

## RESEARCH ARTICLE

# Female lizards (*Eremias argus*) reverse Bergmann's rule across altitude

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## Abstract

The evolution of body size within and among species is 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 covary with ectotherm body sizes across populations with varying local environmental conditions. Here, we used female *Eremias argus* lizards collected from different populations across their wide range in China, and constructed linear mixed models to assess how climatic conditions and/or available resources at different altitudes shape the geographical patterns of lizard body size across altitude. Lizard populations showed significant differences in body size across altitudes. Furthermore, we found that climatic and seasonal changes along the altitudinal gradient also explained variations in body size among populations. Specifically, body size decreased with colder and drier environmental conditions at high altitudes, reversing Bergmann's rule. Limited resources at high altitudes, measured by the low vegetative index, may also constrain body size. Therefore, our study demonstrates that multifarious environmental factors could strongly influence the intraspecific variation in organisms' body size.

## KEYWORDS

climate, geographical gradients, multifarious environments, resource availability, squamates

## TAXONOMY CLASSIFICATION

Evolutionary ecology, Functional ecology

## 1 | INTRODUCTION

Body size is a fundamental and important trait of organisms, and variation in body size within and among species is often tightly linked to life-history traits, such as fecundity, growth, and survival (Deme, Hao, et al., 2022; Deme, Wu, et al., 2022; Lu, Xu,

Jin, et al., 2018; Meiri, 2018; Meiri et al., 2020; Pincheira-Donoso et al., 2008; Roff, 2002; 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

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Blackburn et al., 1999; Freckleton et al., 2003). However, ectotherms often do not (Forsman & Shine, 1995; Norris et al., 2021; Sears & Angilletta, 2004); with some ectotherm species showing no observable clines in body size (Henry et al., 2023), and others reversing Bergmann's rule (Forsman & Shine, 1995; Lu, Xu, Jin, et al., 2018; Meiri et al., 2013; Norris et al., 2021; Olalla-Tárraga & Rodríguez, 2007; Sears & Angilletta, 2004). 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 heat up more slowly as well (Stevenson, 1985). Instead, the proximate underlying factors influencing clines in body size among ectotherms could be complex and diverse (Angilletta, Steury, & Sears, 2004; Pincheira-Donoso et al., 2019; Pincheira-Donoso & Meiri, 2013; Sears & Angilletta, 2004). Thus, unravelling 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, Xu, Jin, et al., 2018; Meiri, 2018; Norris et al., 2021) due to variation in temperature and precipitation across altitude (Anderson et al., 2022; Liang et al., 2021). For instance, studies have found that ectotherms, such as lizards can reverse Bergmann's rule by having bigger body sizes at low elevations (Muñoz et al., 2014). Lower elevations may provide longer growing seasons allowing for increased active time for ectotherms to acquire resources (Anderson et al., 2022; Catalan et al., 2017; Horvátová et al., 2013). Therefore, a potentially important driver of body size variation across ectotherms might be the direct and/or indirect relationship between favorable environmental (climatic) conditions and lizards' foraging behaviour for available resources (Lu, Xu, Jin, et al., 2018; Lu, Xu, Zeng, & Du, 2018). Thus, environments at high altitudes with unfavorable climate conditions which could constrain lizards' foraging behavior for the limited resources might impose underlying constraints on body size within populations of ectothermic species (Velasco et al., 2020).

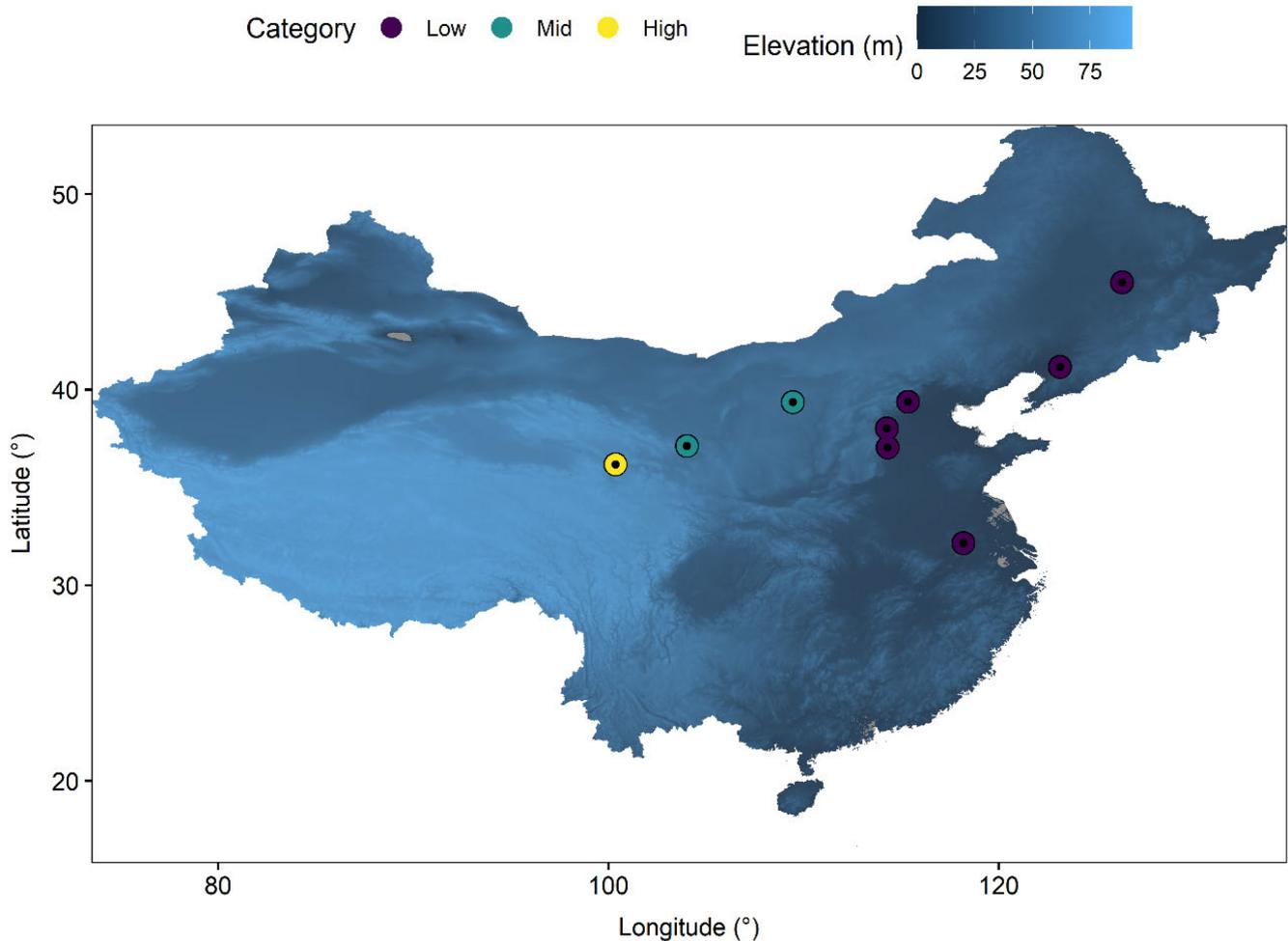
Lizards are excellent models for understanding how climatic conditions along geographic clines influence interspecific variation in body size because of their wide distribution across climatic zones globally (Brusch IV et al., 2023; Feldman & Meiri, 2014; Velasco et al., 2020). China has a rich diversity of over 212 species of lizards belonging to 10 families (Wang et al., 2020; Zhao et al., 1999; Zhou et al., 2019). However, how body size varies with geographic and climatic clines has only recently been explored for this region when considering body size variation across populations (see, Guo, 2016; Liang et al., 2021). For example, female lizards inhabiting colder environments at higher altitudes within China (from tropical to temperate regions) were found to possess small body sizes as a possible response to extreme environmental conditions (Deme, Wu, et al., 2022; Lu, Xu, Jin, et al., 2018), suggesting that the body sizes of lizards in China may as well follow climatic clines for adaptation to environmental (climatic) conditions (Liang et al., 2021). 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., Angilletta, Niewiarowski, et al., 2004; Angilletta, Steury, & Sears, 2004; Ashton & Feldman, 2003; Bruschi IV et al., 2023; Norris et al., 2021; Olalla-Tárraga, 2011; Olalla-Tárraga et al., 2006; Olalla-Tárraga & Rodríguez, 2007; Pincheira-Donoso & Meiri, 2013; Rivas et al., 2018; Sears, 2005; Tarr et al., 2019; Wishingrad & Thomson, 2020; Zamora-Camacho et al., 2014). 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 (30–2975 m above sea level [asl], Figure 1).

Here, we focus only on the female *E. argus* lizards because maternal body size is highly important for maternal fitness, and maternal body of lizards may depend on seasonal, climatic, and geographic variation among populations (Meiri, 2018; Meiri et al., 2013, 2020). For example, the maternal body size of female organisms can directly influence fecundity and maternal investment (Deme, Hao, et al., 2022; Lack et al., 2016). Thus, our study focused on female lizards because we wanted to understand the potential physiological responses of female lizards' body size to spatial and temporal climatic and ecological factors. Female *Eremias argus* lizards occupying high altitudes across China may experience unique local climatic conditions and unpredictable seasonal changes, which may be different for other lizards globally, because of regional differences in climatic conditions in China (see Liang et al., 2021; Wang et al., 2021).

In this study, we set out to ask whether female *E. argus* follow a reverse Bergmann's cline across altitudes due to physiological constraints imposed by local climate. Specifically, we hypothesize that lizards at higher altitudes will have smaller body sizes due to the combined effects of colder conditions affecting growth rates, reductions in foraging and basking time due to shorter unpredictable seasons, and reduced resource availability compared to lizard populations occupying lower altitudes (Angilletta, Steury, & Sears, 2004; Caruso et al., 2014; Muñoz et al., 2017; Sears & Angilletta, 2004). To test this hypothesis, we asked if variation in vegetation index, as a measure of resource availability across altitudes, is negatively associated with lizard body size across altitude, and whether variation in the seasonal environments across altitudes influence the ecological patterns of lizard body size, with shorter unpredictable seasons for growth associated with high altitudes and smaller body sizes. It is important to note that these patterns could be the result of evolutionary change across populations (e.g., in life-history traits such as growth rate and time to maturity) in addition to physiological plasticity (Angilletta, Niewiarowski, et al., 2004; Angilletta, Steury, & Sears, 2004). However, distinguishing between these mechanisms is beyond the scope of this study.

Although population genetic structure and evolutionary history could also affect patterns of body size among populations (i.e., more recently diverged populations could be more similar, regardless of the environment), we only focus our study on understanding if geographical patterns in body size of female lizards occur in response to spatial and temporal climatic variation from the lens of consumer-resource dynamics (Osmond et al., 2017). In



**FIGURE 1** Map showing altitudinal gradients and collection sites of female *Eremias argus* lizards from different altitudes across China. Colored points depict geographical locations where female lizards were sampled, and color gradients of the map represent the square root ( $\sqrt{m}$ ) value of the elevation topology across China.

support of this decision, *E. argus* lizard species appear to have a relatively homogeneous genetic structure (Zhao et al., 2011) while still showing significant variation in morphology, physiology, life histories, and feeding habits across geographic gradients in China (Wang et al., 2020).

## 2 | MATERIALS AND METHODS

### 2.1 | Study system, sites, and collection of lizards

The Mongolian racerunner (*E. argus*), a relatively small (up to 70 mm snout-vent length [SVL]) oviparous lacertid lizard, is widely distributed across China and its environs (Zhao et al., 1999;). The Mongolian racerunner has been reported across the north-northeast to the south (Jiangsu) and the west (Qinghai) of China (Zhao et al., 1999;). Across the Chinese borders, the Mongolian racerunner has also been reported around Lake Baikal in Russia, Mongolia, and Korea (Zhao et al., 2011) within grassland and

farmland habitats and arid and semiarid regions (Zhao et al., 1999;). Mongolian racerunners are widely distributed across altitudes in China (Figure 1), ranging from sea level to ca. 3000 m asl (Zhao et al., 1999).

We collected 432 female *E. argus* lizards between 2011 through 2021 from field locations across China (Figure 1), varying in altitude and environmental conditions. During our field studies from May to July each year, we collected only nongravid female *E. argus* lizards and transported them to field stations in the study areas. To avoid pseudoreplication over our sampling period, we collected from different field sites each time we visited a location. We measured the snout-vent length (SVL;  $\pm 0.01$  mm) of collected female lizards in the field station laboratory, after which we released them at the site where they were captured. We collected and measured the body sizes of *E. argus* female lizards across populations with altitudinal gradients ranging from 30 to 2979 m 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 (Deme et al., 2023).

## 2.2 | Environmental factors

We used the *Raster* package in R to extract environmental variables for each population of lizards (Hijmans & Etten, 2012). In extracting variables (elevation, mean annual temperature, temperature seasonality, mean annual precipitation, and precipitation seasonality), we used the highest resolution within a 2.5 arc min resolution grid (1 × 1 km) from the Worldclim2.1 database (<http://www.worldclim.org>; accessed on August 30, 2021). We obtained the calculated total plant biomass minus the carbon lost to respiration measured in  $\text{gCm}^{-2}\text{year}^{-1}$  from Earth's land surface areas (<https://chelsea-climate.org/bioclim/>; accessed on January 2, 2022) as a measure for net primary productivity (NPP). Our extracted environmental (climate) variables were set at WGS 1984 and projected to UTM Zone 20N geographic spatial reference. We chose to use these climate variables to test for the ecological conditions-induced changes across different populations (Anderson et al., 2022; Meiri et al., 2020; Volynchik, 2014) because these spatial and temporal climate variabilities mostly influence lizards' most active time to scout for resources (Meiri et al., 2013, 2020). Relying on the resource rule, we used plant biomass calculated as net primary productivity (NPP) as the proxy to measure resource availability for species (Huston & Wolverton, 2011; Meiri et al., 2007).

## 2.3 | Data analysis

For this study, we performed all analyses in R 4.2.0 (R Development Core Team, 2021). 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 nonindependence of lizards within populations (Bolker et al., 2009).

First, we fit univariate linear models with each climatic variable (annual mean temperature, annual mean precipitation, temperature seasonality, and precipitation seasonality) as the response variable with altitude as the predictor variable in each case to understand the relationship between climatic conditions and altitude. Next, we analyzed whether the geographical patterns of body size of lizards vary with altitude by constructing a linear model of ln-transformed body size as the response variable with altitude as the predictor variable. We then determined significance with *F* tests using the ANOVA function from the *car* package (Fox & 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 next investigated whether female body size varied with resource availability and/or in response to the changing climatic and seasonal conditions across altitude. Although we found minimal multicollinearity among climatic conditions (with a maximum variance inflation factor of 5.89 for annual mean rainfall), we could not fit a single model for all our predictor variables as the model failed to converge. This could be due to the unequal representation of environmental predictor variables arising from the discontinuous values of the altitude locations in our dataset (Dormann et al., 2013). 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 altitude 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 & Cooper, 2015; Laiolo & Obeso, 2015). Thus, we used the altitude categories: Low (<1000m), mid (1000–2000), and high (>2000) based on ecosystem variations documented in (Zhao et al., 1999). Furthermore, due to the discontinuous nature of the elevational data, modeling it as continuous led to model failure.

## 3 | 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; Figure 2). Also, we found strong evidence that altitudinal variation explained the geographic patterns in the body size of female lizards among populations ( $\chi^2=20.756$ ,  $p<.0001$ ; Figure 3), with our post hoc analysis showing that lizards occupying low altitudes (<1000m) had larger body sizes than those occupying mid (1000–2000m) or high (>2000m) altitudes (Table 2, Figure 3).

### 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 (Figure 4a). Although seasonal temperature changes were apparent across altitudes (Figure 4b), there was no significant relationship between seasonal temperatures and body size ( $\chi^2=0.068$ ,  $p=.955$ ).

TABLE 1 Summary of the body size characteristics, geographical localities, and environmental characteristics of *Eremias argus* in our data across China.

Population	Sample size	Year of sampling	Latitude	Longitude	Net primary productivity	Body size (mm)	Mean annual temperature	Mean annual precipitation	Precipitation seasonality	Temperature seasonality
Chuzhou	44	2012	32.15° N	118.19° E	1512	56.40	15.70	1022	056	091.2
Liaoyang	25	2018	41.20° N	123.00° E	1197	54.3	08.20	747	098	121
Hebei	31	2019	31.02° N	114.28° E	940	59.20	12.20	523	110	103
Shidu	60	2011	39.38° N	115.35° E	793	55.00	12.00	539	135	111
Harbin	36	2012	45.48° N	126.32° E	897	59.10	03.60	558	106	147
Xingtai	26	2014	37.04° N	114.30° E	932	58.90	13.10	564	106	102
Erdos	106	2021	39.36° N	109.46° E	574	53.90	06.70	371	109	112
Jingtai	14	2014	37.11° N	104.03° E	359	60.8	08.20	222	095	102
Gonghe	90	2014	36.17° N	100.37° E	539	54.20	02.50	311	098	088.90

Note: Data values presented in the table are of raw data measured and expressed as means  $\pm$  1 SE.

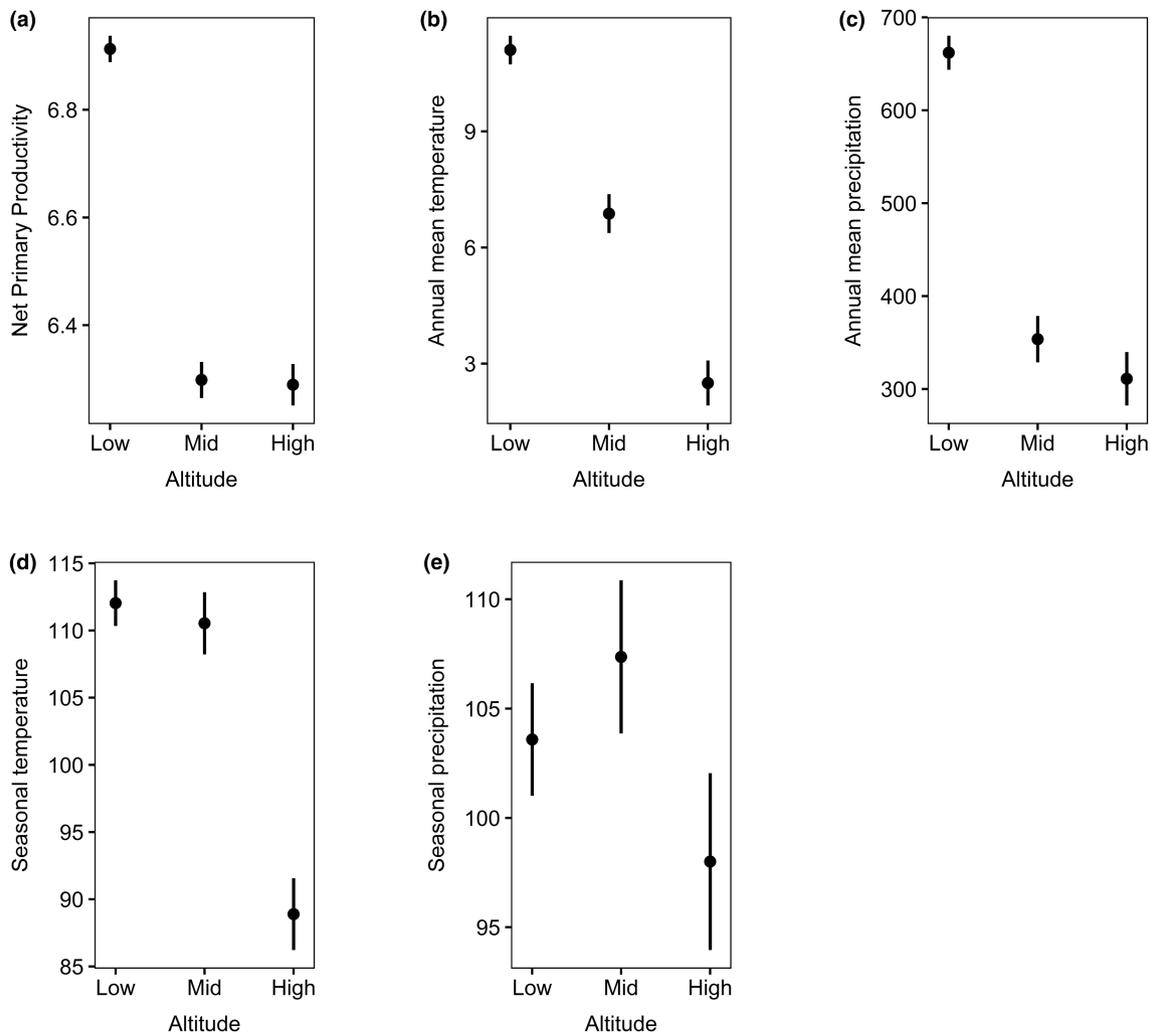
### 3.3 | Lizard body size relationship with environmental conditions across altitude

We found that warmer conditions explained the increased body size of female lizards at low altitudes (Figure 5a). 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 (Figure 5b,c). Although there was a trend, body size did not significantly differ with changes in seasonal temperature across altitudes ( $\chi^2 = 3.719$ ,  $p = .053$ ; Table 3); although seasonal temperatures experienced by lizards' populations at different altitudes were apparent (Figure 5d).

## 4 | DISCUSSION

Association of key life-history traits, such as body size, with environmental factors shape the response of species to local environments (e.g., Hille & Cooper, 2015; Laiolo & Obeso, 2015; Pincheira-Donoso & Tregenza, 2011; Velasco et al., 2020; Volynchik, 2014). 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 physiological response of *E. argus* lizards to the changing environmental conditions. We found that the climate-body size relationship across populations of *E. argus* lizards 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.

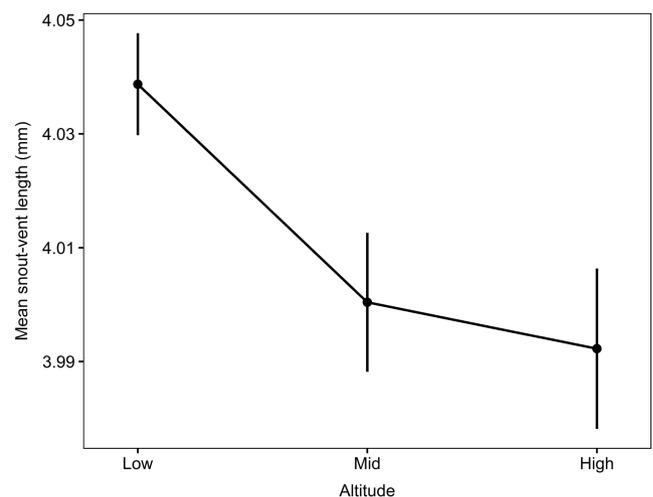
Geographic patterns of body size are thought to be primarily influenced by climatic gradients (Ashton & Feldman, 2003; Bergmann, 1847; Sears, 2005). Based on Bergmann's rule, there is a general understanding that the body sizes of endotherms increase toward high latitudes or altitudes (see Ashton & Feldman, 2003; Freckleton et al., 2003; Meiri & Dayan, 2003; Moreno Azocar et al., 2015; Pincheira-Donoso et al., 2008; Pincheira-Donoso & Meiri, 2013). 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 previous studies showing ectotherms may sometimes reverse Bergmann's rule (Ashton & 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, Niewiarowski, et al., 2004; Angilletta, Steury, & Sears, 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



**FIGURE 2** Relationship between altitudes with (a) net primary productivity, (b) mean annual temperature ( $^{\circ}\text{C}$ ), (c) mean annual precipitation (mm), (d) temperature seasonality ( $^{\circ}\text{C}$ ), or (e) precipitation seasonality (%). Predicted values  $\pm 1$  SE of estimates from the linear regression are represented by dots with error bars showing the standard error of the means.

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; Slavenko et al., 2021; Velasco et al., 2020), since ectotherms with large body sizes that slowly heat up in colder environments show constrained thermoregulatory behavior (Anderson et al., 2022; Pincheira-Donoso et al., 2008; Szymkowiak & Schmidt, 2022).

Expressly, we 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 (Meiri et al., 2020; Slavenko et al., 2021; Valenzuela-Sánchez et al., 2015), 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 (Anderson et al., 2022). Previous studies have shown that abundant available



**FIGURE 3** Relationship between log-transformed body size of lizards with altitudinal clines across populations of lizards. Predicted values  $\pm 1$  SE of estimates from the linear regression model ( $n = 432$ ) that account for population origins of lizards are shown by the connected dots.

**TABLE 2** Results for pairwise contrasts of the linear model with log-transformed lizard body size ( $n=432$ ) and altitudinal gradients (Low altitudes: <1000m; mid altitudes: 1000–2000m; high altitudes: >2000m asl).

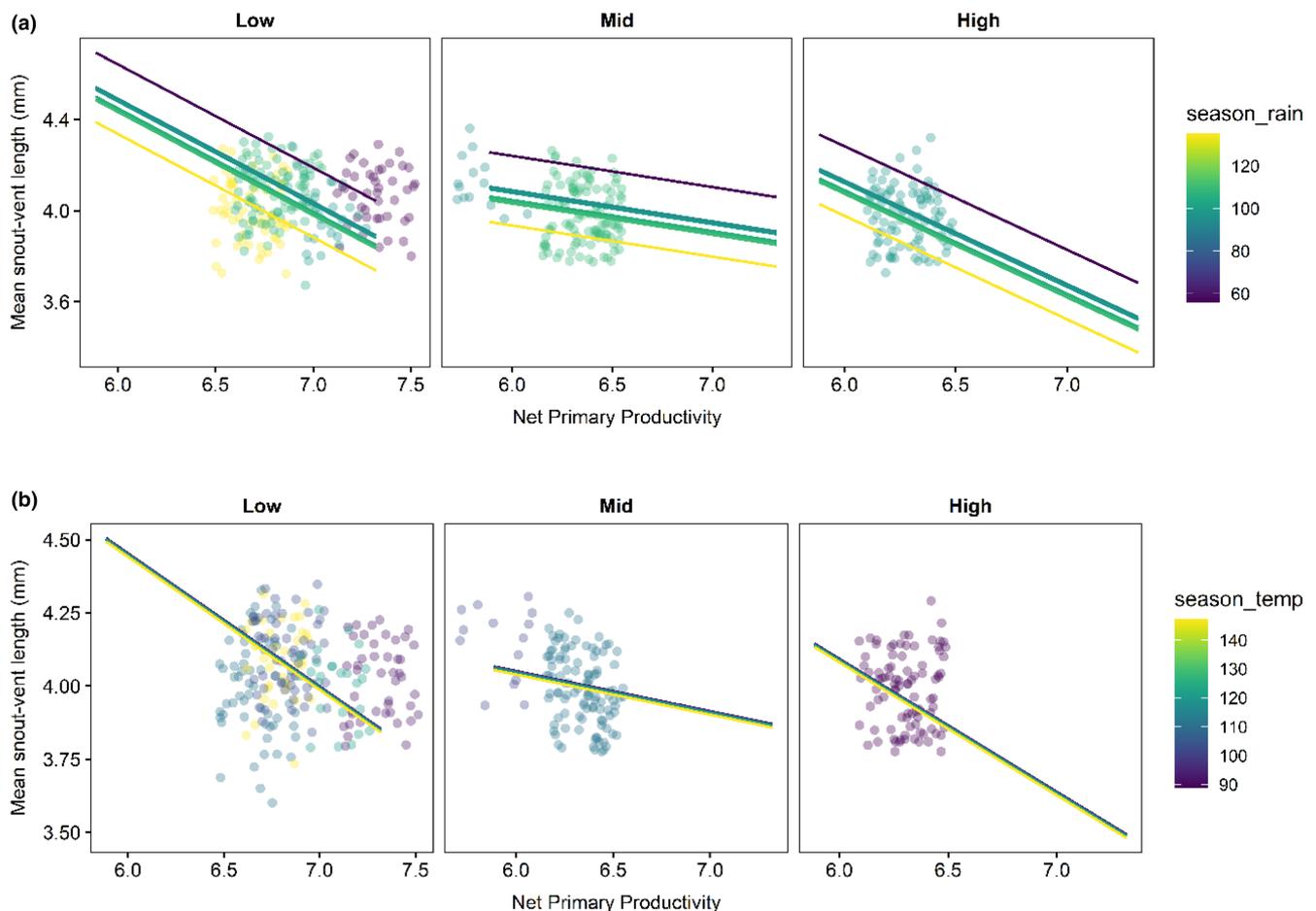
Contrast	Estimates	SE	df	Test statistic	<i>p</i>
Low – Mid	0.038	0.007	429	4.972	<b>&lt;.0001</b>
Low – High	0.046	0.008	429	5.467	<b>&lt;.0001</b>
Mid – High	0.00815	0.00949	429	0.0859	.666

Note: Reported degrees of freedom are for *t* statistics and significant *p*-values are indicated in bold.

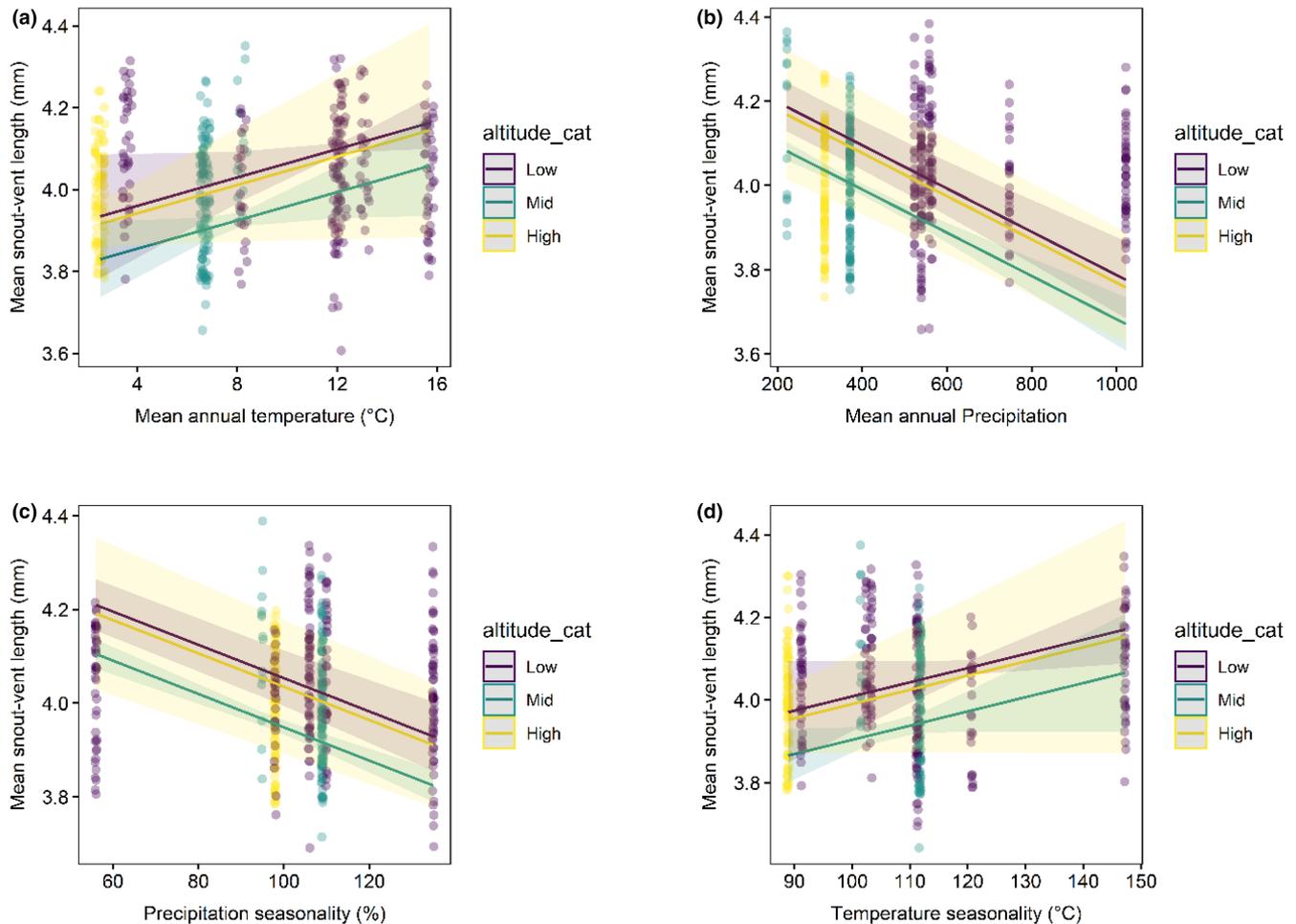
**TABLE 3** Statistical parameters from linear mixed-effects models of body size patterns with (a) seasonally available resources and (b) climatic conditions experienced by different lizard populations across altitudes in China.

Factor	Estimate	SE	df	Test statistic	<i>p</i>
Intercept	5.903	0.589	1	100.197	<b>&lt;.0001</b>
Net primary productivity	-0.239	0.075	1	9.933	<b>.001</b>
Temperature seasonality	0.00004	0.0008	1	0.003	.955
Precipitation seasonality	-0.002	0.0008	1	6.087	<b>.013</b>
Altitude	-0.210	0.064	2	11.011	<b>.004</b>
Intercept	4.170	2.566	1	264.143	<b>&lt;.0001</b>
Annual mean temperature	0.017	0.008	1	4.452	<b>.034</b>
Annual mean precipitation	-0.0005	0.00005	1	100.087	<b>&lt;.0001</b>
Temperature seasonality	0.003	0.001	1	3.719	.053
Precipitation seasonality	-0.003	0.0003	1	88.166	<b>&lt;.0001</b>
Altitude	-0.104	0.033	2	104.320	<b>&lt;.0001</b>

Note: Data presented in the table with significant *p*-values are indicated in bold.



**FIGURE 4** 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  $\pm 1$  SE of estimates from the linear regression model ( $n=432$ ) that accounts for the population origins of lizards. Separate colored trendlines illustrate significant ( $p < .05$ ) relationships between lizard body size seasonal available resources, while single trendlines illustrate nonsignificant relationships between lizard body size seasonal available resources along altitudinal clines.



**FIGURE 5** 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  $\pm 1$  SE of estimates from the linear regression model ( $n=432$ ) that accounts for the population origins of lizards. Separate colored trendlines illustrate significant ( $p < .05$ ) relationships between lizard body size with climatic conditions along altitudinal clines.

resources for lizards to feed mostly impact growth rate along geographic clines, which may result in body size variation in lizards (e.g., Lu, Xu, Jin, et al., 2018; Lu, Xu, Zeng, & Du, 2018), suggesting that non-climatic factors such as available resources can also influence the variation in the body size. For instance, resource availability, as a function of habitat productivity in novel environments, influenced body size variation in other ectotherm species (Laiolo & Obeso, 2015; Morrison & Hero, 2003; Riesch et al., 2018). Perhaps, variation in non-climatic factors across environments also plays a significant role 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 might still be limited.

Clinal variation in body sizes across populations within ectothermic species could result from phenotypic plasticity to changing environmental conditions at a local scale (Riesch et al., 2018).

Organismal body size across most species, as a function of growth and development rates, is influenced by the interplay of intrinsic and extrinsic factors (Duellman & Trueb, 1986). For example, extrinsic and intrinsic factors have been shown to influence the body sizes of ectotherms across environments (Fischer et al., 2003; Horváthová et al., 2013; Laiolo & Obeso, 2015), which ultimately can affect the reproductive ecology of ectotherms (Deme, Hao, et al., 2022; Fielding et al., 1999; Morrison & Hero, 2003; Wu et al., 2022). While the patterns of female body size across altitudes and environments found in our study may be a result of nonadaptive plasticity, or even fixed genetic differences between populations, we suggest that this pattern could be a result of phenotypic plasticity to the rapid environmental changes experienced by organisms (Brusch IV et al., 2023; Freckleton et al., 2003; Ghalambor et al., 2007; Henry et al., 2023; Szymkowiak & Schmidt, 2022), which may influence their reproductive success. 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 respond to future changes in climate (Merilä & 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 & Martin, 2021). In contrast, if body size differences between populations are largely due to evolutionary divergence, these populations may evolve in response to changing climates, but it is unclear whether the rate of evolution could keep pace with the rate of climatic change (Diamond & Martin, 2020).

## 5 | CONCLUSION

In summary, we showed that the body sizes of female lizards are smaller at high altitudes, possibly due to colder and drier climatic conditions, demonstrating a reversal of Bergmann's rule. Further, we showed that the geographical patterns of body sizes between populations of lizards are also potentially influenced by the variation of climatic and seasonality across altitudes. As we predicted, resource availability in highly seasonal environments, such as rainfall along altitudinal clines, was significantly related to the body size variation between populations, suggesting that geographic patterns of female lizards' body sizes, as a phenotypic plastic trait, will help female ectotherms to buffer the costly reproductive-energy output relationship with female body size in response to local extreme environmental conditions as altitude increases.

### AUTHOR CONTRIBUTIONS

**Gideon Gywa Deme:** Conceptualization (lead); data curation (lead); formal analysis (equal); investigation (equal); methodology (equal); software (lead); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Xixi Liang:** Data curation (supporting); investigation (equal); validation (equal); visualization (equal); writing – review and editing (equal). **Joseph Onyekwere Okoro:** Formal analysis (equal); investigation (equal); methodology (equal); software (equal); validation (equal); visualization (equal); writing – review and editing (equal). **Prakash Bhattarai:** Data curation (equal); investigation (equal); methodology (equal); software (equal); validation (equal); writing – review and editing (equal). **Baojun Sun:** Data curation (equal); funding acquisition (equal); investigation (equal); project administration (lead); supervision (equal); writing – review and editing (equal). **Yoila David Malann:** Formal analysis (equal); investigation (equal); methodology (equal); supervision (equal); validation (equal); writing – review and editing (equal). **Ryan A. Martin:** Supervision (equal); validation (equal); writing – original draft (equal); writing – review and editing (equal).

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### CONFLICT OF INTEREST STATEMENT

The authors declare no competing interest.

### DATA AVAILABILITY STATEMENT

Data used for this article are available and published online at Data Dryad; <https://doi.org/10.5061/dryad.41ns1rnkm> (Deme et al., 2023).

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