# Does the Inverse of Bergmann's Rule Apply to the *Hemidactylus* Genus?

By

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A thesis submitted in partial fulfillment
of the requirements of the University Honors Program
University of South Florida St. Petersburg

April 27, 2017

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*Abstract- The applications of Bergmann's rule on nocturnal squamates has rarely been examined. Bergmann's rule states that species increase in size with increasing latitude. The relationship between latitudinal gradients and body size may shed light on the mechanisms these geckos use to function under suboptimal temperatures. This study examined maximum body size in relationship to absolute latitude in 33 of the 132 Hemidactylus species. The objective of the study was to test the inverse of Bergmann's rule, thus testing if lizard body sizes decrease towards higher latitudes. Data was collected from literature and the following two databases, Vertnet and The Reptile Database. I performed a regression analyses to determine whether there is an association between body size and latitudinal gradient. The results indicate no support for the relationship between maximum body size and latitude in the studied species. There was also a lack of support that sexual dimorphism has an effect on the association between maximum body size and latitude. These results support that the inverse of Bergmann's rule does not apply to the studied Hemidactylus species, indicating these species do not require smaller body sizes to function under suboptimal temperatures.*

## Introduction

Bergman's rule is an ecogeographic rule relating geographic variation with the body sizes of animals. Bergmann's rule states that animals will increase in size at higher latitudes and thus, colder climates. The empirical validity of the rule remains hotly contested (see e.g. Rensch, 1938; Scholander, 1955; Mayr, 1956; Ray, 1960; James, 1970; McNab, 1971; Gittleman, 1985; Ralls & Harvey, 1985; Geist, 1987, 1990; Paterson, 1990; Cotgreave & Stockley, 1994; Hawkins, 1995; Hawkins & Lawton, 1995; Van Voorhies, 1996, Teplitsky & Millien 2014). From the many translations and interpretations from Carl Bergmann's original work in 1847 titled "Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse", researchers around the world all have their own opinions on whether this rule is relevant based on energetic considerations. It is important to understand the applicability of Bergmann's rule to elucidate if it can be extended to predict the effects of climate change. If applicable, climate change will lead to a trend with smaller body-sized animals in warmer climates, and larger body sizes in colder climates.

The original translation from Bergmann's original work is "for the amount of warmth, of which an animal can raise itself above its surroundings, 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 surroundings. This law must be of great importance on the mode of life of warm-blooded animals" (Bergmann 1847, p. 600–601) (Translation provided by Watt et al. 2009). This definition has been rewritten most prominently by Rensch (1983) and Mayr (1963), keeping to the original definition by stating "the rule is clearly formulated to pertain to species within a genus”. In further interpretations, researchers such as Belk and Houston (2002) and Scholander (1955) believe this rule mainly applies to the intraspecific and subspecies level. For this paper, I will apply the original reference to species within a genus.

When examining body size in relation to latitude, thereby including temperature, energetic considerations need to be the main premise for which Bergman’s rule is evaluated. The rule was originally written with the application to endotherms. In mammals and birds, there are studies documenting support for Bergmann’s rule (Barnett 1977, Murphy 1985, Langvatn and Albon 1986, Yom-Tov 1986, Dayan et al. 1989, Owen 1989, Yom-Tov 1993, Wigginton and Dobson 1999, Meiri and Dayan 2003, Jones et al. 2005, Lahann et al. 2006). Despite these findings, some still argue that Bergmann’s rule has no basis in fact or theory. Geist (1987) noticed that while mammals did indeed follow a general pattern of larger body sizes in the north and smaller in the south (North America), he argued that “since they do not increase in size from south to north at rates two orders of magnitude greater” then Bergmann’s rule is invalid. Another researcher who documented that Bergmann’s rule is invalid is Scholander (1955). Much like Geist (1987), Scholander doesn’t necessarily question the observation of larger body size in cold environments, but rather questions the validity of the mechanism behind it. He states that the proposed mechanism of increased size and change of body proportion do not explain the conservation of a significant quantity of body heat, but rather attributes it to heat conservation by insulation and vascular control (Scholander 1955).

When examining ectothermic animals, Bergmann’s rule becomes more contentious. Ectotherms, unlike endotherms, do not create their own heat, thus it would be unreasonable to suggest that the mechanism proposed by Bergmann’s rule would explain body size changes in both endotherms and ectotherms (Watt et al. 2009). However, this does not mean that a pattern is not present. Despite ectotherms not being able to create their own heat, some can still be considered as homeotherms. A homeotherm refers to the ability of the organism to maintain body temperature in the face of changing environmental temperatures (Ricklefs and Miller 1999). Many ectotherms are homeotherms through their behavioral regulation of temperature or creating warmth through muscular activity (i.e. Leatherback Sea Turtles, Paladino et al 1990; Female brooding Burmese Pythons, Van Mierop et al 1978; Dragonflies, May 1976). While Watt et al. (2009) argue that even if ectothermic organisms may follow either Bergmann’s rule or its inverse, it does not provide support for Bergmann’s rule due to the original nature of its postulation. In addition, Watt et al. (2009) argue that without a mechanism to describe the trends, there is little value in describing them.

I believe that even if no direct mechanism is fully explained, that the empirical validity of the trend must first be established to further discuss the possible mechanisms behind it, for it can shed light into additional aspects of the organism's biology. This is best illustrated by the work of Ashton and Feldman (2003), who tested the relationship between body size and latitude/elevation and temperature in chelonians (turtles) and squamates (lizards and snakes) for a total of 128 species. What they found is that while 83% of chelonians follow the trend for Bergmann’s rule, 73% of squamates were larger at lower latitudes, supporting the inverse of Bergmann’s rule. In their discussion of the possible mechanisms driving inverse of Begmann’s rule, they proposed fasting endurance, severity of competition, surface area to volume ratios, developmental temperatures, and the influence of other trends such as Cope’s rule (increased body size within a lineage over time; Stanley 1973; Alroy 1998) and Rapoport’s rule (increased geographic range size with increased latitude; Stevens 1989, 1992; Gaston et al. 1998).

The objective of this paper is test if the inverse of Bergmann’s rule applies to the nocturnal genus *Hemidactylus*. These geckos live primarily in darkness and function under suboptimal temperatures. One possible mechanism to their adaptation could be their small size. Bergmann proposes a decrease in surface area to volume ratio resulting in larger body sizes enabling for slower heat loss at higher latitudes, and thus colder climates (Bergmann 1847). The inverse of Bergmann’s rule proposes smaller sized individuals will occur at higher latitudes and colder climates because the increased surface area to volume enables rapid heat gain which may be adaptive to the colder temperatures (Ashton and Feldman 2003). Thus, I test the predictability of the inverse of Bergman’s rule on a nocturnal ectothermic genus, specifically whether *Hemidactylus* species body sizes decrease as latitudes increase in colder environments.

## Study organism

### *Hemidactylus*

The genus *Hemidactylus* belongs to the family *Gekkonidae*. It is considered to be one of the most species rich reptile genera with its 132 currently recognized species (Smid et al 2015). Not only is this genus high in its species numbers, but it also extends across a vast geographic range, with many of its species having become established in new areas of the world by repeated anthropogenic introductions. (Bauer et al 2010). Phylogenetic studies have found that the genus is divided into four divergent clades consisting of the African-Atlantic clade, *H. angulatus* clade, tropical Asian clade, and the arid clade (Bansal & Karanth, 2010; Bauer et al, 2010; Carranza & Arnold, 2006; Moravec et al., 2011) with the arid clade being the most species rich (Smid et al 2015).

The *Hemidactylus* genus is composed of only nocturnal species. Due to being nocturnal, there is a small range of potential temperatures that can be achieved throughout the night, the temperature variation being spatial and not temporal (Hitchcock and McBrayer 2006). This means that they are thermoconformers (proven in *Hemidactylus turcicus*) and are not thermoregulators (Hitchcock and McBrayer 2006). Even though the study was conducted on just *Hemidactylus turcicus*, it is reasonable to apply the same mechanism to other nocturnal geckos since they all share a nocturnal environment and would be constrained to select thermally similar microclimates (Hitchcock and McBrayer 2006). There is evidence that supports that idea that even though *Hemidactylus turcicus* functions at a lower optimum temperature than preferred for locomotion, that other parts of its physiology are likely adapted to low nocturnal temperatures through a decrease in their minimal cost of locomotion (Hitchcock and McBrayer 2006). In addition, they could be exploiting the temperature range available during their diurnal inactive periods to compensate for the low range at night (Hitchcock and McBrayer 2006).

## Data collection and analyses

I collected data from the literature that reported *Hemidactylus* body size (snout vent length in mm) along with latitude and longitude.  Most studies used maximum adult snout vent length as the measure of body size, but some used average snout vent length instead. Those studies that did not report maximum snout-vent length were removed from the data set to keep consistency when comparing body size measurements. Although Bergmann's rule refers to temperature, latitude has been typically used as a proxy (Ashton et al 2000). When coordinates were not given, the coordinates were taken from the centroid of the location given.

Two databases, Vertnet and The Reptile Database, were also utilized to compile the dataset. A dataset with 33 species was composed. A regression test was run between maximum body size (mm) and absolute latitude. In instances where two maximum values were reported for the same absolute latitude, the entry with highest sample size was selected. This was done to increase the statistical validity of the regression test. In addition, regression tests were run separately for male and female data to test if sexual dimorphism had any relationship to body size and latitudinal gradients.

## Results

I tested if there was an effect of sample size on maximum body size. I found no significant relationship ($R^2 = 0.023$, df= 23, F= 0.527, p= 0.475), therefore there is no influence on sample size biasing the maximum body sizes in this study. I then proceeded to test the association between maximum body size and latitude. I found no significant relationship between maximum body size and latitude with the total dataset ($R^2 = 0.0389$, df=32, F=1.255, p=0.271; Fig.1).

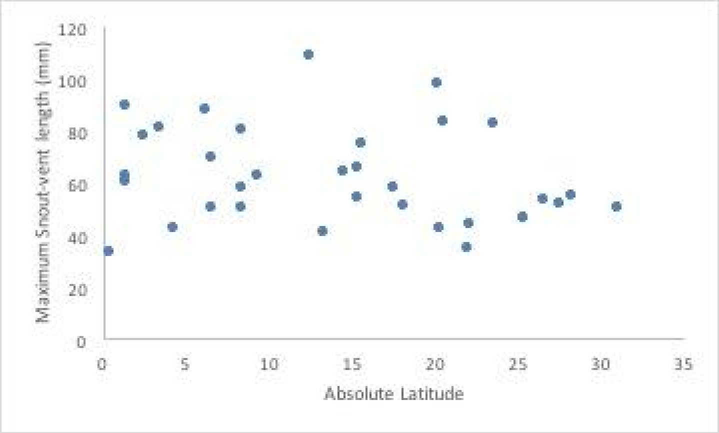

Figure 1. Relationship between snout-vent length of the *Hemidactylus* genus and absolute latitude.

There was no significant relationship between maximum snout-vent length and latitude for males (Males; $R^2$ =0.011, df=12, F=0.118, p= 0.738; Fig. 2).

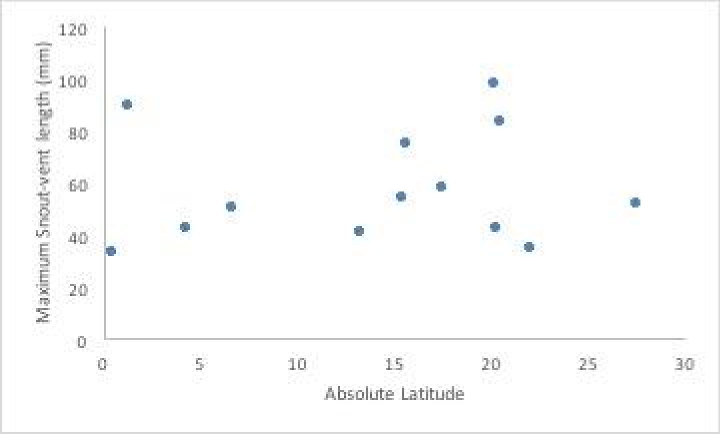

Figure 2. Relationship between male snout-vent length of the *Hemidactylus* genus and absolute latitude.

There was no significant relationship between maximum snout-vent length and latitude for females (Females; $R^2$ = 0.066, df= 10, F= 0.652, p= 0.440; Fig.3).

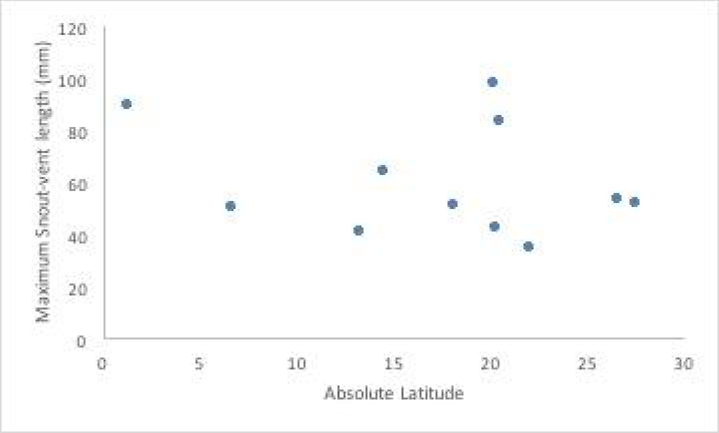

Figure 3 . Relationship between female snout-vent length of the *Hemidactylus* genus and absolute latitude.

In summation, I found no trend for Bergmann’s rule or its inverse in the studied *Hemidactylus* species.

## Discussion

There was no significant relationship between maximum snout-vent length and geographic latitude. The data provides no evidence for patterns associated with either Bergmann's rule or the inverse of Bergmann’s rule. This study supports Pincheira-Donoso and Meiri (2013), which documented certain taxa do not follow the predictions of Bergmann's rule. In addition, sex did not have any significant relationship between maximum snout-vent length and geographic latitude. This supports the idea that there is no influence of sexual dimorphism on Bergmann’s rule. In this study, we find a lack of predictability of Bergmann’s rule to the studied species. Even for endotherms where Bergmann’s rule has been supported, there are exceptions that do not follow any trend (i.e.; large mammals, Geist 1987; Shrews, Yom Tov & Yom Tov 2005; Kangaroo Rat, Sullivan & Best 1997). The lack of correlation between snout-vent length and latitude in certain species within the genus *Hemidactylus* may be due to multiple reasons.

Out of the 132 species in the *Hemidactylus*, only 33 were represented in this study. Thus, the sample size is limited and not a true representation of the genus. Further data is necessary to truly evaluate Bergmann’s rule in *Hemidactylus*. The literature itself also posed limitations, as many of the papers cited were published on the discovery of new species and or new localities for previously known species. Most of these papers had sample size values that were below three could not be used for this study. This is due to the incomplete nature of the information of the

*Hemidactylus* genus. Many of these species have come about in the last ten years due to phylogenetic studies, and morphological data for population studies has yet to be published.

A more complete survey of the *Hemidactylus* genus should still be completed to retest the hypothesis on a larger scale. Even though the study was under represented, the findings most likely will not differ, as the lack of a pattern seems to be characteristic for ectotherms (Pincheira-Donoso and Meiri, 2013). Finding answers to the predictability of Bergmann's rule in *Hemidactylus* species will increase our understanding of the thermoregulatory behaviors of these small elusive geckos. It will also support our understanding of other theories such as whether the resource rule is a better predictor of body size compared to latitudes and temperatures. With many of these species establishing themselves as invasive, understanding the relationship between body size and latitude/temperature could be useful in elucidating how these geckos will adapt in their novel environments. Body size determines metabolic functions, as a larger body size requires more metabolic inputs to keep functioning. If a larger body size is becoming more prevalent at certain latitudes, shifts in diet may be able to be predicted.

One study recorded the introduced species of *Hemidactylus palaichthus* switching from a mostly invertebrate diet to predating on one of the native diurnal geckos.  The authors found a *Hemidactylus palaichthus* on Chacachacare Island off the coast of Trinidad's northwestern peninsula and pulled out an adult male *Gonatodes vittatus* (SVL 32mm) from its mouth, the invader had not had a chance to fully swallow it yet (Charles and Smith 2009). This was the first documentation of the invasive *Hemidactylus palaicthus* predating on the native *Gonatode vittatus*. This was a significant observation because it was an invasive gecko successfully predating on a native species. If the trend continues, *Hemidacylus palaichthus* could predate the native diurnal geckos to extinction since they haven't had the opportunity to adapt to a new nocturnal predator. These types of observations illustrate the threat posed to the environments where *Hemidactylus* species are introduced, with the greatest risk occurring in island environments where restricted niche availability and specialization puts endemic species at a greater risk for extinction (CBD 2004).

In addition, this concept should be explored further to understand how climate change may play a role in the ability of the geckos to adapt to this new future. Testing for the presence, or absence, of an association between body size and latitude can lay the foundation for more in depth studies examining the complexities of how these geckos thermoregulate. Hitchcock and McBrayer (2006) proposed that more studies needed to be conducted to learn more about the thermoregulatory behavior of these ectotherms. By understanding how they physiologically adapt to the narrow and suboptimal temperature range of nocturnal life, it can reveal thermoregulation behavioral patterns as well as physiological mechanisms enabling activity in suboptimal temperatures. This knowledge is important to understanding how global climate change is going to affect the lives of these nocturnal ectotherms.

## Acknowledgments

This paper was completed in partial fulfillment of the requirements of the Honors Thesis for the Undergraduate Honors Program at the University of South Florida St. Petersburg. I would like to acknowledge Alison Gainsbury, Ph.D., who was my primary advisor for this project. She provided the guidance and patience needed to complete this project, without whom it would not have been accomplished. I would also like to acknowledge Melanie Whitmore, Ph.D., who was the secondary advisor for this project and provided review and valuable feedback.

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