

Adherence to Bergmann's rule by lizards may depend on thermoregulatory mode: support from a nocturnal gecko

Sophie Penniket · Alison Cree

Received: 24 February 2014 / Accepted: 14 January 2015 / Published online: 8 February 2015
© Springer-Verlag Berlin Heidelberg 2015

Abstract Bergmann's rule predicts an increase in body size with decreasing environmental temperature; however, the converse pattern has been found in the majority of lizards studied to date. For these ectotherms, small body size may provide thermal benefits (rapid heat uptake when basking), which would be highly advantageous in cold environments. Yet such an advantage may not exist in nocturnal lizards (which do not avidly bask), in which Bergmann's rule has not been closely studied. We have examined whether the body size of a primarily nocturnal gecko, *Woodworthia* "Otago/Southland" changed with elevation and operative temperature (determined using physical copper models). In a laboratory study, we investigated whether thermoregulatory mode (heliothermy or thigmothermy) alters the effect of body size on heating and cooling rates. This gecko followed Bergmann's rule, thereby showing the opposite of the dominant pattern in diurnal lizards. Size at maturity, maximum size of adults and size at birth were larger at higher elevations and at lower operative temperatures. Using physical models, we found that large body size can confer thermal benefits for nocturnal lizards that remain within diurnal retreats. Bergmann's rule should not be dismissed for all lizards. Our results clearly support Bergmann's rule for at least one thigmothermic species, for which large body size may provide thermal benefits. Future

studies on Bergmann's rule in lizards should consider thermoregulatory mode. We advocate that this ecogeographic rule be examined in relation to operative temperature measured at field sites. Finally, we predict that climate warming may weaken the relationship between body size and elevation in this gecko.

Keywords Ectotherm · Elevation · Geographic variation · Life-history traits · Operative temperature

Introduction

The thermal environment has a fundamental effect on animal fitness and body size, such that spatial patterns in body size often correlate with climatic variation over a geographical gradient. Bergmann's rule summarises such a biogeographic pattern, describing increasing animal body size with higher latitude or elevation and, accordingly, with decreasing temperature (Meiri 2011). Originally formulated in 1847, the rule is still hotly debated (Ashton 2001; Meiri 2011; Olalla-Tárraga 2011). Some contend that Bergmann's rule should remain as it was originally framed, namely, a causal rule requiring the original proposed mechanism—heat conservation—to be proven in every case and applied to endotherms only (Pincheira-Donoso 2010; Watt et al. 2010). However, many argue that Bergmann's rule is most useful when framed as a correlative rule, used to describe patterns, not processes (Blackburn et al. 1999; Meiri 2011; Olalla-Tárraga 2011). This broader interpretation allows the rule to be examined in a wide range of taxa, for which a suite of different selective pressures may cause body size clines (Blackburn et al. 1999). In addition to these debates, there is as yet no consensus as to how Bergmann's rule should be investigated (Blackburn et al. 1999;

Communicated by Raoul Van Damme.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-015-3239-0) contains supplementary material, which is available to authorized users.

S. Penniket (✉) · A. Cree
Department of Zoology, University of Otago, P.O. Box 56,
Dunedin, New Zealand
e-mail: sophie.penniket@gmail.com

Gaston et al. 2008; Meiri 2011; Olalla-Tárraga et al. 2010), with three possible methodological approaches: intraspecific (between populations), interspecific (each species as an individual data point) or assemblage-based (using grids to examine variation at the community level) (Gaston et al. 2008).

In light of these debates, it is hardly surprising that there is disagreement as to which taxa adhere to Bergmann's rule. It is strongly contested for terrestrial ectotherms (Pincheira-Donoso 2010), with evidence for a converse trend—that ectotherm body size is smaller at higher latitudes and elevations, where temperatures are lower—or no trend at all [converse-Bergmann's rule (Ashton and Feldman 2003; Blanckenhorn and Demont 2004); no trend (Dillon et al. 2006; Pincheira-Donoso and Meiri 2013); note: only intraspecific studies are listed here]. There are even contrasts within taxonomic groups—for example, intraspecific studies on anurans report all three associations with temperature [no trend (Adams and Church 2008; Ashton 2002); converse-Bergmann's (Cvetković et al. 2009); Bergmann's rule (Schäuble 2004)]. A wide variety of complex processes could be causing these clines in ectotherm body size, including the thermal plasticity of growth rates (Walters and Hassall 2006), local adaptations to achieve more efficient thermoregulation (Ashton and Feldman 2003) or the need to survive periods of extreme cold or drought (Blackburn et al. 1999; Cushman et al. 1993).

Which variation of the rule dominates in lizards is still under intense debate, with most evidence suggesting the converse trend or no trend at all [Ashton and Feldman (2003) and Pincheira-Donoso and Meiri (2013), respectively; both meta-analyses of intraspecific studies). However, studies on lizards have included very few nocturnal species, for which selective forces may differ. Diurnal lizards may have evolved a small body size in cold climates (converse-Bergmann's) because the high surface area relative to volume would permit rapid heat gain when sun-basking (Ashton and Feldman 2003), an inference supported by experimental studies (Carrascal et al. 1992; Martin and Lopez 2003; Martin et al. 1995). However, this small-body advantage may not exist for a nocturnal species that does not gain heat primarily by basking. In fact, large size could be beneficial in cold climates as it could facilitate heat maintenance (Martin and Lopez 2003) when foraging at night. Studies to date on eight nocturnal lizard species show significant relationships (both positive) between body size and environmental temperature in only two species; however, these studies relied on air temperatures and body size data collected several decades apart from museum specimens or from published studies (Ashton and Feldman 2003; Pincheira-Donoso and Meiri 2013). Thus, the existence of trends in nocturnal lizards remains uncertain.

In the past, studies commonly compared body size against geographical gradients only (examples include Blanckenhorn and Demont 2004; Cruz et al. 2005; Pincheira-Donoso et al. 2008), assuming colder conditions at high elevation or latitude (Oufiero et al. 2011) rather than measuring temperature directly. However, the use of geographical gradients to represent temperature is not ideal as the relationship is not always simple and can be influenced by localised weather patterns and physical habitat (Brandt and Navas 2013; Oufiero et al. 2011; Shelomi 2012). Furthermore, as broad geographical ranges regularly contain large variation in other factors that potentially affect body size [for example, biotic interactions (Angilletta et al. 2004) and biome type (Pincheira-Donoso and Meiri 2013)], there could be confounding influences that mask possible trends with temperature. More accurate approaches include comparing body size against a measure of temperature, either air temperature (Meiri et al. 2013) or operative temperature (a measure of temperature that replicates the body temperature of an organism in a given environment; Angilletta 2009). Operative temperature is increasingly being considered a realistic and useful estimate of ectotherm body temperature, using mathematical (Buckley et al. 2013; Huang et al. 2013; Kearney et al. 2014; Sunday et al. 2014) or physical models (Bakken 1992) to incorporate influences such as solar radiation, conduction and wind (Buckley et al. 2013; Sunday et al. 2014). To our knowledge, the large majority of studies on Bergmann's rule in terrestrial ectotherms do not use operative temperatures nor do they physically measure temperature at actual sample sites; rather, they report air temperature commonly taken from interpolated climate databases (examples include: Adams and Church 2008; Feldman and Meiri 2014; Harris et al. 2012; Pincheira-Donoso and Meiri 2013).

Here, we report the results of a field study in which we examined whether a primarily nocturnal lizard follows Bergmann's rule at the intraspecific level, in relation to elevation and to operative temperature. *Woodworthia* "Otago/Southland" (Garman 1901) (a proposed species within the "common gecko" species complex previously known as *Hoplodactylus maculatus*; Nielsen et al. 2011) is a viviparous, long-lived gecko that occurs in the southern regions of temperate New Zealand (Cree 1994; Rock and Cree 2008). This nocturnally foraging gecko is often found by day under rocks, where it gains heat by contact with the uppermost rock surface, although it has been reported to occasionally bask (Rock and Cree 2008; Rock et al. 2002). We studied the variation in body size of adult females and males and of the smallest juveniles. Given that females and males may experience different reproductive constraints and that these constraints can vary with temperature [for example, gestation length (Cree and Hare 2010),

we also investigated whether sexual size dimorphism varied between sites. We placed physical models of lizards at individual sampling sites spanning an elevation range that varied little in latitude, enabling us to investigate how body size correlated with operative temperature with minimal confounding factors [for example, no significant genetic differences (Nielsen et al. 2011)]. Secondly, we conducted a laboratory study to test whether size-related thermal benefits vary between behavioural thermoregulatory positions, by placing lizard models in three different situations (two within a retreat and one openly basking). Overall, we address two predictions: (1) that *W.* “Otago/Southland” will not follow the converse-Bergmann’s rule, as the thermoregulatory benefits proposed for small-sized diurnal lizards in cold environments may not exist for this nocturnal forager; (2) that the most thermally advantageous body size (small vs. large) varies between the thermoregulatory situations available to this primarily nocturnal species.

Materials and methods

Field study: geographic variation in environmental temperatures and body size

Study sites

Seven sites at least 5 km apart and ranging from the coast to approximately 40 km inland were sampled. The sites, which spanned mean elevations from 54 to 1,039 m a.s.l., are labelled here simply as (sites) 1–7 to prevent potential identification by wildlife poachers. Latitudes and longitudes were broadly as follows: Otago Peninsula (two sites)—45°87′S, 170°60′E; vicinity of Macraes Flat (three sites)—45°38′S, 170°43′E; Rock and Pillar range (two sites)—45°51′S, 170°12′E. The regional climate pattern is for milder winters and longer summers at lower elevations, and harsher conditions with shorter activity seasons at higher elevations (Fitzharris 2003).

Operative temperatures

To confirm the extent to which mid-summer temperatures vary with elevation, temperature data loggers were placed for a 4-week period during the austral summer (17 Dec 2010–15 Jan 2011) at six sites (excluding site 3, which was not included due to time constraints). The i-button data loggers (DS1922L-F5 and DS1921G; Maxim Integrated Products, San Jose, CA) were placed inside copper models in the full sun to record temperatures achieved by simulated basking. We acknowledge that such placement does not take into account possible variation in refuge temperatures for geckos that do not bask, but refuge conditions vary so

widely within and among field sites that a meaningful comparison among sites would be extremely challenging. Models were made of copper pipe [110 (long) × 24 (wide) × 11 mm (height)] that had been painted brown (Café Royale; Resene, Wellington, New Zealand) to approximate the size and colour of geckos. One end of the model was crimped closed; the other end was sealed after the i-button logger was placed inside. Loggers took recordings every hour to a precision of 0.5 °C. The models were glued to the upper-side of terracotta tiles [15 × 15 × 1.5 (thickness) cm] and were then placed in the field near where pregnant female geckos were found, with the ‘head’ (crimped) end of the model facing north. These models were validated in the laboratory by placing a copper model with a temperature data logger inside (Stowaway STEBO2; Onset Computer Corp., Bourne, MA) on a rock alongside a gecko (from a laboratory colony founded from the site 6 population) anaesthetised with halothane and with a thermocouple in its cloaca. The rock was placed below a heat lamp, allowing the model and gecko to rise in temperature from 16 to 30 °C, whereupon the heat lamp was turned off and the model and gecko were allowed to cool to room temperature. The mean difference between the resulting temperatures measured at 1-min intervals was 0.19 ± 0.12 °C, and the gecko’s body temperature (y) was strongly related to that of the model (x): $r^2 = 0.961$ ($P < 0.001$).

Body sizes

To obtain measurements of snout–vent length (SVL), we sampled geckos over the austral summer. Sites were sampled twice (once between October and December 2010, once between February and May 2011), except for site 3, which was sampled only in the latter period. Previous studies of this species confirm that these extremely long-lived lizards grow very slowly; for example, at site 6 females are estimated to take 8 years to reach maturity (Sheehan 2002). Thus, we considered that growth over the sampling period at a site was insignificant in comparison with the differences in SVL observed among sites (see “Results”). The broad sampling period also allowed us to measure small juveniles soon after birth, which occurs in spring at site 6 (approx. 650 m a.s.l.) but in late summer or autumn at lower elevation sites in the wider species complex (Cree and Guillelte 1995).

Geckos were hand caught during the daytime by turning over rocks or using artificial retreat sites. Artificial retreats consisted of two or three layers of Onduline roofing material (Onduline, Auckland, New Zealand) separated by small wooden blocks (as used successfully elsewhere for this species complex; Lettink and Cree 2007) and were left in position for no more than 3 weeks. Additionally, at site 2 some geckos were found nearby or under two artificial retreats

that had been placed by the landowner 1 year previously. SVL was measured to the nearest millimetre using a ruler, and elevation (± 4 m) was recorded using a GPS unit. An ID number was drawn on the underside of the abdomen for temporary identification, enabling recaptures prior to moulting to be eliminated. Additionally, each animal's vent–tail length and tail regeneration length, as well the location coordinates, were measured to assist with eliminating inferred recaptures (see below).

For mature females, we obtained minimum, maximum and mean body sizes from samples of 33–59 females per site [Electronic Supplementary Material (ESM) 1]. The presence of reproductive structures detectable by palpation (enlarged vitellogenic follicles in the ovaries, or conceptuses in the uteri) was used to infer the size at maturity of adults at a site. Above this size, females were identified either by palpation or by the absence of the hemipenial sac and enlarged pre-anal pores that are characteristic of adult males (MacAvoy 1976; Towns 1985). Our experience is that palpation in this species has a near 100 % accuracy at detecting reproductive condition and stage of pregnancy (Cree and Guillette 1995; Wilson and Cree 2003). We also report the mean size of mature females that were reproductively active, i.e. vitellogenic or pregnant ($n = 17$ –40 per site as a subset; ESM 1).

For adult males, we obtained minimum, maximum and mean body sizes from samples of at least 10–25 males per site (ESM 1). To estimate size at birth, we measured 8–21 of the smallest juveniles (≤ 40 mm SVL) at each site, including any with obvious placental scars (ESM 1). On release, each animal was returned under the rock from which it was caught, except for a few animals at site 6 which were temporarily retained in captivity for a separate study.

Laboratory study: thermal significance of body size in three thermoregulatory positions

We used painted copper models similar to those used in the field study to simulate geckos of different sizes thermoregulating in three positions relative to their retreat site. Physical models are commonly used to mimic lizards (Shine and Kearney 2001) due to the difficulty of getting a live lizard to assume and hold specific positions. Two sizes of models were used: large [90 (length) \times 21 (width) \times 11 (height)] and small [60 (length) \times 15 (width) \times 8 mm (height)]. The model lengths approximated the SVLs of the smallest and largest adult geckos, respectively, found in the field study. The external probe of a temperature data logger (Stowaway STEBO2; Onset Computer Corp.) was positioned centrally within the airspace inside each model, and the model's open end was then sealed.

Each size of model was then tested in one of three positions ($n = 4$ –5 models of each size per position). A terracotta tile [20 \times 20 \times 0.5 (thickness) cm] was placed over supports to simulate the rock surface of a retreat site (Fig. 1). A heat lamp shone from above each tile to give a tile surface temperature of 31 °C (± 0.5 °C) at or above where the models were placed. This temperature is realistic, as individual *W. "Otago/Southland"* geckos select body temperatures of up to 30 °C on a thermal gradient, and body temperatures of up to 32.1 °C have been observed in the field (Gaby et al. 2011; Rock and Cree 2008; A. Cree unpublished observation). Tile temperatures were measured using an infra-red thermometer (Fluke 568; Fluke Australia Pty Ltd, Sydney, Australia). Room air temperature was controlled at 12 °C, which is representative of mean air temperature in the spring in the coastal Otago region (Wilson and Cree 2003).

Copper models were tested in the following three combinations of position and posture (hereafter simply referred to as positions): 'flat in sun', 'on-toes in wide retreat' and 'flat in tight retreat' (Fig. 1). The 'flat in sun' position simulated direct basking as occasionally observed in field and laboratory studies (Cree et al. 2003; Rock and Cree 2008); here, the model was placed on the tile roof of the retreat directly below the heat lamp. In the 'on toes in wide retreat' position, models simulated a type of thigmothermic behaviour observed in field and laboratory studies in which a gecko raises its body and presses it against the warmed under-surface of a rock, while having an air space underneath the body (Rock et al. 2002). Small wooden blocks [10 \times 10 \times 15 (thickness) mm] were used to prop the models at each end to achieve this position. The depth of the air space under the models depended on the model size (approx. 20 mm for 'small' models and approx. 15 mm for 'large' models). The 'flat in tight retreat' position simulated a second type of thigmothermy, also observed in the field (Rock et al. 2002), in which a gecko in a tight retreat touches a warm rock above and a cooler rock below simultaneously. For this position, models were placed directly between a lower tile that was not heated and an upper tile that received heat from the lamp.

Temperatures inside the models were recorded for a 2-h 'heating' period after the heat lamps were turned on. The heat lamps were then turned off, and temperature was measured for a further 50-min 'cooling' period (tests showed that temperature had plateaued at room temperature by this point).

Statistical analyses

For the 4-week mid-summer field season, we calculated mean daily minimum, mean (24 h) and maximum temperatures for each copper model at each of six sites and then

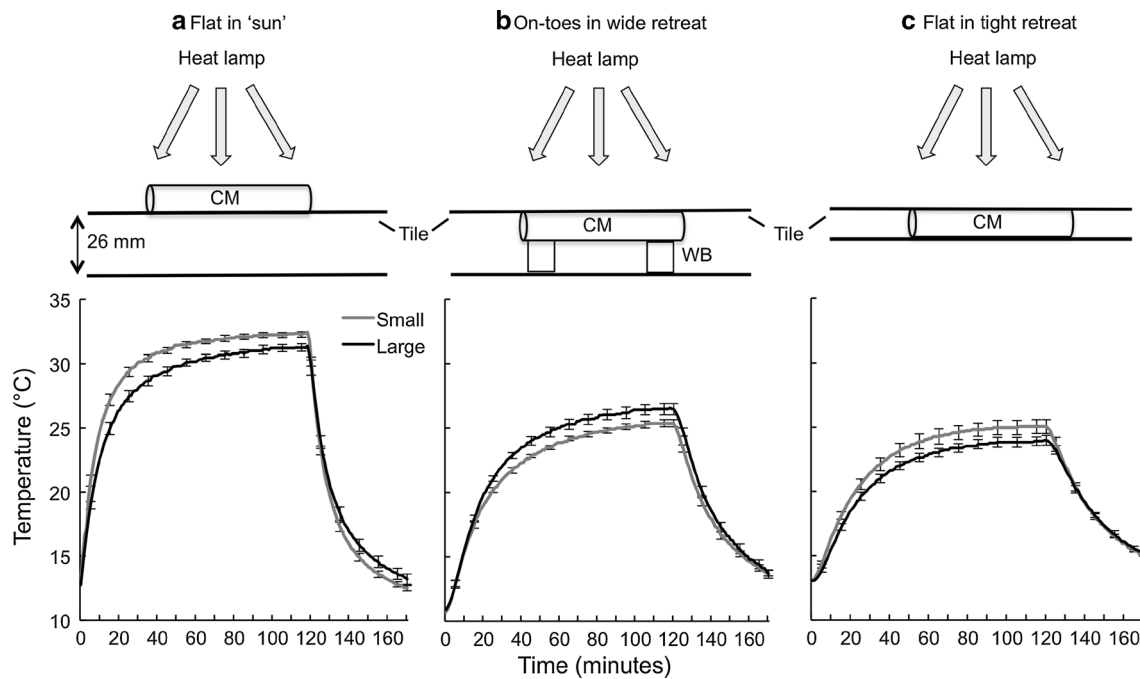


Fig. 1 Physical set-up and thermal profiles for laboratory study testing the effect of body size on heating and cooling rates of simulated geckos in three positions. For each position (**a**, **b**, **c**) the diagram at the top shows the model positions relative to the tiles and heat lamps, and the graph below shows the heating and cooling profiles. The models were placed at the 31 °C temperature spot, and each model was tested in an individual container. Small tiles used to support

the upper terracotta tiles at their edges are not shown. The dimensions given are for large models; the set-up was unchanged for small models (not shown). *CM* Copper model, *WB* wooden block used to hold the 'on-toes' model against the tile undersurface. For the graphs shown at the bottom, $n = 5$ for all positions except for the large models in **b** ($n = 4$). For clarity, the standard error (SE) is shown at 10-min intervals only

averaged the values for loggers to obtain a site mean. Mean daily temperatures (dependent variable) were examined in relation to elevation (independent variable) using regression analysis. Analysis of covariance analyses were used to compare the slopes (i.e. rates of change in temperature, with elevation as a co-variate) for the minimum, mean and maximum temperatures.

For the analysis of gecko body sizes across the field sites, we first eliminated known or inferred recaptures. Recaptures were either known from pen marks or inferred using body measurements and GPS locations in conjunction with the known highly sedentary behaviour of adults in this species complex (adults rarely move >5 m; Lettink 2007; Whitaker 1982). To investigate relationships between SVL measurements and either elevation or copper model temperatures, we performed regression analyses. Sexual dimorphism in terms of minimum, mean and maximum SVL (the difference in SVL between females and males at each site) in relation to elevation and to copper model temperatures was also examined using regression analysis. For these analyses, body size (SVL or sexual dimorphism) was included as the dependent variable, and either elevation or temperature was used as the independent variable. The relationship between size at birth (dependent variable) and

mean size of reproductive females (independent variable) was also examined using regression analysis.

During sampling it became apparent that field site 2 was unusual in terms of both features of habitat and gecko life-history. Rocks at this site were typically found directly on the ground amongst rank grass, whereas at other sites rocks were in stacks or slabs that would allow diurnal basking in crevices (ESM 2). Furthermore, the rock type at site 2 (breccia) has a lower thermal conductivity score than those at the other sites (ESM 3), which would indicate that geckos under rocks at site 2 might have difficulty achieving consistently high body temperatures. Additionally, a concurrent study on variation of reproductive frequency with elevation indicated that while female *W.* "Otago/Southland" at adjacent sites (1, 3 and 4) reproduce annually, females at site 2 reproduce only biennially [as do females at sites 5–7 (S. Penniket, unpublished data), consistent with colder environmental temperatures (Cree 1994)]. Thus, all analyses of body size and elevation or operative temperature are presented both with and without data from site 2.

For the laboratory experiment, we calculated maximum temperature reached, heating rate and cooling rate for each model. Maximum temperature was the temperature at the end of the 2-h heating period, just before the heat lamps

were switched off. Heating rate was calculated for a rapid-heating period (the change in temperature over the first 30 min after the heat lamps were turned on). Two cooling rates were calculated: first, during a ‘fast-cooling’ period (the first 15 min after the heat lamps were turned off); second, over a ‘slow-cooling’ period (the following 35 min). We first confirmed that individual model identity (each model was tested three times, once in each thermoregulatory position) had no significant influence on temperatures and heating rates using general linear models with maximum temperature, heating or cooling rates as dependent variables, positions as a fixed factor and model ID as a covariate factor (all $F_{5,8-9} \leq 2.66$, $P \geq 0.12$). Thus, the analysis was repeated excluding model ID to investigate whether there were significant differences between thermoregulatory positions in maximum temperature and in heating and cooling rates, tested separately for small- and large-sized models. A one-way analysis of variance was used to investigate whether size of model (specified as a fixed factor) affected maximum temperature reached, heating rate or cooling rate (the dependent variable) in each of the different positions.

All statistical analyses were performed in the statistical package SPSS version 19.0 (IBM Corp., New York, NY), with significance accepted at $P \leq 0.05$.

Results

Due to the large number of relationships reported in this section, we present figures primarily for significant trends only. Of the three measures of operative temperature, we focus on mean daily mean temperature (hereafter mean daily temperature), as this had the closest relationships with body size for the majority of analyses. Results for the relationships with mean daily minimum and maximum temperature are given in ESM 4. For the outcomes of all statistical comparisons between gecko body size and environmental variables, see Table 1.

Field study: geographic variation in environmental temperatures and body size

Operative temperatures

For the copper models placed in full-sun positions over a 4-week mid-summer period, mean daily minimum temperature, mean daily temperature and mean daily maximum temperature all showed significant, inverse relationships with elevation (Fig. 2). Although mean daily minimum temperature and mean daily temperature tended to fall by lesser amounts than mean daily maximum temperature with every 100-m rise in elevation (0.4, 0.5 and 1.1 °C

respectively), these differences were not statistically significant ($F_{2,12} = 3.40$, $P = 0.068$).

Relationship between body size and mean elevation

In mature male geckos the minimum size at maturity varied from 60 to 69 mm SVL across the seven sites and did not vary significantly with elevation. However, the minimum SVL of males at site 2 was unexpectedly large (68 mm), and a significant increase with elevation was apparent when the analysis was repeated excluding this site (Table 1; ESM 5). The variation in mean male SVL with elevation ranged from 68 to 81 mm, and maximum SVL varied from 78 to 93 mm. Both mean and maximum male SVL increased significantly with elevation (Table 1; ESM 5).

The minimum size of mature females varied from 60 to 73 mm SVL and increased significantly with elevation (Table 1; ESM 5). The variation in mean SVL across the seven sites was similar for all mature females (range 68–82 mm) and for reproductive (vitellogenic or pregnant) females only (range 68–83 mm). Both measures increased significantly with elevation (Table 1; all females: ESM 5). Maximum female SVL varied from 76 to 91 mm and increased significantly with elevation (Table 1; ESM 5).

Size at maturity was the only measure of sexual size dimorphism that showed a significant relationship with elevation (positive; Table 1; ESM 6). Although for the five lowest elevation sites the reported dimorphism in minimum SVL (defined here as the difference in size at maturity between females and males) was within the measurement error, for the two highest elevation sites the degree of sexual size dimorphism (range 4–6 mm) was greater. The minimum size of juvenile geckos (inferred size at birth) varied across the seven sites from 28 to 34 mm SVL and increased significantly with elevation (Table 1; ESM 5).

Relationship between body size and mean daily temperature

Gecko body size in relation to copper model temperatures in mid-summer was examined at six sites (Fig. 3). The minimum size at maturity of male geckos did not vary significantly with mean daily temperature; however, when site 2 was excluded from the analysis, there was a significant decrease in minimum size at maturity of male geckos with increasing mean daily temperature (Table 1; Fig. 3a). Both mean and maximum male SVL decreased significantly as mean daily temperature rose (Table 1; Fig. 3a).

The minimum size of mature females showed a significant, negative relationship with mean daily temperature (Table 1; Fig. 3b). Mean SVL for all mature females and for reproductive (vitellogenic or pregnant) females only decreased significantly as mean daily temperature rose

Table 1 Statistical results from regression analyses examining relationships between *Woodworthia* “Otago/Southland” gecko body size (snout–vent length) and either elevation or copper model temperatures in the field

Gecko size variables	Gecko population variables	Elevation (m a.s.l.)		Measures of operative temperature					
				Mean daily minimum temperature (°C)		Mean daily mean temperature (°C)		Mean daily maximum temperature (°C)	
		<i>r</i> ²	<i>P</i>	<i>r</i> ²	<i>P</i>	<i>r</i> ²	<i>P</i>	<i>r</i> ²	<i>P</i>
Minimum size	Male	0.27	0.24	0.46	0.14	0.23	0.34	0.001	0.94
	Male excl. site 2	<i>0.86</i>	<i>0.008*</i>	<i>0.90</i>	<i>0.015*</i>	<i>0.83</i>	<i>0.031*</i>	<i>0.63</i>	<i>0.12</i>
	All females	0.67	0.025*	0.79	0.017*	0.76	0.024*	0.41	0.17
	All females excl. site 2	<i>0.82</i>	<i>0.013*</i>	<i>0.81</i>	<i>0.038*</i>	<i>0.88</i>	<i>0.019*</i>	<i>0.85</i>	<i>0.027*</i>
	Juvenile	0.81	0.006*	0.88	0.005*	0.94	0.001*	0.71	0.036*
	Juvenile excl. site 2	<i>0.77</i>	<i>0.021*</i>	<i>0.96</i>	<i>0.004*</i>	<i>0.93</i>	<i>0.009*</i>	<i>0.69</i>	<i>0.081</i>
	SSD	0.64	0.03*	0.41	0.17	0.69	0.042*	0.91	0.003*
	SSD excl. site 2	<i>0.58</i>	<i>0.080</i>	<i>0.45</i>	<i>0.22</i>	<i>0.64</i>	<i>0.106</i>	<i>0.85</i>	<i>0.027*</i>
Maximum size	Male	0.78	0.008*	0.95	0.001*	0.97	0.0001*	0.60	0.069
	Male excl. site 2	<i>0.79</i>	<i>0.019*</i>	<i>0.95</i>	<i>0.004*</i>	<i>0.97</i>	<i>0.001*</i>	<i>0.80</i>	<i>0.040*</i>
	All females	0.81	0.006*	0.79	0.017*	0.87	0.007*	0.64	0.056
	All females excl. site 2	<i>0.87</i>	<i>0.007*</i>	<i>0.78</i>	<i>0.047*</i>	<i>0.87</i>	<i>0.020*</i>	<i>0.92</i>	<i>0.011*</i>
	SSD	0.002	0.93	0.25	0.31	0.20	0.38	0.050	0.61
	SSD excl. site 2	<i>0.003</i>	<i>0.92</i>	<i>0.24</i>	<i>0.41</i>	<i>0.18</i>	<i>0.48</i>	<i>0.028</i>	<i>0.79</i>
Mean size	Male	0.69	0.020*	0.93	0.002*	0.89	0.005*	0.46	0.14
	Male excl. site 2	<i>0.80</i>	<i>0.016*</i>	<i>0.93</i>	<i>0.008*</i>	<i>0.99</i>	<i>0.0001*</i>	<i>0.86</i>	<i>0.024*</i>
	All females	0.80	0.007*	0.82	0.013*	0.87	0.007*	0.58	0.079
	All females excl. site 2	<i>0.88</i>	<i>0.006*</i>	<i>0.81</i>	<i>0.037*</i>	<i>0.92</i>	<i>0.010*</i>	<i>0.96</i>	<i>0.004*</i>
	Reproductive females	0.74	0.013*	0.82	0.013*	0.83	0.011*	0.49	0.12
	Reproductive females excl. site 2	<i>0.88</i>	<i>0.006*</i>	<i>0.83</i>	<i>0.032*</i>	<i>0.94</i>	<i>0.006*</i>	<i>0.97</i>	<i>0.002*</i>
	SSD	0.13	0.43	0.005	0.89	0.007	0.88	0.12	0.50
	SSD excl. site 2	<i>0.090</i>	<i>0.56</i>	<i>0.020</i>	<i>0.82</i>	<i>0.002</i>	<i>0.95</i>	<i>0.065</i>	<i>0.68</i>

All analyses were conducted both with and without (values given in italics) outlier site 2

SSD, Sexual size dimorphism [female snout–vent length (SVL) – male SVL]

* *P* ≤ 0.05

Fig. 2 Daily temperatures (mean ± SE) of copper models in basking positions in relation to elevation [mean metres above sea level (m asl) ± SE] over a 4-week summer period (17 Dec. 2010–15 Jan. 2011). *Dashed line* Daily maximum: $y = -0.011x + 40.894$; $r^2 = 0.74$, $P = 0.027$; *solid line* daily mean: $y = -0.0049x + 19.646$; $r^2 = 0.87$, $P = 0.006$; *dotted line* daily minimum: $y = -0.0042x + 10.417$; $r^2 = 0.79$, $P = 0.018$. At each site $n = 3$ loggers, except sites 1 and 7 (lowest and highest elevation) where $n = 2$

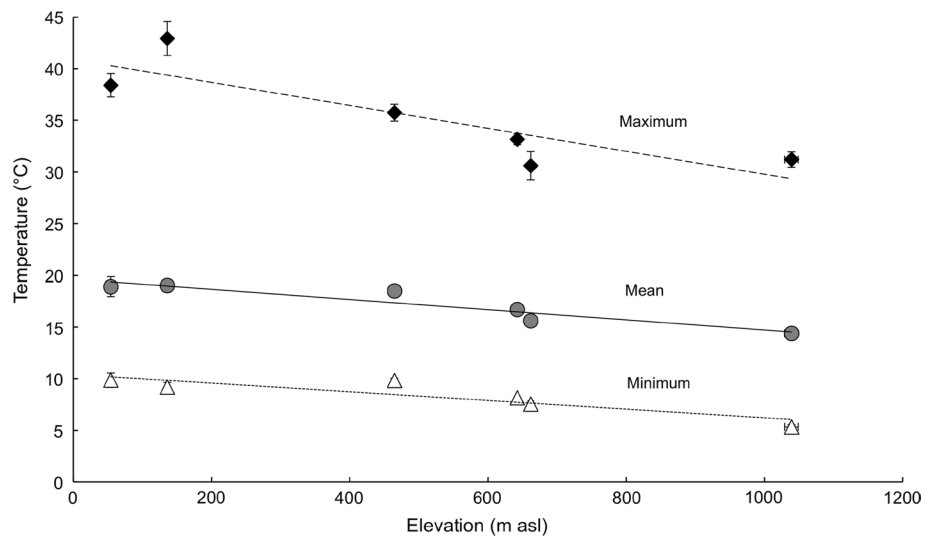


Fig. 3 Maximum, mean (\pm SE) and minimum snout–vent length (SVL) of adult male (**a**; $n = 10$ –25) and female (**b**; $n = 33$ –59) *Woodworthia* “Otago/Southland” geckos in relation to mean daily mean temperature (\pm SE) for a summer period (17 Dec. 2010–15 Jan. 2011) at six field sites (no data for site 3). Minimum SVL of juveniles ($n = 8$ –21) is also shown in **b** (note secondary axis). Site 2 values are shown with *lightshading* and an *asterisk* where their exclusion made a relationship significant. Some y-axis SE bars for mean SVL are smaller than the *symbol size*. See ESM 1 for sample sizes by site. Regression lines are fitted only for significant relationships (*solid line* maximum SVL, *dashed/dotted line* mean SVL, *dotted line* minimum SVL, *dashed line* juvenile minimum SVL)

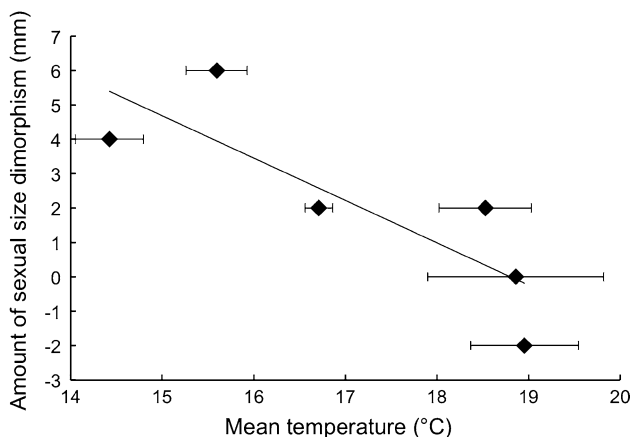
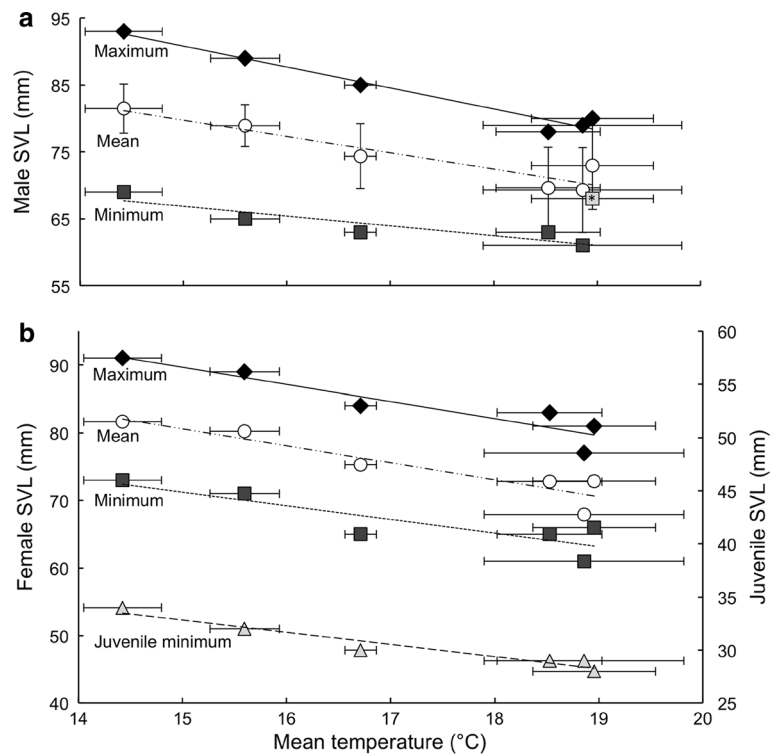


Fig. 4 Sexual size dimorphism in size at maturity (female minimum size – male minimum size) of mature *W.* “Otago/Southland” geckos in relation to mean daily mean temperature (\pm SE) of copper models in summer at six sites (no temperature data available for site 3). For sample sizes, see ESM 1

(Table 1; all females: Fig. 3b). Maximum female SVL declined significantly as mean daily temperature increased (Table 1; Fig. 3b).

Sexual size dimorphism in size at maturity showed a significant relationship with mean daily temperature (negative; Table 1; Fig. 4). The minimum size of juvenile geckos decreased significantly as mean daily temperature rose (Table 1; Fig. 3b).

Relationship between body sizes of juveniles and reproductive females

Mean size of reproductive (vitellogenic or pregnant) females showed a significant and positive relationship with the inferred size at birth of juveniles across the seven sites ($r^2 = 0.75$, $P = 0.011$; ESM 7).

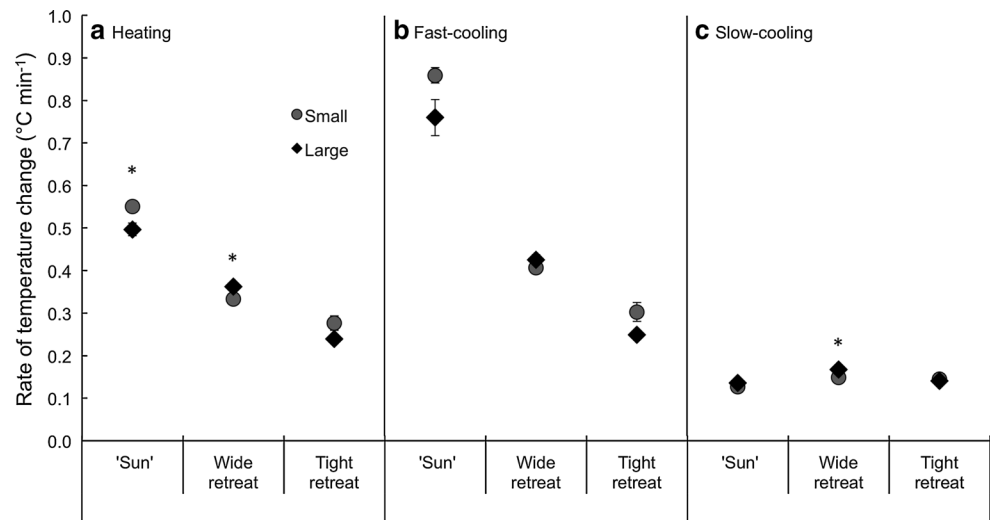
Laboratory study: thermal significance of body size in three thermoregulatory positions

As expected, both small and large models in the ‘flat in sun’ position reached significantly higher temperatures and showed significantly faster heating and ‘fast-cooling’ rates than the models in ‘on-toes in wide retreat’ and ‘flat in tight retreat’ positions (all $F_{2,11-12} \geq 4.74$, $P \leq 0.030$; Fig. 1). However, for both size categories, ‘slow-cooling’ rates were significantly faster in the ‘on-toes in wide retreat’ position than in the other two positions (all $F_{2,11-12} \geq 29.36$, $P \leq 0.001$). The effect of model size within each of these positions is discussed in the following subsections.

‘Flat in sun’ heating position

In this position, the small models reached a significantly higher mean maximum temperature than the large models (32.4 ± 0.2 vs. 31.4 ± 0.3 °C, respectively; $F_{1,8} = 7.44$, $P = 0.026$; Fig. 1). The small models also increased in

Fig. 5 Mean rate of change of temperature (\pm SE) for small and large models in the ‘flat in sun’, ‘on-toes in wide retreat’ and ‘flat in tight retreat’ positions, calculated for the ‘heating’ (a), ‘fast-cooling’ (b) and ‘slow-cooling’ periods (c) (see text for details on periods). For all positions $n = 5$, except the ‘large wide retreat’ position ($n = 4$). Asterisk denotes a $P < 0.05$ in difference between the small and large models



temperature at a slightly but significantly faster rate for the first 30 min of heating ($F_{1,8} = 9.53$, $P = 0.015$; Fig. 5).

Over the 15-min ‘fast-cooling’ period, there was a small and not quite significant difference between model sizes in the mean rate of heat loss ($F_{1,8} = 4.76$, $P = 0.061$; Fig. 5). Over the 35-min ‘slow-cooling’ period, the small and large models decreased in temperature at similar rates ($F_{1,8} = 2.06$, $P = 0.19$; Fig. 5).

‘On-toes in wide retreat’ heating position

Large models reached a significantly higher mean maximum temperature [26.6 ± 0.5 °C (large models) vs. 25.4 ± 0.3 °C (small models); $F_{1,7} = 5.67$, $P = 0.049$; Fig. 1] and heated at a significantly faster mean rate over a 30-min period ($F_{1,7} = 9.06$, $P = 0.02$; Fig. 5).

There was no significant difference in mean cooling rates between the model sizes over the 15-min ‘fast-cooling’ period ($F_{1,7} = 1.17$, $P = 0.32$; Fig. 5). In contrast, over the 35-min ‘slow-cooling’ period, the large models cooled at a significantly faster mean rate than the small models ($F_{1,7} = 11.83$, $P = 0.011$; Fig. 5).

‘Flat in tight retreat’ heating position

In this position, a difference of 1 °C in mean maximum temperatures reached by the two model sizes was not statistically significant [25.0 ± 0.5 °C (small models) vs. 24.0 ± 0.4 °C (large models); $F_{1,8} = 2.54$, $P = 0.15$; Fig. 1). The small and large models did not differ significantly in heating rates over the 30-min heating period ($F_{1,8} = 3.67$, $P = 0.092$; Fig. 5).

Over the ‘fast-cooling’ period there was no significant difference in the mean rates of heat loss between the model sizes ($F_{1,8} = 4.25$, $P = 0.073$, Fig. 5). Over the 35-min

‘slow-cooling’ period, the two model sizes cooled at the same mean rate ($F_{1,8} = 0.32$, $P = 0.59$; Fig. 5).

Discussion

We present a comprehensive investigation, controlling for latitude, to show that Bergmann’s rule is valid for a nocturnally foraging lizard, the viviparous *Woodworthia* “Otago/Southland” gecko of southern New Zealand. A pattern of greater body size at higher elevation is consistent across life-history stages, existing in adult males, adult females and juvenile geckos. Furthermore, this pattern is consistent with declining operative temperature (in a basking situation) at higher elevation. We demonstrate a novel approach of examining an ecogeographic rule against operative temperature measured at sampling sites. In a laboratory study we provide an explanation using physical models as to why both Bergmann’s and converse-Bergmann’s rules can be observed in lizard species.

Size at maturity (minimum adult size) of *W.* “Otago/Southland” geckos was larger at higher elevations and colder temperatures. Given the great longevity (≥ 40 years; Lettink and Whitaker 2006; Sheehan 2002) of geckos in the wider species complex, including *W.* “Otago/Southland”, it is unlikely that this pattern results solely from a difference in activity–season length, as is observed in some short-lived lizard species (Adolph and Porter 1996; Horvathova et al. 2013). Instead, it is probable that environmental temperatures are influencing this cline by affecting lizard growth rates. It is well established that ectotherms exposed to low temperatures during development will often mature later but at larger sizes than those exposed to warm temperatures during development (the temperature–size rule, reviewed in Angilletta 2009). Thus, it is likely that growth

rate varies among *W.* “Otago/Southland” populations, with those exposed to cold environmental temperatures maturing at larger sizes. Mean and maximum adult body sizes may be partly a function of size at maturity—while there is some growth after maturity, growth does slow such that body size reaches an asymptote (Sheehan 2002). Thus, populations that have large sizes at maturity have correspondingly large mean and maximum adult body sizes. However, selective pressures related to reproduction and survival may also drive this large body size, and large body size may confer thermal benefits.

The greater sexual dimorphism in size at maturity observed in gecko populations at high elevations and cold temperatures indicates that female maturation is delayed and occurs at larger sizes than in males at these same sites. It is unlikely that male–male interactions are driving this dimorphism, as within the species complex Todd (2005) found that the two sexes did not differ in incidence of fighting in captivity. Instead, sexual dimorphism may be greater in cold environments because reproductive costs are likely to be greater for females, given that females must expend energy trying to achieve sufficiently warm and consistent body temperatures (Angilletta 2009; Schwarzkopf and Shine 1991) to ensure offspring viability (Cree and Hare 2010; Rock and Cree 2003). Female lizards that have larger energy stores before pregnancy are better able to cope with these energy demands and will have a much higher reproductive output than those with low energy reserves (Doughty and Shine 1998). In harsh alpine and sub-alpine environments, it could be that females with small body sizes have insufficient reserves to cope with the costs of pregnancy. Thus, the selection pressure to become mature at larger sizes may be stronger for females than males, resulting in a significant increase in sexual size dimorphism with elevation. At low elevations, the discrepancy between these reproductive costs may be less, resulting in a smaller sexual dimorphism. A similar pattern has been reported by Volynchik (2014), who noted that females displayed a stronger response to temperature than males in an intraspecific study on Bergmann’s rule in four lacertid species.

An additional explanation for larger female size at maturity at high elevation is that offspring size could be influencing female size. Larger neonates may have survival advantages in the cold temperatures and short activity seasons that occur at high elevations (Uller et al. 2011), such as having sufficient energy reserves to withstand periods of starvation (Civantos et al. 1999). At the lower and warmer sites, this advantage may not be as crucial, as conditions are less severe (Uller et al. 2011). Within a population (field site), larger individual female *W.* “Otago/Southland” produce larger offspring (Rock and Cree 2003), and this relationship is also seen in our study when mean sizes among populations (field sites) are compared. Thus, it could be

that selection for large juvenile body size may be a factor driving large female size at maturity at high-elevation sites. Of all the life-history traits examined in this study, minimum size of juveniles showed the most consistent trends with elevation and operative temperatures, suggesting that it is strongly linked with temperature and has important evolutionary consequences.

At site 2, all measures of adult body size were unusual in relation to elevation and operative temperatures. It is possible that the high mean daily maximum copper model temperature recorded at this site may not represent temperatures actually available to the geckos. Vegetation shading at this site might strongly limit sun-basking in rock crevices (Rock and Cree 2008); in addition, the rock type, breccia (Martin 2000), has a low thermal conductivity score compared to the rock types found at other sites (Clauser and Huenges 1995). Therefore, geckos at site 2 may not consistently achieve high body temperatures, causing slow growth rates that result in larger adult body sizes. Temperature loggers placed in a variety of positions under rocks could help determine the potential thermal opportunities for geckos at this site. It would be even more informative to implant temperature-sensitive devices into the lizards themselves; however, this remains technically challenging given the small body sizes involved (Rock and Cree 2008). In contrast to adult body size, the size of juveniles at site 2 was not unusually large. It is likely that conditions at this site would still be mild in comparison to those at high elevation, such that small neonate size may not be disadvantageous, thereby relaxing selective pressures on offspring size. Uller et al. (2011) found that selection on offspring size at birth in a viviparous skink (*Niveoscincus ocellatus*) was weak or absent at low-elevation sites in comparison to a strong selective pressure driving large neonate size at high elevation. Therefore, although a possible low body temperature of geckos at site 2 may cause a slow growth rate, it may not be affecting offspring size at birth. This aberrant site demonstrates the importance of including multiple sites when investigating Bergmann’s rule.

We confirm that the intraspecific converse-Bergmann’s pattern seen in a great number of diurnal lizard species (Ashton and Feldman 2003) is plausibly explained by the thermal benefits of small body size at high elevations and/or cold temperatures. Under direct radiant heat, a higher surface area relative to volume meant that the small models gained heat more quickly than the large models, meaning that a small, diurnal lizard would be able to spend less time thermoregulating and reach the preferred temperature sooner. However, we found no such thermal benefit to small size in under-cover positions (thigmothermy). In fact, in the position simulating a lizard thermoregulating by pressing itself against a warm upper-surface, large models gained heat more quickly and reached a higher temperature

than the small models. One possible explanation is that the large models received more heat from conduction, yet experienced reduced convective cooling under the tile due to a low surface area to volume ratio, relative to the small models. In contrast, in the second thigmothermic position—a model touching a cold and warm tile simultaneously—a large model might experience equal amounts of heat loss and gain, resulting in a net heat balance that would not be significantly different from that of the small models. In the natural environment these processes may be more complex, as a gecko could change positions within its three-dimensional habitat to maximise heating and minimise cooling. However, this might result in a further disadvantage to small size, as a smaller gecko would have to move a greater distance within a retreat to do this. Thus, for the nocturnally foraging *W.* “Otago/Southland”, small body size may not confer thermal benefits. Instead, large body size may be beneficial at cold temperatures as it may permit faster heat gain when thermoregulating by thigmothermy and, furthermore, reduce heat loss when foraging at night. While the biological relevance of these observed thermal benefits may not seem great, it is likely that the cumulative effect is important, especially when considering the extreme length of pregnancy at cold sites (up to 14 months; Cree and Guille 1995) and the delayed maturity. At low-elevation sites, the advantage of large body size may be reduced, as warmer air temperatures would allow preferred body temperatures to readily be achieved during the day and may also facilitate heat conservation, regardless of body size.

Therefore, variation in the thermal advantage of large body size may be influencing the Bergmann’s rule pattern observed in this primarily nocturnal lizard. It would be informative to explore body size trends in other nocturnal lizards to see if Bergmann’s rule holds among these species also. Aguilar and Cruz (2010) demonstrated that diurnal retreat site temperatures affect nocturnal performance in a cold-climate population of the South American nocturnal gecko *Homonota darwini*. It is conceivable that large body size would be advantageous in a cold environment for this species also. Additionally, Feldman and Meiri (2014) have recently shown that interspecific adherence to Bergmann’s rule in Australian snake species is partly dependent on activity time—nocturnal snakes showed Bergmann’s rule or the converse (depending on habitat use), whereas diurnal snakes showed no trend. We do not, however, mean to imply that every lizard species that exhibits Bergmann’s rule does so because it is nocturnal. Indeed, there are a number of studies that report positive Bergmann’s trends in diurnal lizards (Angilletta et al. 2004; Olalla-Tárraga et al. 2006; intra- and interspecific levels, respectively) for which there are a range of potential explanations, including local benefits to large body size at cold sites or differences in juvenile survivorship (Sears and Angilletta 2004) and

female fecundity (Wapstra et al. 2001). Due to the large variation in the habitats and habits of lizards worldwide, it is unlikely that there would be one overriding explanation for when the rule does or does not apply (Olalla-Tárraga 2011). We propose only that Bergmann’s rule may be more likely than the reverse trend in nocturnal lizard species. In any case, it is clear that an examination of Bergmann’s rule in any species must involve consideration of its specific characteristics and habitat.

Changes in body size in response to climate warming have been reported for a variety of endothermic and ectothermic taxa, including lizards (Chamaille-Jammes et al. 2006; Ohlberger 2013; Teplitsky and Millien 2014). Such change has been documented world-wide; for example, in New Zealand mean body mass of a population of red-billed gulls (*Larus novaehollandiae scopulinus*) has decreased over time, as ambient air temperature has increased (Teplitsky et al. 2008). In our study region, annual air temperatures are predicted to increase by 0.8–2.5 °C over the next 100 years (depending on the level of future carbon emissions; Reisinger et al. 2010). With such an increase in environmental temperature, it is possible that the body size of *W.* “Otago/Southland” geckos might decrease over time, as a warming climate might relax constraints on offspring survival and adult reproduction in populations that are currently experiencing cold environmental temperatures. Thus, as environmental temperatures rise, we might first observe a decrease in size at birth at high elevation sites, which in turn could relax selective pressures on female size at maturity and so decrease the amount of sexual size dimorphism. Warmer temperatures would cause increased growth rates, which may result in a decrease in male and female size at maturity and, consequently, in mean and maximum adult size. Currently, most of the low-elevation populations are not strongly constrained by environmental temperature; therefore, body size at these sites may not respond to climate change to the same degree as those at high elevations. Eventually, we may observe a decrease in the strength of the relationship between body size and elevation in *W.* “Otago/Southland” and in its adherence to Bergmann’s rule. Thus, climate change may act as a natural experiment to further discern the influences of the thermal environment on the life-history traits of lizards.

Author contribution statement SP and AC conceived and designed the study. SP led the fieldwork and experiments, performed the statistical analyses and drafted the manuscript; AC provided supervision, fieldwork and editorial advice.

Acknowledgments This research was carried out with permission from the Department of Conservation (OT-28494-FAU) and the

University of Otago Animal Ethics Committee (55/10), and following consultation with the Ngai Tahu Consultation Committee and Kati Huirapa Runaka ki Puketeraki. A student research grant from the Society for Research on Amphibians and Reptiles in New Zealand and support from OURG grant ORG0110-0312 to AC helped to fund this study. We thank the many landowners who kindly allowed us access and also thank all of our field assistants. Thank you to all the staff in the Department of Zoology, particularly to Murray McKenzie for help with equipment, to Kim Garrett for fieldwork support and to Ken Miller for graphical expertise. We are grateful to the anonymous reviewers, two examiners for comments on the Masters thesis that preceded this manuscript and to Steve Adolph, Jo Monks and the Cree lab group for discussions and comments.

References

- Adams DC, Church JO (2008) Amphibians do not follow Bergmann's rule. *Evolution* 62:413–420. doi:10.1111/j.1558-5646.2007.00297.x
- Adolph S, Porter W (1996) Growth, seasonality, and lizard life histories: age and size at maturity. *Oikos* 77:267–278
- Aguilar R, Cruz FB (2010) Refuge use in a Patagonian nocturnal lizard, *Homonota darwini*: the role of temperature. *J Herpetol* 44:236–241. doi:10.1670/08-270.1
- Angilletta MJ Jr (2009) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, New York
- Angilletta MJ Jr, Niewiarowski PH, Dunham AE, Leaché AD, Porter WP (2004) Bergmann's clines in ectotherms: illustrating a life-history perspective with sceloporine lizards. *Am Nat* 164:E168–E183. doi:10.1086/425222
- Ashton KG (2001) Are ecological and evolutionary rules being dismissed prematurely? *Divers Distrib* 7:289–295. doi:10.1046/j.1366-9516.2001.00115.x
- Ashton KG (2002) Do amphibians follow Bergmann's rule? *Can J Zool* 80:708–716. doi:10.1139/z02-049
- Ashton K, Feldman C (2003) Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution* 57:1151–1163. doi:10.1111/j.0014-3820.2003.tb00324.x
- Bakken GS (1992) Measurement and application of operative and standard operative temperatures in ecology. *Am Zool* 32:194–216. doi:10.1093/icb/32.2.194
- Blackburn TM, Gaston KJ, Loder N (1999) Geographic gradients in body size: a clarification of Bergmann's rule. *Divers Distrib* 5:165–174. doi:10.1046/j.1472-4642.1999.00046.x
- Blanckenhorn WU, Demont M (2004) Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? *Integr Comp Biol* 44:413–424. doi:10.1093/icb/44.6.413
- Brandt R, Navas C (2013) Body size variation across climatic gradients and sexual size dimorphism in Tropicurinae lizards. *J Zool* 290:192–198. doi:10.1111/jzo.12024
- Buckley LB, Miller EF, Kingsolver JG (2013) Ectotherm thermal stress and specialization across altitude and latitude. *Integr Comp Biol* 53:571–581. doi:10.1093/icb/ict026
- Carrascal LM, Lopez P, Martín J, Salvador A (1992) Basking and antipredator behaviour in a high altitude lizard: implications of heat exchange rate. *Ethology* 92:143–154. doi:10.1111/j.1439-0310.1992.tb00955.x
- Chamaille-Jammes S, Massot M, Aragon P, Clobert J (2006) Global warming and positive fitness response in mountain populations of common lizards *Lacerta vivipara*. *Glob Change Biol* 12:392–402. doi:10.1111/j.1365-2486.2005.01088.x
- Civantos E, Salvador A, Veiga JP (1999) Body size and microhabitat affect winter survival of hatchling *Psammodromus algirus* lizards. *Copeia* 4:1112–1117. doi:10.2307/1447988
- Clauser C, Huenges E (1995) Thermal conductivity of rocks and minerals. In: Ahrens TJ (ed) *Rock physics and phase relations: a handbook of physical constants*. American Geophysical Union, Washington DC
- Cree A (1994) Low annual reproductive output in female reptiles from New Zealand. *N Z J Zool* 21:351–372. doi:10.1080/03014223.1994.9518005
- Cree A, Guillelte L (1995) Biennial reproduction with a fourteen-month pregnancy in the gecko *Hoplodactylus maculatus* from southern New Zealand. *J Herpetol* 29:163–173
- Cree A, Hare K (2010) Equal thermal opportunity does not result in equal gestation length in a cool-climate skink and gecko. *Herpetol Conserv Biol* 5:271–282
- Cree A, Tyrrell CL, Preest MR, Thorburn D, Guillelte LJ Jr (2003) Protecting embryos from stress: corticosterone effects and the corticosterone response to capture and confinement during pregnancy in a live-bearing lizard (*Hoplodactylus maculatus*). *Gen Comp Endocrinol* 134:316–329. doi:10.1016/S0016-6480(03)00282-X
- Cruz F, Fitzgerald L, Espinoza R, Schulte I (2005) The importance of phylogenetic scale in tests of Bergmann's and Rapoport's rules: lessons from a clade of South American lizards. *J Evol Biol* 18:1559–1574. doi:10.1111/j.1420-9101.2005.00936.x
- Cushman JH, Lawton JH, Manly BF (1993) Latitudinal patterns in European ant assemblages: variation in species richness and body size. *Oecologia* 95:30–37. doi:10.1007/BF00649503
- Cvetković D, Tomašević N, Ficetola GF, Crnobrnja-Isailović J, Miuad C (2009) Bergmann's rule in amphibians: combining demographic and ecological parameters to explain body size variation among populations in the common toad *Bufo bufo*. *J Zool Syst Evol Res* 47:171–180. doi:10.1111/j.1439-0469.2008.00504.x
- Dillon ME, Frazier MR, Dudley R (2006) Into thin air: physiology and evolution of alpine insects. *Integr Comp Biol* 46:49–61. doi:10.1093/icb/icj007
- Doughty P, Shine R (1998) Reproductive energy allocation and long-term energy stores in a viviparous lizard (*Eulamprus tympanum*). *Ecology* 79:1073–1083. doi:10.2307/176602
- Feldman A, Meiri S (2014) Australian snakes do not follow Bergmann's rule. *Evol Biol* 41:327–335. doi:10.1007/s11692-014-9271-x
- Fitzharris B (2003) Climate. In: Darby JT, Fordyce RE, Mark AF, Probert PK, Townsend C (eds) *The natural history of southern New Zealand*. University of Otago Press, Dunedin, pp 65–86
- Gaby MJ, Besson AA, Bezzina CN, Caldwell AJ, Cosgrove S, Cree A, Haresnape S, Hare KM (2011) Thermal dependence of locomotor performance in two cool-temperate lizards. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol* 197:869–875. doi:10.1007/s00359-011-0648-3
- Gaston KJ, Chown SL, Evans KL (2008) Ecogeographical rules: elements of a synthesis. *J Biogeogr* 35:483–500. doi:10.1111/j.1365-2699.2007.01772.x
- Harris R, McQuillan P, Hughes L (2012) Patterns in body size and melanism along a latitudinal cline in the wingless grasshopper, *Phaulacridium vittatum*. *J Biogeogr* 39:1450–1461. doi:10.1111/j.1365-2699.2012.02710.x
- Horváthová T, Cooney CR, Fitze PS, Oksanen TA, Jelić D, Ghira I, Uller T, Jandzik D (2013) Length of activity season drives geographic variation in body size of a widely distributed lizard. *Ecol Evol* 3:2424–2442. doi:10.1002/ece3.613
- Huang SP, Chiou CR, Lin TE, Tu MC, Lin CC, Porter WP (2013) Future advantages in energetics, activity time, and habitats predicted in a high-altitude pit viper with climate warming. *Funct Ecol* 27:446–458. doi:10.1111/1365-2435.12040
- Kearney MR, Shamakhy A, Tingley R, Karoly DJ, Hoffmann AA, Briggs PR, Porter WP (2014) Microclimate modelling at macro scales: a test of a general microclimate model integrated with

- gridded continental-scale soil and weather data. *Methods Ecol Evol* 5:273–286. doi:10.1111/2041-210x.12148
- Lettink M (2007) Detectability, movements and apparent lack of homing in *Hoplodactylus maculatus* (Reptilia: diplodactylidae) following translocation. *N Z J Ecol* 31:111–116
- Lettink M, Cree A (2007) Relative use of three types of artificial retreats by terrestrial lizards in grazed coastal shrubland, New Zealand. *Appl Herpetol* 4:227–243
- Lettink M, Whitaker A (2006) *Hoplodactylus maculatus* (common gecko). Longevity. *Herpetol Rev* 37:223–224
- MacAvoy ES (1976) The physiology of lizards from arid regions in Central Otago. PhD thesis. University of Otago, Dunedin
- Martin U (2000) Eruptions and deposition of volcanoclastic rocks in the Dunedin Volcanic Complex, Otago Peninsula, New Zealand. PhD thesis. University of Otago, Dunedin
- Martin J, Lopez P (2003) Ontogenetic variation in antipredator behavior of Iberian rock lizards (*Lacerta monticola*): effects of body-size-dependent thermal-exchange rates and costs of refuge use. *Can J Zool* 81:1131–1137. doi:10.1139/z03-094
- Martin J, Lopez P, Carrascal LM, Salvador A (1995) Adjustment of basking postures in the high-altitude Iberian rock lizard (*Lacerta monticola*). *Can J Zool* 73:1065–1068. doi:10.1139/z95-126
- Meiri S (2011) Bergmann's rule—what's in a name? *Glob Ecol Biogeogr* 20:203–207. doi:10.1111/j.1466-8238.2010.00577.x
- Meiri S, Bauer AM, Chirio L, Colli GR, Das I, Doan TM, Feldman A, Herrera FC, Novosolov M, Pafilis P (2013) Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. *Glob Ecol Biogeogr* 22:834–845. doi:10.1111/geb.12053
- Nielsen SV, Bauer AM, Jackman TR, Hitchmough RA, Daugherty CH (2011) New Zealand geckos (Diplodactylidae): cryptic diversity in a post-Gondwanan lineage with trans-Tasman affinities. *Mol Phylogenet Evol* 59:1–22. doi:10.1016/j.ympev.2010.12.007
- Ohlberger J (2013) Climate warming and ectotherm body size—from individual physiology to community ecology. *Funct Ecol* 27:991–1001. doi:10.1111/1365-2435.12098
- Olalla-Tárraga MÁ (2011) “Nullius in Bergmann” or the pluralistic approach to ecogeographical rules: a reply to Watt et al. (2010). *Oikos* 120:1441–1444. doi:10.1111/j.1600-0706.2011.19319.x
- Olalla-Tárraga MÁ, Rodríguez MÁ, Hawkins BA (2006) Broad-scale patterns of body size in squamate reptiles of Europe and North America. *J Biogeogr* 33:781–793. doi:10.1111/j.1365-2699.2006.01435.x
- Olalla-Tárraga MÁ, Bini LM, Diniz-Filho JAF, Rodríguez MÁ (2010) Cross-species and assemblage-based approaches to Bergmann's rule and the biogeography of body size in *Plethodon* salamanders of eastern North America. *Ecography* 33:362–368. doi:10.1111/j.1600-0587.2010.06244.x
- Oufiero CE, Gartner GE, Adolph SC, Garland T (2011) Latitudinal and climatic variation in body size and dorsal scale counts in *Sceloporus* lizards: a phylogenetic perspective. *Evolution* 65:3590–3607. doi:10.1111/j.1558-5646.2011.01405.x
- Pincheira-Donoso D (2010) The balance between predictions and evidence and the search for universal macroecological patterns: taking Bergmann's rule back to its endothermic origin. *Theory Biosci* 129:247–253. doi:10.1007/s12064-010-0101-0
- Pincheira-Donoso D, Meiri S (2013) An intercontinental analysis of climate-driven body size clines in reptiles: no support for patterns, no signals of processes. *Evol Biol* 40:562–578. doi:10.1007/s11692-013-9232-9
- Pincheira-Donoso D, Hodgson D, Tregenza T (2008) The evolution of body size under environmental gradients in ectotherms: why should Bergmann's rule apply to lizards? *BMC Evol Biol* 8:68
- Reisinger A, Mullan B, Manning M, Wratt D, Nottage R (2010) Global and local climate change scenarios to support adaptation in New Zealand. In: Nottage RAC, Wratt DS, Bornman JF, Jones K (eds) *Climate change adaptation in New Zealand: future scenarios and some sectoral perspectives*. N Z Clim Change Cent, Wellington, pp 26–43
- Rock J, Cree A (2003) Intraspecific variation in the effect of temperature on pregnancy in the viviparous gecko *Hoplodactylus maculatus*. *Herpetologica* 59:8–22. doi:10.1655/0018-0831(2003)059[0008:IVITEO]2.0.CO;2
- Rock J, Cree A (2008) Extreme variation in body temperature in a nocturnal thigmothermic lizard. *Herpetol J* 18:69–76
- Rock J, Cree A, Andrews RM (2002) The effect of reproductive condition on thermoregulation in a viviparous gecko from a cool climate. *J Therm Biol* 27:17–27. doi:10.1016/S0306-4565(01)00011-0
- Schäuble CS (2004) Variation in body size and sexual dimorphism across geographical and environmental space in the frogs *Limnodynastes tasmaniensis* and *L. peronii*. *Biol J Linn Soc* 82:39–56. doi:10.1111/j.1095-8312.2004.00315.x
- Schwarzkopf L, Shine R (1991) Thermal biology of reproduction in viviparous skinks, *Eulamprus tympanum*: why do gravid females bask more? *Oecologia* 88:562–569. doi:10.1007/BF00317720
- Sears MW, Angilletta MJ Jr (2004) Body size clines in *Sceloporus* lizards: proximate mechanisms and demographic constraints. *Integr Comp Biol* 44:433–442. doi:10.1093/icb/44.6.433
- Sheehan H (2002) Age at maturity, longevity and sexual dimorphism in a sub-alpine population of common geckos (*Hoplodactylus maculatus*): a comparison with warmer populations. Honours dissertation. University of Otago, Dunedin
- Shelomi M (2012) Where are we now? Bergmann's rule sensu lato in insects. *Am Nat* 180:511–519. doi:10.1086/667595
- Shine R, Kearney M (2001) Field studies of reptile thermoregulation: how well do physical models predict operative temperatures? *Funct Ecol* 15:282–288. doi:10.1046/j.1365-2435.2001.00510.x
- Sunday JM, Bates AE, Kearney MR, Colwell RK, Dulvy NK, Longino JT, Huey RB (2014) Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc Natl Acad Sci USA* 111:5610–5615. doi:10.1073/pnas.1316145111
- Teplitsky C, Millien V (2014) Climate warming and Bergmann's rule through time: is there any evidence? *Evol Appl* 7:156–168. doi:10.1111/eva.12129
- Teplitsky C, Mills JA, Alho JS, Yarrall JW, Merilä J (2008) Bergmann's rule and climate change revisited: disentangling environmental and genetic responses in a wild bird population. *Proc Natl Acad Sci USA* 105:13492–13496. doi:10.1073/pnas.0800999105
- Todd AC (2005) The social mating system of *Hoplodactylus maculatus*. *N Z J Zool* 32:251–262. doi:10.1080/03014223.2005.9518417
- Towns DR (1985) A field guide to the lizards of New Zealand. N.Z. Wildlife Service Occasional Publication No. 7. New Zealand Wildlife Service, Department of Internal Affairs, Wellington, pp 8–9
- Uller T, While GM, Cadby CD, Harts A, O'Connor K, Pen I, Wapstra E (2011) Altitudinal divergence in maternal thermoregulatory behaviour may be driven by differences in selection on offspring survival in a viviparous lizard. *Evolution* 65:2313–2324. doi:10.1111/j.1558-5646.2011.01303.x
- Volynchik S (2014) Climate-related variation in body dimensions within four lacertid species. *Int J Zool* 2014. doi:10.1155/2014/795387
- Walters RJ, Hassall M (2006) The temperature-size rule in ectotherms: may a general explanation exist after all? *Am Nat* 167:510–523. doi:10.1086/501029
- Wapstra E, Swain R, O'Reilly JM (2001) Geographic variation in age and size at maturity in a small Australian viviparous skink. *Copeia* 2001:646–655. doi:10.1643/0045-8511(2001)001[0646:GVIAAS]2.0.CO;2
- Watt C, Mitchell S, Salewski V (2010) Bergmann's rule; a concept cluster? *Oikos* 119:89–100. doi:10.1111/j.1600-0706.2009.17959.x

- Whitaker AH (1982) Interim results from a study of *Hoplodactylus maculatus* (Boulenger) at Turakirae Head, Wellington. In: Newman DG (ed) New Zealand herpetology. N.Z. Wildlife Service Occasional Publication No. 2. New Zealand Wildlife Service, Department of Internal Affairs, Wellington, pp 363–374
- Wilson J, Cree A (2003) Extended gestation with late-autumn births in a cool-climate viviparous gecko from southern New Zealand (Reptilia: *Naultinus gemmeus*). Austral Ecol 28:339–348. doi:[10.1046/j.1442-9993.2003.01293.x](https://doi.org/10.1046/j.1442-9993.2003.01293.x)