Habitat selection by the highly endangered long-horned beetle *Rosalia alpina* in Southern Europe: a multiple spatial scale assessment. *Journal of Insect Conservation*. doi: 10.1007/s10841-010-9366-3. [The first habitat selection study done on the most charismatic, highly threatened European beetle]
- Ryder O. (1986). Species conservation and systematics: the dilemma of subspecies. *Trends in Ecology and Evolution* 1: 9–10. [The introduction of the “Evolutionary Significant Unit” concept in conservation biology]
- Sama G. (2002) *Atlas of Cerambycidae of Europe and Mediterranean Area*. Zlín: Kabourek. 173 p. [Reference work on long-horned beetles of Europe and the Mediterranean]
- Schmidt J.H., Lindberg M.S., Johnson D.S., Conant B. and King J. (2009). Evidence of Alaskan trumpeter swan population growth using Bayesian hierarchical models. *Journal of Wildlife Management* 73: 720–727. [Bayesian models are used here to estimate population trends in trumpeter swans based on datasets with missing data, showing that population size is increasing especially at higher latitudes]
- Scott J.A. (1986). *The Butterflies of North America*. Stanford University Press, Stanford, CA. [A presentation of butterflies in the Northern American continent]
- Serrat M.A., King D. and Lovejoy C.O. (2008). Temperature regulates limb length in homeotherms by directly modulating cartilage growth. *Proceedings of the National Academy of Sciences of the United States of America* 105:19348–19353. [A study showing the influence of temperature on the development of limb cartilage in ectotherm embryos]
- Shenbrot G., Krasnov B. and Lu L. (2007). Geographical range size and host specificity in ectoparasites: a case study with *Amphipsylla* fleas and rodent hosts. *Journal of Biogeography* 34: 1679–1690. [A study on range size of fleas parasitizing rodents, showing that the main determinant of the geographical range

size of a flea species is the size of its host's geographical range. Potential competitors in determining the geographical range size are more important for host-specific than for host-opportunistic fleas]

Sherrill-Mix S.A., James M. and Myers R.A. (2007). Migration cues and timing in leatherback sea turtles. *Behavioral Ecology* 19: 231–236. [A satellite-tracking study of leatherback turtles reveals that latitude, longitude, mean sea surface temperature, and chlorophyll concentration influence departure timing]

Sites J.W. and Marshall J.C. (2004). Operational criteria for delimiting species. *Annual Review of Ecology, Evolution, and Systematics* 35: 199–227. [A reference review setting the operational criteria to delimit species]

Stevens, G. C. (1989). The latitudinal gradients in geographical range: how so many species co-exist in the tropics. *American Naturalist* 133: 240–256. [The study introducing Rapoport's rule and applying it to species diversity in the tropics]

Stone G.S., Katona S.K. and Tucker E.B. (1987). History, migration and present status of humpback whales, *Megaptera novaeangliae*, at Bermuda. *Biological Conservation* 42: 122–145. [Title is self-explanatory]

Symonds M.R. and Tattersall G.J. (2010). Geographical variation in bill size across bird species provides evidence for Allen's rule. *American Naturalist* 176: 188–197. [A rare evidence for Allen's rule from beak size in several avian taxa]

Taberlet, P., Fumagalli, L., Wust-Saucy, A.-G. and Cosson, J.-F., (1998). Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology* 7: 453–464. [A study looking at phylogeographic patterns in ten animal and plant taxa determined by Quaternary cold periods showing that the northern regions were mostly colonized from the Iberic and Balkanic refugia and the Italian lineages were often isolated by the Alps]

Udvardy M.D.F. (1969). *Dynamic zoogeography*. London: Van Nostrand Reinhold. [The book reviews several important zoogeography topics (dispersal, colonization, dynamic zoogeography, i.e. the explanation to why animals migrate)]

Vaughan T.A., Ryan J.M. and Czaplewski N.J. (2011) *Mammalogy*. Massachusetts: Jones and Bartlett Publishers. [A comprehensive, state-of-art monograph on mammals]

Veech J.A., Small M.F and Baccus J.T. (2011). The effect of habitat on the range expansion of a native and an introduced bird species. *Journal of Biogeography* 38: 69–77. [A paper testing the geographical spread of two model dove species, concluding that range expansion and the extent to which ranges are saturated depend on the species' habitat availability but also on factors acting at larger geographical scales]

Wahungu G.M., Mumia E.N. and Manoa D. (2003). The effects of flock size, habitat type and cattle herd sizes on feeding and vigilance in cattle egrets (*Ardeola ibis*). *African Journal of Ecology* 41: 287–288. [A study looking at the relationship between cattle herd sizes and egret flock sizes and assessing whether vigilance in this bird depend on flock size]

Weng K., Boustany A., Pyle P., Anderson S., Brown A. and Block B. (2007). Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. *Marine Biology* 152: 877–894. [A detailed analysis of great white shark movements from satellite telemetry data]

Yako L.A., Mather M.E. and Juanes F. (2002) Mechanisms for migration of anadromous herring; providing an ecological basis for an effective conservation plan. *Ecological Applications* 12: 521–534. [a study on river herring in North America aiming to analyze migration patterns, cues triggering migration, effects of ecosystem alteration on this fish and advice on the development of conservation actions]

Yom-Tov Y. and Yom-Tov J. (2005) Global warming, Bergmann's rule and body size in the masked shrew *Sorex cinereus* in Alaska. *Journal of Animal Ecology* 74: 803–808. [Patterns of body size distribution of masked shrews in Alaska contradict Bergmann's rule. Body size also increased during the second half of the twentieth century, apparently due to the higher food availability in winter]

Zuffi M.A.L. (1999). *Salamandrina terdigitata* (Lacépède, 1788) – *Brillensalamander*. Handbuch der Reptilien und Amphibien Europas, Band 4/1 chwanzlurche (Urodela) I. K. Grossenbacher and B. Thiesmeir, eds., Aula-Verlag, Wiesbaden, 229–246. [A monograph on the spectacled salamander, an endemism of the Italian peninsula]

Biographical Sketch

Danilo Russo is an animal ecology scientist based at the University of Naples Federico II, Italy. He obtained his PhD in zoology at the University of Bristol (U.K.) in 2002 and is still honorary member of that academic institution. He is a well-recognized specialist in bat ecology and conservation biology. His scientific interests also cover the effects of land use change on animal distribution patterns and the ecology of management-dependent long-horned beetles.

Since 2007 Danilo has been teaching conservation biology and nature reserve management at the University of Naples Federico II. He also teaches zoology (University of Salerno, Italy) and applied zoology (Second University of Naples).

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