Bergmann's rule: a biophysiological rule examined in birds

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(Abstract)

The most studied ecogeographic rule is Bergmann's rule, but aspects of the original paper are often presented incorrectly even though Bergmann (1847) is explicitly cited. The goal of this paper is to 1) summarize the contents of Bergmann's paper, supported by direct translations, and 2) to discuss the main issues surrounding Bergmann's rule based on Bergmann's intentions and early definitions of the rule.

Although Bergmann himself never formulated an explicit rule, based on Bergmann's (1847) intentions and early definitions of Bergmann's rule, Bergmann's rule is: "Within species and amongst closely related species of homeothermic animals a larger size is often achieved in colder climates than in warmer ones, which is linked to the temperature budget of these animals." Bergmann (1847) assumed that the surface area of an animal is a measure for heat dissipation and an animal's volume a measure of its heat production. As body size increases, an animal's surface area increases less than its volume; however, modifications in morphology and behaviour will also influence the temperature budget. Bergmann hypothesized that when everything but size is equal, the smaller animals should live in warmer areas. This was supported by empirical data on >300 bird species belonging to 86 genera.

Recommendations for use of the term Bergmann's rule include 1) inclusion of a thermoregulatory mechanism, 2) application only to homoeothermic animals, 3) but to any taxonomic group, 4) tests of the rule should test the assumption that larger animals have to produce less heat to increase body temperatures, and 5) future authors should either go back to the original publication (Bergmann 1847) when referring to it or simply not cite it at all.

Introduction

How body size and body proportions are shaped by environmental conditions in which animals live has been one of the key questions of zoogeography (e.g. Allen 1876, v. Boetticher 1915, Mayr 1956, Rosenzweig 1968, Atkinson and Sibly 1997, Sheridan and Bickford 2011, Smith and Lyons 2011). The most influential early empirical study that tested a prediction about the distribution of size along an environmental gradient based on a biophysical law was published by Bergmann (1847). Bergmann (1847, page 682-683) concluded "for animals with the greatest structural similarities, the influence of the size relationship is manifested insofar that the smaller species within a genus are more susceptible to cold and live in warmer areas than the larger ones". This gradual association of body size with temperature or its surrogate latitude or altitude was termed 'Bergmann's rule' by later authors and is one of the best known ecogeographical rules. Its actual meaning is, however, subject to much debate (Rensch 1938, Mayr 1956, Geist 1987, Watt et al. 2010, Meiri 2010, Olalla-Tárraga 2011, Watt and Salewski 2011).

The discussion surrounding ecogeographic rules concerning size trends "has approached a near-chaotic intellectual state" (McNab 2010). With respect to 'Bergmann's rule' those disputing its many facets all root their arguments in a single publication (Bergmann 1847), but "because Bergmann's paper is seldom read, the meaning of the term is somewhat obscure" (Meiri 2010). Therefore, a presentation and discussion of the contents of Bergmann's (1847) paper is timely to clarify these misunderstandings. James (1970), Watt et al. (2010) and Clauss et al. (2013) provided translations of parts of Bergmann's paper, but the translated excerpts were short and the lack of context gave rise to misunderstandings. We have read Bergmann's (1847) original paper thoroughly. While we do not aim to translate Bergmann's entire paper we provide a description of the main aspects of his work, with background context. After pointing out some of the most widespread errors in relation to Bergmann (1847) and a descriptive section of contents of the original publication, we discuss Bergmann's paper with respect to the most controversial questions: (1) what was 'Bergmann's rule' for Bergmann (1847) including a review of the evolution of the term "Bergmann's rule", (2) was Bergmann's (1847) rule applied only to endotherms or also to ectotherms, (3) at which taxonomic level should the rule be applied according to Bergmann (1847), and (4) is Bergmann's rule valid. Finally, we give recommendations for the use of the term 'Bergmann's rule'. Superscript numbers in the text refer to an original citation and its translation in the Supplementary material Appendix 1 Table 1, while footnotes are depicted with capital letters. Our goal is that this discussion will shed some light on Carl Bergmann's original research and ideas, being the often cited but hardly read, foundation of 'Bergmann's rule'.

The need to reexamine Bergmann (1847)

The accelerated global change during the late 20th century (IPCC 2014) has left profound impacts on the earth's ecosystems (Parmesan and Yohe 2003, Bradshaw and Holzapfel 2006) and putative morphological responses of animals to rising temperatures have been the focus of a number of recent studies (e.g. Yom-Tov and Yom-Tov 2005, Smith and Betancourt 2006, Millien et al. 2006, Yom-Tov et al. 2008, Meiri et al. 2009, Van Buskirk et al. 2010, Salewski et al. 2014). This has led to an increased interest in Bergmann's work and a growing number of papers referring to 'Bergmann's rule'. A search in the web of knowledge for "Bergmann's rule" in the topic (includes title, abstract, and keywords) revealed that 701 papers were published on the topic from 1929 to April 2016. Approximately 432 papers have cited Bergmann (1847)[A] explicitly despite the fact that most authors are probably not able to read German of the mid-19th century. This is most likely the reason that many statements referring to Bergmann's publication are not justified when comparing them with the contents of the original paper. Erroneous claims include for example: (1) that the rule was established by Bergmann for mammals (King 1989, McNab 2010, Olalla-Tárraga 2011, Chauvaud et al. 2012, Berke et al. 2013). In fact, Bergmann tested an *a priori* predicted size pattern empirically on birds. (2) That Bergmann used body mass as the surrogate for size (Meiri and Dayan 2003, Goodman et al. 2012), whereas Bergmann used mainly wingspan as a surrogate for size; and (3) that Bergmann's originally interspecific interpretation of a size pattern should be regarded as an intraspecific one because the taxonomic units considered as species by Bergmann would be considered as populations within species by modern taxonomists (Mayr 1956, Meiri 2010). Instead, the great majority of species mentioned by Bergmann are still valid by modern taxonomists. Additionally, there have been some general statements with respect to Bergmann's rule that would not have

[A] This is an approximation because many authors cite Bergmann differently, (i.e. Bergmann, K. versus Bergmann, C., and there are various citations referring to the journal volume as 3 or 1). The most common version of the citation has been cited 432 times.

been made had the contents of the original paper been known to the authors. Examples include: (1) “the first general review of Bergmann’s rule for birds was by Rensch (1936)” (Ashton 2002), yet the first who tested Bergmann’s predicted size pattern on birds was Bergmann himself (1847). (2) “This clear separation between empirical findings and interpretation has not always been observed by some of the early authors (e.g. Bergmann) …” Mayr (1956) and “Bergmann observed that smaller-bodied endotherms in general inhabit warmer areas than larger-bodied species and proposed that this was because of the smaller surface area to volume ratios of larger bodied species” (Thomas 2009; similar Olalla-Tárraga 2011). In fact, Bergmann first explained a biophysical law on which he based his hypothesis about size clines that he then tested empirically and included a complex discussion why the predicted results were not observed in many cases. (3) “It seems that Bergmann’s own inferred focus on interspecific patterns was based not on mechanism, but on what he found empirical support for” (Meiri 2010). Rather, Bergmann tested a predicted pattern based on a general biophysical law (i.e. a mechanism) without any taxonomic focus both at the inter- and intra-specific level. (4) “Bergmann never mentioned the converse of smaller organisms in warmer environments ...” (Sheridan and Bickford 2011). On the contrary, Bergmann wrote explicitly that of two species being as similar as possible, the larger one would need a colder and the smaller would need a warmer climate. (5) “Temperature is responsible for generating latitudinal clines in body size ... but perhaps in a more complex way than Bergmann originally thought” (Stillwell 2010). In fact, Bergmann based his hypothesis about size clines on the condition that “if we were to enlarge an animal …and leave the conditions of warmth dissipation (fur etc,) the same” though he noted “we do not find this in nature” and discussed many aspects that could mask the pattern predicted by ambient temperature alone. Some previous authors have wondered about certain details of Bergmann’s paper that could have been solved by reading the paper. For example: (1) “Bergmann … might have suggested the mechanism of thermoregulation” (Shelomi 2012). Bergmann did: his main intention was to write about “warmth economy” (i.e. thermoregulation), and the predicted size cline because of thermoregulatory needs was one of several aspects of thermoregulation discussed. (2) Blackburn et al. (1999) wrote “whether he [Bergmann] intended the example he gave of ‘species within a genus’ to be literal is unclear”. In fact, Bergmann compared species within the taxonomic units that were considered genera at the time and mentioned explicitly when there were doubts about certain taxonomic classifications. Furthermore, some authors speculate about Bergmann’s own intentions (Blackburn et al. 1999, Meiri & Thomas 2007, Meiri 2010, Michael et al. 2014), which could be avoided had the contents of the paper been known. Our goal is to reexamine Bergmann's paper to help avoid the above mentioned errors and misinterpretations of Bergmann's research in the future.

Bergmann (1847) – what's in the paper?

Bergmann's paper was published in 1847 in the "Göttinger Studien", a journal that was published only in that year (C. Pfordt, pers. comm.). It contains the footnote "Göttinger Studien. Abthl. I." on some pages, indicating that this volume was the first section of the Göttinger Studien, which contained mathematical and natural history treatises. The author's name was written as "Carl Bergmann", so the correct citation should be "Bergmann, C. 1847. Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Göttinger Studien 1: 595-708". The translation of the title is: "On the relationship of the warmth economy of animals to their size". Important for the understanding of Bergmann's paper and intentions is that 'Wärmeökonomie' should be translated as 'warmth economy' (modern authors would probably use 'thermoregulation') and not 'heat conservation' (Daufresne et al. 2009, Gür and Kart Gür 2012). Bergmann's paper includes explanations for how animals increase and reduce heat production, as well as heat dissipation, through behaviour and morphology. A reprint of Bergmann's paper from 1848 is available on the internet at http://books.google.com/books?id=EHoAAAAcAAJ&pg=PA1#v=onepage& q&f=false. The reprint is identical to Bergmann's original paper except the pages are numbered from 3 (Bergmann's original title page) to 116 and the "Göttinger Studien. Abthl. I." footnote is missing.

Bergmann's paper has a clear structure. After an untitled part that modern authors would call an introduction it is divided into three main chapters indicated by the roman numbers I. and II., and an Appendix. These sections may be further divided into sub-sections (Table 1). We base all details in the following section on Bergmann's original statements without any interpretation or discussion of facts by us, unless explicitly stated.

"Introduction"

In the first sentence of the paper Bergmann states that the occurrence of warm-bloodedness in animals offers a wide field for investigation[1]. He explains that with respect to the question of where an animal's heat is coming from, it is probably produced during the process of oxygen bonding. The temperature budget is important for maintaining a constant inner temperature, and because of this, Bergmann criticizes investigations that merely measured the loss of heat as a proxy for heat production. Bergmann also advises against use of the term warm-bloodedness because it implies that the production and dissipation of heat are the same at any time. In the next section, Bergmann provides an explanation of the importance of the surface area : volume ratio for warm-blooded animals[2] and begins with an explanation of the role of an animal's surface area for the dissipation of heat[3] and the volume as a limiting factor for heat production[4]. Then he describes the allometric scaling that in general an increase in linear dimensions by 1 : 2 is accompanied by an increase of the surface area by 1 : 4 and of the volume by 1 : 8 [(5)]. After this explanation Bergmann formulates the law ("Gesetz") that larger animals have to produce less heat in relation to their size to raise their temperature to a certain degree above the environment[6]. If only body dimensions are considered and other factors, such as fur, are ignored, an animal with increased body size should be warmer. However, this is not the case and in warm-blooded animals internal temperatures do not differ to a large extent. Therefore, different factors must be responsible for these relatively constant temperatures[7] and these include reduced respiration (modern physiologists would probably use the term "metabolism") in larger animals[8] and increased food intake in smaller animals[9]. Bergmann completes the "introduction" by stating that the largest and smallest warm-blooded land animals are found at the same latitudes. This must be a result of the different scales of heat production and dissipation in a comparable volume of the animal and through a comparable surface area respectively[10]. Finally, Bergmann poses the question of whether a minimal and/or a maximal possible body size has been reached by any warm-blooded organism[11].

"Chapter" I.

Bergmann compares cold- and warm-blooded animals, but states these terms do not describe the situation appropriately[12]. He explains that the production of heat is a common character of all animals and discusses that cold-blooded animals can maintain higher body temperatures than the external environment (e.g. hearts of tunas and sharks). He hypothesizes that it should be easier to raise the internal temperature of large cold-blooded animals above the temperature of the environment[13] compared to small cold-blooded animals.

Following this, Bergmann summarizes his ideas and states that the difference between warm- and cold-blooded animals is not the total amount of heat produced[14] but rather that warm-blooded animals maintain a constant internal temperature unlike cold-blooded animals[15]. Morphology and behaviour help warm-blooded animals maintain a constant temperature, but there are exceptions, such as hibernating mammals plus birds and mammals during their first days of life. Differences in warm- and cold-blooded animals' capability of maintaining a constant temperature inspired Bergmann to propose changing the terms cold- and warm-blooded to homeotherm and poikilotherm, respectively[16]. From this point on in the paper Bergmann hardly uses the terms cold- and warm-blooded. Later in this section Bergmann discusses the relationship between the sizes of animals and whether they are homeotherms or poikilotherms, assuming the production and dissipation of heat must have some [unspecified] limits. With a reduction of body size, the volume that produces heat decreases faster than the surface area that dissipates heat and this leads to an assumed lower size limit for homeothermic animals. Bergmann explains that hummingbirds are close to this limit and therefore, for the plethora of animals that are smaller than hummingbirds, homeothermy is not possible. The limiting body size may be higher for animals living in water, which explains why so many fish are much larger than the smallest homeothermic animals.

"Chapter" II.

This chapter contains several subdivisions indicated by the numbers 1, 2, and 3; the latter is divided into A., B., and C. (Table 1). The chapter focuses on whether the relationship between homeothermy and body size limits the size of homeothermic animals. The surface area : volume ratio is important for maintaining an internal temperature, but factors related to the production (through quality and quantity of food) and dissipation (temperature and evaporation of the skin, structure of fur, mode of life, the environment) of heat are also important. Bergmann states that in general, the more the dissipation of heat is limited and the production of heat increased, the smaller the animal. Given this principle, Bergmann poses the question whether there are body size limits because of extremes in the relationship between production and dissipation of heat[17]. Three approaches are followed to deal with this question in the subdivisions of chapter II.

"Subchapter" 1.

Bergmann explains that he aims to discuss the largest and the smallest homeothermic animals and their respective modes of life[18]. The largest potential body size, with respect to heat dissipation, is not reached in homeothermic animals, as exemplified by whales, because of limited food supply. Whales are an exception, however, because they live in water and therefore have relatively low muscular activity. Since an increase in muscular activity leads to an increase in oxygen bonding and therefore increased heat production, conditions should be prevailing in large animals that reduce muscular activity. With respect to hummingbirds, the smallest homeothermic animals, two factors are important: (1) they live in hot tropical America although some are migrants to higher latitudes, and (2) they are extremely active leading to an extraordinary amount of muscular activity. Small animals need less muscular activity for their movements and therefore it is difficult to increase their heat production. Many small birds have extra ornamental feathers that increase load and drag, and in turn, a proportionally larger muscle mass is needed. Bergmann states the smallest homeothermic animals are birds instead of mammals because birds are able to produce a sufficient amount of heat through their proportionately large muscles. He concludes that small birds increase heat production while reducing heat dissipation, which results in them being close to the lower size limit for homeothermic animals.

"Subchapter" 2.

Bergmann considers the distribution of larger and smaller homeothermic animals over the earth's surface and in the oceans to test whether the size distribution follows the described law or whether the opposite is the case because of other factors[19]. Since the body size limits of homeotherms that live in water are greater than the corresponding limits for those living on land, this provides support for the law. However, Bergmann states that land animals show inconsistent results. The largest pachyderms live in a hot climate, which indicates the largest possible sizes are not realized at higher latitudes for unknown reasons, whereas some small animals are found far north. For a more detailed investigation Bergmann says that it is necessary to determine the conditions under which an animal lives, for example, how it actively avoids or seeks sunshine or how it escapes the winter coldness by becoming poikilothermic during hibernation[20] or denning[21]. On the other hand, the large animals of the tropics spend ample time in the water, have hardly any fur, and tend to be active at night. It seems therefore that size limits are reached in the tropics, or even exceeded, as these animals need to bathe to control their temperature. Bergmann states that we know the least about how the quality and quantity of food impacts body size, but it seems that the smaller the animal and the colder the climate, the more the animal forages. Body shape also has to be considered. For example, the round form of pachyderms results in a relatively small surface area in relation to its volume. Those large animals would therefore not be ideally shaped for heat dissipation as a result of their mechanical constraints. In contrast, bats have a large surface area : volume ratio because of their extended wing surface; Bergmann suggests this is possible because they hibernate and their wings have low blood flow and therefore probably a low temperature.

"Subchapter" 3.

This is the part of Bergmann's paper in which he tests a predicted size pattern and which has attracted most attention by later scientists. Bergmann states at the beginning that he attempted to investigate, using a different approach, how the discussed "law" is expressed in nature[22]. Note that for Bergmann the "law" is the biophysical rule that animals have to produce less heat the larger they are to raise their temperature above that of the environment; it is not a latitudinal size cline. Bergmann notes that homeothermic animals of different sizes are found in the same climate, which must be caused by differences in factors influencing production and dissipation of heat[23]. These differences, based only on animal structure, must be reduced the more similar the respective animals are[24]. After these comments, the subchapter is divided into three sections A., B., and C.

Section A. discusses the scenario that if there were two species of animals that differ only in size, the smaller would need a warmer and the larger a colder climate[25], and that if there were genera whose species differ only in size the smaller would need a warmer climate proportional to their difference in size[26]. This will rarely be the case, and when species differ in morphology and behaviour this will consequently mask the predicted pattern[27]. It is possible that these factors are related to size itself, additionally decreasing or increasing the size effect. Bergmann was inspired by birds in Iceland as a putative example of the expression of the law: in the "raptors" only the smallest species leaves Iceland in winter, whereas in the "ravens" only the largest stays. However, there are also counter-examples of the predicted size pattern, such as the distribution of cat species. Bergmann further mentions that it seems that amongst birds more similar species are more often found within a genus than in mammals, which is the reason why he wanted to examine the geographical distribution of body sizes in relation to climate in birds[28]. Consideration of mammals would not have tested the "law" per se, for its expression would have been masked through modifications in their organization and mode of life, which would have been difficult to define.

Bergmann used the information from Naumann's "Naturgeschichte der Vögel Deutschlands" (Naumann 1820-1860[B]) to rank species by size within a genus, using primarily wingspan as a surrogate for size[29]. In some cases Bergmann splits Naumann's genera according to the more recent views of Keyserling and Blasius (1840). In the following presentation of empirical data Bergmann discusses bird species from 86 genera. He mentioned 284 bird species by name and 26 additional species can be identified from Naumann (1822-1860). For example, Bergmann, assuming that readers would have a detailed knowledge of Naumann's books, wrote about the "two Graculi", which are *Corvus pyrrhocorax* and *C. graculus* in Naumann, known by modern taxonomists as *Pyrrhocorax graculus* Linnaeus 1766 and *P. pyrrhocorax* Linnaeus 1758 respectively (Supplementary material Appendix 2 Table A2). We listed all species of Bergmann's genera and used the illustrations and descriptions in Naumann (1820-1860) to determine their modern names (Supplementary material Appendix 2 Table A2). The great majority of the 310 species listed by Bergmann retain species status in modern taxonomy and only ten (3% of Bergmann's species) would not have been recognized according to modern taxonomy.

The empirical component of Bergmann's paper spans thirty pages (pages 646-676). For each genus Bergmann describes whether the species show a distribution in relation to their size as expected according to the "law". In cases where there are deviations from the expected pattern, i.e. the smaller species is living farther north compared to the larger species, Bergmann explains why this may be the case. Examples are (Supplementary material Appendix 2 Table A2 for current taxonomy): (1) that the species listed by Naumann (1820-1860) as belonging to the same genus may not be as closely related to each other as previously thought (vultures, owls, *Corvus*, larks, *Fringilla*, *Perdix*, bustards), (2) the influence of altitude (rough-legged eagles, swallows, *Cypselus*), (3) the proportionally longer wings of some species that may mask real size differences (true falcons, doves), (4) migration (ruticillae, *Motacilla*, larks, buntings, *Aegialites*, *Anas*), (5) the quantity of food consumed (currucae, phyllopseusten, *Salicaria*) and (6) the quality of plumage (titmice, *Fringilla*, *Tringa*, *Somateria*). The only species for which Bergmann mentions intra-specific size variation is the White-tailed

[B] Naumann published volumes 1 to 12 of the "Naturgeschichte der Vögel Deutschlands" between 1820 and 1844. Chapters of volume 13 were then published separately by Naumann before he died in 1857. Therefore Bergmann had access to the first chapters of volume 13 in 1847, although it was not published in a single volume until 1860, when J. H. Blasius, E. Baldamus and F. Sturm published Naumann's pre-published chapters together with additional information and corrections.

Sea Eagle (*Haliaeetus albicilla* Linnaeus 1758), in which it seems that the larger individuals are mainly found in the north and smaller ones in the south.

Section B. of the subchapter 3. deals with intra-specific comparisons. After a paragraph summarizing the previous part, i.e. that despite exceptions on average the smaller species can stand less cold than the larger species, Bergmann states that this trend should be evident in races of animals, which may be more similar than species in genera; nevertheless, he finds this is not the case[30]. However, Bergmann only deals with races of domesticated animals and explains that there are very different conditions in races, especially in the development of fur and feathers, which influence temperature budgets. For instance, young chicks lose their down feathers quickly in tropical America, and sheep in this region lose their wool and develop goat-like hair. The differences are especially pronounced in dogs, which he says are a special case because they often live with humans. Horses in Iceland and the Shetland Islands provide an example of races becoming smaller in the north (but also in the south as on Timor and Corsica) for unknown reasons, although they do have well-developed fur, that could aid in heat retention. Bergmann mentions the “miserable life”, the lack of care when breeding and that horses on Iceland must look after themselves during the winter as reasons for the size reduction in the north.

In section C. Bergmann discusses how small (young) animals can live in the same climate as larger ones: young animals are often not homeothermic, instead they acquire heat from their parents and protection in nests and dens. Young animals are also raised during warmer times of the year, and are voracious, which aids in heat production. Bergmann then provides a summary of his paper. Since large animals can maintain a constant temperature[31] with less effort it follows that poikilothermic animals are often much smaller than homeothermic animals (especially when animals that live in the same climate and medium are compared), and that the small poikilothermic animals cannot be homeothermic because of their body size[32]. In homeothermic animals the smallest possible body size is probably reached in birds[33], but the largest possible sizes are not realized in any homeothermic species[34]; however, these limits may be reached with respect to some climates and mediums. Taking the organization of animals and not the climate into consideration, Bergmann found for species within a genus that the smaller ones are more often found in warmer climates[35]. This statement is supported by results of the study regarding the size - distribution relationship in birds, which found the smaller species live further south in the majority of examples, although there are exceptions.

Appendix

The appendix has the subtitle “about another relation of size to organization”. Bergmann explains that homeothermic animals must have certain mechanisms for maintaining their temperature budget. For example, if one of two similar sized animals possesses factors, e.g. different food, that result in greater heat production, the other animal must compensate its heat production for them to have similar body temperatures[36]. Compensation may come from muscles or the skeletal elements, but muscles and bones must also have some size restrictions that may limit body size. After a detailed discussion of the function of muscles, Bergmann argues that muscles should be mechanically less effective if a body is larger[37]. Therefore, the muscle mass must be enlarged at a much higher ratio (no such allometric ratio is provided by Bergmann) when the mere dimensions of an animal are increased[38]. Additionally, the skeletal mass must be increased at a higher ratio than the body mass to carry the body[39]. Bergmann states this must have a pronounced effect on the bones of the limbs when animals are enlarged at a constant rate. There must also be an additional limit on the capacity of the digestive and respiration systems, which have to maintain an enlarged muscle and skeletal mass. Another aspect is reproduction in relation to size. Small animals have relatively larger testes and ovaries, and more offspring. Therefore, extra nutrition is necessary with the consequently higher activity and size of the organs required to capture, manipulate, and digest food. As a result, the larger the animal is, muscular and skeletal mass has to be conserved through the reduction of reproduction[40]. Furthermore, Bergmann states that the extremities must be relatively stronger the heavier the body and, in this context, discusses that the largest mammals live in water and the largest birds are flightless. With respect to mammals, the smaller ones have a greater variety of modes of locomotion, many of which are especially energy consuming (Bergmann apparently thought that energetic modes of locomotion, as well as ornaments in small birds, are adaptive because the increased muscular activity linked to them increases heat production), and their fur, although absolutely shorter, is heavier and denser in relation to the body. In order to save muscle mass the extremities become simpler in large mammals. In a final paragraph Bergmann states there is an interaction between the various aspects of his paper: warm-blooded animals have to produce more heat per unit volume the smaller they are[41]. However, the muscular system, which is tightly connected to heat production, should be relatively more developed in large animals. This problem is avoided by the simpler organization of large compared to small animals[41].

Discussion

The evolution of Bergmann's rule

With the plethora of definitions by later authors 'Bergmann's rule' became a concept cluster with multiple meanings and contrasting definitions (Watt et al. 2010). The approach to the question of what Bergmann's rule is includes two aspects: what was Bergmann's intention and how did later authors define it?

Bergmann himself never defined a general 'rule' with respect to a size cline. Based on the different rate of increase of volume and surface with increasing size[5], Bergmann concluded that larger animals have to produce less warmth in relation to their size to increase their temperature above the temperature of their environment[6]. Only the latter was termed a "law"[C] by Bergmann[6]. Based on this 'law', Bergmann formulated a hypothesis about size clines in homeothermic animals[25,26] which he tested empirically with an analysis that modern ecologists would call a macroecological approach. Finally, he summarized his results by stating that larger animals can keep a constant temperature with relatively less effort compared to smaller ones[31]. Therefore, for Bergmann, the predicted size cline with temperature was only the consequence of a biophysical law that he described[22]. It was this biophysical law which was at the centre of his study, rather than the discovery of a size pattern for which he needed an explanation. Bergmann's study is not merely a description of an empirical pattern (Mayr 1956, Meiri and Dayan 2003, Meiri 2010, Gür and Kart Gür 2012), but is founded on an explicitly formulated mechanism, irrespective of whether the underlying assumptions still hold when tested by modern scientific methods. The need for the separation between a pattern and a mechanism in Bergmann's rule (Mayr 1956, Olalla-Tárraga 2011) is based on Mayr's (1956) erroneous assumption that Bergmann observed a pattern first and then tried to find an explanation for the pattern.

[C] Bergmann used the term "Gesetz" (law) also in connection with the statement that of two animals as similar as possible the larger one would need relatively more muscle mass than the smaller one (page 625) and in connection with the statement that in general smaller animals reproduce faster compared to larger ones (page 698).

The history of the idea of temperature-related size clines and the term “Bergmann’s rule” is complex. It is difficult to determine who first used the term and defined a ‘Bergmann’s rule’. Some authors (e.g. Smith and Betancourt 2003, Millien et al. 2006) refer to Sarrus and Rameaux[D] (1838) in connection with Bergmann’s rule and latitudinal body size clines, leaving the impression that Sarrus and Rameaux (1838) predated Bergmann’s reasoning. This is not the case. Although Sarrus and Rameaux (1838) stated that “all else being equal, bodies of the same nature lose, at each instant, quantities of heat which are proportional to the extent of their free surface“[E] (translation by Smith and Betancourt 1998), their paper does not deal with general thermoregulation and its consequences for size clines of animals. Rather, it addresses the relationship between the production of warmth and size-dependent lung volume, which is discussed in connection with the role of breathing and heart beat rates for oxygen consumption, which is proportional to heat production. With respect to North American mammals, Allen (1876) referred to the “general supposition” that among representatives of the same species, size decreases with decreasing latitude, and wrote that “it seems fair to suppose that decrease in size southward may be directly due to the enfeebling influences of increase of temperature”, but without referring to Bergmann’s paper or temperature budgets (Allen 1877). Von Boetticher (1913, 1915) explicitly wanted to test the “hypothesis” formulated by Bergmann that in birds and mammals the larger “forms” of a “closer group” find better living conditions in colder climates compared to smaller forms, but v. Boetticher (1913) did not formulate a specific rule. As far as we are aware, Klatt (1913) used the term Bergmann’s law (“Bergmann’sches Gesetz”) first, but only by mentioning that v. Boetticher (1913) confirmed its validity in birds. Hesse (1921) was the first author, to our knowledge, who used the term “Bergmann’s rule” and connected it with a definition: “Carl Bergmann was the first to point to the fact that a species of homeothermic animals – and the explanation is restricted only to those– often achieve a larger size in colder climates than in warmer ones, and that amongst closely related species, the larger one is often found further north, and he linked this relationship to the temperature budget of animals. It is therefore recommended to

[D] The cited authors actually refer to ‘Rameaux & Sarrus (1838)’, but the paper in question has the heading:”*Rapport sur un mémoire adressé à l’Académi royale de médicine* par MM. Sarrus, professeur de mathématiques à la Faculté des sciences de Strasbourg, et Rameaux, docteur en médicine et ès-sciences.”. Therefore we prefer to refer to this paper as ‘Sarrus & Rameaux (1838)’.

[E] Sarrus & Rameaux 1838, page 1095: “Toute chose étant égale d’ailleurs, des corps de même nature perdent à chaque instant des quantités de chaleur qui sont proportionnelles à l’étendue de leur surface libre.”

summarize this complex of facts with the term 'Bergmann's rule'."[F] It is remarkable that this first definition already included aspects that have been debated in recent years (Watt et al. 2010, Meiri 2010, Pincheiro-Donoso 2010, Olalla-Tárraga 2011). According to Hesse (1921) the rule is formulated for homeothermic animals only, it is formulated for the intra-specific as well as for the interspecific level, and the "complex of facts" includes an explanation for the size pattern. Another early definition of Bergmann's rule is from Rensch (1924): "the Bergmann 'law' explains in brief as follows: in closely related species that differ only through quantitative differences from each other the larger forms always live in colder and the smaller forms in warmer climates"[G]. Later, Rensch (1938) reformulated Bergmann's rule as: "within a Rassenkreis [ring-species] of warm-blooded animals the races living in cooler climates are generally larger than the races living in warmer regions" (see also Rensch 1936) and as being applicable at the intra-specific level, but without the absolute aspect ("generally" rather than "always") of his 1924 definition. Mayr (1956) adopted this definition without reference to Rensch (1938) and wrote that Bergmann's rule states "races of warm blooded vertebrates from cooler climates tend to be larger than races of the same species from warmer climates". The use of quotation marks by Mayr implies a citation, but this sentence is not found in Bergmann's paper. Mayr apparently relied solely on Rensch for information about Bergmann's paper. This is further suggested by Mayr's (1970) note that the application of Bergmann's rule depends on "other things being equal" according to Rensch (1938), even though this was a prime condition for the realization of the predicted size cline by Bergmann himself. Although Mayr's formulation is a great modification of Bergmann's original concept (James 1970) it has been referred to as Bergmann's rule in a number of studies (McNab 1971, Ashton et al. 2000, Ochocińska and Taylor 2003, Kaneko 2015, Roseman and Auerbach 2015), along with numerous other definitions and reformulations (see Watt et al. 2010 for a review).

Should Bergmann's rule be applied only to endothermic animals?

[F] Hesse (1921, page 105): „Carl Bergmann hat zuerst auf die Tatsache hingewiesen, daß dieselbe Art homöothermer Tiere – und auf solche beschränkt sich die Erklärung – in kälterem Klima häufig eine bedeutendere Größe erreicht als in wärmeren, und dass von nahe verwandten Arten die größeren meist weiter nordwärts vorkommen, und er hat dies Verhalten zu dem Wärmehaushalt der Tiere in Beziehung gesetzt. Es empfiehlt sich daher diesen Tatsachenkomplex unter der Bezeichnung „Bergmannsche Regel" zusammenzufassen."

[G] Rensch (1924, page 139): „Das Bergmann'sche „Gesetz" besagt kurz folgendes: Bei nahverwandten Spezies, die im wesentlichen nur durch quantitative Unterschiede voneinander abweichen, leben stets die großen Formen in kälteren und die kleinen in wärmeren Klimaten."

Central to Bergmann's paper is the biophysical 'law' connecting body size with the amount of heat needed to be produced to raise an animal's temperature above that of the environment[6]. Bergmann states that this 'law' must be of great influence on the mode of life of "warm-blooded animals"[6]. However, Bergmann also states that probably all "cold-blooded animals" produce heat through their metabolism[14] and that they should also be able to raise their temperature above the environment the larger they are[13] (but see Bennett et al. 2000, Brown and Au 2009). The only difference between cold- and warm-blooded animals is that the latter are able to maintain a constant inner temperature[15]. Despite these explanations it is not merely heat production through metabolism that is the focus of Bergmann's reasoning, but the temperature budget, i.e. to keep a constant temperature. Although Bergmann discusses ectothermic animals in section I, the analysis of the consequences of the "law"[6] in section II is restricted to endotherms (birds and mammals). Therefore, and in line with early descriptions of 'Bergmann's hypothesis' (v. Boetticher 1915) and definitions of Bergmann's rule (Hesse 1921, Rensch 1938), investigations of temperature – body size relationships in ectotherms (e.g. Ray 1960, de Queiroz and Ashton 2004, Ho et al. 2010, Berke et al. 2012, Shelomi 2012) should not be connected to the term 'Bergmann's rule' regardless of the size pattern they may reveal. However, we do not simply "reject a possible thermoregulatory explanation for the observed patterns in ectotherms" (Olalla-Tárraga 2011), instead we argue that while ectotherms may show a size pattern similar to that expected by Bergmann for endotherms, the term Bergmann's rule is tightly linked to heat production and thermoregulation (see also Watt and Salewski 2011).

Should Bergmann's rule be applied inter- or intra-specifically?

There has been an intensive debate whether Bergmann's rule was formulated for interspecific or intraspecific comparisons; both interspecific and intraspecific versions of the rule have been defined (Blackburn et al. 1999, Blackburn and Hawkins 2004, Freckleton et al. 2003). Those who would include an intraspecific application of Bergmann's rule point out that there are fewer structural differences influencing the temperature budget in members of the same species than in species within genera (v. Boetticher 1915). They mention Rensch's (1938) 'reformulation' of Bergmann's rule, Mayr's (1956) intraspecific definition (Ashton 2002, Ochocińska and Taylor 2003, Gür and Kart Gür 2012), and Mayr's (1956) unsustained argument that most of Bergmann's species "are considered geographic races by modern authors" (Meiri 2010). Opposite to the latter opinion, v. Boetticher (1915) aimed for a revision of Bergmann's empirical study in birds because he argued that in Bergmann's time many species that were not closely related were included within the same genera. However, Rensch (1938), without any reference to Bergmann (1847), wrote of 'races' within a 'Rassenkreis': "in the time of Darwin most of these geographical representatives were looked upon as species ... but nowadays nearly all such geographical representatives are only looked upon as geographical races." Later in the same paper Rensch (1938) 'reformulated' his own earlier, strictly interspecific definition of Bergmann's rule which was later repeated by Mayr (1956). Probably it was the former statement that Mayr (1956) erroneously applied to Bergmann's species in general and which was later repeated by Meiri (2010) as being a fact. In contrast, supporters of a purely interspecific interpretation of Bergmann's rule argue with Bergmann's formulation of the hypothesis that when two species do not differ in other aspects than size, the smaller one would need a warmer climate[25,26]. This formulation was already translated by James (1970), Watt et al. (2010) and Clauss et al (2013); however, it is misleading without the context of the entire paper.

Bergmann intended to compare animals of different sizes that are as similar as possible. To his knowledge the most similar animals of different sizes were the different species of birds within genera. This does not mean, however, that Bergmann did not consider the possibility of an intraspecific size cline; indeed, this is shown both by the structure of the paper and the fact that he did discuss potential intra-specific size clines. Bergmann devotes two equivalent subdivisions of his paper to interspecific comparisons (chapter II, 3, A) and intraspecific comparisons (chapter II, 3, B). The fundamental difference between the two subchapters is their length and this is due to a lack of intraspecific examples. For Bergmann, the lack of an obvious intra-specific size pattern was surprising, but simply the result of morphological or behavioral traits masking the consequence of the biophysical law rather than an argument against the law. Bergmann did not intend to treat intra- and interspecific patterns of the hypothesized size cline as separate phenomena, nor did he focus on interspecific patterns simply because he found empirical support for them (contrary to Meiri 2010).

Bergmann put some emphasis on the argument that a temperature-dependent size cline should be more easily found the more similar the compared animals are[23-26,30]. There is, however, only one example where he briefly mentions an intraspecific size difference in a wild bird species (see above). That this cline is mentioned more as a curiosity and that he compared only domestic animals intraspecifically, can lead only to one conclusion: Bergmann was not aware of intraspecific size clines in wild animals. He probably would have been very excited to read papers that found his predicted size-pattern within species of birds (v. Boetticher 1913, Stresemann 1916, Rensch 1924, 1936, James 1970, Ashton 2002), and mammals both in association with latitude (Rensch 1936, Klein 1986, Ashton et al. 2000, Storz et al. 2001, Meiri and Dayan 2003, Gürt and Kart Gürt 2012) and temperature fluctuations over time (Klein 1986, Smith and Betancourt 1998, 2003, 2006). However, other studies that do not confirm his predicted pattern (Reinig 1939, Hamilton 1958, Zink and Remsen 1986, King 1989, Yom-Tov and Yom-Tov 2005, Ochocińska and Taylor 2003) would not have disappointed Bergmann greatly because then he would have assumed that the animals studied in such examples probably differ in their "warmth economy", thereby masking the predicted trend just as he suggested in some of his own examples. Therefore, the entire discussion about whether Bergmann's rule applies to interspecific or intraspecific comparisons is irrelevant when the proponents argue on the base of Bergmann's paper (Mayer 1956, Blackburn et al. 1999, Meiri & Thomas 2007, Watt et al. 2010, Meiri 2010). Recognizing Bergmann's rule as a general rule of temperature – body-size association with no restriction on phylogenetic scale (Pincheira-Donoso 2010) meets Bergmann's original intentions best (see also Clauss et al. 2013), despite the possibility that intra- and interspecific gradients in body size may represent different phenomena (Blackburn et al. 1999). This was acknowledged by early authors who published their work in German (v. Boetticher 1913, Stresemann 1916, Hesse 1921), but the definitions of Rensch (1938) and Mayr (1956) became more widely known presumably because they were published in English.

Is Bergmann's (1847) rule valid?

A plethora of studies have tested whether Bergmann's rule is valid by investigating a great variety of endothermic taxa. These studies lead to mixed results, either supporting (e.g. v. Boetticher 1913, 1915, Rensch 1936, Blackburn and Gaston 1996, Ashton et al. 2000, Stortz et al. 2001, Ashton 2002, Meiri and Dayan 2003, Blackburn and Hawkins 2004, Jones et al. 2005) or rejecting (e.g. Reinig 1939, Hamilton 1958, McNab 1971, Zink and Remsen 1986, Geist 1987, Ochocińska and Taylor 2003, Cotgreave and Stockley 1994) the rule.

Studies that could not find Bergmann's size pattern have invoked numerous factors to explain why body size does not follow temperature or latitudinal gradients. Scholander (1955) criticised Bergmann's rule and argued that "the factors that count are the thermal properties of the surface – its insulation, exposure, vascularization, and ability to tolerate a cold tissue temperature" instead of the area of the surface. Later authors discussed factors such as food availability, migration, selection of suitable microhabitat, and burrowing habits and hibernation (Mayr 1963, King 1989, Geist 1987, Meiri and Dayan 2003, Ochocińska and Taylor 2003, Blackburn and Hawkins 2004, Meiri et al. 2007) as being important for the temperature budget of animals and potentially being the reason for the species they studied failing to conform to 'Bergmann's rule'. However, Bergmann formulated his biophysical rule and the derived hypothesis about size clines in relation to climate explicitly under the conditions "if we were to enlarge an animal to the same degree in all its dimensions and … leave the conditions of heat dissipation (fur etc.) the same …"[7] and "if there were genera, in which the species differed as much as possible … only by size"[26]. Bergmann added "we do not find this in nature"[7] and "besides size, the species differ in aspects of their organization and mode of life which influence heat production and dissipation"[27]. Bergmann explicitly points out the development of fur[7] including its association with size. He discusses quantity and insulation quality of feathers and food availability when explaining inverse size patterns in species within bird genera (pp 655, 660, 664, 667, 676). Foraging behaviour, both in terms of quality (pp 623, 628, 635, 639, 688[36]) and quantity (p. 633), is identified as impacting temperature budgets. Habitat selection and/or microhabitat (pp 631, 632, 633), burrowing behaviour[21] (p 631), and hibernation[20] are also factors Bergmann considers influencing the temperature budget of animals. It is evident that Bergmann was well aware that size is not the only factor that influences an animal's temperature budget and there is no reason to assume he overlooked the complexity of the relationship between temperature and latitudinal clines in body size (Stillwell 2010). Therefore, for Bergmann, the failure to find a size gradient would not have led to rejection of the rule.

Many of the above mentioned papers merely repeated Bergmann's own empirical test. For instance, Blackburn and Gaston (1996) and Ashton (2002) investigated spatial patterns in body size of bird species in the New World and worldwide, respectively. Probably without being aware of the contents of Bergmann (1847), these authors repeated Bergmann's analysis that focused on Old World bird species. Blackburn and Gaston (1996) used a different surrogate for size (mass instead of wingspan) and both studies used sophisticated statistical analyses considering several covariates. However, the conclusions of studies conducted about 150 years apart are very similar: "the geometric mean mass of species is lowest around the equator, and increases towards the poles" (Blackburn and Gaston 1996) and "birds in general have a strong intraspecific tendency towards larger body sizes at higher latitudes and in cooler environments" (Ashton 2002) versus "for animals with the greatest structural similarities, the influence of the size relationship is manifested insofar that the smaller species within a genus are more susceptible to cold and live in warmer areas than the larger ones"[35] (Bergmann 1847). Instead of following the same approach taken by Bergmann to study the predicted body size pattern, it would be useful to investigate the causes of varying body size, such as competition, environmental predictability, resource availability, varying primary production, habitat fragmentation, exposure to the earth's magnetic field, and interactions among these factors (Rosenzweig 1968, McNab 1971, Lindstedt and Boyce 1985, Geist 1987, Dayan & Simberloff 1998, Tornberg et al. 1999, Meiri and Dayan 2003, Schmidt & Jensen 2003, Jones et al. 2005, Meiri et al. 2007, Nishimura et al. 2008, McNab 2010, Houston and Wolverton 2011, see also the flow chart in Yom-Tov and Geffen 2011, for factors acting on body size).

Nevertheless, there remain serious issues regarding the validity of Bergmann's arguments regardless of any size patterns. These concern Bergmann's assumption of a constant rate of heat production per unit body mass. Lindstedt and Boyce (1985) argued that large mammals have proportionally more body fat, are better insulated, and have a broader range of thermoneutrality (see also Scholander 1955). Although Bergmann discusses the potential of some of these or related factors to influence the temperature budget of animals[10, page 639], they could render the surface area : volume ratio invalid. Even more problematic is that Bergmann assumes the volume of an animal is a measure for the production of heat and disregards the possibility that heat production per unit volume may depend on other factors potentially correlated with volume[4, but see 10, page 618, 639]. This assumption may not withstand a critical examination. Several authors have recognized that large endotherms lose more heat and expend more energy at all temperatures compared to small endotherms because metabolism and heat loss increase with body mass (Kendeigh 1969, McNab 1971), culminating in the statement that "mass-specific rates [of metabolism] are intellectual abstractions that have no ecological reality" (McNab 2010). Let us assume this also holds for volume-specific rates and/or there is a positive association of volume and size with body mass. Bergmann assumed that heat production and dissipation are associated with an animal's volume and surface area; if this assumption is not met and larger animals do not have to produce less heat compared to smaller animals to gain an increase of body temperature then

Bergmann’s (1847) rule would indeed be invalid, irrespective of later definitions or any size clines found in empirical studies (Geist 1990).

Recommendations for the use of the term ‘Bergmann’s rule’

Summarizing the discussion above, we argue that based on Bergmann (1847) and first definitions of the rule (Hesse 1921, Rensch 1924), Bergmann’s rule is: “Within species and amongst closely related species of homeothermic animals a larger size is often achieved in colder climates than in warmer ones, which is linked to the temperature budget of these animals.” Other concepts about size clines in animals deviating from this original meaning should not be called Bergmann’s rule, especially when they lack a mechanism and/or include ectotherms. We argue against adding further confusion by providing new definitions of Bergmann’s rule to adjust the term to the hypotheses studied. Alternatively, different terms have been coined to name associations of body size factors other than temperature such as resource availability (resource rule, McNab 2010), and net primary production (eNPP rule, Huston and Wolverton 2011). Finally, there is simply no need to cite Bergmann (1847) in every study about animal body size especially when the original paper has not been read nor its contents understood.

It is important to note that we do not plea for a static view of scientific concepts, including those related to geographic size distribution among animals. Concepts and ideas have to evolve and must be dynamic to enhance progress in science, and current scientific questions cannot be answered with concepts of the mid-19th century. Nevertheless, Bergmann (1847) is explicitly cited as a reference for the definition of a concept, to reject the assumption of a simple size-temperature relationship, to justify the use of a certain methodology, or to explain facts, by a number of authors as recent as e.g. Ashton et al. (2000), Meiri & Dayan (2003), Ochocińska & Taylor (2003), Meiri & Thomas (2007), Thomas (2009), McNab (2010), Pincheira-Donoso (2010) and Stillwell (2010), apparently without being aware of the contents of Bergmann’s (1847) original paper. Despite this widespread appreciation of Bergmann’s original work there have been a number of proposals for new definitions of Bergmann’s rule (Watt et al. 2010 for review). We are not arguing against a pluralistic approach to questions related to patterns and factors affecting size distributions of animals (Olalla-Tárraga 2011). We argue, however, that concepts with multiple meanings lead to confusion when a single name may indicate different approaches to a scientific problem. Therefore, we give the following recommendations for the use of the term ‘Bergmann’s rule’:

- Bergmann’s rule includes the mechanism of thermoregulation. Therefore, studies investigating size clines linked to other factors are not studies of Bergmann’s rule and can not support or refute the rule.
- Studies investigating size clines in ectotherm animals should not be linked to Bergmann’s rule.
- Studies on Bergmann’s rule are not restricted to any taxonomic unit.
- Studies about the validity of Bergmann’s rule should focus on the mechanism rather than searching for specific size patterns.
- In order to avoid wrong conclusions, similar to those made in the past, future authors should either go back to the original publication when referring to it or simply not cite Bergmann (1847) at all. In any scientific study it is good practice to “check all parts of every reference against the original publication” (Day 1994), unfortunately this is lacking in much of the general scientific literature (MacRoberts and MacRoberts 1996).

A note of caution

Bergmann’s publication includes lengthy discussions that are probably not of great interest for modern readers. Therefore we translated only selected sections of the paper, biased by our intention to answer what we considered were the most important questions related to Bergmann’s rule, and to clarify misinterpretations of his original paper. Bergmann’s paper is written in the German of the mid-19th century. At places it is difficult to understand the meaning immediately, even for a native German speaker of the early 21st century. However, we are confident that our translations reflect the intentions of the original text because all translations were conducted by a native German speaker (VS) who is fluent in English, and counter-checked by a native English speaker (O. Muise) who is fluent in German. Nevertheless, translations by other people may deviate from our interpretations and the original paper contains many different aspects and details we have not discussed. Our translation and discussion should therefore be seen as an indication of Bergmann's original intention rather than the last word about every aspect of his paper.

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Supplementary material (available online as Appendix oik-xxx at < www.oikosjournal.org/appendix/oik-xxx >). Appendix 1–2.

Table Legend

Table 1. The structure of Bergmann's paper. Pages refer to the page numbers of Bergmann's original 1847 paper, and in brackets the page numbers of the reprint from 1848. Short title may be a title that modern authors would give the respective chapters today and content is a very brief summary of the contents of the respective chapters.

Bergmann's structure	Pages	Short title	Content
	595-604 (3-12)	The surface area : volume ratio and its implication for the heat-economy of animals.	An increase in all dimensions of a body by 1 : 2 will lead to an increase of the surface area by 1 : 4 and of the volume by 1 : 8. Therefore, larger animals have to produce less heat in relation to their size to raise their temperature above the ambient temperature. If only body dimensions are considered and other factors, like fur, are ignored, an animal with increased body size should be warmer.
I	604-622 (12-30)	A comparison of cold- and warm-blooded animals.	All animals produce heat, but the difference between warm- and cold-blooded animals is that warm-blooded animals maintain a constant temperature. Therefore, the terms cold- and warm-blooded should be changed to homeotherm and poikilotherm

				respectively. Is there a size limit for homeothermic animals?
II		622-687 (30-95)	Size limits in homeothermic animals.	The more the dissipation of heat is limited and the production of heat increased the smaller the animal should be and when the opposite is the case the animal should be larger. Are there therefore size limits because of extremes in the relation between production and dissipation of heat? The approach to the question can be threefold.
	1	624-629 (32-37)	Comparison of the largest and smallest homeothermic animals.	The largest potential size with respect to dissipation of heat is not reached in homeothermic animals. The smallest and most active homeothermic animals live in the tropics. They are birds because they can create enough heat through their relatively large muscle mass but reach the lower size limit for homeothermy.
	2	629-637 (37-45)	The geographical distribution of the smallest and largest homeothermic animals.	The lower and upper size limits of homeotherms in water are above the respective limits of those living on land.

				At higher latitudes the largest possible size is not realized for unknown reasons, but the upper size limit is reached in the tropics.
3		637-687 (45-95)	The geographical distribution of animals in relation to their size.	Homeothermic animals of different sizes are found in the same climate, which must be caused by differences in factors influencing production and dissipation of heat under exclusion of climate. These differences, based only on the structure of the animals, must be reduced the more similar the respective animals are.
	A	638-676 (46-84)	Interspecific comparison.	In an empirical approach 310 bird species of 86 genera are compared to test whether the smaller species of a genus have a more southerly distribution compared to the larger ones.
	B	677-680 (85-88)	Intraspecific comparison	The same approach is performed with races of domestic animals and it is discussed why races do not show the expected distribution.

C	680-687 (88-95)	Summary and discussion.	It is easier for large animals to maintain a constant temperature, therefore: I. the small poikilothermic animals cannot be homeothermic because of their body size; II. 1. the smallest possible body size is reached in birds, but the largest possible sizes are not realized; however, 2. these limits may be reached with respect to some climates and mediums, and 3. for species within a genus the smaller ones are more often found in warmer climates.
Appendix	687-708 (95-116)	About a different relation of size to organization	The muscle mass must be enlarged at a much higher ratio when the dimensions of an animal are increased. Additionally, the skeletal mass must be increased at a higher ratio than the body mass to carry the body. Muscle and bones must have size limits that in turn limit the size of animals. The contradiction between the influence of size and development of muscles on body temperature is solved by the relatively more complex structure of smaller animals.