

Bergmann's rule reviewed for Endotherms & Ectotherms



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Abstract

A lot of research has been done regarding Bergmann's rule. Bergmann's rule means that from the surface area to volume ratio it becomes clear that warm-blooded animals, from the same species, tend to be larger at higher latitudes and in cooler climates. But in the literature Bergmann's rule is revised in the time and also the mechanism behind the pattern of latitudinal body size variation is debated among researchers. Therefore this thesis deals with two goals. The first goal is to give a first impression whether both endotherms and ectotherms are following the trend of larger size at higher latitudes in the same strength. Therefore I compiled correlation coefficients of endothermic and ectothermic species of the literature. I found that endotherms are strongly following the pattern of large size at higher latitudes (~90%), whereas ectotherms follow it (50%), but not as strong as the endotherms. The second goal is to discuss whether the heat conservation mechanism, as originally proposed by Bergmann is a more or less valid explanation for latitudinal body size variation than other proposed mechanisms in the literature. I suggest that a combination of abiotic factors (i.e. temperature) and biotic factors (i.e. food quality and food abundance) is responsible for latitudinal body size variation in animals, instead of one mechanism (i.e. heat conservation). This is supported by the fact that latitude alone is not the explanation for body size variation among latitudes, but that a combination of factors, i.e. temperature and precipitation, drives latitudinal body size variation. Therefore I encourage further studies to look at the interaction between abiotic and biotic factors to explain the mechanism behind Bergmann's rule, in which it is important to investigate the effects of global warming on vegetation types and the direct and indirect effects on food quality and food abundance.

Key-words: Bergmann's rule, endotherms, ectotherms, body size, latitude, explanations, mechanisms.

Cover pictures show red fox (*Vulpes vulpes*) sparrow hawk (*Accipiter nisus*) and sand lizard (*Lacerta agilis*). Pictures are from AGAMI 'IMAGES of BIRDS & NATURE' <http://agami.nl/index.php>

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Introduction

Imagine a fox in a warm tropical area and a fox on a cold arctic region. It might be clear, that both foxes experience very different temperatures between the two regions. The fox in the arctic region would suffer more from the cold than the fox in the tropical region, which will of course have more disadvantage of heat. This means that both foxes should have different body plans from each other to be able to balance their heat budget to ensure survival in the different areas. Therefore it is possible that both foxes differ for example in size and thickness of fur.

With this in mind, we might in part empathize what Carl Bergmann (1814-1865), a German biologist, was thinking about when he published his paper "Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse", translated into English "About the relation of warm economics of animals to their size". In this paper Bergmann mentioned: "for the amount of warmth, of which an animal can raise itself above its surrounding, the relation of its volume to its surface is of course of great importance" and "it is thus clear, that animals have to create less warmth in relation to their size the larger they are, to gain a certain increase in temperature above the one of their surrounding. This law must be of great importance on the mode of life of warm-blooded animals" (Bergmann 1847, p. 600-601). Besides, Bergmann stated that "If there would be genera, which species are distinguished as much as possible only by size, the smaller species need a warmer, the larger species a colder climate" (Bergmann 1847, p. 638). This means that from the surface area to volume ratio it becomes clear that warm-blooded animals, from the same species, tend to be larger at higher latitudes and in cooler climates. This is also known as Bergmann's rule.

A lot of research has been done after Bergmann introduced his ideas, but his rule is revised in the time, as becomes clear from Blackburn et al (1999) and Watt et al (2010). First Rensch (1938) revised the definition to "within a complex of races of warm-blooded animals the races living in colder climates are generally larger than the races living in warmer regions" (cited in Blackburn et al, 1999). But, as Rensch mentioned by himself, with this definition the rule is reduced to the geographical races of a species. Mayr (1956) reformulated the definition of Rensch to "races from cooler climates tend to be larger in species of warm-blooded vertebrates than races of the same species living in warmer climates" (cited in Blackburn et al, 1999). This last definition of Mayr, which is reduced to races of vertebrates, is the most common used definition among researchers. But in time, Bergmann's rule is not only examined on warm-blooded vertebrates, but for example also on cold-blooded vertebrates (Ashton, 2002a; Ashton & Feldman, 2003; Laugen et al, 2005). Furthermore James (1970) noted that Bergmann's rule fitted also at the intraspecific level of body size variation in birds, whereas Bergmann's own expectation of latitudinal body size variation only was based on the interspecific level.

Because of the confusion surrounding Bergmann's rule, i.e. should we study it on the interspecific or intraspecific level, Blackburn et al (1999) and Watt et al (2010) give clarity regarding Bergmann's rule. Both papers are in agreement that Bergmann's rule has to be intended as interspecific, but they did not agree if the rule has to be applied only to endotherms. Watt et al (2010) argues that some ectotherms follow a similar pattern, but that ectotherms do not conform the rule, whereas Blackburn et al (1999) states that Bergmann's rule has not to be restricted to homeotherms.

In this thesis I will not discuss which definition is more useful for Bergmann's rule. But I think it is worth to know that Bergmann's rule is not generally used in one way.

To my opinion Bergmann's rule has to be intended as interspecific and only for endotherms, as originally proposed by Bergmann himself. However, it is not my intention that research has to be restricted at the interspecific level and endotherms. I think that the pattern also can be examined on other taxonomic levels, i.e. intraspecific as already shown for mammals and birds that follow Bergmann's rule (studied by Ashton et al, 2000; and Ashton, 2002b respectively). But then it is important not to look if these results support or reject Bergmann's rule in the way it is originally proposed by Bergmann.

In addition to describing a pattern, Bergmann also provided a mechanism for his rule. Bergmann (1847) stated that larger endothermic animals are better cold adapted than smaller animals, because they are able to conserve heat due to a lower surface area to volume ratio. This is also called the heat conservation mechanism (explained in a later section), but is also debated in the literature. Ashton (2002b) and Brodie (1975) suggested that fasting endurance is a better explanation for Bergmann's rule. Another mechanism, food abundance, is proposed as an explanation for the converse of Bergmann's rule (Erlinge, 1987; Ochocinska & Taylor, 2003; Yom-Tov & Yom-Tov, 2005). In this thesis I will discuss whether the original mechanism of Bergmann for his rule is a more or less valid explanation than other proposed mechanisms in the literature.

Bergmann (1847) proposed that homeothermic and poikilothermic are more useful terms to classify animals instead of warm-blooded and cold-blooded respectively. These terms are based on whether animals have internal temperatures that vary widely (poikilotherm) or that they have relatively stable internal temperatures (homeotherm). Nowadays the terms endotherm and ectotherm are used to distinguish animals from each other. These terms are not based on whether animals have constant or variable internal temperatures, but on the source of heat used to maintain body temperature (Campbell & Reece, 2005). The endothermic term means that endotherms, mainly birds and mammals, regulate their own body temperature by producing heat through metabolism in their own tissues, and that they maintain a high and very stable body temperature within a narrow range, even when the temperature of the environment fluctuates (figure 1, Campbell & Reece 2005). The ectothermic term on the other hand, means that ectotherms, most invertebrates, fishes, amphibians, reptiles, use behavioural adaptations to absorb heat from external sources (i.e. the sun) to gain body heat, and that they tolerate a wide range in internal temperatures compared to endotherms (Campbell & Reece 2005).

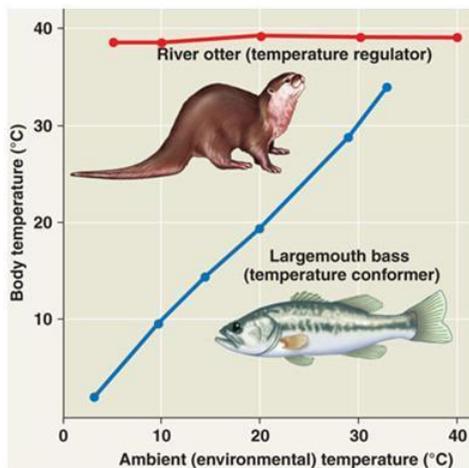


Figure 1. Effect of ambient temperature (°C) on body temperature (°C) for a river otter and a largemouth bass. The river otter, an endotherm, maintains a very stable internal body temperature independent of the environment, while the largemouth bass, an ectotherm, assumes the temperature of the environment. (from Campbell & Reece, 2005, figure 40.12, page 834)

Endothermic and ectothermic are part of bio-energetic strategies, which means that the flow of energy through an animal ultimately limits his behavior, growth and reproduction, and determines how much food it needs (Campbell & Reece, 2005). The bio-energetic 'strategy' of an animal is closely related to its metabolic rate (Campbell & Reece, 2005). The metabolic rate (the amount of energy an animal uses in a unit of time) is higher in endotherms compared to ectotherms, because of the higher energy expenditure for heating or cooling the body of the endotherm. Because of his high metabolic rate, the endothermic animal is able to generate enough heat to keep his body warmer than the surrounding.

It is important to know that both bio-energetic strategies are not exclusively opposite (Campbell & Reece, 2005). This is probably best understood when we imagine a bird which is warming itself in the sun on a cold morning. The bird is an endotherm, but it may warm itself in the sun as much as an ectothermic lizard does. Therefore I think that we have to be careful in strictly dividing animals to which kind of thermoregulatory term they belong. This is supported by the fact that animals, regardless if they are endotherm or ectotherm, have to balance heat gain and heat loss to regulate their body temperature, which is a critical factor for survival. The process, in which heat gain and heat loss are balanced, is also called thermoregulation (Campbell & Reece, 2005).

Watt et al (2010) found that 28 of 47 endotherm species and 17 of the 28 ectotherm species follow Bergmann's rule. This means that the pattern of larger size at higher latitudes and in cooler areas occurs in approximately 60% of endotherms and ectotherms. However, Watt et al (2010) based this conclusion on whether species are following Bergmann's rule or show the converse to Bergmann's rule. But it might be better to look to the magnitude and direction of body size variation with latitude (Ashton & Feldman, 2003). Therefore the main goal of this thesis is to give a first impression whether both endotherms and ectotherms are following the trend of larger size at higher latitudes in the same strength. I compare endotherms and ectotherms on the interspecific level, following the original intention of Bergmann's rule.

Latitudinal body size variation in endotherms and ectotherms

To see if endotherms and ectotherms follow the pattern of larger size at higher latitudes in the same strength, I compiled correlation coefficients (r) of size and latitude for birds, mammals, amphibians (caudata and anura) and reptiles (chelonians and squamata) from articles of Ashton et al (2000), Ashton (2002a, 2002b) and Ashton & Feldman (2003). Because there are different ways in measuring body size of an animal, only correlation coefficients were used in which body size was measured as wing length for birds; body mass, total length, head + body length for mammals; and plastron length, carapace length and snout-vent length for ectotherms. Correlation coefficients were given in the literature for both sexes (table 1), or separated for males and females, or only given for males or females (table 2 and 3). Therefore I created three graphs: one for both sexes (figure 2a), one for males (figure 2b) and one for females (figure 2c). For some species more data were present than for other species. Therefore it was decided to place all the correlation coefficients of one genus on one rank-number on the x-axis in the graphs to make the graphs conveniently arranged. Only data are used from sedentary birds, because of ignorance if correlation coefficients of migratory birds are given for their overwintering or breeding place.

Some remarks have to be made when we look to relations between species: First studies are based on different sample sizes. This might influence the strength and direction of body size variation in species, because a large sample size comprises more variation than a small sample size. Secondly, the geographic range of the species studied might influence the direction of body size variation with latitude. To illustrate this, Laugen et al (2005) found that mean body size of frogs (*Rana temporaria*) increased until 65° N, but declined markedly above latitudes 65° N (figure 5a). Therefore they found a weak positive correlation between body size and latitude for *R. temporaria*. However, another study on *R. temporaria* (reviewed in Ashton, 2002a) found a positive correlation between body size and latitude. However, none of the studies reviewed in Ashton (2002a) considered latitudinal gradients beyond 55° N. This means that two studies on the same species, but on different geographic ranges, can present different conclusions. Therefore I suggest that it is important to include the whole geographic range of a species under study, because it is already known that the magnitude and direction of body size trends may vary with latitude (Ashton & Feldman, 2003). Laugen et al (2005) controlled for age effects in their study, which means that age of *R. temporaria* does not explain body size variation with latitude (figure 5b).

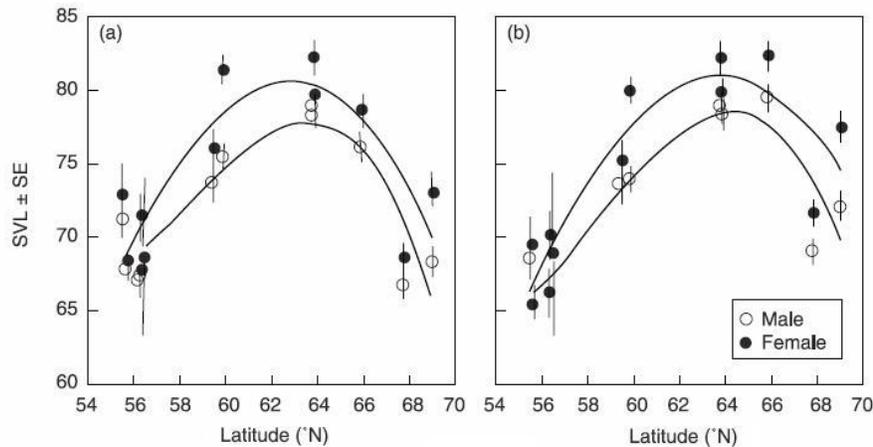


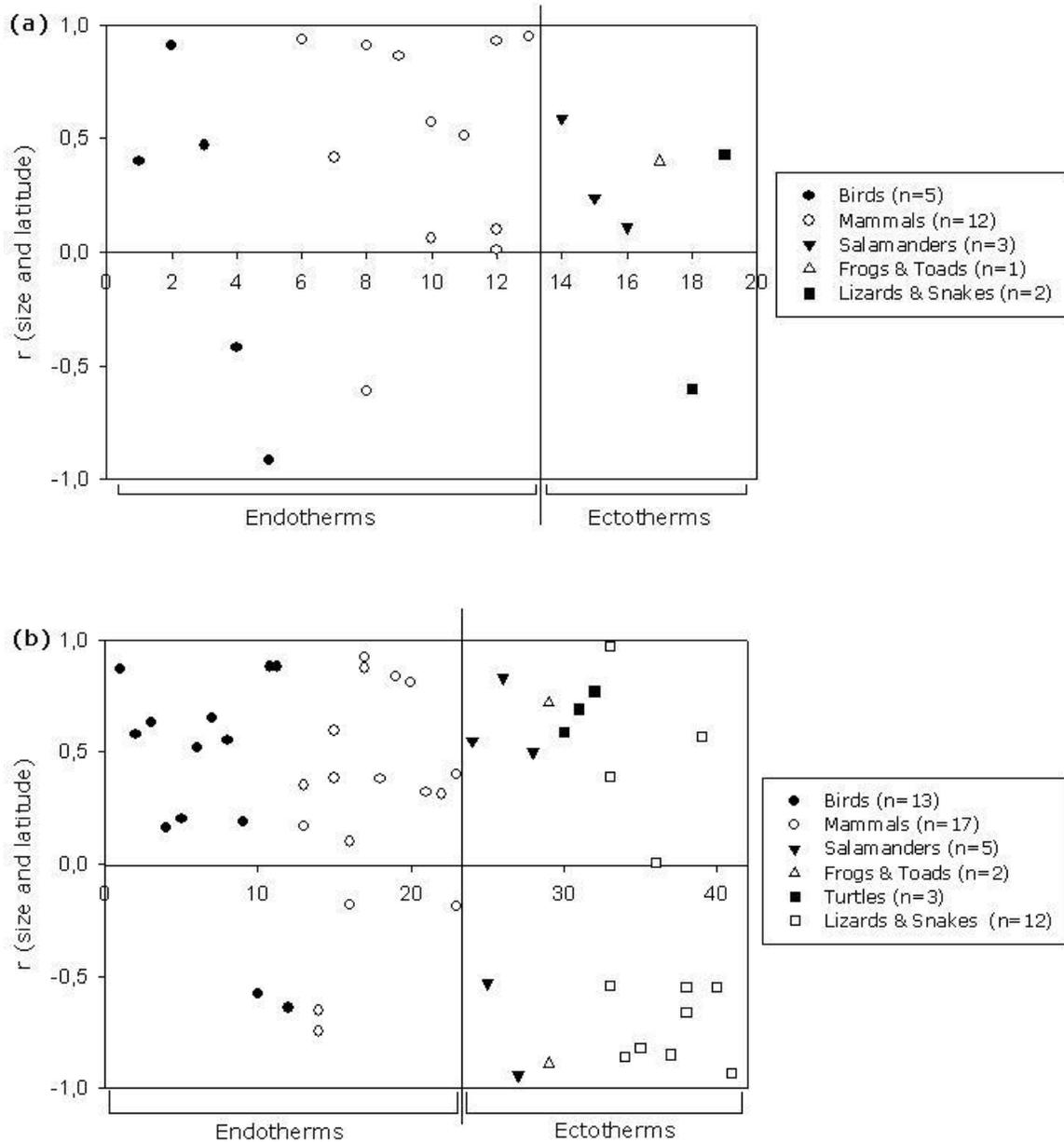
Figure 5. Mean adult size (snout-vent length, SVL+standard error) of male and female frogs (*Rana temporaria*) as a function of latitude (a). In (b) accounted for age effects. Mean adult size increased until 65° N and declined after 65° N. (modified from Laugen et al, 2005, figure 2).

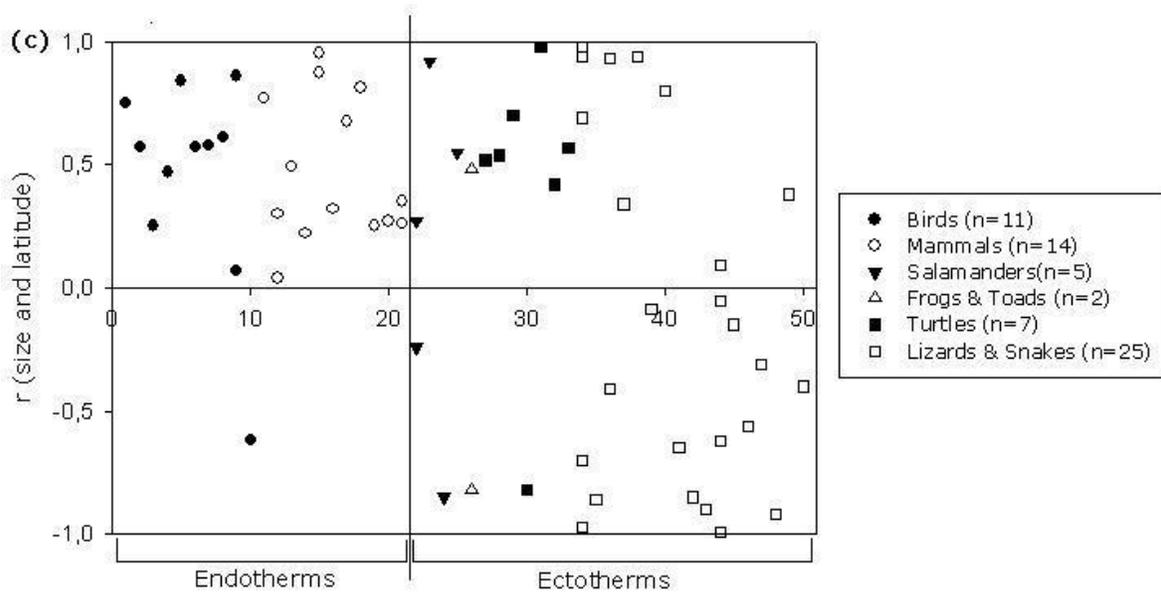
Thirdly, related species may show similar body size trends (Ashton et al, 2000; Ashton 2002b). However, it is also possible that within a genus two species can be very different from each other. To illustrate this, the female Little striped Whiptail (*Cnemidophorus inornatus*) shows an almost perfect positive correlation between size and latitude ($r = 0,98$), whereas the female Checkered Whiptail (*Cnemidophorus tesselatus*) has an almost perfect negative correlation between size and latitude ($r = 0,97$) (data from Ashton 2002a, also see figure 2c and table 3). This means that data analysis should be done using phylogenetic and non-phylogenetic methods (Ashton et al, 2000; Ashton 2002b).

The graphs I present in this thesis are a first impression to see whether both endotherms and ectotherms are following the trend of larger size at higher latitudes in the same strength. I did not include sample sizes, and performed no statistical analysis, because this is beyond the scope of this thesis.

Results

Figure 2. Correlation coefficients (r) of size and latitude for endotherms (birds and mammals) and ectotherms (salamanders, frogs and toads, turtles, lizards and snakes) are presented for **(a)** both sexes, **(b)** males, and **(c)** females. The number on the x-axis corresponds with one species name, which are included in table 1 for both sexes, in table 2 for males and in table 3 for females (see for tables the appendix).





Birds and mammals have the highest r -values compared to ectotherms when data of both sexes are included (figure 2a). It is conspicuous that birds did not have r -values between 0,40 and -0,40. Mammals have by far the most positive correlation between size and latitude, 11 of the 12 values (figure 2a).

Male birds, mammals and ectotherms have positive and negative correlation coefficients (figure 2b). The highest and lowest r -values are for ectotherms, which have, except for one r -value (0,0069), a gap between -0,53 and 0,39 (figure 2b).

Female ectotherms show a uniform distribution of r -values, whereas mammals only have positive r -values and birds have only one negative r -value (figure 2c).

In the graphs of males and females it seems that 50% (11 of 22 for males, 19 of 39 for females) of the ectotherms is positively correlated with latitude, whereas this percentage in male and female birds and mammals is around 90% (24 of 30 (80%) for male birds and mammals, 24 of 25 (96%) for female birds and mammals).

To summarize the findings: birds and mammals almost only have positive correlation coefficients, although there are some notable exceptions, whereas ectotherms have almost the same number of positive and negative r -values, so a much more uniform distribution. This means that birds and mammals are strongly following the pattern of large size at higher latitudes, whereas ectotherms follow it but not as strong as the endotherms. This results supports that it is better to look to the magnitude and direction of body size variation with latitude, as also mentioned in Ashton & Feldman (2003). The findings of this first analysis do not fully correspond with the findings of Watt et al (2010) that on average 60% of endotherms and ectotherms are following Bergmann's rule. But I think this is due to the fact Watt et al (2010) based his conclusion whether species are following Bergmann's rule or show the converse to Bergmann's rule.

Explanations for latitudinal body size variation in endotherms and ectotherms

Is latitude effect a temperature effect?

Before an explanation can be given for Bergmann's rule, it is first important to discuss if latitude alone drives body size variation. It might be that other factors, i.e. temperature varies with latitude and that therefore latitudinal body size variation occurs. In a study on 12 species of birds in the eastern and central United States, James (1970) found that the patterns of size variation are highly correlated with climatic gradients that are combined effects of temperature and humidity. Therefore James (1970) suggested that wet-bulb temperature is a better indicator than dry-bulb temperature. This means that the combined effects of temperature and humidity are more related to body size variation than temperature or latitude alone. This is supported by Ashton (2002a), they argued that precipitation and humidity could be selective factors behind latitudinal and altitudinal body size variation in adult amphibians. Ashton (2002a) suggested that for amphibians the temperature during development may partly explain larger body size in cooler areas, because also humidity and precipitation levels contribute to body size in amphibians, because amphibians are constrained by water availability because of the need to keep their skin moist to allow respiration. This two studies underline that latitude alone is not the explanation for body size variation among latitudes, but that a combination of factors, i.e. temperature and precipitation, drives latitudinal body size variation.

Heat conservation mechanism

Bergmann's own explanation for his rule is that large endothermic animals are better cold adapted because of a lower surface area to volume ratio (Bergmann, 1847). A low surface area to volume ratio means that an animal has a relatively low heat loss. This is because the relationship between surface and volume is $2/3$. This means that when all parts of the body are enlarged proportionally from 1 till 2, the surface will increase from 1 till 4 and the volume from 1 till 8. The surface area to volume ratio is important in two ways in a cold environment. First a lower surface area to volume ratio means reduced heat loss per unit mass, and thus a lower mass-specific metabolic rate, which is favourable when food sources are scarce and unpredictable. Secondly a larger bird has more volume per unit surface area. This is important because larger body content permits larger organs which process the food and create the warmth in an endothermic animal. Thus, volume and surface area are important factors in determining heat gain and heat loss respectively. So the larger the animal, the more favourable the ratio of surface area to volume to reduce the loss of heat to the environment. This is also known as the heat conservation mechanism.

But researchers have argued some other mechanism's to explain Bergmann's rule in endotherms (and ectotherms). This is discussed below. Keep in mind that the explanation proposed by Bergmann yields not for ectotherms, because they use no metabolic heat to maintain body temperature.

Fasting endurance hypothesis

From a physiological perspective, insulation is a more important mechanism to conserve heat instead of changes in body size. Steudel et al (1994) used a thermal simulation model to determine the effects of increasing body mass and increasing

pelage insulative properties on mass-specific metabolic rate. They found that smaller animals have lower fur depths, maybe of biomechanical constraints. This seems logic, because for small animals a fur of equal thickness is a much greater burden than for a large animal, because it amounts a larger proportion of his total body mass (Bergmann, 1847). Therefore a change in body size has a greater influence on smaller animals because they rely more on increased body size to conserve heat, whereas larger animals benefit from a large pelage in terms of heat transfer (Steudel et al, 1994). Thus, from the heat conservation mechanism, smaller animals should follow Bergmann's rule more strongly than larger animals (Steudel et al, 1994).

A meta-analytical study by Ashton et al (2000) showed a positive correlation between body size and latitude for 78 of 100 (71%) mammalian species, and 48 of 64 (75%) mammals showed a negative correlation between body size and temperature. This supports that Bergmann's rule is a general trend for mammals. However, Ashton et al (2000) suggested that heat conservation couldn't be the explanation for Bergmann's rule, because they did not find that smaller mammals conform stronger to Bergmann's rule than larger mammals. In a meta-analysis on birds, Ashton (2002b) found that 76 of 100 species are larger at higher latitudes and 20 of 22 species are larger in cooler areas. But also in this study, Ashton (2002b) showed no relationship between the strength of Bergmann's rule and body size. From the studies of Ashton et al (2000) and Ashton (2002b), which have reviewed a great part of the literature, it suggests that another explanation holds true for Bergmann's rule. Ashton (2002b) argued that fasting endurance is probably a more likely explanation for Bergmann's rule, then the originally proposed heat conservation mechanism.

The fasting endurance hypothesis means that large size is favoured in seasonal environments because larger individuals can store more fat and are able to use this fat storage during food shortages in the environment. Although this hypothesis seems true, it is not mentioning that larger individuals also need more food in absolute terms, because a large body requires more calories. But it might be that during long periods of food exclusion, larger individuals are able to reduce their metabolic rate, such as occurs during hibernation. Ashton (2002b) mentioned that because of the scaling of fat stores and metabolism with body size, larger animals have an absolutely longer fasting endurance, which enables them to survive long periods of cold (Ashton, 2002b). Furthermore, Brodie (1975) found that Antarctic fin whales (*Balaenoptera physalus*) are larger compared with those of the Northern hemisphere. Brodie (1975) suggested that this result was explained by the fact that Antarctic fin whales were selected for body proportions that reduce metabolic rate and establish an optimal surface area for deposition and efficient utilization of lipid reserves during exclusion from feeding grounds. This means that Brodie (1975) also supports the fasting endurance hypothesis instead of the heat conservation mechanism.

To summarize, I think that Ashton (2002b) is right with mentioning that the fasting endurance hypothesis has the additional advantage to explain Bergmann rule-like patterns in ectotherms. I think that the fasting endurance hypothesis can be a valid explanation for Bergmann's rule in endotherms, but only when they are able to reduce their metabolic rate during periods of food exclusion. However, it seems not applicable to ectotherms. Ectotherms have on average a more or less high surface area to volume ratio, in that way they are able to gain and lose heat very rapidly. Therefore their body is not able to deposit a lipid layer which is efficient enough to resist the cold at high latitudes.

Food quality and food abundance

Behind the heat conservation mechanism and the fasting endurance hypothesis, a nutritional hypothesis is proposed by Langvatn & Albon (1986) to explain Bergmann's rule. Langvatn & Albon (1986) found that red deer (*Cervus elaphus*) are heavier with increasing latitude, because the red deer's adapt their behavior in such a way that they maximize the food intake of digestible energy and high quality nutrients. Furthermore, they found that body weights were negatively correlated with temperature and precipitation. This means that higher quality forage places at higher latitudes and in cooler and drier climates might enhance the possibilities for red deer to increase in size. The results of this study might intend that a high primary productivity of an area (i.e. high quality of plants) increases size in mammals. In contrast with this last statement are the findings of Erlinge (1987) on stoats (*Mustela erminea*). Erlinge (1987) found that stoats in central Europe are larger than those in southern Sweden, which are in turn larger than stoats in northern Sweden. These results are contradicting with Bergmann's rule. Erlinge (1987) found a positive correlation between body size variation in stoats and regional variations in sizes of their prey, i.e. large size of stoats is linked to large size of prey. Therefore Erlinge (1987) proposes that body size variation in stoats is an adjustment to regional variations in sizes of available prey, and not to prey diversity.

Yom-Tov & Yom-Tov (2005) showed that body size of Alaskan masked shrews (*Sorex cinereus*) decreases with increasing latitude and cold January temperature, thus contradicting Bergmann's rule, but that body size increased during the second half of the twentieth century. Yom-Tov & Yom-Tov (2005) suggested that this was the result of higher food availability in winter, as a result of higher temperatures, higher precipitation and extended growth seasons due to global warming in Alaska. This is supported by the positive correlation between high January temperatures and body size. It is known that shrews are very common in the cool and damp forest of North America, where they forage on soil invertebrates, but that too cold temperatures (i.e. in winters) reduce these food source, which then might result in a decline in body size of shrews.

In a study by Ochocinska & Taylor (2003) the condylobasal length of the skull (CBL) in four of five shrews of Palearctic *Sorex* species was negatively correlated with latitude and positively correlated with temperature. This is in contrast with the heat conservation mechanism for Bergmann's rule and Ochocinska & Taylor (2003) hypothesized that scarcity of food in winter is a major factor selecting for smaller body size in shrews in northern latitudes, because smaller individuals should require less food. Under conditions of low food availability, especially during the winter, small shrews might be better able to meet their food requirements compared to larger shrews. But, as becomes clear from the surface area to volume ratio, small shrews are losing more heat and have a high metabolic rate and therefore a low fasting endurance. This raises the question why small shrews are able to cope with low temperatures in the northern hemisphere? This might be explained for two reasons. First small shrews have the ability to forage on microhabitats which are relatively stable, and therefore predictable, because they are covered with snow (Ochocinska & Taylor, 2003). Secondly, it is also possible that small animals can better handle small prey, compared to large animals.

Ho et al (2010) argued that research has focused too much on abiotic factors to explain the latitudinal variation in body size, and that therefore they have overlooked biotic factors as explanations for Bergmann's rule. In a study of Ho et al (2010) on

three herbivores, it was shown that the plant hopper (*Prokelisia marginata*) and the sea hare (*Aplysia juliana*), but not the long-horned grasshopper (*Orchelimum fidicinium*) were larger at high latitudes, and this could be influenced by latitudinal variation in plant quality. In the laboratory, Ho et al (2010) found that all three species grew larger or faster on high-latitude plants. One of the species, the sea hare, increased growth rate by 55% at a high-latitude diet compared to a low-latitude diet. I think these findings can be extended to higher tropical levels, as also suggested by Ho et al (2010). This is also supported by Erlinge (1987) on stoats, in which stoats of larger size are feeding on larger prey. Also Ho et al (2010) mentioned that larger herbivores might support larger body size in predators.

Summarizing, food quality and food abundance are proposed in the literature as explanations for Bergmann's rule. It means that a high quality and great amount of food enhances the possibilities for animals to increase in size. Evidence for a nutritional hypothesis comes from studies on red deer (Langvatn & Albon, 1986), stoats (Erlinge, 1987), shrews (Yom-Tov & Yom-Tov, 2005; and Ochocinska & Taylor, 2003) and herbivores (Ho et al, 2010).

Competition and maintenance of preferred body temperature

Ashton & Feldman (2003) found that chelonians (turtles) follow Bergmann's rule, whereas squamates (lizards and snakes) show the opposite of Bergmann's rule. First they proposed competition as an alternative process to explain Bergmann's rule. Ashton et al (2000) suggested that competition is negatively associated with latitude which leads to larger body sizes in mammals at higher latitudes. However, it is also possible that animals evolve toward smaller body sizes when they are released from competition, which might be the case for squamates (Ashton & Feldman, 2003). In stoats, Erlinge (1987) did not find support for the competition hypothesis. Erlinge (1987) suggested that a lot of potential competitors, other than their own conspecifics, can act as competitors for stoats. Secondly Ashton & Feldman (2003) mentioned maintenance of preferred body temperature, which acts also on ectotherms, as an alternative process. For example, squamates are able to heat and cool their body very rapidly, because of their high surface area to volume ratio; on the contrary chelonians are better in heat conservation because of their shell, density and size (Ashton & Feldman, 2003). Therefore Ashton & Feldman (2003) suggested that selection for maintenance of preferred body temperature is accomplished by size variation to conserve heat (mammals, birds, turtles) or increase heat gain (lizards and snakes). From the two examples mentioned above, it becomes clear, that a process responsible for body size variation can have different effects on different groups of animals. Therefore I think that it is important to look from different point of views when a process is considered for a mechanism or pattern.

It is difficult to give one general explanation for Bergmann's rule, because all given explanations in the literature have some kind of evidence. Therefore I think that Bergmann's rule cannot be explained only by the heat conservation mechanism, as originally proposed by Bergmann himself. I think that a combination between abiotic (i.e. temperature) and biotic (i.e. food quality and food abundance) factors, as supported by Ho et al (2010), is a better explanation for larger size at higher latitudes and in cooler climates, than that one mechanism (i.e. heat conservation) is a more or less valid explanation than other mechanisms. In view of the interaction between a lot of abiotic factors in the field, I think that it is not right to rule out some abiotic factors when the pattern of latitudinal body size variation is investigated. This is supported by the fact that latitude alone is not the explanation for body size

variation among latitudes, but that a combination of factors, i.e. temperature and precipitation, drives latitudinal body size variation.

Laugen et al (2005) suggested that behind environmental factors also genetic factors might be important in determining body size. In their study on frogs *R. temporaria* they found a positive correlation between metamorphic and adult body sizes, which suggest that latitudinal body size variation in adult *R. temporaria* could be genetically driven. This finding also supports that it is worth to look at a combination of factors by investigating a pattern or mechanism.

In the time Bergmann was proposing his rule, he only applied it to endotherms, because he argued that only this kind of animals were able to generate heat to sustain the cold of the arctic environment. But it is known that ectotherms have benefits compared to endotherms when food supplies are limited, which is a common situation in cold environments. This is because endotherms need more food as a result of higher metabolic rates, because they have to generate heat by their own, which is a serious disadvantage if food supplies are limited (Biology, 2005). Also with the proposed shifting of climate zones by Hughes (2000, see later section), it becomes possible that some kinds of ectotherms can live further northwards. Furthermore, Ray (1960) found that at least 13 of 17 poikilotherm species (76,5%) showed body size variation inversely proportional to temperature, conforming Bergmann's rule, and when he compiled all the data present at that moment in the literature (including his own observations) he found that Bergmann's rule was applicable to 27 of 36 species (75 %). Thus in 1960 it was still clear that also ectotherms are following the pattern of large size at higher latitudes in cooler climates.

Future studies

Global mean surface temperatures are increased 0.6 °C since the late 19th century (figure 6), and the warming of the earth has been greatest over latitudes between 40° N and 70° N (Houghton et al, 2001; Hughes, 2000). Due to global warming, the physiology, distribution and phenology are changing in animals and plants (Hughes, 2000). Hughes (2000) also expected that animal and plant species are moving upward in elevation or toward the poles in latitude in response to shifting climate zones. Therefore I think that with longer growing seasons due to increased temperatures at high latitudes in the northern hemisphere, and a greater diversity of food because of increased invasion of plant and animal species, animals that are already present at higher latitudes in the northern hemisphere have access to a greater amount and different composition of food which enables them to grow larger. Also energetic costs of foraging will be lower when a greater amount of food is available, which might favour allocation of resources to growth.

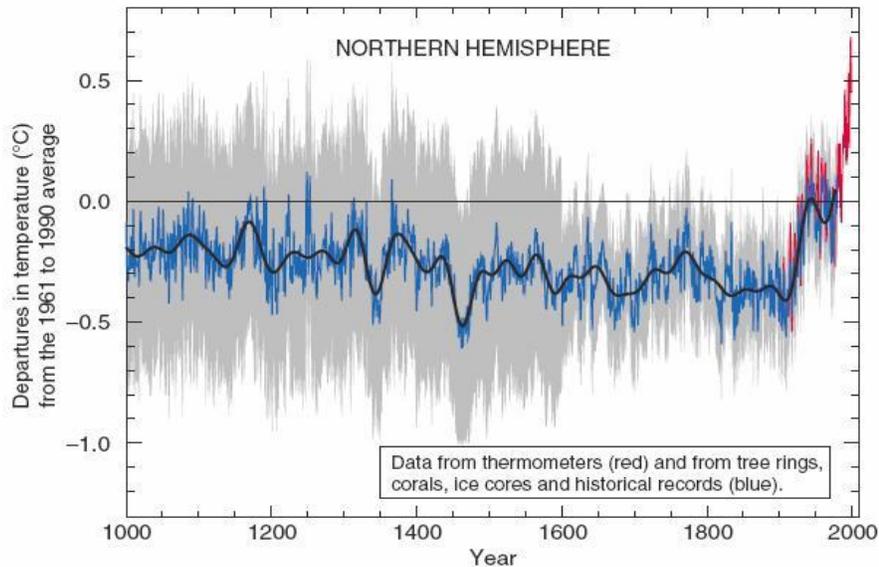


Figure 6. Variations of the earth’s surface temperature in the northern hemisphere over the last millennium. Blue line represents year by year variations; black line represents 50 year average variation; grey background represents 95% confidence interval. It is clear that temperatures increased more in the 20th century compared to the previous nine centuries. (modified from Houghton et al, 2001, figure 1).

Therefore, I suggest for further research, to focus on the appearance of vegetation types in habitats. Questions like what kind of food is present in an area? in which quantities?, and what is the energetic value of the food? will become more and more important when the effects of global warming will become more obvious. It might be clear that not only the quantity of food but also the quality of food (its energetic value) determines the growth of individuals, as already suggested by Ho et al (2010), which found that plant quality at high latitudes might support better growth of herbivores. This process might also operate on other tropic levels which feed on herbivores. More research is needed to support the findings of Ho et al (2010) to see if food quality is a good explanation for Bergmann’s rule.

Conclusion

A first impression of correlation coefficients between size and latitude for endotherms and ectotherms shows that birds and mammals (endotherms) strongly follow the pattern of larger size at higher latitudes (~90%), whereas ectotherms follow it (50%), but not as strong as endotherms. I think that a combination between abiotic (i.e. temperature) and biotic (i.e. food quality and food abundance) factors is a better explanation for latitudinal body size variation in animals, instead of one mechanism (i.e. heat conservation). This is supported by the fact that latitude alone is not the explanation for body size variation among latitudes, but that a combination of factors, i.e. temperature and precipitation, drives latitudinal body size variation. Therefore, I encourage further studies to look at the interaction between abiotic and biotic factors to explain the mechanism behind Bergmann’s rule, in which it is important to investigate the effects of global warming on vegetation types and the direct and indirect effects on food quality and food abundance.

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Appendix

Table 1. Relationship between body size and latitude for **both sexes** of sedentary birds, mammals and ectoterms. Species are arranged based on birds, mammals, caudata (salamanders), anura (frogs and toads), chelonia (turtles) and squamata (lizards and snakes) and then alphabetically by genus and species within these categories. r (lat.) = correlation coefficient between size and latitude. Rank-number corresponds with symbols in figure 2a. WL = wing length. BL = body length. TL = total length. SVL = snout-vent length.

	Latin name		English name	r (Lat.)	Rank-	Size
	Genus	Species			number	measure
Birds	<i>Dacelo</i>	<i>gigas</i>	Kookaburra	0,4	1	WL
	<i>Meliphaga</i>	<i>virescens</i>	Singing honey Eater	0,91	2	WL
	<i>Myiagra</i>	<i>inquieta</i>	Restless Flycatcher	0,47	3	WL
	<i>Perisoreus</i>	<i>canadensis</i>	Gray Jay	-0,42	4	WL
	<i>Picoides</i>	<i>pubescens</i>	Downy Woodpecker	-0,915	5	WL
Mammals	<i>Dipodomys</i>	<i>agilis</i>	Agile Kangaroo Rat	0,9334	6	head + BL
	<i>Heteromys</i>	<i>gaumeri</i>	Gaumer's Spiny Pocket Mouse	0,417	7	TL
	<i>Lycalopex</i>	<i>culpaeus</i>	Culpeo Fox	0,91	8	BL
	<i>Lycalopex</i>	<i>griseus</i>	Argentine gray Fox	-0,61	8	BL
	<i>Myotis</i>	<i>californicus</i>	California Bat	0,861	9	TL
	<i>Neotoma</i>	<i>cinerea</i>	Bushy-tailed Woodrat	0,57	10	mass
	<i>Neotoma</i>	<i>lepida</i>	Desert Woodrat	0,06	10	mass
	<i>Perognathus</i>	<i>penicillatus</i>	Desert pocket Mouse	0,51	11	TL
	<i>Peromyscus</i>	<i>californicus</i>	California Mouse	0,93	12	mass
	<i>Peromyscus</i>	<i>eremicus</i>	Cactus Mouse	0,01	12	mass
	<i>Peromyscus</i>	<i>maniculatus</i>	Deer Mouse	0,1	12	mass
	<i>Sigmodon</i>	<i>hispidus</i>	Hispid cotton Rat	0,949	13	mass
Caudata	<i>Aneides</i>	<i>flavipunctatus</i>	Black Salamander	0,59	14	SVL
	<i>Desmognathus</i>	<i>ochrophaeus</i>	Allegheny mountain dusky Salamander	0,24	15	SVL
	<i>Eurycea</i>	<i>bislineata</i>	Northern two-lined Salamander	0,11	16	SVL
Anura	<i>Hyla</i>	<i>regilla</i>	Pacific Treefrog	0,4	17	SVL
Squamata	<i>Loxocemus</i>	<i>bicolor</i>	Mexican burrowing Pythons	-0,6	18	TL
	<i>Sauromalus</i>	<i>obesus</i>	Chuckwalla	0,43	19	SVL

Table 2. Relationship between body size and latitude for **males** of sedentary birds, mammals and ectoterms. Species are arranged based on birds, mammals, caudata (salamanders), anura (frogs and toads), chelonia (turtles) and squamata (lizards and snakes) and then alphabetically by genus and species within these categories. r (lat.) = correlation coefficient between size and latitude. Rank-number corresponds with symbols in figure 2b. WL = wing length. BL = body length. TL = total length. SVL = snout-vent length. CL = carapace length. PL= plastron length.

	Latin name		English name	r (Lat.)	Rank-	Size
	Genus	Species			number	measure
Birds	<i>Accipter</i>	<i>nisus</i>	Sparrow Hawk	0,87	1	WL
	<i>Bubo</i>	<i>virginianus</i>	Great-Horned Owl	0,58	2	WL
	<i>Cyanocitta</i>	<i>stelleri</i>	Steller's Jay	0,63	3	WL
	<i>Diglossa</i>	<i>carbonaria</i>	Grey-bellied Flowerpiercer	0,16	4	WL
	<i>Empidonax</i>	<i>hammondii</i>	Hammond's Flycatcher	0,2	5	WL
	<i>Otus</i>	<i>asio</i>	Screech Owl	0,52	6	WL
	<i>Parus</i>	<i>carolinensis</i>	Carolina Chickadee	0,65	7	WL
	<i>Passer</i>	<i>domesticus</i>	House Sparrow	0,55	8	WL
	<i>Picoides</i>	<i>villosus</i>	Hairy Woodpecker	0,19	9	WL
	<i>Quelea</i>	<i>quelea</i>	Red-billed Ouelea	-0,58	10	WL
	<i>Sitta</i>	<i>carolinensis</i>	White-breasted Nuthatch	0,88	11	WL
	<i>Sitta</i>	<i>pulsilla</i>	Brown-headed Nuthatch	0,88	11	WL
	<i>Thryothorus</i>	<i>ludovicianus</i>	Carolina Wren	-0,64	12	WL
Mammals	<i>Canis</i>	<i>latrans</i>	Coyote	0,17	13	head + BL
	<i>Canis</i>	<i>lupus + niger</i>	Gray Wolf	0,35	13	head + BL
	<i>Dipodomys</i>	<i>peninsularis</i>	Kangeroo Rat	-0,746	14	BL
	<i>Dipodomys</i>	<i>peninsularis</i>	Kangeroo Rat	-0,655	14	TL
	<i>Macropus</i>	<i>fuliginosus</i>	Western gray Kangeroo	0,5941	15	mass
	<i>Macropus</i>	<i>giganteus</i>	Eastern gray Kangeroo	0,3826	15	mass
	<i>Martes</i>	<i>americanus</i>	American Marten	0,1	16	head + BL
	<i>Martes</i>	<i>pennanti</i>	Fisher	-0,18	16	head + BL
	<i>Procyon</i>	<i>lotor</i>	Raccoon	0,871	17	fall mass
	<i>Procyon</i>	<i>lotor</i>	Raccoon	0,922	17	spring mass
	<i>Rattus</i>	<i>rattus</i>	Black Rat	0,38	18	head + BL
	<i>Scapanus</i>	<i>latimanus</i>	Broad-footed Mole	0,837	19	TL
	<i>Tachyglossus</i>	<i>vulpecula</i>	Echidna	0,8077	20	mass
	<i>Taxidea</i>	<i>taxus</i>	Badger	0,32	21	head + BL
	<i>Urocyon</i>	<i>cinereoargenteus</i>	Gray Fox	0,31	22	head + BL
	<i>Vulpes</i>	<i>velox + macrotis</i>	Swift Fox	-0,19	23	head + BL
	<i>Vulpes</i>	<i>vulpes</i>	Red Fox	0,4	23	head + BL
Caudata	<i>Desmognathus</i>	<i>fuscus</i>	Dusky Salamander	0,55	24	SVL
	<i>Eurycea</i>	<i>longicauda</i>	Long-tailed Salamander	-0,53	25	SVL
	<i>Plethodon</i>	<i>cinereus</i>	Red-backed Salamander	0,83	26	SVL
	<i>Taricha</i>	<i>granulosa</i>	Roughskin Newt	-0,94	27	SVL
	<i>Triturus</i>	<i>marmoratus</i>	Marbled Newt	0,5	28	SVL
Anura	<i>Rana</i>	<i>catesbeiana</i>	North American Bullfrog	-0,89	29	SVL
	<i>Rana</i>	<i>septentrionalis</i>	Mink Frog	0,72	29	SVL

Table 2 *continued.*

	Latin name		English name	r (Lat.)	Rank-	Size
	Genus	Species			number	measure
Chelonia	<i>Clemmys</i>	<i>insculpta</i>	North American wood Turtle	0,59	30	CL
	<i>Chrysemys</i>	<i>picta</i>	Painted Turtle	0,69	31	PL
	<i>Emys</i>	<i>blandingii</i>	Blanding's Turtle	0,77	32	CL
Squamata	<i>Cnemidophorus</i>	<i>gularis</i>	Texas spotted Whiptail	-0,54	33	SVL
	<i>Cnemidophorus</i>	<i>inornatus</i>	Little striped Whiptail	0,97	33	SVL
	<i>Cnemidophorus</i>	<i>tigris</i>	Western Whiptail	0,39	33	SVL
	<i>Coleonyx</i>	<i>variegatus</i>	Western banded Gecko	-0,86	34	SVL
	<i>Gonatodes</i>	<i>humeralis</i>	Bridled forest Gecko	-0,82	35	SVL
	<i>Lampropholis</i>	<i>delicata</i>	Garden Skink	0,0069	36	SVL
	<i>Phrynosoma</i>	<i>douglasi</i>	Short horned Lizard	-0,85	37	SVL
	<i>Sceloporus</i>	<i>graciosus</i>	Sagebrush Lizard	-0,66	38	SVL
	<i>Sceloporus</i>	<i>merriami</i>	Canyon Lizard	-0,55	38	SVL
	<i>Scincella</i>	<i>lateralis</i>	Little brown Skink	0,57	39	SVL
	<i>Thamnophis</i>	<i>sirtalis</i>	Garter Snake	-0,55	40	SVL
	<i>Trimorphodon</i>	<i>biscutatus</i>	Western lyre Snake	-0,93	41	TL

Table 3. Relationship between body size and latitude for **females** of sedentary birds, mammals and ectoterms. Species are arranged based on birds, mammals, caudata (salamanders), anura (frogs and toads), chelonia (turtles) and squamata (lizards and snakes) and then alphabetically by genus and species within these categories. r (lat.) = correlation coefficient between size and latitude. Rank-number corresponds with symbols in figure 2c. WL = wing length. BL = body length. TL = total length. SVL = snout-vent length. CL= carapace length. PL= plastron length.

	Latin name		English name	r (Lat.)	Rank-	Size
	Genus	Species			number	measure
Birds	<i>Accipiter</i>	<i>nisus</i>	Sparrow Hawk	0,75	1	WL
	<i>Bubo</i>	<i>virginianus</i>	Great Horned Owl	0,57	2	WL
	<i>Diglossa</i>	<i>carbonaria</i>	Grey-bellied Flowerpiercer	0,25	3	WL
	<i>Empidonax</i>	<i>hammondii</i>	Hammond's Flycatcher	0,47	4	WL
	<i>Otus</i>	<i>asio</i>	Screech Owl	0,84	5	WL
	<i>Parus</i>	<i>carolinensis</i>	Carolina chickadee	0,57	6	WL
	<i>Passer</i>	<i>domesticus</i>	House Sparrow	0,58	7	WL
	<i>Picoides</i>	<i>villosus</i>	Hairy Woodpecker	0,61	8	WL
	<i>Sitta</i>	<i>carolinensis</i>	White-breasted Nuthatch	0,068	9	WL
	<i>Sitta</i>	<i>pulsilla</i>	Brown-headed Nuthatch	0,86	9	WL
	<i>Thryothorus</i>	<i>ludovicianus</i>	Carolina Wren	-0,62	10	WL
Mammals	<i>Alces</i>	<i>alces</i>	Moose	0,77	11	carcass mass
	<i>Canis</i>	<i>latrans</i>	Coyote	0,04	12	head + BL
	<i>Canis</i>	<i>lupus + niger</i>	Gray Wolf	0,3	12	head + BL
	<i>Macropus</i>	<i>giganteus</i>	Eastern gray kangaroo	0,4913	13	mass
	<i>Martes</i>	<i>americanus</i>	American Marten	0,22	14	head + BL
	<i>Procyon</i>	<i>lotor</i>	Raccoon	0,871	15	fall mass
	<i>Procyon</i>	<i>lotor</i>	Raccoon	0,951	15	spring mass
	<i>Rattus</i>	<i>rattus</i>	Black Rat	0,32	16	head + BL
	<i>Scapanus</i>	<i>latimanus</i>	Broad-footed mole	0,673	17	TL
	<i>Tachyglossus</i>	<i>vulpecula</i>	Echidna	0,8129	18	mass
	<i>Taxidea</i>	<i>taxus</i>	Badger	0,25	19	head + BL
	<i>Urocyon</i>	<i>cinereoargenteus</i>	Gray Fox	0,27	20	head + BL
	<i>Vulpes</i>	<i>velox + macrotis</i>	Swift Fox	0,26	21	head + BL
	<i>Vulpes</i>	<i>Vulpes</i>	Red fox	0,35	21	head + BL
Caudata	<i>Eurycea</i>	<i>longicauda</i>	Long-tailed Salamander	-0,24	22	SVL
	<i>Eurycea</i>	<i>lucifuga</i>	Cave Salamander	0,27	22	SVL
	<i>Plethodon</i>	<i>cinereus</i>	Red-backed Salamander	0,92	23	SVL
	<i>Taricha</i>	<i>granulosa</i>	Roughskin Newt	-0,85	24	SVL
	<i>Triturus</i>	<i>marmoratus</i>	Marbled Newt	0,55	25	SVL
Anura	<i>Rana</i>	<i>catesbeiana</i>	North American Bullfrog	-0,82	26	SVL
	<i>Rana</i>	<i>septentrionalis</i>	Mink Frog	0,48	26	SVL
Chelonia	<i>Clemmys</i>	<i>insculpta</i>	North American wood Turtle	0,52	27	CL
	<i>Chelydra</i>	<i>serpentina</i>	Snapping Turtle	0,54	28	CL
	<i>Chrysemys</i>	<i>picta</i>	Painted Turtle	0,7	29	PL
	<i>Kinosternon</i>	<i>flavescens</i>	Yellow mud Turtle	-0,82	30	CL
	<i>Mauremys</i>	<i>leprosa</i>	Pond Turtle	0,98	31	CL

Table 3 continued.

	Latin name		English name	r (Lat.)	Rank-	Size
	Genus	Species			number	measure
	<i>Terrapene</i>	<i>carolina</i>	Box Turtle	0,42	32	CL
	<i>Testudo</i>	<i>hermanni</i>	Hermann's Tortoise	0,57	33	CL
Squamata	<i>Cnemidophorus</i>	<i>gularis</i>	Texas spotted Whiptail	0,94	34	SVL
	<i>Cnemidophorus</i>	<i>inornatus</i>	Little striped Whiptail	0,98	34	SVL
	<i>Cnemidophorus</i>	<i>sexlineatus</i>	Six-lined Racerunner	-0,7	34	SVL
	<i>Cnemidophorus</i>	<i>tesselatus</i>	Checkered Whiptail	-0,97	34	SVL
	<i>Cnemidophorus</i>	<i>tigris</i>	Western Whiptail	0,69	34	SVL
	<i>Coleonyx</i>	<i>variegatus</i>	Western banded Gecko	-0,86	35	SVL
	<i>Crotalus</i>	<i>viridis</i>	Western rattle Snake	0,93	36	SVL
	<i>Crotalus</i>	<i>oreganus</i>	Rattle snake	-0,41	36	SVL
	<i>Crotaphytus</i>	<i>collaris</i>	Collared Lizard	0,34	37	SVL
	<i>Lacerta</i>	<i>agilis</i>	Sand Lizard	0,94	38	SVL
	<i>Lampropholis</i>	<i>delicata</i>	Garden Skink	-0,085	39	SVL
	<i>Nerodia</i>	<i>rhombifer</i>	Diamond-backed Watersnake	0,8	40	SVL
	<i>Opheodrys</i>	<i>vernalis</i>	Smooth green Snake	-0,65	41	SVL
	<i>Phrynosoma</i>	<i>douglasi</i>	Short horned Lizard	-0,85	42	SVL
	<i>Pseudemys</i>	<i>concinna</i>	River cooter	-0,9	43	PL
	<i>Sceloporus</i>	<i>undulatus</i>	Fence Lizard	0,09	44	SVL
	<i>Sceloporus</i>	<i>graciosus</i>	Sagebrush Lizard	-0,62	44	SVL
	<i>Sceloporus</i>	<i>magister</i>	Spiny Lizard	-0,99	44	SVL
	<i>Sceloporus</i>	<i>merriami</i>	Canyon Lizard	-0,053	44	SVL
	<i>Scincella</i>	<i>lateralis</i>	Little brown Skink	-0,15	45	SVL
	<i>Thamnophis</i>	<i>sirtalis</i>	Garter Snake	-0,56	46	SVL
	<i>Trachemys</i>	<i>scripta</i>	Slider	-0,31	47	PL
	<i>Trimorphodon</i>	<i>biscutatus</i>	Western lyre Snake	-0,92	48	TL
	<i>Urosaurus</i>	<i>ornatus</i>	Tree Lizard	0,38	49	SVL
	<i>Uta</i>	<i>stansburiana</i>	Side-blotched Lizard	-0,4	50	SVL