

1 **Not playing by the rules: mixed support of ecogeographic rules in an arid-adapted**
2 **African ground squirrel**

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12 Running head: Ecogeographic variance in body size

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Abstract

Body size impacts nearly all aspects of an animal's life and can be subject to considerable variation in response to differences in climate and resource availability. We studied the impact of temperature and resource availability on arid-living Cape ground squirrels (*Xerus inauris*), relative to body size and degree of sexual dimorphism, over three locations differing in annual rainfall and temperature to test Bergmann's rule, the resource rule and Rensch's rule. We found that squirrels were the largest where resources were the highest and temperatures were the lowest but squirrels were similar in mass where resources were medium or low and temperatures medium and highest, partially supporting Bergmann's rule and the resource rule. Hind-feet were the largest where resources were medium and temperatures medium and similarly small in low and high resource and high and low-temperature areas. The degree of sexual dimorphism of hind-foot and mass was constant no matter the resource abundance or temperature, suggesting no impact of resource availability or temperature on the degree of sexual dimorphism, contradicting Rensch's rule. Our findings suggest that, while resource availability and temperature may have an impact on body size, other mechanisms may be important in limiting both body size and degree of sexual dimorphism in this species.

Keywords: Bergmann's rule, Rensch's rule, resource rule, hind-foot, *Xerus inauris*, sexual dimorphism

Introduction

Body size is an important characteristic of the biology of a species, affecting many aspects of their life, including reproduction and survival (Schulte-Hostedde *et al.*, 2005). Intraspecifically, size is often subject to considerable spatial and temporal variation (Boast *et al.*, 2013). Several hypotheses have been advanced to explain such spatial and temporal variation both inter- and intraspecifically. Perhaps the most well known and widely discussed hypothesis is Bergmann's rule, which stipulates that body sizes tend to increase with increasing latitude (Bergmann, 1847), which has been suggested to be a result of heat retention as latitude and temperature are correlated (Meiri, 2011; Kamilar *et al.*, 2012). This hypothesis generally holds in endotherms, where larger-bodied animals exhibit a lower surface area to volume ratio, minimizing heat-loss and metabolic needs, meaning that larger-bodied animals can better adapt to cold temperatures (Brown, Kotler, & Porter, 2017). Though often resting on thermodynamic explanations in endotherms, Bergmann's rule also applies to some ectotherms (Ashton & Feldman, 2003; Pincheira-Donoso *et al.*, 2019), suggesting other non-thermoregulatory explanations may apply to these species, including food scarcity, primary productivity and environmental predictability (Tomlinson & Withers, 2008; Meiri, 2011). The fasting endurance hypothesis suggests that larger-bodied animals are better able to endure periods of food scarcity, which occurs more frequently at higher latitudes (i.e., colder temperatures; Ashton & Feldman, 2003; Boyce, 1979; Cushman *et al.*, 1993). This hypothesis explains patterns supporting Bergmann's rule in both endotherms and ectotherms (Boyce, 1979; Cushman, Lawton, & Manly, 1993). The basis of this hypothesis rests on strategies for maintaining homeostasis, that is, smaller animals consume less food but must do so more

frequently than larger animals, while larger-bodied animals must consume larger quantities of food but can do so at longer intervals (Millar & Hickling, 1990). Thus, availability of resources can have an important influence on body size and therefore may have a role in explaining variation. McNab (2010) suggested the “resource rule”, where variation in primary productivity due to variation in temperature, rainfall and seasonality can impact the energetics of endotherms and thus their body size. This rule predicts that decreasing resource availability causes a decrease in body size intraspecifically, both spatially and temporally (McNab, 2010). In Molina’s hog-nosed skunks (*Conepatus chinga*), body size variation is related to net primary productivity and not to temperature, supporting the resource rule but not Bergmann’s rule (Schiaffini, 2016). The Australian sandy inland mouse (*Pseudomys hermannsburgensis*) and the house mouse (*Mus domesticus*), while very similar in body mass, general ecology and distribution, differ in their response to temperature, aridity and rainfall (Tomlinson & Withers, 2008). The Australian sandy inland mouse does not conform to Bergmann’s rule, nor is its body mass affected by rainfall availability, but body mass is influenced by aridity, while the house mouse conforms to Bergmann’s rule and is also influenced by rainfall and aridity (Tomlinson & Withers, 2008).

Body size can also differ between sexes of the same species, termed sexual dimorphism (Isaac, 2005). In mammals, males are more often the larger sex, known as male-biased sexual dimorphism (Shine, 1988). Most commonly, male-biased sexual dimorphism is accredited to sexual selection, wherein males compete for mating opportunities with females (Darwin, 1871; Ulian & Rossi, 2017). Alternatively, female-biased sexual dimorphism, when females are the larger sex, is often attributable to

fecundity selection (Ulian & Rossi, 2017). Rensch's rule is an allometric rule that predicts that if there is male-biased sexual dimorphism, sexual size dimorphism will increase with increasing body size and the opposite is predicted if sexual dimorphism is female-biased (Rensch, 1950; Bubadu   et al. 2018). This rule has been interpreted to indicate a positive relationship between resource availability and the degree of sexual dimorphism when males are larger than females and a negative relationship when females are the larger sex (Dale *et al.*, 2007). Rensch's rule assumes that male size varies more than female size, as males generally experience stronger sexual selection than females, while females may invest energy from additional resources into the size and number of their offspring (Wu *et al.*, 2014). In keeping with both the resource rule and Rensch's rule, cheetahs (*Acinonyx jubatus*) decreased in both height and mass with decreasing resource abundance (Boast *et al.*, 2013). Boast *et al.* (2013) found that cheetahs, where males are generally larger than females, only exhibited male-biased sexual dimorphism at a high resource site. Similar patterns exist in a number of other mammalian species (Boast *et al.*, 2013).

Cape ground squirrels (*Xerus inauris*) are distributed throughout the Namib Desert (Namibia), the Kalahari (Namibia and Botswana) and central South Africa (Herzig-Straschil, 1978), regions exhibiting low, medium and high abundance of rain, respectively (Pettitt, Waterman & Wheaton, 2008; Ewacha *et al.*, 2016). Temperatures in the Namib are generally warmer than the Kalahari, which in turn are warmer than temperatures in central South Africa (Mendelsohn et al., 2002; Jury, 2013;).

Cape ground squirrels are cooperative breeders with females living in kin groups of up to five adult females and their offspring (Skurski & Waterman, 2005; Hillegass,

Waterman, & Roth, 2008). Natal dispersal is male-biased, with unrelated dispersed males forming social groups that live apart from female groups (Pettitt & Waterman, 2011). Males tend to be 8-12% larger than females (Skurski & Waterman, 2005; Waterman, 1996).

Herzig-Straschil & Winkler (1991) studied over 300 Cape ground squirrel skulls and found that skulls tend to become smaller on an east to west cline from South Africa to Namibia. These results, combined with what we know about temperature and rainfall gradients, and consequential differences in resource availability, suggest that body sizes will be smaller in regions with lower resource availability and high temperatures compared to those inhabiting colder, higher resource areas. We may also expect to see a greater level of sexual dimorphism in South Africa due to larger body sizes, and a higher abundance of resources, than in Namibia or the Kalahari.

We examined the effects of resource availability and temperature on the body size and the degree of sexual dimorphism in Cape ground squirrels at low resource/high temperature (Namib), medium resource/medium temperature (Kalahari) and high resource/low temperature (central South Africa) sites. Our objective was to determine if Cape ground squirrels follow the resource rule and/or Bergmann's rule, and if they do, whether Rensch's rule applies in terms of sexual dimorphism. In keeping with this objective, we tested the following hypotheses/predictions: 1) Size is influenced by resource availability, predicting smaller individuals, in terms of hind-foot length and body mass, in the Namib, medium-sized individuals in the Kalahari, and larger individuals in South Africa; 2) body size is influenced by temperature, predicting smaller individuals, in hind-foot length and body mass, in the Namib, medium-sized individuals

in the Kalahari and larger individuals in South Africa; and 3) the degree of sexual dimorphism is influenced by resource availability, predicting that the degree of sexual dimorphism, of hind-foot length and body mass, increases from the Namib to South Africa.

Assessing these rules with capture data provides an opportunity to investigate the patterns of body size variation and sexual dimorphism with both skeletal (hind-foot) and mass measurements. In addition, with mass measurements, we may observe both spatial and temporal patterns for a better overall understanding of the selective factors driving variation.

Methods

Study sites

Data were collected at three sites differing in mean minimum annual temperature, annual rainfall and associated resource abundance. The correlation between rainfall and resource abundance in arid environments, such as these study sites, is particularly high (Pettitt *et al.*, 2008). The low resource/high-temperature site in the Namib Desert was in the NamibRand Nature Reserve, a 185,000 ha reserve (16°02'E, 25°20'S; Ewacha *et al.*, 2016). The medium resource/medium-temperature site was in the Kalahari-bushveld region of east-central Namibia (300 km from the Namib site) on a private 3,500-ha farm 185 km southeast of Windhoek, Namibia (23°25'S, 18°00'E; Waterman, 1995). The high resource/low-temperature site, in South Africa, was in the S. A. Lombard Nature Reserve (27°35'S, 25°35'E), a 3,660-ha reserve consisting primarily of Kalahari grassland approximately 880km from the Kalahari site (Pettitt & Waterman, 2011). Annual rainfall

data were recorded from rain gauges located at each site. Rainfall data for the Namib site was available from 1967 to 2008, for the Kalahari site from 1980 to 2011, and for the central South Africa site from 1952-2011. For the Namib site, we used annual minimum temperatures recorded from 1998 to 2008 at a NamibRand Nature Reserve weather station 45 km north of our study site. For the Kalahari site, we used annual minimum temperatures recorded from 2000 to 2011 at a site 55 km south of our study site (Hoachanas, downloaded from <https://freemeteo.nl>; no temperature data were available for 2004). For the central South Africa site, we used minimum annual temperatures recorded from 1979 to 2011 at the study site (no temperature data were available from 2000-2001).

Trapping and handling

Live-trapping was conducted in all three locations, during the years 2004-2007 in South Africa, 2004-2006 in the Kalahari, and 2004-2008 in the Namib. Squirrels were trapped using Tomahawk (15 X 15 X 50 cm; Tomahawk Live Trap Inc., WI, USA) live-traps baited with peanut butter and bird-seed (Waterman, 1995). Individuals were weighed (± 5.0 g; Pesola AG spring scale, Baar, Switzerland), injected with a Passive Integrated Transponder (PIT; AVID Inc., Norco, CA, USA; Hillegass *et al.*, 2008) tag for permanent identification, aged, assessed for sex and reproductive condition, and the left hind-foot measured with electronic callipers (mm; Mitutoyo Inc., Tokyo, Japan) before being released at site of capture, as described by Waterman (1995). We only included adults, who had reached full body size and were reproductive, in our analysis to control for any differences between reproductive adults and non-reproductive sub-adults (Waterman, 1996). All procedures were approved by the University of Manitoba's

Animal Care and Use Committee and followed the guidelines of the American Society of Mammalogists (Gannon *et al.*, 2007). Permission for the project was provided by Northwest Province Parks Board in South Africa and the Namibian Ministry of Environment and Tourism.

Statistical analysis

All statistical tests were run with JMP Pro 13 (SAS Institute Inc., Cary, NC, USA). We analysed mass and hind-foot measurements separately to observe their different patterns of variation. As the majority of individuals were trapped multiple times within each location, we used mixed models with squirrel ID as a random effect. Hind-foot length was normally distributed (Shapiro-Wilk: $W = 0.98$, $P = 0.0002$) and homoscedastic so we used a mixed model ANOVA with sex and location as fixed effects and an interaction term to test for variation in the degree of sexual dimorphism by location. We calculated the degree of sexual dimorphism for each location by dividing the average hind-foot length of males, the larger individuals, by the average hind-foot length of females (Lockwood *et al.*, 1996).

To examine the effects of temperature and rainfall, we used prior month's average minimum temperature as our temperature effect and total rainfall of previous rainy season (October – April) as our rainfall variable. To determine whether body mass was influenced by location, sex, temperature, rainfall or a combination thereof, a mixed model ANOVA with a reduced maximum likelihood approach was used with ID as a random effect to account for repeated measures of the same individuals. As with the hind-foot length analysis, an interaction term between sex and location tested for variation in the

degree of sexual dimorphism by location. We included location-rainfall and location-temperature interactions, accounting for the possibility that, in keeping with Rensch's rule, the degree of sexual dimorphism may be affected by rainfall and/or temperature within locations. Residuals were normally distributed (Shapiro-Wilk: $W = 0.98$, $P = 0.0001$) and homoscedastic. We calculated the degree of sexual dimorphism by dividing the average mass of males, the larger individuals, by the average mass of females for each location (Lockwood *et al.*, 1996). All results are presented in mean \pm standard error and a 0.05 probability of a Type I error was considered significant.

Results

Average annual rainfall and average annual minimum temperature differed among sites (rainfall: $F_{2, 131} = 172.28$, $P < 0.0001$, Tukey HSD $P < 0.0001$ for all comparisons; temperature: $F_{2, 50} = 50.18$, $P \leq 0.001$, Tukey HSD Namib vs. Kalahari, $P < 0.0001$, Kalahari vs. South Africa, $P < 0.0001$, Namib vs Kalahari, $P = 0.0009$; Fig. 1). The central South Africa experiences average minimum temperatures 1.9 °C colder than the Kalahari, and 3.7 °C cooler than the Namib, while the Kalahari experiences average minimum temperatures nearly 1.8 °C colder than the Namib.

We trapped 325 individuals in South Africa from 2004 to 2007. Individuals in South Africa were trapped an average of 5.64 ± 0.39 times (ranging 1 - 39 captures). At our Kalahari site, we trapped 183 individuals from 2004 to 2006, an average of 4.46 ± 0.35 times per individual (range 1 - 22 captures). We trapped 114 individuals in the Namib from 2004 to 2008, trapping individuals on average 4.51 ± 0.43 times (range 1 – 25 captures).

Hind-foot length was influenced by both location ($F_{2,465} = 58.19$, $P < 0.0001$) and sex ($F_{1,492} = 50.18$, $P < 0.0001$); however, their interaction was not significant ($F_{2,489} = 0.01$, $P = 0.99$; Fig. 2). Male Kalahari squirrels had larger feet (61.59 ± 0.24 mm) than both male Namib squirrels (59.65 ± 0.26 mm; Tukey HSD, $P < 0.0001$) and male South African squirrels (59.47 ± 0.17 mm; Tukey HSD, $P < 0.0001$), but male squirrels from the Namib and South Africa did not differ (Tukey HSD, $P = 0.99$). Similarly, female Kalahari squirrels (60.23 ± 0.21 mm) had larger feet than both their Namib (58.36 ± 0.29 mm; Tukey HSD, $P < 0.0001$) and South African (58.17 ± 0.16 mm; Tukey HSD, $P < 0.0001$) counterparts, but female Namib and South African squirrels did not differ (Tukey HSD, $P = 0.99$). The male-biased sexual dimorphism ratio for hind-foot length was 1.02 at all three locations.

Mass was influenced by location ($F_{2,1375} = 97.81$, $P < 0.0001$), sex ($F_{1,579} = 154.34$, $P < 0.0001$), temperature ($F_{1,2540} = 30.31$, $P < 0.0001$), and rainfall ($F_{1,2716} = 4.33$, $P = 0.04$; Fig. 3). The interaction between location and rainfall was significant ($F_{2,2711} = 3.24$, $P = 0.04$). The interaction between location and sex was not significant ($F_{2,573} = 1.47$, $P = 0.23$), nor was the interaction between location and temperature ($F_{2,2536} = 0.33$, $P = 0.72$). Male South African squirrels (699.22 ± 4.04 g) were heavier than male Kalahari squirrels (615.98 ± 6.88 g) and male Namib squirrels (625.74 ± 9.54 g; Tukey HSD, $P < 0.0001$), but male squirrels from the Namib and the Kalahari did not differ in mass (Tukey HSD, $P = 0.96$). Similarly, female South African squirrels (635.86 ± 3.98 g) were larger than both Kalahari females (566.40 ± 6.19 g; Tukey HSD, $P < 0.0001$) and Namib females (575.98 ± 10.02 g; Tukey HSD, $P < 0.0001$), but female squirrels from the Kalahari and the Namib did not differ (Tukey HSD, $P = 0.97$). The ratio of

male-biased sexual dimorphism for mass was 1.09 for the Namib and Kalahari, and 1.10 for South Africa and did not differ significantly among sites ($F_{2,573} = 1.47$, $P = 0.23$).

Discussion

Our investigation into the effects of resource abundance and temperature on body size made use of two estimates: hind-foot length and mass, which differed in their results. Hind-foot length results showed that foot sizes were the largest in the medium resource, medium-temperature Kalahari site and did not differ between the high resource and low temperature South African site and the low resource, high-temperature Namib site. These findings suggest that foot size does not follow the resource rule nor does it follow Bergmann's rule, in that foot size does not increase with increasing resource availability or with decreasing temperature. These findings indicate that hind-foot length results rather from a combination of selective pressures more complex than biogeographic rules can explain. One of the selection pressures likely to influence hind-foot length is locomotion, which may be affected by density, composition and characteristics of vegetation on or off burrow systems. Montane akodonts (*Akodon montensis*) have larger feet in environments with an open understory, possibly allowing for them to run faster to evade predators (Rosalino *et al.*, 2013). Open environments also have fewer predators, resulting in different predatory selective pressures (Rosalino *et al.*, 2013). The Kalahari features bushes and small trees (Waterman, 1995), while in the Namib Desert and the South African grassland bushes and trees are rare (Unck *et al.*, 2009; Ewacha *et al.*, 2016). In northern quolls (*Dasyurus hallucatus*) larger feet correspond to higher manoeuvrability, helping to better evade predators (Wynn *et al.*, 2015). A detailed

comparison of vegetation on burrow systems among the three sites, as well as the behaviour of predators and analysis of manoeuvrability relative to foot length, would be necessary to evaluate this hypothesis in Cape ground squirrels. Furthermore, research addressing this puzzling pattern would be required to determine if larger foot sizes translate to larger measures of other body size indicators across all three study sites, and to determine the evolutionary driver of larger feet in this location. Foot length can in some cases be a good indicator of body size (Garel *et al.*, 2010). However, our findings suggest that hind-foot length may be influenced by more complex combinations of selection pressures, and as a result should not be used to examine biogeographic rules. Our results also indicate that future research with Cape grounds squirrels cannot confidently use foot length as an indication of overall body size. Rather these studies should use a standardized measure of body length such as spine length, skull length or head-body length to minimize residual and observer error (Stephens *et al.*, 2015).

Contrary to hind-foot length results, the heaviest squirrels were at the highest resource and lowest temperature site, in South Africa, and those in the medium resource and medium-temperature Kalahari site and the low resource, high-temperature Namib site did not differ in mass. Our results are also somewhat in accordance with Bergmann's rule and the resource rule, as individuals were largest in the lowest temperature and highest resource area. Two main factors diverge from the predictions of these rules. Firstly, contradicting Bergmann's rule, individuals in higher and medium temperature sites did not differ in mass. Similarly, contrary to the resource rule, squirrels inhabiting sites with medium and low resource areas were similar in size, though one site receives, on average, almost twice as much rain as the other. According to the fasting endurance hypothesis,

larger-bodied individuals require larger quantities of food but can endure longer periods of food scarcity, while smaller individuals require more frequent but less abundant feeding (Millar & Hickling, 1992). That said, the consistent seasonality of resources in the South African grassland habitat may select for larger-bodied squirrels, while the more scarce resource availability of the Namib and Kalahari deserts may similarly limit body size (Pettitt *et al.*, 2008, Ewacha *et al.*, 2016).

Not only does seasonality of rainfall affect body size, but the predictability of annual rainfall can significantly influence body size (Boyce, 1978). While rainfall may be more variable among years in the desert, particularly the Namib desert, resources are consistently low (Ewacha *et al.*, 2016), potentially favouring smaller individuals who can subsist off of fewer nutrients (Millar & Hickling, 1990). In contrast, in the South African grasslands, rainfall is generally restricted to the rainy season but it is relatively consistent from year to year (Pettitt *et al.*, 2008), selecting for larger individuals who can withstand periods of food scarcity (Millar & Hickling 1990). Similarly, highly variable rainfall patterns among years select for smaller body sizes in muskrats (*Ondatra zibethicus*), while consistent seasonality selects for large body sizes (Boyce, 1978). These potentially more significant limiters may mask the effects of resource availability and temperature. Overall, our findings suggest that resource availability, combined with seasonality, may play a role in explaining body size variation and that mass may be influenced by temperature. Notably, hind-foot length and mass results suggest that resource availability plays a role in explaining body size variation, but that the resource rule is limited in its ability to entirely predict said variation, without considering the effects of seasonality and rainfall variability.

Our investigation into the relationship between resource availability and the degree of sexual dimorphism included hind-foot length and mass data. Our results for both models indicated that the degree of sexual dimorphism did not differ among the three locations. These results are inconsistent with the hypothesis that sexual dimorphism is affected by resource availability and inconsistent with Rensch's rule. If Rensch's rule were at play in this species, we would expect to see the degree of sexual dimorphism of hind-foot lengths at its highest where hind-feet are the largest, in the Kalahari, and similarly, the degree of sexual dimorphism of mass would be the largest where squirrels are the heaviest, in South Africa. Consistent with our results, Matějů & Kratochvíl (2013) tested Rensch's rule in 63 species of ground squirrels (excluding the Cape ground squirrel) and found that ground squirrels generally do not conform to Rensch's rule, nor do they feature high degrees of sexual dimorphism overall. The relatively constant degree of sexual dimorphism, in Cape ground squirrels and other species of ground squirrel, may be attributable to the need for males to be able to fit into burrows dug by females (Matějů & Kratochvíl, 2013; Martínez et al. 2016; Wang, 2017), for refuge or to copulate with females. Similarly, Wang (2017) suggests that female Mongolian gerbils (*Meriones unguiculatus*) may have smaller body sizes than their male conspecifics allowing them to fit into burrows dug by males. Thus for semi-fossorial or fossorial species, burrowing may constrain sexual size dimorphism (Martínez et al. 2016). Isaac (2005) suggests that several factors from reproductive strategies to competition for resources may also influence sexual dimorphism. Male Cape ground squirrels are rarely aggressive and do not exhibit much pre-copulatory competition (Waterman, 1998), possibly explaining why sexual dimorphism ratios for both hind-foot length and mass are relatively small. The

degree of sexual dimorphism may not increase with increasing resource availability if reproductive competition amongst males does not increase from one location to the next. Since operational sex ratios (which reflect reproductive competition) do not differ between South Africa and the Namib, reproductive competition is also most likely similar (Manjerovic, 2010, Manjerovic & Waterman, 2015). Larger males may also be subject to higher mortality due to selective predation, where predators may be more likely to see larger individuals and may prefer them to smaller prey (Isaac, 2005), though in Namibia male Cape ground squirrels had better survival than females (Waterman, 1995). Overall, the intensity of sexual dimorphism in hind-foot and mass were not influenced by resource availability, indicating that Rensch's rule does not appear to apply to Cape ground squirrels.

Body size affects most aspects of an animal's biology (Schulte-Hostedde *et al.*, 2005), and is often limited by resource availability and/or temperature, resulting in larger individuals where resource abundance is the highest (McNab, 2010) and where temperatures are the lowest (Schiaffini, 2016). Body size is often subject to sexual dimorphism, which may increase with increasing resource availability, particularly when dimorphism is male-biased (Dale *et al.*, 2007). Somewhat contrary to the abovementioned patterns, Cape ground squirrels had the largest feet in an area with medium resources and medium temperatures, and similarly small feet in low and high resource and high and low-temperature areas, suggesting that a more complex interaction of environmental conditions is likely at play in determining hind-foot length. Consistent with the resource rule and Bergmann's rule, Cape ground squirrels were the heaviest at the coldest, highest resource site, but were similar in size at the medium and low resource

sites, which are the medium and high-temperature sites respectively, indicating that another limiting factor may be important in these harsher desert areas. Lastly, sexual dimorphism was consistent, in both hind-foot sizes and mass, among all three locations, possibly because larger squirrels may be selected as prey and may not fit down burrows constructed by smaller females. However, the small number of locations in our study may limit our conclusions, and sampling over more locations may shed light on these patterns and possible mechanisms. This investigation provided insight into the roles and limitations of the resource rule, Bergmann's rule and Rensch's rule in explaining variation in body size and the degree of sexual dimorphism, particularly in seasonal, arid environments. Further research into the interactions among ecogeographical rules and other ecological constraints in fossorial and semi-fossorial species would assist in understanding the limitations of these rules.

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References

Ashton, K. G., & Feldman, C. R. (2003). Bergmann's rule in nonavian reptiles: Turtles follow it, lizards and snakes reverse it. *Evolution*, **57**, 1151–1163.

Balčiauskas, L., Amshokova, A., Balčiauskienė, L., Benedek, A.M., Cichocki, J., Csanády, A., Mendonça, P.G. & Nistoreanu, V. (2019). Geographical clines in the size of the herb field mouse (*Apodemus uralensis*). *Integr. Zool.* 1749-4877.12407

Bergmann C. (1847). Über die verhältnisse der warmekonomie der tiere zu ihrer grosse. *Gottinger Studien*. **3**, 595–708.

Bergmann, P.J., Pettinelli, K.J., Crockett, M.E. & Schaper, E.G. (2017). It's just sand between the toes: how particle size and shape variation affect running performance and kinematics in a generalist lizard. *J. Exp. Biol.* **220**, 3706–3716.

Boast, L.K., Houser, A.M., Good, K. & Gusset, M. (2013). Regional variation in body size of the cheetah (*Acinonyx jubatus*). *J. Mammal.* **94**, 1293–1297.

Boyce, M.S. (1978). Climatic variability and body size variation in the Muskrats (*Ondatra zibethicus*) of North America. *Oecologia*, **36**, 1–19.

Boyce, M.S. (1979). Seasonality and patterns of natural selection for life histories. *The Amer. Nat.*, **114**, 569–583.

Brown, J.S., Kotler, B.P., & Porter, W P. (2017). How foraging allometries and resource dynamics could explain Bergmann's rule and the body-size diet relationship in mammals. *Oikos*. **126**, 224–230.

413 Bubadu , J. de M., Polidoro, G.L.S., Melo, G., Sponchiado, J., Serio, C., Melchionna, M.,
 414 Mondanaro, A., Castiglione, S., Meloro, C., Raia, P., C ceres, N.C. & Carotenuto,
 415 F. (2018). Rensch’s and Bergmann’s rules in Cis-Andean South-American howler
 416 monkeys (Mammalia: Alouatta). *Hystrix*, **29**, 122–127.

417 Cushman, J. H., Lawton, J. H., & Manly, B. F. J. (1993). Latitudinal patterns in European
 418 ant assemblages: Variation in species richness and body size. *Oecologia*, **95**, 30–37.

419 Dale, J., Dunn, P.O., Figuerola, J., Lislevand, T., Szekely, T. & Whittingham, L.A.
 420 (2007). Sexual selection explains Rensch’s rule of allometry for sexual size
 421 dimorphism. *Proc. R. Soc. B Biol. Sci.* **274**, 2971–2979.

422 Darwin, C. (1871). *The Descent of Man, and Selection in Relation to Sex* (Reprint 1981).
 423 London: J. Murray.

424 Ewacha, M.V.A., Kaapehi, C., Waterman, J.M. & Roth, J.D. (2016). Cape ground
 425 squirrels as ecosystem engineers: Modifying habitat for plants, small mammals and
 426 beetles in Namib Desert grasslands. *Afr. J. Ecol.* **54**, 68–75.

427 Gannon, W.L., Sikes, R.S. & Animal Care and Use Committee of the American Society
 428 of Mammalogy. (2007). Guidelines for the American Society of Mammalogists for
 429 the use of wild mammals in research. *J. Mammal.* **88**, 809–823.

430 Garel, M., Gaillard, J.M., Chevrier, T., Michallet, J., Delorme, D. & Van Laere, G.
 431 (2010). Testing reliability of body size measurements using hind foot length in roe
 432 deer. *J. Wildl. Manage.* **74**, 1382–1386.

433 Herzig-Straschil, B.B. (1978). On the biology of *Xerus inauris* (Zimmermann, 1780). *Z.*
 434 *Saugetierkd.* **43**, 262–278.

435 Herzig-Straschil, B., & Winkler, H. (1991). A morphometric analysis of the skulls of

436 *Xerus inauris* and *Xerus princeps* (Rodentia; Sciuridae). *Z. Saugetierkd.* **56**, 177–
 437 187.

438 Hillegass, M.A., Waterman, J.M., & Roth, J.D. (2008). The influence of sex and sociality
 439 on parasite loads in an African ground squirrel. *Behav. Ecol.* **19**, 1006–1011.

440 Isaac, J.L. (2005). Potential causes and life-history consequences of sexual size
 441 dimorphism in mammals. *Mamm. Rev.* **35**, 101–115.

442 Jury, M.R. (2013). Climate trends in southern Africa. *S. Afr. J. Sci.* **109**, 1–11.

443 Kamilar, J.M., Muldoon, K.M., Lehman, S.M. & Herrera, J.P. (2012). Testing
 444 Bergmann’s rule and the resource seasonality hypothesis in Malagasy primates using
 445 GIS-based climate data. *Amer. J. Phys. Anthropol.* **147**, 401–408.

446 Lockwood, C.A., Richmond, B.G., Jungers, W.L. & Kimbel, W.H. (1996).
 447 Randomization procedures and sexual dimorphism in *Australopithecus afarensis*. *J.*
 448 *Hum. Evol.* **31**, 537–548.

449 Manjerovic, M.B. (2010). The influence of sexual selection on behavioral and
 450 physiological mechanisms underlying reproductive success in male Cape ground
 451 squirrels (*Xerus inauris*). Ph.D. thesis, University of Central Florida, Orlando.

452 Manjerovic, M.B. & Waterman, J.M. (2015). “Failure to launch”: Is there a reproductive
 453 cost to males living at home? *J. Mammal.* **96**, 144–150.

454 Martínez, P.A. & Bidau, C.J. (2016). A re-assessment of Rensch’s rule in tuco-tucos
 455 (Rodentia: Ctenomyidae: Ctenomys) using a phylogenetic approach. *Mamm. Biol.*
 456 **81**, 66–72.

457 Matějů, J. & Kratochvíl, L. (2013). Sexual size dimorphism in ground squirrels
 458 (Rodentia: Sciuridae: Marmotini) does not correlate with body size and sociality.

459 *Front. Zool.* **10**, 27.

460 McNab, B.K. (2010). Geographic and temporal correlations of mammalian size
 461 reconsidered: A resource rule. *Oecologia* **164**, 13–23.

462 Meiri, S. (2011). Bergmann ' s Rule – what ' s in a name ? *J. Macroecol.* **20**, 203–207.

463 Mendelsohn, J., Jarvis, A., Roberts, C. & Robertson, T. (2002). Atlas of Namibia. A
 464 Portrait of the Land and its People. Cape Town: D. Philip Publ.

465 Millar, J.S., & Hickling, G J. (1990). Fasting endurance and the evolution of mammalian
 466 body size. *Funct. Ecol.*, **4**, 5–12.

467 Millar, J.S., & Hickling, G.J. (1992). The fasting endurance hypothesis revisited. *Funct.*
 468 *Ecol.*, **6**, 496–498.

469 Pettitt, B.A., Waterman, J.M. & Wheaton, C.J. (2008). Assessing the effects of resource
 470 availability and parity on reproduction in female Cape ground squirrels: Resources
 471 do not matter. *J. Zool.* **276**, 291–298.

472 Pettitt, B.A. & Waterman, J.M. 2011. Reproductive delay in the female Cape ground
 473 squirrel (*Xerus inauris*). *J. Mammal.* **92**, 378–386.

474 Pincheira-Donoso, D., Meiri, S., Jara, M., Olalla-Tárraga, M.Á., & Hodgson, D.J. (2019).
 475 Global patterns of body size evolution are driven by precipitation in legless
 476 amphibians. *Ecography*, **42**, 1682–1690.

477 Rensch, B. (1950). Die Abhängigkeit der relativen Sexualdifferenz von der Körpergröße.
 478 *Bonn. zool. Beitr.*, **1**:58-69.

479 Rosalino, L.M., Martin, P.S., Gheler-Costa, C., Lopes, P.C. & Verdade, L.M. (2013).
 480 Allometric relations of neotropical small rodents (Sigmodontinae) in anthropogenic
 481 environments. *Zool. Sci.* **30**, 585–590.

482 Schiaffini, M.I. (2016). A test of the Resource's and Bergmann's rules in a widely
 483 distributed small carnivore from southern South America, *Conepatus chinga*
 484 (Molina, 1782) (Carnivora: Mephitidae). *Mamm. Biol.* **81**, 73–81.
 485 Schulte-Hostedde, A.I., Zinner, B., Millar, J.S. & Hickling, G.J. (2005). Restitution of
 486 mass – size residuals : validating body condition indices. *Ecology* **86**, 155–163.
 487 Shine, R. (1988). The evolution of large body size in females : A critique of Darwin's
 488 "fecundity advantage " model. *Amer. Nat.* **131**, 124–131.
 489 Skurski, D.A. & Waterman, J.M. (2005). *Xerus inauris*. *Mamm. Species* **781**, 1–4.
 490 Stephens, R.B., Karau, K.H., Yahnke, C.J., Wendt, S.R. & Rowe, R.J. (2015). Dead mice
 491 can grow - Variation of standard external mammal measurements from live and
 492 three postmortem body states. *J. Mammal.* **96**, 185–193.
 493 Tomlinson, S.A., & Withers, P.C. (2008). Biogeographical effects on body mass of native
 494 Australian and introduced mice, *Pseudomys hermannsburgensis* and *Mus*
 495 *domesticus*: an inquiry into Bergmann's rule. *Aust. J. Zool.*, **56**, 423–430.
 496 Ulian, C.M. V, & Rossi, M.N. (2017). Intraspecific variation in body size and sexual size
 497 dimorphism, and a test of Rensch's rule in bats. *Acta Zoologica.* **98**, 377–386.
 498 Unck, C.E., Waterman, J.M., Verburgt, L. & Bateman, P.W. (2009). Quantity versus
 499 quality : how does level of predation threat affect Cape ground squirrel vigilance?
 500 *Anim. Behav.* **78**, 625–632.
 501 Wang, G. (2017). Sexual size dimorphism of group-living Mongolian gerbils *Meriones*
 502 *unguiculatus* (Muridae: Gerbillinae). *Eur. Zool. J.* **84**, 536–540.
 503 Waterman, J.M. (1995). The social organization of the Cape ground squirrel (*Xerus*
 504 *inauris*; Rodentia: Sciuridae). *Ethology* **101**, 130–147

- Waterman, J.M. (1996). Reproductive biology of a tropical, non-hibernating ground squirrel. *J. Mammal.* **77**, 134–146.
- Waterman, J.M. (1998). Mating tactics of male Cape ground squirrels, *Xerus inauris*: Consequences of year-round breeding. *Anim. Behav.* **56**, 459–466.
- Wu, H., Jiang, T., Huang, X., Lin, H., Wang, H., Wang, L., Niu, H. & Feng, J. (2014). A test of Rensch's rule in greater horseshoe bat (*Rhinolophus ferrumequinum*) with female-biased sexual size dimorphism. *PLoS One*, **9**, 1–7.
- Wynn, Mn.L., Clemente, C., Nasir, A.F.A.A. & Wilson, R.S. (2015). Running faster causes disaster: trade-offs between speed, manoeuvrability and motor control when running around corners in northern quolls (*Dasyurus hallucatus*). *J. Exp. Biol.*, **218**, 433–439.

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Figure 2. Hindfoot length (mean \pm SEM) of female and male adult Cape ground squirrels

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Figure 3. Mass (mean \pm SEM) of female and male adult Cape ground squirrels (*Xerus*

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