

Living in difficult situations: Lizards living in high altitudes have smaller body sizes due to extreme climatic conditions and limited resources

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Abstract

The evolution of body size, both within and between species, has been long predicted to be influenced by multifarious environmental factors. However, the specific drivers of body size variation have remained difficult to understand because of the wide range of proximate factors that consistently covary with ectotherm body sizes across populations with varying local environmental conditions. Here, we used a widely distributed lizard (*Eremias argus*) collected from different populations situated across China to assess how climatic conditions and/or available resources at different altitudes shape the geographical patterns of lizard body size across populations. We used body size data from locations differing in altitudes across China to construct linear mixed models to test the relationship between lizard body size and ecological and climate conditions across altitudes. Lizard populations showed significant differences in body size across altitudes. Furthermore, we found that variation in body size among populations was also explained by climatic and seasonal changes along the altitudinal gradient. Specifically, body size decreased with colder and drier environmental conditions at high altitudes, resulting in a reversal of Bergmann's rule. Limited resources at high altitudes, as measured by net primary productivity, may also constrain body size. Therefore, our study demonstrates that the intraspecific variation in female lizards' body size may be strongly influenced by multifarious local environments as adaptive plasticity for female organisms to possibly maximise reproductive ecology along geographic clines.

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more, we found that variation in body size among populations was also explained by climatic and seasonal changes along the altitudinal gradient. Specifically, body size decreased with colder and drier environmental conditions at high altitudes, resulting in a reversal of Bergmann's rule. Limited resources at high altitudes, as measured by net primary productivity, may also constrain body size. Therefore, our study demonstrates that the intraspecific variation in female lizards' body size may be strongly influenced by multifarious local environments as adaptive plasticity for female organisms to possibly maximise reproductive ecology along geographic clines.

Keywords: Bergmann's rule, Squamates, Resource availability, Geographical gradients, Climate

1.0 Introduction

Body size is a fundamental but critical trait of organisms, and variation in body size within and between species is often tightly linked to important life history traits, such as fecundity, growth, and survival (Roff, 2002; Pincheira-Donoso et al., 2008; Meiri, 2018; Lu et al., 2018a; Meiri et al., 2020; Deme et al., 2022a; 2022b; Wu et al., 2022). Originally described for endothermic species, Bergmann's rule predicts that species occupying colder environments will have larger body sizes when compared to species occupying warmer environments (Bergmann, 1847). Indeed, almost all endotherms adhere to Bergmann's rule (see reviews by Blackburn et al., 1999; Freckleton et al., 2003). However, ectotherms often do not (Forsman and Shine, 1995; Sears and Angilletta, 2004; Norris et al., 2021); with some ectotherm species showing no observable clines in body size and others reversing Bergmann's rule (Forsman and Shine, 1995; Sears and Angilletta, 2004; Olalla-Tárraga and Rodríguez, 2007; Meiri et al., 2013; Lu et al., 2018a; Norris et al., 2021). This is perhaps not surprising, as the original explanation for Bergman's rule does not apply to ectotherms (Watt et al., 2010), since they generate little internal body heat, and a larger body would therefore heat up more slowly as well (Stevenson, 1985). The proximate underlying factors influencing clines in body size among ectotherms are instead likely complex and multifarious (Sears and Angilletta, 2004; Pincheira-Donoso and Meiri, 2013; Pincheira-Donoso et al., 2019). Thus, unraveling the specific factors explaining clines of body size in ectotherms is necessary to properly understand the evolution of body size and its ecological consequences (Collar et al., 2010).

Plastic and evolutionary responses to altitudinal clines may influence inter- and intraspecific variation in body size among ectotherms (Lu et al., 2018a; Meiri, 2018; Norris et al., 2021; Giovanna et al., 2022), due to the often rapid changes in annual and seasonal variation in temperature and precipitation across altitude (Liang et al., 2021; Anderson et al., 2022). For instance, studies have suggested that ectotherm body sizes may increase at low elevations with optimal seasonal environments (seasonal environments that allow ectotherms to have more active time) (Slavenko et al., 2019), likely because optimal seasonal environments allow for increased time available for ectotherms to acquire resources (Horváthová et al., 2013). Moreover, lizard species at high altitudes may have small body sizes due to short warmer seasons, unfavourable conditions, and constrained active time (Meiri et al., 2013; Meiri, 2018). Therefore, a potentially important driver of body size variation across ectotherms may be the direct and/or indirect relationship between favourable environmental (climatic) conditions and lizards' foraging behaviour for available resources (van der Meer, 2019; Lu et al., 2018a; Lu et al., 2018b). Thus, environments at high altitudes with unfavourable climate conditions that may constrain lizards' foraging behaviour for the limited resources may impose underlying constraints on body size within populations of ectothermic species (Velasco et al., 2020; Giovanna et al., 2022).

As their wide distribution across climatic zones globally, lizards are excellent models for understanding how climatic conditions along geographic clines influence interspecific variation in body size (Velasco et al., 2020). China, has a rich diversity of over 212 species of lizards belonging to 10 families (Zhao et al., 1999; Zhou et al., 2019; Wang et al., 2020). However, how body size varies with geographic and climatic clines has only recently been explored for this region, especially when considering body size variation across populations (see, Guo, 2016; Liang et al., 2021). For example, female lizards inhabiting colder environments at higher gradients within China (from tropical to temperate regions) were found to possess small body sizes as adaptive plasticity for reproductive ecology (Lu et al., 2018a; Deme et al., 2022b), suggesting that the

body sizes of the female lizards may as well follow climatic clines for adaptation to environmental (climatic) conditions (Feldman and Meiri, 2014; Bruschi et al., 2022). Indeed, this is a large gap considering that the impact of climate conditions on lizard body size has been extensively studied in other regions of the world (e.g., Ashton and Feldman, 2003; Angilletta et al., 2004; Sears, 2005; Olalla-Tárraga et al., 2006; Olalla-Tárraga and Rodríguez, 2007; Olalla-Tárraga, 2011; Pincheira-Donoso and Meiri, 2013; Zamora-Camacho et al., 2014; Rivas et al., 2018; Slavenko et al., 2019; Tarr et al., 2019; Wishingrad and Thomson, 2020; Norris et al., 2021). To address this gap in our knowledge, we set out to evaluate the predictors of female body size within populations of the Lacertid lizard, the Mongolia racerunner (*Eremias argus*), a widespread species occupying a wide altitudinal range across China (30 m to 2975m asl, Figure 1).

Here, we focus only on the female *E. argus* lizards because maternal body size is highly important for maternal fitness, which may depend on seasonal, climatic, and geographic variation among populations (Deme et al., 2022b). *Eremias argus* lizard populations occupying high altitudes across China may experience unique local climatic conditions and unpredictable seasonal changes (Deme et al., 2022a), which may be different for other lizards globally, because of regional differences in climatic conditions (see, Sinervo et al., 2010; Meiri et al., 2013; Meiri, 2018). As studies have suggested that lizard populations across China that occupy unfavourable environments, which may reduce lizards' body size (Liang et al., 2021; Wang et al., 2021), we set out to ask (i) whether *E. argus* follow a reverse Bergmann's cline across altitudes to physiologically adapt to local environmental changes? (ii) if variation in resource availability, climate, and seasonality across altitudes will explain the patterns of lizards' body sizes. We predict that a) lizards in colder environments will have small body sizes as physiological adaptive plasticity to reduce physiological costs along altitudes (Meiri et al., 2020; Bruschi et al., 2022), with lizard species occupying high altitudes may have small body sizes, thereby reversing Bergmann's rule; b) high altitudes with rapid transitions between seasons may constraint the body sizes of lizards since short seasonal changes at high altitudes may imply less active time and fewer resources available for species (Ashton and Feldman, 2003; Sears, 2005; Meiri et al., 2007; Slavenko et al., 2021).

2.0 MATERIALS AND METHODS

2.1 Study system, sites and collection of lizards

The Mongolian racerunner (*E. argus*), a relatively small (up to 70mm snout-vent length [SVL]) oviparous lacertid lizard, is widely distributed across China and its environs (Zhao, 1999). The Mongolian racerunner has been reported across the north-northeast to the south (Jiangsu) and the west (Qinghai) of China (Zhao, 1999). Across the Chinese borders, the Mongolian racerunner has also been reported around the region of Lake Baikal in Russia, Mongolia, and Korea (Zhao et al., 2011) within grassland and farmland habitats and arid and semiarid regions (Zhao, 1999). Mongolian racerunners are widely distributed across altitude in China (Fig. 1), ranging from sea level to ca. 3000 m asl (Zhao et al., 1999). The Mongolian racerunner lizard populations across China are relatively homogeneous in their genetic structure (Zhao et al., 2011) but show significant variation in morphology, physiology, life histories, and feeding habits across geographic gradients (Wang et al., 2020).

We collected 432 female *E. argus* lizards between 2011 through 2021 from nine field locations across China, varying in altitude and environmental conditions (Fig. 1). During our field studies from May to July each year, we collected only non-gravid female *E. argus* lizards and transported them to field stations in the study areas. We measured the snout-vent length (SVL; ± 0.01 mm) of collected female lizards in the field station laboratory, after which we released them at the site from where they were captured. We collected and measured the body sizes of *E. argus* female lizards across populations with altitudinal gradients ranging from 30 – 2979m above sea level (asl), with 60 records from Shidu, 26 from Xingtai, 14 from Jingtai, 36 from Harbin, 31 from Hebei, 25 from Liaoyang, 44 from Chuzhou, 106 from Erdos, and 90 from Gonghe (Table S1).

2.2 Environmental factors

For the extraction of environmental variables (i.e., elevation, mean annual temperature, temperature seasonality, mean annual precipitation, precipitation seasonality, net primary productivity) for each population

of lizards, we used the *Raster* package in R (Hijmans and Etten, 2012). We elected to use the annual mean temperature and precipitation because these climate variables represent the mean yearly climate conditions that can influence some life-history traits of lizards across populations (Volynchik, 2014; Anderson et al., 2022). Thus, tested for a relationship between body size variation across populations of female lizards and these climatic variables (Volynchik, 2014; Deme et al., 2022a). Furthermore, temperature seasonality and precipitation seasonality were used because these variables represent the annual variation in climate conditions, with lower annual variability indicating more stable climates and greater active time for scouting for resources (Meiri et al., 2013; Meiri et al., 2020). To extract these environmental factors, we used the highest resolution within a 2.5 arc minute resolution grid (1 x 1 km) from the Worldclim2.1 database (<http://www.worldclim.org>; accessed on 30 August 2021). For the net primary productivity, we extracted data using the highest resolution within 2.5 arc minutes from the Earth’s land surface areas (<http://chelsa-climate.org/>; accessed on 2 January 2022). Finally, our extracted environmental (climate) variables were set at WGS 1984 and projected to UTM Zone 20N geographic spatial reference.

2.3 Data analysis

For this study, we performed all analyses in R 4.2.0 (R Development Core Team, 2022). We improved the residual normality and reduced the heteroscedasticity of our data by log-transforming (natural logarithm) female snout-vent length. To answer our central questions regarding the determinants of intraspecific variation in female body size across geographical gradients, we constructed linear mixed models using the *lmer* function implemented in the *lme4* package (Bates et al., 2015). For each model, we used the lizard population origin as a random intercept; because this allows us to account for the non-independence of lizards within populations (Bolker et al., 2009).

First, we asked whether the geographical patterns of body size at the intraspecific level of lizards vary with altitude; to achieve this, we constructed a simple linear model of ln-transformed body sizes of lizards as the response variable with altitude (binned into three categories) as the predictor variable. We then determined the significance using the *Anova* function from the *car* package (Fox and Weisberg, 2019). Further, we constructed a post hoc test for our model using the *emmeans* function from the *emmeans* package (Lenth, 2019) to specifically test for differences in body size between our three levels of altitude.

we then fit univariate linear models of each environmental factor (annual mean temperature, annual mean precipitation, temperature seasonality, and precipitation seasonality) as the response variable with the altitude as the predictor variable in each case to understand the relationship between climatic conditions and altitude in our study.

Next, we asked whether female body size varied with resource availability and/or in response to the changing climatic and seasonal conditions across altitudes. However, we could not achieve a single model for all our predictor variables due to the significant collinearity between net primary productivity and annual mean temperature ($r = 0.70$; $p < 0.0001$) and net primary productivity and annual mean precipitation ($r = 0.96$; $p < 0.0001$), which resulted in all linear mixed models failing to converge. Thus, we fit two alternative models to explore climate-body size relationships: (1) with net primary productivity, temperature seasonality, and precipitation seasonality; and (2) with annual mean temperature, annual mean precipitation, temperature seasonality, precipitation seasonality and altitude as our predictor variables. In all our fitted models, we included altitudes as a covariate because climatic and seasonal changes that influence the life-history traits of species significantly vary across geographic gradients such as altitudes (Hille and Cooper, 2015; Laiolo and Obeso, 2015).

We binned elevation in our models because of the discontinuous elevational distribution of the lizards (Fig. 1). Due to the discontinuous nature of the elevational data, modeling it as continuous led to model failure. Therefore, we follow the approach of Bhat et al. (2020) to categorize the lizard populations in our data into three altitudinal levels (low altitudes: <1,000m; mid altitudes: 1,000–2,000 m; high altitudes: >2,000 m asl).

3. 0 RESULTS

3.1 Lizard body sizes relationships with altitude

We found that the environmental conditions significantly vary across altitude, with high altitudes characterized by limited resources, colder and drier climatic conditions, and less seasonal change compared to low altitudes with more resources, warmer and wetter climatic conditions, and high seasonality (Table 1; Table S1). We found strong evidence that altitude explained variation in body size across populations ($\eta^2 = 20.756$, $p < 0.0001$; Fig. 2). Post hoc comparisons showed that female lizards occupying low altitudes (<1,000m) had larger body sizes than female lizards occupying mid (1,000–2,000m) or high (>2000m) altitudes (Table 2).

3.2 Lizard body size relationship with resource availability and seasonality across altitudes

We found that the geographical pattern in the body size of female lizards is significantly related to changes in net primary productivity across altitude (Table 3). Specifically, we found that less seasonal precipitation and limited available resources that characterized environments at higher altitudes were associated with reduced body size (Fig. 3a; Table 3). Although seasonal temperature changes were apparent along altitudes (Fig. 3b), there was no significant relationship between seasonal temperatures and body size ($\eta^2 = 0.068$, $p = 0.955$).

3.3 Lizard body size relationship with environmental conditions across altitude

We found that warmer conditions explained the increased body size of female lizards at low altitudes (Fig. 4a; Table 3). Further, we found that drier conditions due to decreased annual precipitation and with less seasonal variation in precipitation were significantly associated with decreased female body size of lizards at high altitudes (Fig. 4b & 4c; Table 3). Although there was a trend, body size did not significantly differ with changes in seasonal temperature along altitudinal clines ($\eta^2 = 3.719$, $p = 0.053$); although seasonal temperatures experienced by lizards' populations at different altitudes were apparent (Fig. 4d).

Discussion

Association of key life history traits, such as body size, with environmental factors shape the adaptation of species to local environments (e.g., Blackburn et al., 1999; Freckleton et al., 2003; Morrison and Hero, 2003; Pincheira-Donoso and Tregenza, 2011; Meiri et al., 2013; Volynchik, 2014; Hille and Cooper, 2015; Laiolo and Obeso 2015; Lack et al., 2016; Meiri et al., 2020; Velasco et al., 2020; Wang et al., 2021; Deme et al., 2022a; Giovanna et al., 2022; Szymkowiak and Schmidt, 2022). Indeed, we found that geographical patterns of female body size were influenced by the coupling effects of the seasonal and annual changes in the climatic conditions along altitudinal gradients, suggesting a possible adaptation of *E. argus* lizards to the changing environmental conditions. The climate-body size relationship across populations of *E. argus* lizards in our study showed a reversal of Bergmann's rule: female lizards occupying warmer environments at low altitudes had bigger body sizes. Further, we found that populations at low latitudes with an abundance of available resources and highly seasonal environments, such as increased precipitation, had significantly larger body sizes. Thus, our study suggests that the intraspecific variation in the geographical patterns of body size along altitudinal clines was primarily driven by multifarious local environmental conditions such as climatic conditions, highly seasonal environments and available resources.

Geographic patterns of body size are thought to be primarily influenced by climatic gradients, as summarized by Bergmann's rule (Bergmann, 1847; Ashton and Feldman, 2003; Sears, 2005). Based on Bergmann's rule, there is a general understanding that the body sizes of endotherms increase toward high latitudes or altitudes (see Ashton and Feldman, 2003; Meiri and Dayan, 2003; Pincheira-Donoso et al., 2008; Pincheira-Donoso and Meiri, 2013; Moreno Azocar et al., 2015). In a reversal to Bergmann's rule, we found evidence that female lizards at lower altitudes in warmer environments had larger body sizes. Our finding concurs with other previous studies showing ectotherms may sometimes reverse Bergmann's rule (Ashton and Feldman, 2003; Sears, 2005). In contrast studies have shown some ectotherms follow Bergmann's rule, possessing large body sizes at high latitudes (e.g., Angilletta et al., 2004). The original explanation for Bergman's rule did not account for the peculiarity of ectotherms (Watt et al., 2010) in their inability to generate significant

internal body heat, and consequently that a larger bodied ectotherm would therefore heat up more slowly (Stevenson, 1985) and would lack the ability to conserve heat in colder environments (Liang et al., 2021). Further, possessing larger bodies in colder environments may be deleterious to some ectotherm species (Jadin et al., 2019; Velasco et al., 2020; Slavenko et al., 2021); since ectotherms with large body sizes that slowly heat up in colder environments show constrained thermoregulatory behavior (Pincheira-Donoso et al., 2008; Anderson et al., 2022; Szymkowiak and Schmidt, 2022).

Expressly, our results found evidence for the influence of both resource availability and seasonality (i.e., precipitation seasonality) on female body size, with smaller body sizes associated with decreased seasonality and lower primary productivity. Previous studies have suggested that highly seasonal changes in rainfall significantly influence the abundance of available resources for female lizards (Valenzuela-Sanchez et al., 2015; Meiri et al., 2020; Slavenko et al., 2021), which is positively related to large body sizes (Liang et al., 2021). Perhaps this is not surprising since unpredictable seasonal changes at high altitudes may suggest scarce resources for lizards (Deme et al., 2022a; Anderson et al., 2022). Previous studies have shown that abundant available resources for lizards to feed mostly impact the growth rate along geographic clines, which may be a function of body size variations in lizards (e.g., Lu et al., 2018a, 2018b), suggesting that non-climatic factors such as available resources can also influence the variation in the body sizes of lizards. For instance, available resources as a function of habitat productivity in novel environments influenced body size variations in other ectotherm species like insects, fishes and amphibians (Morrison and Hero, 2003; Laiolo and Obeso, 2015; Riesch et al., 2018; Giovanna et al., 2022). Perhaps, the variations in non-climatic factors across environments also play significant roles in determining shifts in phenotypic traits, such as variation in the body size of species. However, our understanding of how the variations of these climatic and non-climatic factors along geographic clines can directly or indirectly impact ectotherms' body sizes in the context of rapidly changing climates may still be limited.

Thus, clinal variation in body sizes across populations within ectothermic species may be a result of adaptive plasticity to changing environmental conditions (Riesch et al., 2018; Giovanna et al., 2022). Organismal body size, as a function of growth and development rates, is influenced by the interplay of intrinsic and extrinsic factors (Duellman and Trueb 1986). For example, extrinsic and intrinsic factors such as temperature, habitat type, food availability, egg size, yolk reserves, and competition have all been shown to influence the body sizes of ectotherms across environments (Fischer et al., 2003; Laiolo and Obeso, 2015; Riesch et al., 2018), which ultimately can affect the reproductive ecology of ectotherms (Fielding et al., 1999; Morrison and Hero, 2003; Deme et al., 2022a). While the patterns of female body size across altitudes and environments found in our study may be a results of non-adaptive plasticity, or even fixed genetic differences between populations, we suggest that this pattern may be a result of adaptive phenotypic plasticity (Ghalambor et al., 2007; Szymkowiak and Schmidt, 2022). However, further experiments, such as common garden studies, would be needed to test this hypothesis. Understanding the underlying cause of the altitudinal body size differences is important in order to predict how these populations will response to future changes in climate (Merila and Hendry, 2014). The pace of climate change is expected to be more rapid at high altitudes (Pepin *et al.*, 2015). Phenotypic plasticity in body size may allow lizard populations to quickly respond to changes in climatic conditions across populations, but may consequently shield body size from selection, slowing the pace of evolutionary change (Diamond and Martin 2021). In contrast if body size differences between populations is largely due to genetic divergence, these population may evolve on response to changing climates, but it is unclear whether the rate of evolution could keep pace with the rate of climatic change (Diamond and Martin 2020).

Conclusion

In sum, we showed that the body sizes of female lizards were smaller at high altitudes due to colder and drier climatic conditions, which is a reversal of Bergmann's rule. Further, we showed that the geographical patterns of body sizes within populations of lizards are largely influenced by the variation of climatic and seasonality along altitudinal clines. As expected, resource availability in highly seasonal environments such as rainfall along altitudinal clines significantly influenced the body's variations within populations of female

lizards, suggesting that the variations in the geographic patterns of female lizards' body sizes may be largely driven by multifarious environments as adaptive plasticity for organisms to possibly buffer physiological costs along geographic clines.

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Figure legends

Table 1; Summary results of univariate linear models showing the relationships between available resources (net primary productivity), annual mean precipitation, annual mean temperature, temperature seasonality or precipitation seasonality with altitudes.

Table 2; Results for pairwise contrasts of the linear model with log-transformed lizard body size ($n = 432$) and altitudinal gradients (low altitudes: $<1,000\text{m}$; mid altitudes: $1,000\text{--}2,000\text{ m}$; high altitudes: $>2,000\text{ m asl}$). Reported degrees of freedom is for t statistics.

Table 3; Statistical parameters from linear mixed-effects models of body size patterns with seasonally available resources across different altitudes accounting for lizards' population origins. Results presented are for the model with resource availability (net primary productivity), seasonality (temperature seasonality and precipitation seasonality), altitudes and the interaction between resource availability with altitudes as predictors.

Table 4; Statistical parameters from linear mixed-effects models of body size patterns with environmental conditions across different altitudes accounting for lizards' population origins. Results presented are for the model with climatic conditions (annual mean temperature and annual mean precipitation), seasonality (temperature seasonality and precipitation seasonality), altitudes and the interaction between resource availability with altitudes as predictors

Figure 1; Map showing altitudinal gradients and collection sites of female *Eremias argus* lizards from different altitudes across China. Color gradients represent China's altitudinal gradients in square meters, with colored points depicting the geographical locations across China occupied by female lizards in our study

Figure 2; Relationship between log-transformed body size of lizards with altitudinal clines across populations of lizards. Predicted values ± 1 SE of estimates from the linear regression model ($n = 432$) that account for population origins of lizards are shown by the connected dots.

Figure 3; The relationship between log-transformed lizard body size with (a) net primary productivity and seasonal precipitation along altitudinal clines; (b) net primary productivity and changes in seasonal temperature along altitudinal clines. Color gradient of points represents the changes in the pattern of log-transformed body size of lizards with seasonally available resources at different altitudes. Color gradient trendlines represent predicted values ± 1 SE of estimates from the linear regression model ($n = 432$) that accounts for the population origins of lizards. Separate coloured trendlines illustrate significant ($P < 0.05$) relationships between lizard body size seasonal available resources while single trendlines illustrate non-significant relationships between lizard body size seasonal available resources along altitudinal clines.

Figure 4; Relationship between lizard body sizes with a) annual mean temperature, b) annual mean precipitation, c) precipitation seasonality and d) temperature seasonality at different altitudes. Color gradient of points represents the changes in the pattern of log-transformed body size of lizards with climatic conditions at different altitudes. Color gradient trendlines represent predicted values ± 1 SE of estimates from the linear regression model ($n = 432$) that accounts for the population origins of lizards. Separate colored trendlines illustrate significant ($P < 0.05$)relationships between lizard body size with climatic conditions along altitudinal clines.

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