

An Intercontinental Analysis of Climate-Driven Body Size Clines in Reptiles: No Support for Patterns, No Signals of Processes

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Abstract Climatic gradients impose clinal selection on animal ecological and physiological performance, often promoting geographic body size clines. Bergmann's rule predicts that body size increases with decreasing environmental temperatures given the need to retain body-heat through adjustments of body-mass-to-surface-area ratio. This prediction generally holds for endotherms, but remains controversial for ectotherms. An alternative interpretation, the 'resource rule', suggests that food abundance, primary productivity and precipitation (which, unlike temperature, do not necessarily correlate with geography), drive body size clines. We investigate geographic variation in body size within 65 species of lizards and snakes (squamates) based on an intercontinental dataset (6,500+ specimens belonging to 56 Israeli species, and multiple populations of nine *Liolaemus* species from Argentina and Chile). Bergmann's rule is only rarely supported by our data (in four species, 6 %), whereas six species (9 %) follow its converse (hence, it is unsupported in 94 % of cases). Similarly, size increases with resource abundance in only 12 species (18 %). Therefore, although neither of the rules is supported, factors suggested by the resource rule are better predictors of body size than

temperature. Surprisingly, we show that some measures of the extent of a species' climatic envelope do not affect the likelihood of it showing a size-climate relationship. We conclude that negative size-temperature associations are an exception rather than a generality among squamates.

Keywords Macroecology · Bergmann's rule · Resource rule · Climatic variability · Geographic variation in body size · Lizards · Snakes · *Liolaemus*

Introduction

Animal body size influences fitness through most ecological, life-history and metabolic functions, and is therefore simultaneously influenced by multiple selection demands (Peters 1983; Schmidt-Nielsen 1984). Given that environmental variation along geographic gradients has also consistently been observed to influence life-history and metabolism (Lovegrove 2000; Meiri et al. 2012, 2013), a strong interaction between animal distributions and body size is expected by macroecological theory (Blackburn and Gaston 2003).

The most influential hypothesis related to body size variation, Bergmann's rule, predicts that animal body size increases as a function of declining environmental temperatures that demand thermoregulatory optimizations through adjustments of the body-mass-to-surface-area ratio (Bergmann 1847; James 1970; Meiri and Dayan 2003). Although extensively studied, multiple aspects of the conceptual structure of Bergmann's rule, and hence the direction of predictions, remain controversial and intensely debated (Blackburn et al. 1999; Pincheira-Donoso 2010; Watt et al. 2010; Meiri 2011; Olalla-Tarraga 2011). Such controversy stems primarily from the conflicting support that the rule receives among studies, from different

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approaches to the taxonomic scale such studies should be carried out at, and from the still limited knowledge on the specific factors that drive climate-related size clines. Most empirical studies reveal that endotherms (birds and mammals) tend to follow the rule (Ashton et al. 2000; Meiri and Dayan 2003). Evidence from ectotherms, however, is conflicting (Ashton and Feldman 2003; Blanckenhorn and Demont 2004; Cruz et al. 2005; Dillon et al. 2006; Pincheira-Donoso et al. 2007, 2008a; Adams and Church 2008; Pincheira-Donoso 2010; Oufiero et al. 2011). Similarly, although body size differences among species (and hence, body size clines) are likely to be strongly influenced by multivariate natural selection on multiple components of fitness, it remains largely unclear whether the same clines within species are adaptive, driven by phenotypic plasticity, or are, to an extent, a result of both (i.e., adaptive plasticity; Partridge and Coyne 1997).

The complex effects of body size on multiple components of fitness (i.e., survival, mating success and fecundity) suggest that the observed variation in animal size is influenced by a number of factors other than temperature. Indeed, an alternative interpretation for Bergmann's rule, the 'resource rule', suggests that body size is fundamentally influenced by food availability, which, in turn, varies geographically as a function of variation in primary productivity and precipitation (Lindsey 1966; Rosenzweig 1968; Yom-Tov and Geffen 2006; Meiri et al. 2008; McNab 2010; Huston and Wolverson 2011; Gur and Gur 2012). This interpretation has increasingly gained interest, with several authors advocating resource availability as a primary determinant of intraspecific size clines in the direction predicted by Bergmann's rule (McNab 2010; Gur and Gur 2012). For example, based on analyses of Israeli mammals, Yom-Tov and Geffen (2006) claimed that, in arid regions, rainfall is the primary determinant of resource availability, and as such it is expected to be positively correlated with body size.

In reptiles, the relationship between productivity, rainfall, and body size remains poorly studied. Amarello et al. (2010) recently showed that size in the snake *Crotalus atrox* increases in colder and wetter (i.e., more productive) areas. On the other hand, Oufiero et al. (2011) and Volynchik (2012) found that size of *Sceloporus* lizards and of the viper *Vipera palaestinae*, respectively, increased in arid areas, while Tracy (1999) found no association between size and food abundance in the lizard *Sauromalus obesus* (= *S. ater*). Therefore, evidence for the resource rule is as conflicting as evidence for Bergmann's rule. A primary difference between the supporting evidence reported for these two hypotheses is that while Bergmann's rule has extensively been studied, only a few studies have investigated the resource rule.

Overall, independent of the mechanism underlying body size trends, squamates (lizards and snakes) often show size patterns reversing or falsifying the predicted Bergmannian

clines at both inter- and intra-specific scales. At the assemblage level, European lizards have been found to conform to Bergmann's rule and snakes its converse, whereas both clades show more complex patterns in North America (Olalla-Tarraga et al. 2006). At the interspecific level, Cruz et al. (2005) provided the first phylogenetic evidence supporting Bergmann's rule in squamates, based on species of the lizard genus *Liolaemus*. However, two subsequent phylogenetic studies falsified the rule when the number of sampled *Liolaemus* species was increased (Pincheira-Donoso et al. 2007, 2008a). Analyses of thermoregulatory physiology further revealed that Bergmann's rule is unlikely for *Liolaemus*, as lizard operative temperatures (T_e) and climatic categories (tropical, continental, Mediterranean and oceanic) were found to exert no influence on their body sizes (Labra et al. 2009). At a larger-scale, Ashton and Feldman (2003) conducted a meta-analysis of the prevalence of intra-specific cases of Bergmann's rule across squamates. Their dataset consisted mostly of populations of North American and European species. These authors found that squamate size increases, in general, with temperature, thus reversing Bergmann's rule. However, Ashton and Feldman's (2003) data and analyses are not suitable for drawing conclusive evidence for the prevalence of size clines within squamate species. Although 104 squamate species were included in that study, data for most species (taken from the literature) were based on only two populations, and often the size differences between populations in their sample were qualitative only. For just 20 species did the sample of Ashton and Feldman (2003) meet their criterion of at least ten individuals in each of at least three populations. Consequently, the general nature of intraspecific body size clines in squamates in relation to climatic and ecological factors remains unclear.

Here, we investigate trends in body size within multiple squamate species based on a two-continental geographic setting including biogeographically, and phylogenetically, independent faunas from Israel and from southern South America (Argentina and Chile). We test the hypotheses that (1) intraspecific variation in body size responds to clinal selection arising from variation in environmental temperatures (Bergmann's rule), and (2) size increases as a function of higher resource abundance within a species' geographic range (the resource rule). The mechanistic basis of both hypotheses differs importantly. While Bergmann's rule focuses on thermoregulation-dependent body size adjustments, the resource rule predicts a link between energy abundance and body size. Given that advantages of large body size in cold-environment ectotherms (thermal inertia) may be negated by prolonged heating time and hence, by prolonged exposure to predators and reduced time for foraging and reproduction, we expect no general

relationships between body size and temperature in the way predicted by Bergmann's rule. In contrast, given that organisms may directly benefit from higher resource abundance when natural or sexual selection favours larger body size, we expect a stronger link between size and resource abundance. Therefore, if these expectations are met, the resource rule may provide an alternative hypothesis to explain variation in body size within (and potentially among) species. Primary productivity, a common measure of resource abundance, however, may translate poorly into the amount of energy available for animals at high trophic levels (Huston and Wolverton 2011). Likewise, prey size may exert a strong selective pressure on predator size (Vezina 1985; Raia and Meiri 2006; Costa et al. 2008), irrespective of food abundance. Only further empirical tests of this theory, therefore, can identify its value as a factor behind animal body size evolution. Finally, we investigate the hypothesis that conspecific populations exposed to greater climatic variability across their range, and are, thus, exposed to stronger selection differentials on body size along their ranges, tend to vary clinally in response to these factors more than do species inhabiting less variable environments (Meiri and Thomas 2007; Pincheira-Donoso 2010).

Materials and Methods

Study Species, Geographic Settings and Body Size Data

We investigate spatial gradients of body size among adult conspecific specimens or populations of 56 species of squamates (lizards and snakes) from Israel (and adjacent areas) and of nine species from South America (Argentina and Chile; Appendix 1). The Israel dataset comprises 30 lizard and 26 snake species belonging to 13 monophyletic families. The South American dataset comprises nine species of the *Liolaemus* lizard adaptive radiation, one of the largest genera among living amniotes (Pincheira-Donoso et al. 2013), and which has extensively dispersed across large geographic ranges (Pincheira-Donoso et al. 2008b). This comparative perspective provides an ideal opportunity to replicate tests of intraspecific body size clines both among unrelated groups occurring in different continents, and among related species occupying the same geographic areas within each continent.

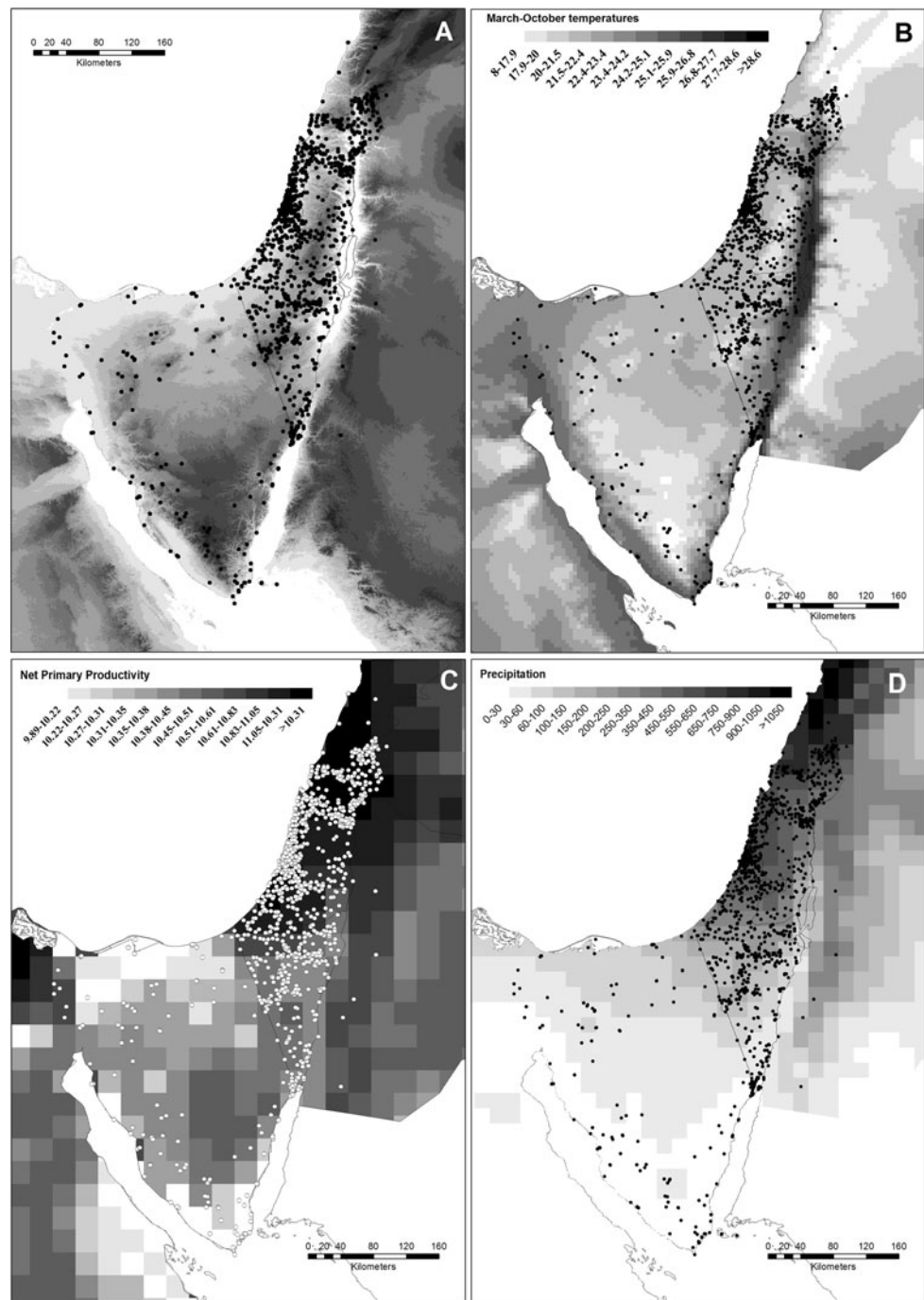
The Israeli data comprise of individuals housed at the National Museum of Natural History, Tel Aviv University (TAUM). The specimens were collected between 1950 and 2012. They originate mostly from Israel (92 %) but some specimens are from neighbouring countries, especially from Sinai (Egypt, 7 %), and also from the Palestinian authority, Lebanon, and Jordan (all henceforth

referred to as “Israel” for simplicity, no political agenda intended; Fig. 1). We used data from all species in the museum for which we had at least 30 adult individuals with at least five known collection localities (mean: 45, median 37 localities). Age data were only given for ~9 % of the specimens and maturity is difficult to verify in reptiles without damaging the specimens. We therefore examined literature data on the size at maturity (e.g., Mendelssohn 1963; Frankenberg and Werner 1992; Goldberg 2012a, b), and used data of the larger sex in species where females and males are known to mature at different sizes. Where such data were unavailable we only used specimens that were larger than the second smallest individual designated as adult in the collection. These procedures left us with data on 5,068 individuals belonging to 56 species (mean 91, median 58 individuals per species, range 30–678; Appendix 1) in 13 squamate families (taxonomy after Uetz 2012). This dataset thus represents 68 % of the 82 squamate species currently recognized in Israel (Bar and Haimovitch 2011).

The South American (*Liolaemus*) dataset consists of 1,472 specimens from nine of the widest geographically spread species of the genus (Pincheira-Donoso 2011). The unit of intraspecific analyses for these lizards is populations distributed in different latitudes and elevations. The number of conspecific populations per species ranges from five to eleven (mean = 8.2; Appendix 1; Fig. 2). The criteria employed to set population boundaries are based on arbitrary geographic areas where extensive field work has been conducted. Many large ecosystems (e.g., the Andes, Patagonia) where *Liolaemus* species occur are difficult to survey in a continuous fashion and hence, areas where access is viable tend to be repeatedly sampled. These sites of active field work are, therefore, better represented in collections and were treated as different populations.

Whereas we view weight as the best measure of size in interspecific studies (Meiri 2010; Feldman and Meiri 2013), we argue that length is a more suitable body size proxy in within-species analyses such as the one presented herein, because the shape of conspecifics is relatively similar, and weight may manifest variation related to feeding, phenology, and reproductive status (Meiri 2008). Snout-vent length (SVL, the length of the body from the tip of the snout to the cloaca) is the most extensively used body size index for lizards. It is tightly correlated with multiple life-history, ecological and physiological functions (Peters 1983; Meiri 2008), and it allows measurements of specimens in which the tail has been lost (Pincheira-Donoso et al. 2011). We therefore use SVL (in mm, log-transformed) as a measure of size in both the Israeli and South American samples. All measurements were taken on preserved museum specimens

Fig. 1 Distribution of the studied Israeli squamate reptiles in relation with topography (in meters of elevation, **a**), March–October temperature (in °C, **b**), net primary productivity (NPP in gram carbon, **c**), and precipitation (in mm, **d**)

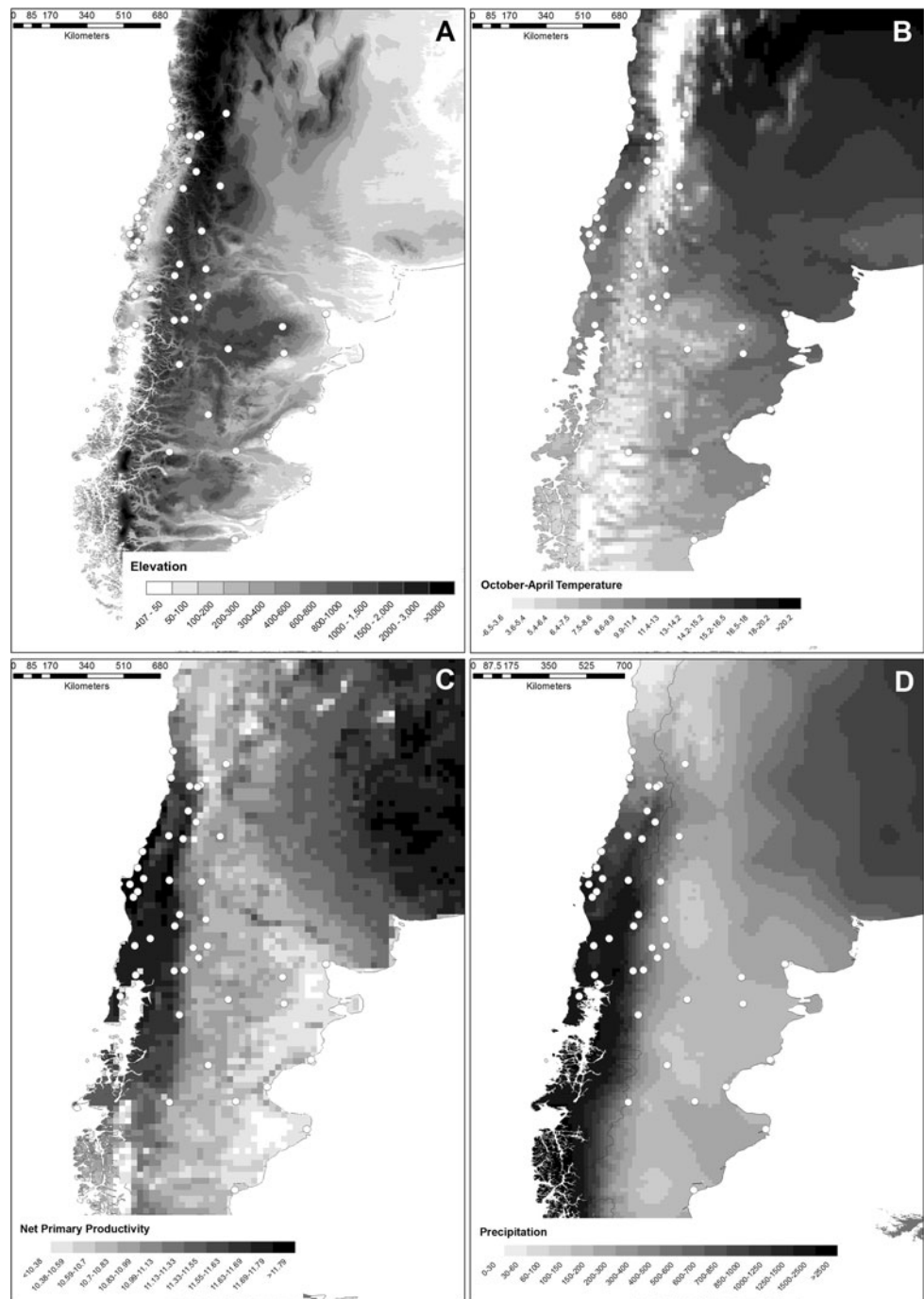


using 0.01 mm precision Mitutoyo digital callipers. Measurements of Israeli specimens were taken by museum personnel using similar tools and techniques, and hence inter-observer variation (Roitberg et al. 2011) is expected to be minimal (older technicians tutored younger ones). Measurements of *Liolaemus* specimens were all taken by one of us (DPD) using the same procedure, and for which only the largest 2/3 of the specimens per population in the analyses were included, in order to avoid effects of body size from immature specimens.

Climatic and Environmental Data

To investigate the relationships between intraspecific variation in body size and environmental factors, we obtained variables that reflect the thermal environment and resource abundance at adequate scales. To examine the effects of temperature on size, we used Worldclim data (at a 2.5-min resolution; Hijmans et al. 2005). We aimed to obtain mean “activity season” temperatures (i.e., temperatures in the months in which reptiles are active). For the Israeli species,

Fig. 2 Distribution of the studied populations of nine *Liolaemus* lizard species in Argentina and Chile, in relation with topography (in meters of elevation, **a**), October–April temperature (in °C, **b**), net primary productivity (NPP in gram carbon, **c**), and precipitation (in mm, **d**)



we averaged mean temperatures between March and October (the main reptile activity season in Israel; Meiri, pers. obs.), for each collection locality, then assigned these to each specimen (Fig. 1). For the South American dataset we averaged the mean temperatures between October and April as our estimate of their activity season. We assigned the obtained climatic data to each studied population within each *Liolaemus* species (Fig. 2). To examine the effects of resource availability on size we used two measures: mean annual precipitation (total yearly precipitation, in mm per

year, on a spatial resolution of $1/6^\circ$, assumed to be positively associated with productivity in the generally arid areas we study) and net primary productivity (NPP, the net amount of solar energy converted to plant organic matter through photosynthesis—measured in units of elemental carbon per year, on a spatial resolution of 0.25°). Precipitation data are from Worldclim (Hijmans et al. 2005), and NPP data (log-transformed) are from Imhoff et al. (2004). To assign these resource abundance proxies, we followed the same procedure described for temperatures, in which

data for Israeli species was based on localities per specimens, while for the *Liolaemus* dataset we obtained data for each population. These climatic data were assigned to each collection locality by intersecting the distribution data with the climatic layers in ArcGIS 9.3.1.

Statistical Analyses

We used multiple OLS regression to simultaneously determine the association between the three environmental predictors (Temperature, NPP, Precipitation), and log-transformed SVL of populations (South America) and individuals (Israel). We used backwards stepwise elimination based on P -values (cutoff: $P < 0.05$) to simplify the models and arrive at a minimum adequate model. Multi co-linearity was moderately strong with the Israeli data, especially because, across all cells in the region there is a substantial correlation between NPP and precipitation ($R^2=0.77$, VIF 4.8, for precipitation 5.6 and for temperature 1.4). We nevertheless used both measures together because common rules of thumb regarding the effects of even stronger VIFs (i.e., of 10) have recently been criticized (O'Brien 2007). Furthermore, NPP and precipitation only rarely feature in the same model after simplification (we tried to substitute them when a model included just one, and selected the resulting model based on AIC, analyses not shown). We nonetheless take this issue into account when interpreting our results. Collinearity was low in the South American dataset (all VIFs < 2.3).

After obtaining a model for each species we examined whether there any generalities emerge with respect to the response of size to temperature, precipitation and productivity. We compare the number of significant positive and significant negative association with each variable by means of a binomial test. We investigate the hypothesis that higher climatic variability across the range of a species results in stronger signal for predictable variation in body size (Meiri et al. 2004). We do this by comparing the ranges of the environmental predictors in species that varied with them versus the ranges across the range of species that did not, by means of t tests. Then we compared the number of Israeli species showing size clines versus the ones that do not, in relation to the biomes they inhabit using Chi squared tests (the mesic Mediterranean region, the arid desert regions, and species distributed in both; biomes present within the geographic range sampled was determined by intersecting the sample localities with a map of Israeli biomes).

Data on sample sizes, means and range of body sizes, mean values and ranges of all climatic data, and the ecological and biogeographic attributes we tested for all species are presented in “Appendix 1”. All statistical analyses were conducted in R 2.15.

Results

Environment-Size Relationships

Body size of most species does not vary predictably with climatic measures in either Israel or South America (Table 1; Fig. 3; Appendix 2). Overall, body size variation was found to be explained by at least one of the three factors in 30 out of the 65 species sampled (46 % of the cases; Fig. 3). Among Israeli squamates, 30 species showed no relationship between size and climate, size of 21 species was correlated with one variable, the size of two species was correlated with two variables, and in three species the minimum adequate model included all three predictors (Table 1). For the significant associations there is no significant excess of either positive or negative relationships with any of the three environmental variables (binomial tests, $P > 0.2$ in all three tests). In these reptiles, Bergmann's rule was only observed in three species (*Platyceps rogersi*, *Pseudotrapelus sinaitus*, and *Trachylepis vittata*), while body size in six other species (2 lizards, 3 snakes) decreases in colder climates. In the remaining 47 Israeli species, temperature was not significantly correlated with SVL. Seven species significantly increase in size with increasing precipitation, while the sizes of seven others decrease (and that of 42 does not vary with precipitation). Finally, the size of eight species increases with NPP, that of three decreases and the other 45 species show no size-NPP relationship. Intriguingly, in all four species in which both precipitation and NPP are both significant predictors of size (*P. rogersi*, *T. vittata*, *Psammophis schokari* and *Stenodactylus sthenodactylus*), the signs of the regression for NPP and precipitation differ (one positive, the other negative)—although both are indices of productivity. In the latter two species this may stem from a multicollinearity of NPP and precipitation (VIFs = 6.1 for *P. schokari* and 5.2 for *S. sthenodactylus*), but for the former two multicollinearity is not an issue (VIFs = 1.98 for *P. rogersi* and 1.01 for *T. vittata*). We conclude that the resource rule is not supported by our data (Fig. 3).

The tendencies observed among South American *Liolaemus* are similar (Fig. 3). In four out of the nine species body size varied predictably with at least one of the three factors. In three of these species sizes were predicted by one single factor (size of *L. pictus* increases with NPP as expected by the resource rule, but decreases with precipitation in *L. chiliensis* and *L. elongatus*, the opposite of the predicted direction; Table 1). In *Liolaemus tenuis*, all three factors are significantly correlated with body size (size varies negatively with temperature and precipitation, but positively with NPP; Table 1). See

Table 1 Qualitative summary of results of the minimum adequate models for each species from both continents

Species	Body response to			Model R^2
	Temperature	NPP	Precipitation	
Israel				
<i>Ablepharus rueppellii</i>	None	None	None	–
<i>Acanthodactylus beershebensis</i>	None	None	None	–
<i>Acanthodactylus boskianus</i>	None	Increase	None	0.024
<i>Acanthodactylus schreiberi</i>	None	None	None	–
<i>Acanthodactylus scutellatus</i>	None	Increase	None	0.145
<i>Atractaspis engaddensis</i>	None	None	None	–
<i>Bunopus tuberculatus</i>	None	None	Increase	0.134
<i>Cerastes cerastes</i>	None	None	Increase	0.132
<i>Cerastes gasperettii</i>	None	None	None	–
<i>Cerastes vipera</i>	None	None	None	–
<i>Chalcides guentheri</i>	None	Decrease	None	0.119
<i>Chalcides ocellatus</i>	None	None	Decrease	0.028
<i>Chalcides sepsoides</i>	None	None	None	–
<i>Chamaeleo chamaeleon</i>	Increase	None	None	0.088
<i>Daboia palaestinae</i>	None	None	None	–
<i>Dolichophis jugularis</i>	None	None	None	–
<i>Echis coloratus</i>	None	None	None	–
<i>Eirenis coronelloides</i>	None	None	None	–
<i>Eirenis decemlineatus</i>	None	None	None	–
<i>Eirenis rothii</i>	None	None	None	–
<i>Eryx jaculus</i>	None	None	None	–
<i>Eumeces schneideri</i>	None	Increase	None	0.081
<i>Hemidactylus turcicus</i>	Increase	None	Increase	0.209
<i>Hemorrhoids nummifer</i>	None	None	None	–
<i>Laudakia stellio</i>	None	None	Decrease	0.113
<i>Lytorhynchus diadema</i>	None	Increase	None	0.202
<i>Malpolon insignitus</i>	None	None	None	–
<i>Mediodactylus kotschy</i>	None	Decrease	None	0.251
<i>Mesalina guttulata</i>	None	Increase	None	0.132
<i>Mesalina olivieri</i>	None	None	None	–
<i>Micrelaps muelleri</i>	None	None	None	–
<i>Natrix tessellata</i>	None	None	Decrease	0.098
<i>Ophisops elegans</i>	None	None	Increase	0.162
<i>Phoenicolacerta laevis</i>	None	None	Increase	0.069
<i>Platycephs collaris</i>	None	None	None	–
<i>Platycephs rogersi</i>	Decrease	Increase	Decrease	0.159
<i>Psammophis schokari</i>	None	Increase	Decrease	0.061
<i>Pseudocerastes fieldi</i>	None	None	None	–
<i>Pseudotrapelus sinaitus</i>	Decrease	None	None	0.047
<i>Ptyodactylus guttatus</i>	None	None	None	–
<i>Ptyodactylus puiseuxi</i>	None	None	None	–
<i>Rhynchocalamus melanocephalus</i>	None	None	None	–
<i>Spalerosophis diadema</i>	None	None	None	–
<i>Stenodactylus doriae</i>	None	None	None	–
<i>Stenodactylus petrii</i>	None	None	None	–
<i>Stenodactylus sthenodactylus</i>	Increase	Decrease	Increase	0.072

Table 1 continued

Species	Body response to			Model R^2
	Temperature	NPP	Precipitation	
<i>Telescopus dhara</i>	Increase	None	None	0.155
<i>Telescopus fallax</i>	None	None	None	–
<i>Trachylepis vittata</i>	Decrease	Increase	Decrease	0.117
<i>Trapelus mutabilis</i>	None	None	None	–
<i>Trapelus savignii</i>	Increase	None	None	0.114
<i>Tropiocolotes nattereri</i>	None	None	Increase	0.116
<i>Typhlops vermicularis</i>	None	None	None	–
<i>Uromastix ornata</i>	None	None	None	–
<i>Varanus griseus</i>	None	None	Decrease	0.167
<i>Walterinnesia aegyptia</i>	Increase	None	None	0.088
South America				
<i>Liolaemus bibronii</i>	None	None	None	
<i>Liolaemus boulengeri</i>	None	None	None	–
<i>Liolaemus chiliensis</i>	None	None	Decrease	0.608
<i>Liolaemus elongatus</i>	None	None	Decrease	0.597
<i>Liolaemus fitzingerii</i>	None	None	None	–
<i>Liolaemus lemniscatus</i>	None	None	None	–
<i>Liolaemus pictus</i>	None	Increase	None	0.729
<i>Liolaemus schroederi</i>	None	None	None	–
<i>Liolaemus tenuis</i>	Decrease	Increase	Decrease	0.774

Significant terms are in boldface (model R^2 provided)

Increases or decreases refer to the response of body size to the predictor variables temperature, net primary productivity (NPP), and precipitation See [Appendix 2](#) for full parameter estimates of the minimum adequate models

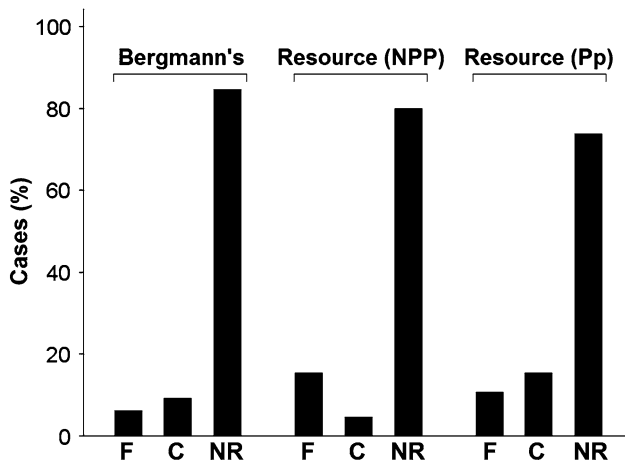


Fig. 3 Summary of species cases (in percentage) that follow (*F*), follow the converse of (*C*), or show no relationship with (*NR*), body size clines predicted by Bergmann's rule, and the resource rule for net primary productivity (*NPP*) and precipitation (*Pp*)

[Appendix 2](#) for parameter estimates in the minimum adequate models. Collinearity of the predictors is not an issue in the *Liolaemus* dataset (all VIF scores <3).

Correlates of Size Change

Few factors readily predict which species will show size clines and which will not. All nine Israeli genera with >1 species in which at least one species shows a significant trend also have at least one species not showing any trend (in the two *Ptyodactylus* and three *Eirenis* species in our sample no species shows a size cline with any predictor). Lizards, however, seem to more readily respond to climate than snakes (19 lizard species responding to climate, 11 not, vs. 7 snake species with significant correlations, 19 without, $\chi^2 = 7.42$, $P < 0.01$). Furthermore, species inhabiting the mesic, Mediterranean, climate in Israel tend to vary clinally less than desert species, whereas wide-spread species (inhabiting both major biomes) show the greatest tendency to vary in size with climate (26, 48 and 80 % of species showing clines, respectively, $\chi^2 = 7.65$, $P < 0.05$).

Diurnal species tend to decrease in size with increasing rainfall (seven species, vs. none that increase in size), but increase in size with increasing NPP (seven species, vs. one that decreases in size), even though both factors are thought to reflect resource availability. Nocturnal species

tend to show opposite trends to diurnal ones: five species increase in size with precipitation, and two decrease. The size of one nocturnal species decreases with NPP, and that of two increases. All three nocturnal species in which size varied with temperature followed the converse to Bergmann's rule, whereas three diurnal species followed the rule and three others followed its converse.

Species showing a size-NPP cline are distributed over a greater productivity range than NPP-indifferent species (1.14 vs. 0.87 log units, $t = 2.34$, $P = 0.02$). Surprisingly, however, precipitation-sensitive species do not range over significantly greater precipitation gradients than precipitation-indifferent ones (547 vs. 454 mm; $t = 1.43$, $P = 0.16$), and the pattern is much the same for temperature (7.6 vs. 7.7 °C; $t = 0.07$, $P = 0.94$).

Overall, small and large species are as likely to show body size clines. For example, both the largest and smallest Israeli lizards (*Varanus griseus* and *Tropicolotes nattereri*, respectively, both desert dwellers) change in size with precipitation (the diurnal monitor decreasing in size in arid areas, the nocturnal gecko size increasing), while other large and small lizards (e.g., *Ablepharus ruepellii* and *Uromastix ornatus*) do not respond to any climatic variable. Likewise, none of the largest (*Dolichophis jugularis*, *Daboia palaestinae*, *Malpolon insignatus*) or smallest (*Eirenis* spp., *Typhlops vermicularis*) snakes in our dataset changed size with any climatic variable. The mean body length of species showing some clines was marginally non-significantly shorter than that of those showing no clines (200 vs. 376 mm, $t = 1.83$, $P = 0.07$). However as the former mainly include lizards and the latter group has a greater proportion of snakes, and snakes are generally lighter than lizards of similar length, this distinction will probably not be apparent when masses are compared.

Within *Liolaemus* species (all diurnal) we found no tendency of species responding to any of the variables to have wider distribution along the gradient of this variable. The mean range in NPP of species showing clines is 0.776 versus 0.396 of species showing no clines ($t = 1.91$, $P = 0.098$). The mean range of precipitation is actually (non-significantly) wider in species showing no clines (1,310 mm, vs. 724 in species changing in size with precipitation, $t = 1.83$, $P = 0.110$). The single species varying in size with temperature, *L. tenuis*, has a temperature range of 7.78 °C, well within the 95 % confidence interval of species not showing such a cline ($6.50 \text{ °C} \pm 0.77_{\text{SE}}$). Thus it does not seem as if very drastic climatic ranges are required for size to respond to climate.

Discussion

Our intercontinental analyses reveal that body size within species of squamate reptiles seldom increases as a function

of decreasing environmental temperatures (i.e., predominantly falsifying Bergmann's rule), or increasing net primary productivity (NPP) or rainfall (i.e., predominantly falsifying the 'resource rule'). In most cases no predictable body size clines were observed, and cases of support for the converse of the predicted clines occur in similarly low frequencies to clines running in the other direction. However, for both Israeli and South American squamates, the factors suggested by the resource rule are more often better predictors of clinal body size than temperature, although not necessarily in the expected direction (Table 1; Fig. 3). Our results further suggest that the tendency to evolve size clines is not greatly influenced by phylogeny, as most multi-species genera and all families included both species showing size clines and ones that do not.

Bergmann's Rule

Overall, our findings are consistent with previous studies where body size trends predicted by Bergmann's rule are only rarely conformed by ectotherms (in contrast to endotherms), and among squamates in particular, irrespective of the underlying mechanisms (Pincheira-Donoso 2010). Our findings are also similar to results obtained at the interspecific level in squamates (Pincheira-Donoso et al. 2007, 2008a; Oufiero et al. 2011). Consequently, these results reinforce the view that Bergmann's rule is likely to be a phenomenon more common to endotherms (as it was originally established; Bergmann 1847).

The formulation of hypotheses explaining differential tendencies to follow Bergmann's rule observed between physiologically different groups (endotherms vs. ectotherms) has contributed to identify general factors underlying the contrasting relationships between body size and environmental demands among such groups. The way organisms interact with environmental temperature is, in general, regarded as one of the primary explanations. For example, large body size in cold climate endotherms facilitates heat conservation (Bergmann 1847; Mayr 1956), while in ectotherms large body size also reduces heating rates in the first place (Ashton and Feldman 2003; Pincheira-Donoso et al. 2008a). However, a different (and challenging) question is, why within the same functional or phylogenetic groups some sets of species or populations show Bergmann's rule, while others do not show any cline, and yet others follow a reverse one. Our results reflect this conundrum (Table 1). Such inconsistencies in the tendency to follow Bergmann's rule are particularly common among ectotherms (e.g., Ashton and Feldman 2003; Pincheira-Donoso 2010). Temperature influences most organismal activities linked to fitness. However, when thermal selection on body size is relaxed (e.g., where environmental temperature are high and close enough to animal thermal

optima to enable reptiles of any size to efficiently thermoregulate), the impact of other factors (e.g., food, sexual selection, life histories) with major fitness effects on body size may override the influence of temperature. These factors, therefore, are likely to deviate variation of body size from the expected trends that would be expected to emerge if temperature was the only agent of selection on size (see next subsection for more details). For example, contrasting natural selection on offspring survival (and maturation schedule) among two *Sceloporus* lizard species has been shown to result in one of them following Bergmann's rule while the other its converse (Sears and Angilletta 2004). Likewise, while range size and latitude (as a traditional proxy for temperature) are the primary factors shaping geographic size variation among mammalian Carnivora, strong influences of competition and food availability at local scales can result in some species deviating from the general tendency (Dayan et al. 1989; Raia and Meiri 2006; Meiri et al. 2007). In addition, within major functional and taxonomic groups, both lineage-specific and area-specific factors that influence the ways body size interact with the environment can result in conflicting evidence for Bergmann's rule. For example, within Syngnathid fish, the polygamous mating system of *Syngnathus* pipefish species promotes conformity to the rule, while body size variation is not predicted by latitude among the monogamous *Hippocampus* seahorse species (Wilson 2009).

Resource Rule

Our results do not support the 'resource rule'. Within most species body size is uncorrelated with either NPP or precipitation. In general, these factors (and hence this rule) explain body size clines in more squamate species than does temperature (Bergmann's rule), in both Israeli and South American squamates (Table 1; Fig. 3).

We suggest that a major difference between both studied rules is that the resource rule offers a more integrative influence of multiple interacting factors (food abundance, humidity, NPP) as drivers of body size variation across space (Yom-Tov and Geffen 2006; Meiri et al. 2008). Hence, an important conceptual aspect of the resource rule is that it, intrinsically, does not necessarily predict a relationship between body size and geography, in contrast to Bergmann's rule. Although the spatial distribution of resources sometimes correlate with latitude and elevation (as temperatures strongly do), this correlation can often be weak. For example, at the same latitudes and elevations, there are humid and hot forests with abundant resources, and dry and hot deserts where resources are poor. Human

settlements, for example, can also artificially increase food abundance in arid areas further breaking the association between climate and the resources available to animals on a very local scale (Yom-Tov 2003). It follows, therefore, that the mechanistic basis of both rules as explanations for large-scale body size patterns can be discordant (although not necessarily mutually exclusive). A question that remains open is whether the resource rule, similar to Bergmann's rule, is more prevalent among endotherms than among ectotherms.

The Complexities of Body Size Clines

It has been suggested that geographic size clines are more likely to express among (conspecific or closely-related heterospecific) animals spread over larger geographic ranges, where different populations are exposed to greater climatic differentials and hence, face larger differential selection pressures between them (Blackburn and Ruggiero 2001; Meiri et al. 2007; Pincheira-Donoso 2010). However, we found that the range of temperatures, NPP or rainfall, across the range of the species we examined was not consistently associated with a tendency for size to vary with these predictors. In Israeli squamates we did find such a relationship between size variation and productivity. We also found a greater tendency of species ranging across biomes to vary in size in relation to species found in a single biome. Temperature and rainfall ranges, however, are unrelated to the tendency of size to vary with them. We suggest that the overall range of temperature or rainfall may be a poor measure of climatic variability. If the mean annual rainfall across the range of a species varies between 50 and 350 mm, for example, it will make the huge difference: from a desert environment to a Mediterranean environment. Within one biome an even greater difference (e.g., within the Mediterranean climate belt from 400 to 800 mm) may affect the perception of the environment by an animal less than a smaller difference across biomes. When we examine the variation in precipitation as the ratio of the highest to the lowest value, the median value for species that show a precipitation gradient is 28.4, and for those that do not it is 6.8 (although this difference is not significant, $P = 0.09$). In addition, environmental variability underlying body size variation does not necessarily require extensive areas. It can result from contrasting selection regimes demanding adaptations to divergent niche dimensions in restricted geographic areas. Indeed, multiple conspecific populations spread along geographic gradients can evolve diverse body sizes at each site as a result of local interactions as part of different assemblages (Dayan et al. 1989) where natural selection regimes vary,

but this variation is not necessarily linearly related with geography. Such spatial variation may be influenced by, for example, divergent competitive character displacement, or differences in sexual selection interactions (via e.g., differences in operational sex ratios), which do not necessarily respond to the studied environmental variables. In these cases, the predictability of the body size-geography relationship is expected to be altered by ecological and sexual interactions taking place at local scale, making geographic clines less likely. Such scenarios are in fact observed in *Liolaemus*, where some widespread species (*Liolaemus bibronii*, *Liolaemus lemniscatus*, *L. tenuis*) interact with largely different lizard assemblages in different geographic locations (Cei 1993; Pincheira-Donoso and Núñez 2005).

In trying to seek generalities as to which taxa are likely to show size clines and which do not, we did not take phylogenetic relatedness into account, for two main reasons: (1) While body size is certainly influenced by shared ancestry, and range size may also be (Webb and Gaston 2003; Waldron 2007), size clines are not shared from an ancestor. Under peripatric cladogenesis, species ranges are small upon speciation, and their sizes are thus unlikely to vary clinally. Size clines may evolve as ranges expand. Thus clines evolve independently, and are not inherited as some non-emergent traits (e.g., body size, metabolic rate) are. While some groups may share traits that predispose them to evolve size clines, this evolution is nonetheless independent. Therefore, species can be treated as independent data-points. (2) In our data (see above) there is likely little phylogenetic signal (e.g., in every genus with >1 species that has a species showing a cline, there is also at least one species not showing clines), and thus we have no evidence that the tendency to evolve size clines has a basis in shared ancestry.

Collectively, our major conclusion is that the formulation of precise predictions of body size evolution involving large spatial contexts is an enormous challenge. First, because most fitness components are influenced by body size, this complex trait is sensitive to many more factors than those accounted for by traditional macroecological generalizations, such as traditional Bergmann's (or even the resource) rule. Second, because large areas and ranges with great climatic variation reflect large selection gradients arising from both climatic demands and from ecological interactions. Such large scale climatic variation does not necessarily exert the same effects on body size as do local-scale contexts. Therefore, although climatic factors exert major effects on fitness through ecophysiological demands on body size across space, multiple additional

factors that operate at local scales also impose substantial selection pressures on size (e.g., sexual selection).

Actual measures of food abundance and prey size are probably necessary to correctly test the resource rule. Large-scale measures such as NPP and rainfall may not be well correlated with the amount of food available to animals. Furthermore, predator ability to subdue and swallow their prey exerts a selective force on size which may be independent of resource abundance. Likewise, the dependence of herbivorous diet on temperature in lizards is thought to influence body size adaptations. Voluminous guts for efficient plant digestion are globally attained by warm climate herbivorous lizards, which tend to be large-sized (Iverson 1982; King 1996), given that thermal constraints on their maximum body sizes are relaxed. Herbivory in cold climate lizards (e.g., *Liolaemus*), in contrast, requires smaller body sizes to accelerate heating rates, and consequently, rates of plant digestion (Espinoza et al. 2004). Therefore, in these organisms temperature is likely to interact with diet to drive patterns of body size, rather than having a direct effect on it. In addition, these relationships between lizard herbivory and temperature in general (i.e., requirements for larger sizes in warm climates) run against Bergmann's rule expectations (Pincheira-Donoso et al. 2008a; but see Meiri et al. 2013). In conclusion, Bergmann's and resource rules (as many other patterns in macroecology) can only be recognized as partial generalizations, more likely to hold in some groups (endotherms) than in others (ectotherms), depending on their differences in the way they respond to varying selection across space. Therefore, we argue that these rules can only be generalized within the phylogenetic and biological limits of particular groups, rather than in a more abstract way across all forms of life.

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Appendix 1

See Tables 2 and 3.

Table 2 The Israeli sample

Taxa	N	SVL (mm)		Temperature		NPP		Rainfall		Activity	Climate zone
		Mean	Range	Mean	Range	Mean	Range	Mean	Range		
Lizards											
Agamidae											
<i>Laudakia stellio</i>	100	115	54	21.1	14	10.98	1.28	378	878	Diurnal	Widespread
<i>Pseudotrapelus sinaitus</i>	106	76	50	24.1	10.9	10.45	0.3	74	318	Diurnal	Desert
<i>Trapelus mutabilis</i>	154	65	36	22.1	8.1	10.57	0.96	165	309	Diurnal	Desert
<i>Trapelus savignii</i>	79	88	57	22.1	4	10.64	1.11	174	530	Diurnal	Desert
<i>Uromastix ornata</i>	43	158	72	25	10.8	10.32	0.59	20	34	Diurnal	Desert
Chamaeleonidae											
<i>Chamaeleo chamaeleon</i>	74	115	79	22.4	6.2	11.1	1.32	441	806	Diurnal	Widespread
Gekkonidae											
<i>Bunopus tuberculatus</i>	32	49	22	26.4	1.4	10.42	0.09	48	32	Nocturnal	Desert
<i>Hemidactylus turcicus</i>	74	47	24	22.9	8.1	10.75	1.45	267	775	Nocturnal	Widespread
<i>Mediodactylus kotschy</i>	36	41	17	22.2	4.8	11.12	0.83	558	381	Nocturnal	Mediterranean
<i>Stenodactylus doriae</i>	34	59	18	26.2	5.5	10.43	0.37	56	182	Nocturnal	Desert
<i>Stenodactylus petrii</i>	32	61	19	22.1	5.5	10.52	0.49	165	181	Nocturnal	Desert
<i>Stenodactylus sthenodactylus</i>	104	50	15	23.3	8.3	10.62	1.37	185	566	Nocturnal	Widespread
<i>Tropicolotes nattereri</i>	43	24	8	24.2	7.5	10.48	0.65	112	382	Nocturnal	Desert
Lacertidae											
<i>Acanthodactylus beershebensis</i>	143	66	40	21.9	1.6	10.66	0.81	218	151	Diurnal	Desert
<i>Acanthodactylus boskianus</i>	254	63	40	22.3	13.4	10.47	1.33	129	377	Diurnal	Desert
<i>Acanthodactylus schreiberi</i>	144	69	45	22.3	0.9	11.31	0.83	532	422	Diurnal	Mediterranean
<i>Acanthodactylus scutellatus</i>	199	56	32	22.2	4.7	10.9	1.25	346	549	Diurnal	Desert
<i>Mesalina guttulata</i>	185	46	43	21.6	11.8	10.5	1.14	165	520	Diurnal	Desert
<i>Mesalina olivieri</i>	71	44	16	22.3	7.4	10.59	1.32	205	561	Diurnal	Desert
<i>Ophisops elegans</i>	171	48	20	20	13.8	11.11	1.14	543	898	Diurnal	Widespread
<i>Phoenicolacerta laevis</i>	89	63	30	18.7	12.7	11.19	0.83	667	485	Diurnal	Mediterranean
Phyllodactylidae											
<i>Ptyodactylus guttatus</i>	130	74	32	22.5	10	10.75	1.46	266	568	Cathemeral	Widespread
<i>Ptyodactylus puiseuxi</i>	30	70	23	20.2	11.4	11.31	0.44	644	512	Diurnal	Mediterranean
Scincidae											
<i>Ablepharus rueppellii</i>	60	33	16	21.9	9.2	11.17	1.14	497	847	Diurnal	Widespread
<i>Chalcides guentheri</i>	37	126	97	21.7	7.4	11.3	0.83	561	393	Diurnal	Mediterranean
<i>Chalcides ocellatus</i>	145	93	110	22.3	8.7	10.78	1.28	290	762	Diurnal	Widespread
<i>Chalcides sepsoides</i>	34	87	29	23.1	6.6	10.62	1.22	199	543	Cathemeral	Desert
<i>Eumeces schneideri</i>	53	148	115	21.9	10.9	11.16	1.07	470	750	Diurnal	Widespread
<i>Trachylepis vittata</i>	116	76	40	20.1	10.4	11.24	0.72	591	620	Diurnal	Mediterranean
Varanidae											
<i>Varanus griseus</i>	32	418	265	22.9	6	10.88	1.35	301	670	Diurnal	Desert
Snakes											
Boidae											
<i>Eryx jaculus</i>	52	498	384	22.4	3.8	11.27	0.86	478	480	Nocturnal	Mediterranean
Colubridae											
<i>Dolichophis jugularis</i>	57	1,222	1,240	22.1	7.6	11.24	0.83	541	489	Diurnal	Mediterranean
<i>Eirenis coronelloides</i>	45	214	110	21.9	6.8	10.52	0.78	182	269	Diurnal	Desert
<i>Eirenis decemlineatus</i>	31	432	303	22	2.7	11.29	0.92	475	548	Diurnal	Mediterranean
<i>Eirenis rothii</i>	49	201	166	21.7	8.4	11.31	0.9	547	721	Cathemeral	Mediterranean
<i>Hemorrhois nummifer</i>	46	719	600	22.3	7.6	11.26	0.83	525	538	Nocturnal	Mediterranean

Table 2 continued

Taxa	N	SVL (mm)		Temperature		NPP		Rainfall		Activity	Climate zone
		Mean	Range	Mean	Range	Mean	Range	Mean	Range		
<i>Lytorhynchus diadema</i>	34	322	152	22.2	4.2	10.88	1.32	316	548	Nocturnal	Desert
<i>Natrix tessellata</i>	42	623	350	22.6	7.6	11.17	0.75	525	489	Diurnal	Mediterranean
<i>Platyceps collaris</i>	50	598	400	21.8	10.9	11.3	0.51	548	517	Diurnal	Mediterranean
<i>Platyceps rogersi</i>	61	561	629	22.1	6.4	10.56	1.14	171	313	Diurnal	Desert
<i>Rhynchocalamus melanocephalus</i>	33	329	206	22.2	4.9	11.25	1.15	498	871	Cathemeral	Mediterranean
<i>Spalerosophis diadema</i>	79	807	915	22.6	8.6	10.68	1.11	188	502	Cathemeral	Desert
<i>Telescopus dhara</i>	33	728	750	23.9	6.7	10.63	1.08	179	386	Diurnal	Desert
<i>Telescopus fallax</i>	51	450	480	22.1	7.2	11.28	0.44	497	489	Nocturnal	Mediterranean
Elapidae											
<i>Walterinnesia aegyptia</i>	48	899	340	22.8	7.4	10.51	0.84	151	305	Nocturnal	Desert
Lamprophiidae											
<i>Atractaspis engaddensis</i>	46	550	436	24.1	6.3	10.76	0.76	230	382	Nocturnal	Desert
<i>Malpolon insignitus</i>	59	1,043	973	21.9	10.9	11.22	0.92	511	661	Diurnal	Mediterranean
<i>Micrelaps muelleri</i>	30	390	292	22.5	4.5	11.28	0.76	520	382	Nocturnal	Mediterranean
<i>Psammophis schokari</i>	79	572	486	22.8	10.9	10.82	1.54	281	631	Diurnal	Widespread
Typhlopidae											
<i>Typhlops vermicularis</i>	77	211	227	22.2	8.3	11.31	0.83	547	543	Cathemeral	Mediterranean
Viperidae											
<i>Cerastes cerastes</i>	47	544	275	24.2	10.5	10.42	1.36	27	162	Nocturnal	Desert
<i>Cerastes gasperettii</i>	71	603	335	26.1	5.7	10.42	0.12	52	112	Nocturnal	Desert
<i>Cerastes vipera</i>	85	221	105	22.3	5.6	10.58	0.67	146	209	Nocturnal	Desert
<i>Daboia palaestinae</i>	678	853	590	22.8	8.1	11.31	0.83	507	586	Nocturnal	Mediterranean
<i>Echis coloratus</i>	343	552	515	25.6	8.6	10.5	1.27	115	418	Nocturnal	Desert
<i>Pseudocerastes fieldi</i>	38	605	360	21.3	7.3	10.44	0.13	149	164	Nocturnal	Desert

Sample size (number of individuals), and means and ranges of body size (Snout vent lengths, in mm), temperature (mean March–October temperatures across the parts of the geographic range sampled, in °C), net primary productivity (NPP, across the parts of the geographic range sampled, in grams elemental carbon per year, after logarithmic transformation) and annual precipitation (across the parts of the geographic range sampled, in mm per year)

The range in precipitation is computed both as a difference (highest minus lowest annual precipitation across the range, in mm) and as a ratio (highest precipitation divided by the lowest precipitation, unit free)

Activity is classified as either diurnal or nocturnal, and climatic zone refers to the two major biomes in Israel: the northern, mesic, Mediterranean region and the southern, arid desert

“Widespread” means the species inhabits both regions

Table 3 The South American sample (*Liolaemus* lizards)

Species	N	SVL (mm)		Temperature		NPP		Rainfall	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range
<i>Liolaemus bibronii</i>	10	57.1	10.93	12.8	5.7	10.90	0.55	283	353
<i>Liolaemus boulengeri</i>	5	65.0	8.203	13.5	9.1	10.78	0.56	269	353
<i>Liolaemus chiliensis</i>	7	90.5	15.66	13.9	8.2	11.54	1.16	1,070	1,550
<i>Liolaemus elongatus</i>	8	83.8	9.935	13.5	5.2	11.09	0.59	450	1,065
<i>Liolaemus fitzingerii</i>	9	95.9	8.053	14.4	8.4	10.63	0.72	207	107
<i>Liolaemus lemmiscatus</i>	10	49.4	6.827	15.1	7.4	11.60	1.15	869	1,192
<i>Liolaemus pictus</i>	7	66.7	2.865	11.8	2.5	11.70	0.35	1,714	1,320

Table 3 continued

Species	N	SVL (mm)		Temperature		NPP		Rainfall	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range
<i>Liolaemus schroederi</i>	7	61.6	7.7	12.8	5.5	11.55	0.71	923	1,019
<i>Liolaemus tenuis</i>	11	58.5	8.64	14.6	7.8	11.71	0.44	1,018	1,316

Sample size (number of populations), and population means and ranges of body size (Snout-vent lengths, in mm), temperature (mean October to April temperatures across the parts of the geographic range sampled, in °C), net primary productivity (NPP, across the parts of the geographic range sampled, in grams elemental carbon per year, after logarithmic transformation) and annual precipitation (across the parts of the geographic range sampled, in mm per year)

The range in precipitation is computed both as a difference (highest minus lowest annual precipitation across the range, in mm) and as a ratio (highest precipitation divided by the lowest precipitation, unit free)

All species are diurnal

Appendix 2

See Table 4.

Table 4 Full parameter estimates of the minimum adequate models for each studied species from both continents

Species	Temperature				NPP				Precipitation				Model R ²	Best model predictors
	Slope	SE	t	P	Slope	SE	t	P	Slope	SE	t	P		
Asia														
<i>Ablepharus rueppellii</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Acanthodactylus beershebenensis</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Acanthodactylus boskianus</i>	Na	Na	Na	Na	0.04	0.02	2.49	0.013	Na	Na	Na	Na	0.02	NPP
<i>Acanthodactylus schreiberi</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Acanthodactylus scutellatus</i>	Na	Na	Na	Na	0.05	0.01	5.78	<0.001	Na	Na	Na	Na	0.15	NPP
<i>Atractaspis engaddensis</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Bunopus tuberculatus</i>	Na	Na	Na	Na	Na	Na	Na	Na	0.001	0.001	2.16	0.039	0.13	Pre
<i>Cerastes cerastes</i>	Na	Na	Na	Na	Na	Na	Na	Na	0.0005	0.0002	2.62	0.012	0.13	Pre
<i>Cerastes gasperettii</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Cerastes vipera</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Chalcides guentheri</i>	Na	Na	Na	Na	-0.14	0.06	2.18	0.036	Na	Na	Na	Na	0.12	NPP
<i>Chalcides ocellatus</i>	Na	Na	Na	Na	Na	Na	Na	Na	-0.0001	0.00003	2.02	0.045	0.03	Pre
<i>Chalcides sepsoides</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Chamaeleo chamaeleon</i>	0.023	0.009	2.63	0.010	Na	Na	Na	Na	Na	Na	Na	Na	0.09	Tem
<i>Daboia palaestinae</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Dolichophis jugularis</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Echis coloratus</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Eirenis coronelloides</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Eirenis decemlineatus</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Eirenis rothii</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Eryx jaculus</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Eumeces schneideri</i>	Na	Na	Na	Na	0.06	0.03	2.12	0.039	Na	Na	Na	Na	0.08	NPP
<i>Hemidactylus turcicus</i>	0.010	0.003	2.96	0.004	Na	Na	Na	Na	0.0001	0.00003	4.12	<0.001	0.21	Tem, Pre
<i>Hemorrhoids nummifer</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Laudakia stellio</i>	Na	Na	Na	Na	Na	Na	Na	Na	-0.0001	0.00002	3.53	0.001	0.11	Pre
<i>Lytorhynchus diadema</i>	Na	Na	Na	Na	0.06	0.02	2.84	0.008	Na	Na	Na	Na	0.20	NPP
<i>Malpolon insignitus</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Mediodactylus kotschyi</i>	Na	Na	Na	Na	-0.07	0.02	3.38	0.002	Na	Na	Na	Na	0.25	NPP
<i>Mesalina guttulata</i>	Na	Na	Na	Na	0.09	0.02	5.28	<0.001	Na	Na	Na	Na	0.13	NPP

Table 4 continued

Species	Temperature				NPP				Precipitation				Model R^2	Best model predictors
	Slope	SE	<i>t</i>	<i>P</i>	Slope	SE	<i>t</i>	<i>P</i>	Slope	SE	<i>t</i>	<i>P</i>		
<i>Mesalina olivieri</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Micrelaps muelleri</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Natrix tessellata</i>	Na	Na	Na	Na	Na	Na	Na	Na	−0.0002	0.0001	2.08	0.044	0.09	Pre
<i>Ophisops elegans</i>	Na	Na	Na	Na	Na	Na	Na	Na	0.0001	0.00001	5.71	<0.001	0.16	Pre
<i>Phoenicolacerta laevis</i>	Na	Na	Na	Na	Na	Na	Na	Na	0.0001	0.00004	2.54	0.013	0.07	Pre
<i>Platyceps collaris</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Platyceps rogersi</i>	−0.022	0.011	2.02	0.048	0.27	0.08	3.22	0.002	−0.001	0.0003	2.84	0.006	0.16	Tem, NPP, Pre
<i>Psammophis schokari</i>	Na	Na	Na	Na	0.09	0.04	2.20	0.031	−0.0002	0.0001	2.10	0.039	0.06	NPP, Pre
<i>Pseudocerastes fieldi</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Pseudotrapelus sinaitus</i>	−0.003	0.001	2.26	0.026	Na	Na	Na	Na	Na	Na	Na	Na	0.05	Tem
<i>Ptyodactylus guttatus</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Ptyodactylus puiseuxi</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Rhynchocalamus melanocephalus</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Spalerosophis diadema</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Stenodactylus doriae</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Stenodactylus petrii</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Stenodactylus sthenodactylus</i>	0.004	0.002	2.29	0.024	−0.05	0.02	2.21	0.029	0.0001	0.00005	2.47	0.051	0.07	Tem, NPP, Pre
<i>Telescopus dhara</i>	0.019	0.008	2.39	0.023	Na	Na	Na	Na	Na	Na	Na	Na	0.16	Tem
<i>Telescopus fallax</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Trachylepis vittata</i>	−0.011	0.003	3.66	0.0004	0.10	0.04	2.52	0.013	−0.0001	0.00005	2.29	0.024	0.12	Tem, NPP, Pre
<i>Trapelus mutabilis</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Trapelus savignii</i>	0.032	0.010	3.15	0.002	Na	Na	Na	Na	Na	Na	Na	Na	0.11	Tem
<i>Tropicolotes nattereri</i>	Na	Na	Na	Na	Na	Na	Na	Na	0.0001	0.0001	2.32	0.026	0.12	Pre
<i>Typhlops vermicularis</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Uromastix ornata</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Varanus griseus</i>	Na	Na	Na	Na	Na	Na	Na	Na	−0.0001	0.00005	2.45	0.020	0.17	Pre
<i>Walterinnesia aegyptia</i>	0.006	0.003	2.11	0.040	Na	Na	Na	Na	Na	Na	Na	Na	0.09	Tem
South America														
<i>Liolaemus bibronii</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Liolaemus boulengeri</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Liolaemus chiliensis</i>	Na	Na	Na	Na	Na	Na	Na	Na	−0.0001	0.000	−2.8	0.039	0.61	Pre
<i>Liolaemus elongatus</i>	Na	Na	Na	Na	Na	Na	Na	Na	−0.0001	0.000	−2.9	0.003	0.597	Pre
<i>Liolaemus fitzingerii</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Liolaemus lemniscatus</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Liolaemus pictus</i>	Na	Na	Na	Na	0.045	0.01	3.68	0.014	Na	Na	Na	Na	0.729	NPP
<i>Liolaemus schroederi</i>	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	Na	None
<i>Liolaemus tenuis</i>	−0.0001	0.002	−3.3	0.013	0.212	0.06	3.82	<0.01	−0.0001	0.000	−4.8	0.002	0.774	Tem, NPP, Pre

Last column details the best predictor of the model, in bold

Predictors are temperature, net primary productivity (NPP), and precipitation

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