Environmental extremes at high altitudes drive clutch size patterns in a wide-ranging lizard

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Abstract

Latitudinal patterns in reproductive output such as clutch size are linked to resource abundance and seasonal climate variation across taxa. Understanding if these patterns hold across local altitudinal gradients and within species can provide insight into key drivers of life-history evolution across scales. In this study, we examined geographical variations in clutch size and climate conditions in a wide-ranging lizard. We collected clutch data from ten populations of E. argus of varying elevation in China from both field observation and from the literature. A total of 369 clutches were obtained and generalized linear mixed-effects models were used to test the relationship between clutch size with body mass, habitat type, elevation, and climate conditions. Body mass strongly correlated with clutch size across all populations. Females from populations at high altitudes with low mean annual temperature and variability, and drier conditions had smaller clutches, while females at lower altitudes with higher mean temperatures and rainfall had larger clutch sizes. Poor climate conditions at high altitudes suggest fewer resources for females to invest in larger clutch sizes, likely due to reduced foraging and activity times, and growth under unfavourable conditions. These constraints match macroecological patterns of clutch size diversity in egg-laying taxa, suggesting local climate constraints can translate across scales to explain the diversity of reproductive output.

Introduction

Female investment in reproduction is an energetic expensive component of their life history (Sibly et al., 2012; Healy et al 2019), and within and between egg-laying species, there is substantial variation in reproductive output such as clutch size, clutch numbers, and clutch intervals (Roff, 2002; Shine and Greer, 1991; Pincheira-Donoso and Hunt, 2017; Meiri et al., 2020; Bansal & Thaker, 2021; Fisher et al., 2021; Pincheira-Donoso et al., 2021). Clutch size is the most common reproductive output trait measured and linked to maternal body size, resource availability, and environmental conditions (Lack, 1947; Jetz et al., 2008; Pincheira-Donoso and Hunt, 2017; Meiri et al., 2020; Caracalas et al., 2021). For example, clutch size among egg-laying squamates positively correlates with maternal traits such as body size, age, and growth rate (Tinkle et al., 1970; Pincheira-Donoso and Tregenza, 2011; Scharf et al., 2015; Liang et al., 2021). However, size-dependent clutch size is often constrained and dependent by other reproductive parameters where larger eggs or multiple clutches can result in smaller clutch size (e.g., Shine and Greer, 1991; King, 2000; Shine and Greer, 1991; Werneck et al., 2009; Siliceo and Diaz, 2010; Meiri et al., 2012; Slavenko et al., 2015; Meiri, 2018).

Environmental variation can also impact reproductive investment for ectotherms that depend on the environment to regulate their body temperature (Shine, 2005; Parmesan, 2006; Meiri et al, 2013; Meiri, 2018). For example, ectotherms raised under warmer temperatures often result in smaller body sizes which then leads to lower reproductive output (Fitch, 1970; Gibbons and McCarthy, 1986; Atkinson, 1994; Barneche et al., 2018; Meiri, 2018; Wu et al., 2022). In macroecology studies, variations in climate at large scales are often represented by geographic latitude (Boyer et al., 2010; Griebeler et al., 2010; Laiolo and Obeso 2015). At higher latitude, the climate is generally warmer and consistent throughout the year and becomes colder and more variable at lower latitude. Studies have shown patterns in clutch size and latitude, where clutch size increases at higher latitude among reptile species (e.g., Cody, 1966; Lack, 1947; Tinkle et al., 1970; Fitch, 1985; Iverson et al., 1993; Boyer et al., 2010). For example, lizards at high latitudes lay large clutch sizes primarily by the highly seasonal environment, favouring suitable breeding periods (Cody, 1966; Fitch, 1985). Therefore, the variation in the degree of seasonality may influence clutch size patterns across lizard species (Tinkle et al., 1970; Hao et al., 2006; Meiri et al., 2013; Mesquita et al., 2016; Meiri et al., 2020).

However, there is still substantial variation in clutch size within a similar latitude range (Fitch, 1970; Fitch, 1985; Du et al., 2014; Laiolo and Obeso 2015). It is likely that local scale variation in climates contributes to these clutch size variations. Altitudinal gradients have been incorporated as an alternative proxy to latitudinal patterns in life-history, especially to explain variation within broad wide-ranging lizard species (Griebeler et al., 2010; Roitberg et al., 2013). Unlike the latitudinal gradients in environmental conditions at the macroscale, altitudinal gradients can have greater impact life-history traits at local scales due to synergetic interactions of decreasing air temperature, oxygen levels, and greater variation in weather conditions such as sudden snowstorms and short summers (Fitch, 1985; Morrison and Hero, 2003; Beall, 2014; Hille and Cooper, 2015; Lack et al., 2016). Since life history patterns such as reproduction depend on the environment for ectotherms, the unique climate at high altitude is expected to lead to differentiation of life-history strategies that may impose evolutionary constraints on reproduction (Lack, 1947; Laiolo and Obeso 2015).

Understanding the impact of the environment on reproductive investment has mainly been focused on global patterns and annual averages in environmental conditions (Araújo et al., 2006; Hille and Cooper, 2015; Laiolo and Obeso 2015; Meiri et al., 2020). Local scale studies that examine environmental variation can provide more direct mechanistic explanations of clutch size diversity. This is because maternal investment is directly influenced by resource availability (Vitt and Congdon, 1978; Griebeler et al., 2010; Bansal and Thaker, 2021). In energetic models, greater accumulation of food prior to breeding provides females with more energy resources for reproduction (Forseth et al., 1994; *Lika and Kooijman, 2003*). At high altitude, food resource is generally scarce and maybe the primary limiting factor for reproductive investment. Additionally, unpredictable weather conditions at high altitudes such as high seasonal temperature and precipitation variability can reduce the window of opportunity to forage (Fitch, 1970; Urban et al., 2014; Burner et al., 2020; Anderson et al., 2022), limiting an individual's ability to accumulate sufficient energetic resources for egg production (Tinkle et al., 1970; Vitt and Congdon, 1978). Such trends in reproductive investment and environmental variability have been observed at global scales (Andrew et al. 2013; Crozier and Hutchings, 2014; Urban et al., 2014), however, this pattern is not consistent across species (Lyon et al., 2008). Therefore, the need for intraspecific studies at local levels can provide a mechanistic link for within-species variation in clutch size diversity and global patterns in clutch size diversity. If the prediction on clutch diversity at high altitudes holds true at an intraspecific level, populations at high altitudes are expected to lay smaller clutches relative to populations closer to sea level.

In this study, we examined the relationship between clutch size and environmental variables from ten populations of a wide-ranging lizard, *Eremias argus* from China. *E. argus* is a small (~70 mm snout-vent length [SVL]; Zhao et al., 1999), an oviparous lizard that lays several clutches of two to five parchment-shelled eggs per clutch. This species occurs throughout China and other Asian countries across altitudinal gradients between 0–2,900 m above sea level (Zhao et al., 1999), providing an excellent model system to examine the influence of altitude climates on the clutch size within species. We hypothesized that clutch size will: (i) positively correlate with maternal body mass, and (ii) will be lower at higher elevations due to lower temperatures and precipitation and greater climate variability. Understanding the extent to which these hypotheses hold for clutch size diversity within species allows inference of whether the relationship between clutch size with geographic distribution conforms to the global patterns across taxa as seen in Meiri et al. (2020).

Materials And Methods

2.1 Study site and lizard collection

We collected clutch size, the number of clutches per female, and female body mass (in grams) from 369 individuals across ten populations of differing altitudinal gradients (Zhao et al., 1999). The ten populations sampled from Shidu, Erdos, Xingtai, Jingtai, Harbin, Hebei, Handan, Linfen, Chuzhou, and Gonghe provided a representative range of *E. argus* range distribution across China (**Fig. 1**; Zhao et al., 1999). For data on the Handan and Linfen populations, we collected the representative clutches and female body mass (smallest and largest clutch size) reported from Hao et al. (2006) and Ma et al. (2019). Populations were grouped into three altitude categories: low (<1,000 m), mid (1,000–2,000 m), or high (>2,000 m).

Gravid females *E. argus* were captured by hand during the early reproductive season from two different locations (Harbin County, Heilongjiang: 500 m asl, 45°48’ N, 126°32’ E; and Erdos County, Inner Mongolia: 1300 m asl, 39°36’ N, 109°46’ E). Description of how lizards, body mass, and clutch size were collected for other locations was provided in Hao et al. (2006), Ma et al. (2019), Sun et al. (2013), Wang et al. (2021), Zhao et al. (1999), Once captured, all gravid females were transferred to the nearby field laboratories where they were immediately weighed (body mass [BM]; ±0.01 g). Each female was housed individually in glass terraria (600 x 300 x 400, L x W x D mm) filled with 10 mm of moist sand and pieces of clay tile that served as shelters. All lizards were maintained in rooms at the field laboratories with a constant light cycle that alternated between 10L:14D (0800 h on and 1800 h off) for an average of 7 days before clutches were produced. Each enclosure contained a 100 W light bulb suspended above to provide them with additional heat for thermoregulation from 0800 h to 1800 h. Lizards were fed *ad libitum* with mealworms and crickets dusted with additional vitamins and minerals, and fresh water was provided daily. We checked each terrarium four times a day for freshly laid eggs (0800 h, 1100 h, 1400 h, and 1800 h) and counted the number of eggs laid in a single clutch once found. Once the females had laid eggs, we measured their postpartum body mass (BM; ±0.01 g) and then released them at the site from where they had been captured.

2.2 Habitat and climatic condition

Environmental factors in the analysis included habitat type, latitude, temperature (°C), and precipitation (mm yr ¹). Habitat type was classified for each population as either farmland, grassland, semiarid, or arid based on the climate conditions experienced (Zhao et al., 1999). The annual mean and seasonal variation in temperature and precipitation for each population location was extracted from the Worldclim2.1 database (http://www.worldclim.org; accessed on 21 December 2021). We calculated the overlapping spatial coordinates of the sampled sites by setting the geographic spatial reference at WGS 1984 and projecting to the UTM Zone 20N to extract the climate variables within a 2.5 arc minute resolution grid (1 × 1 km). The annual mean temperature and precipitation represent the average yearly climate conditions that the lizards experience and correlate with ecosystem productivity, while the temperature and precipitation seasonality represent annual variation in climate conditions. Lower annual variability indicates more stable climates.

2.3 Data analysis

All analyses were performed using *R* 4.0.5 (R Development Core Team, 2021). To improve the residual normality and reduce heteroscedasticity of our data in our models, we log-transformed (natural logarithm) clutch size and body mass. For the relationship between maternal body mass and clutch size, we ran a linear mixed-effects model using the *lmerTest* package (Kuznetsova et al., 2017) with body mass set as random-slope and random-intercept across populations which accounts for within population variation in intercept and slope. To understand the effect of latitude and habitat type on the clutch size diversity, we used generalized linear mixed-effects models using the ‘glmer.nb’ function from the *lme4* package (Bates et al., 2015). In this model, we set latitude and habitat type as fixed effects and clutch number and population origin as random factors to account for the nested effect of clutch number variations within different populations in our data (Bolker et al., 2009).

2.3.1 Principal component analysis

Since temperature and precipitation variables are correlated, we ran a principal component analysis (PCA) to project all environmental variables in the dataset (elevation, mean annual temperature, temperature seasonality, mean annual precipitation, precipitation seasonality) into lower dimensions using the ‘prcomp’ function in *R*. PCA applies a linear transformation to a set of *n* features to output a set of *n* orthogonal principal components that are uncorrelated, and each explains a percentage of the total variance in the dataset. The environmental data were centered and scaled to avoid biasing the PCA due to differences in magnitude and scale between each environmental value. The first and second PC scores (PC1 and PC2 respectively) combined explained 81.16% of the total variation, where for PC1, positive values indicate higher elevation with lower mean temperature and precipitation, while for PC2, positive values indicate more seasonal variation in temperature and precipitation at lower elevation. We extracted the PC1 and PC2 scores as a proxy for climate condition across altitude and ran a linear model on clutch size (ln-transformed) using a generalized linear mixed-effects model with habitat type as a covariate, and clutch number and population origin as random factors to account for the nested effect of clutch number variations within different populations.

Results

3.1 Clutch size relationship

Clutch size varied from 1 to 6 eggs per female from our dataset. There was a positive relationship between the clutch size with maternal body mass across populations (slope = 0.65, $t_{(9.2)}$ = 3.8, P = 0.003; **Fig. 2**). Within populations, the slope of the relationship all followed a similar trend with the exception of the Hebei population where clutch size did not positively associate with body mass (**Fig. 2**). However, this is likely due to the low sample size in this population (n = 8). There was a positive correlation between clutch size with latitudinal gradients ($X^2_{(1)}$ = 6.147, P = 0.013; **Table 1a**), but not habitat types along latitudes ($X^2_{(3)}$ = 3.836, P = 0.280; **Table 1a**).

3.2 Altitudinal seasonality and environmental correlates

Principal component analysis revealed two climatic trends associated with altitude. PC1 explained 51.27% of the variation and showed a positive association of temperature and precipitation seasonality with elevation, while mean annual temperature and precipitation was negatively associated with high elevation (**Fig. 3a**; **Table 2**). In PC2 which explained 29.89% of the variation, temperature and precipitation seasonality was negatively associated with elevation. The relationship with clutch size showed a negative correlation with PC1 (β = -0.163±0.067, $t_{\mathrm{df}\,=\,1}$ = -2.445, P = 0.015; **Fig. 3b**; **Table 1b**), while clutch size was positively correlated with PC2 (β = 0.225±0.084, $t_{\mathrm{df}\,=\,1}$ = 2.691, P = 0.007; **Fig. 3c**; **Table 1b**).

3.3 Habitat type

The environmental condition of different habitat types occupied by female lizards along altitudinal gradients significantly contributed to the intraspecific variations of lizard clutch size (ANOVA: $F_{\mathrm{df}\,=\,3,\,369}$ = 14.110, P = 0.003; **Table 1b**), where female lizards living in semiarid habitats at high altitudes laid smaller clutches (**Fig. 4; Table S1**).

Discussion

Local climatic gradients can have profound effects on an organism's life history. We show that climatic differences associated with high altitudes can influence clutch size among our lizard populations. In particular, low temperature and precipitation at higher altitudes were the primary drivers of clutch size, followed by temperature and precipitation seasonality.

Body size is inherently a key driver of clutch size variation. Larger females had larger clutch sizes in our populations of *E. argus*, consistent with other squamate species at both local (Nussbaum 1981; Angilletta *et al.* 2001; Du and Shou 2008; Du et al., 2014) and global scale (Meiri et al., 2020). Not surprisingly, larger females have more space to produce and hold eggs, and since egg size does not increase proportionally with maternal size (Stearns, 1992; Shine, 2005; Kratochvil and Kubicka, 2007), larger females can produce more eggs (Broderick et al., 2003; Du et al., 2005a; Griebeler et al., 2010). Latitude also showed an effect on clutch size in our study system, where higher latitudes are positively related to clutch size within our lizard populations. These latitude patterns are consistent with the wider literature for multiple taxa groups (Fitch, 1970; Fitch, 1985; Du et al., 2005b; Forsman and Shine 1995; Ji and Wang 2005; Boyer et al., 2010; Du et al., 2014; Hille and Cooper, 2015; Meiri et al., 2020).

However, altitudinal variation showed a stronger effect on our study system, where populations at higher altitudes produced smaller clutches. Ectotherms occupying high altitudes are expected to cope with these distinctive environmental conditions that can impose physiological and locomotory costs (Pincheira-Donoso and Hunt, 2017; Anderson et al., 2022), and in turn, affect resources allocated for reproduction (Fitch, 1985). The primary hypothesis to elevation dependency in clutch size is environmental conditions (Tinkle et al., 1970; Sun et al., 2013; Hille and Cooper, 2015; Deme et al., 2022). Because colder, drier conditions at high altitudes result in low ecosystem productivity, this can lead to less food available for females to invest in reproduction (Fitch, 1985). Our findings on low temperature and variation at higher altitudes leading to smaller clutch size are in agreement with studies that showed coupling effects of short foraging seasonal activity and depressing climate conditions (colder and less rainfall) associated with high altitudes constrain female lizards to lay smaller clutch (Sun et al., 2013; Novosolov & Meiri, 2013). Therefore, clutch size differences may be due to short seasonal foraging activity and unfavourable climate conditions that negatively influence available resources allocated for reproduction (Cody, 1966; Fitch, 1985; Meiri et al., 2013).

In presence of changing climates along altitudinal clines, most ectotherms take advantage of periods of favourable climate conditions to increase their body condition (Anderson et al., 2022; Li and Wiens, 2022). We found support for the idea that highly seasonal changes in the environments at low altitudes with warmer temperatures, and higher rainfall lead to larger clutches. It is likely that favourable climate conditions at low altitudes increase foraging activity by female lizards to enable them to invest more in reproduction. For example, studies have shown that populations at low altitudes have longer foraging activities than high altitude populations (Tinkle et al., 1970; Fitch, 1985; Cooper et al., 2005; Morrongiello et al., 2012; Hille and Cooper, 2015). We suggest within-population variation in clutch size along altitudinal clines is driven by environmental productivity and optimum climate conditions (Sun et al., 2013; Bansal and Thaker, 2021; Li and Wiens, 2022). However, whether the presumption holds for the clutch size variation between sympatric species that coexist in local environments along altitudinal clines requires further investigation. This is because sympatric species might evolve unique life-history traits due to the interactive relationships between species' habitats and life histories (Dawson et al., 2002; Dawson, 2014).

When grouping populations based on habitat type, we found the clutch size to be more constrained in populations occupying habitats with drier conditions along altitudinal clines. Hot, short days, low prey availability, and low seasonality of drier conditions represent the semiarid conditions of Gonghe habitats (Wang et al., 2021). In contrast, moderate temperatures, long days, high seasonality, food availability, and low predation are represented by grassland or farmland habitats (Zhao et al., 1999). Such extreme environmental clines of the drier Gonghe habitats can strain thermoregulation and foraging activity of ectotherms (Bansal and Thaker, 2021; Anderson et al., 2022; Li and Wiens, 2022). Evidence for climate-induced constrains on clutch size can be seen in *Chelonia mydas*, where female *C. mydas* produce smaller clutches in seasonal environments with prevailing sub-optimal environmental conditions that compressed their foraging activity (Broderick et al., 2001). The small clutch size laid by the Gonghe populations may be related to the continental drier climatic conditions with less rainfall, more aridity, and low temperature during the spring and summer reproductive seasons. Presumably, female lizards cannot maintain the optimum ecological performance in such extreme climate conditions. Thus, this may impede their ability to acquire more food or shuttle more efficiently between basking and foraging activities to increase their reproductive investments (Tinkle et al., 1970; Fitch, 1985). However, we acknowledge that female reproduction among ectotherms occupying different habitat types with changing climates may be influenced by other factors such as vegetation cover, parasite load, predation risk, and population density (Griebeler et al., 2010; Burner et al., 2020; Meiri et al., 2020).

Overall, smaller clutch sizes produced by females in high altitude regions with poor climate conditions suggests low resources available for females invest reproductive output, Conversely, the highly seasonal environments coupled with favourable climate conditions at low altitudes may provide a wider range of suitable conditions for female lizards to invest in reproductive output. Changing climate conditions along altitudinal gradients match macroecological patterns of clutch size diversity in egg-laying taxa, suggesting climate constraints can translate across scales to explain the diversity of reproductive output.

Declarations

Authors' contributions: GGD conceived the study; GGD, XH, and BS collected the data; GGD and NCW designed the methodology and analyzed the data; GGD and NCW wrote the manuscript. All authors interpreted the results, provided comments, and approved the final manuscript draft for submission.

Ethical Approval: The collection, handling, and husbandry of lizards were approved by Animal Ethics Committees of the Institute of Zoology, Chinese Academy of Sciences with approval no: IOZ14001

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Data availability statement: Data and code will be available in an online repository with DOI provided upon acceptance.

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Tables

Table 1; ANOVA results of ecological and environmental predictors of clutch size: a) shows ANOVA results of a latitudinal model; b) shows ANOVA results of a climate model. Differences in clutch size between each habitat type were further expanded in Supporting Information Table S1.

Factors	**df**	**Sum Sq**	**Mean Sq**	***χ^2-value***	***p-value***
1. **ANOVA: Latitude model**					
Latitude	1	0.217	0.217	6.147	0.013
Habitat type	3	3.640	1.213	3.836	0.280
2. **ANOVA: Climate model**					
PC1	1	0.196	0.196	5.979	0.015
PC2	1	0.092	0.092	7.244	0.007
Habitat type	3	4.775	1.592	14.110	0.003

Table 2; Principal component loadings from the PCA of climate variables, seasonal environments, and altitudes of lizard populations. Principal components loadings ≥0.45 were bolded to show the main factors of each PC.

Factors	PC1	PC2	PC3	PC4	PC5
Altitude	**0.502**	**-0.475**	0.062	-0.249	**-0.676**
Mean temperature	**-0.557**	0.003	**-0.482**	0.339	**-0.585**
Seasonal temperature	0.158	**0.696**	**0.504**	0.248	**-0.418**
Mean precipitation	**-0.570**	0.050	0.337	**-0.731**	-0.159
Seasonal precipitation	0.297	**0.535**	**-0.630**	**-0.477**	-0.038
Eigenvalue	1.601	1.223	0.890	0.373	0.105
Percentage variance	51.30	29.90	15.80	2.80	0.20

Figures

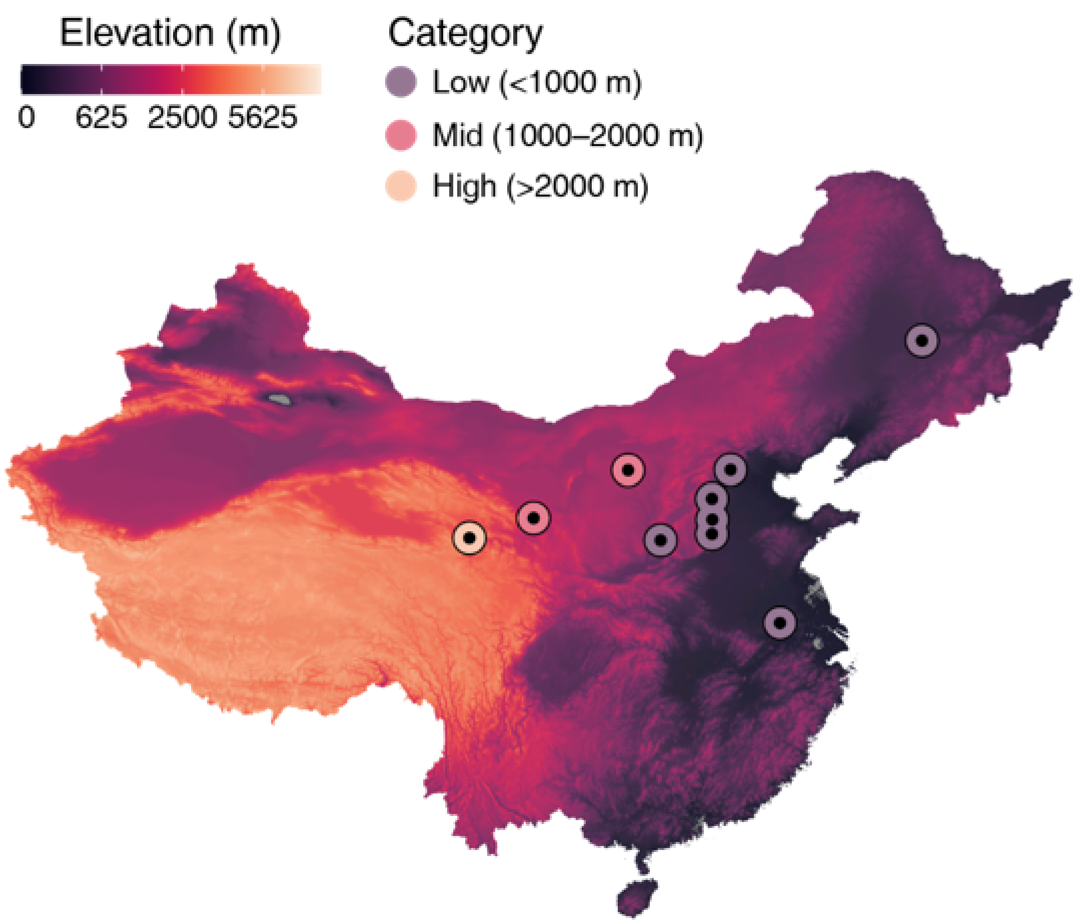

Figure 1

Collection sites of ten *Eremias argus* populations from different altitudes in China. Coloured circles represent populations collected either from low altitude (<1,000 m), mid-altitude (1,000–2,000 m), or high altitude (>2,000 m) environments. Colour-filled gradients represent the elevation topology of China.

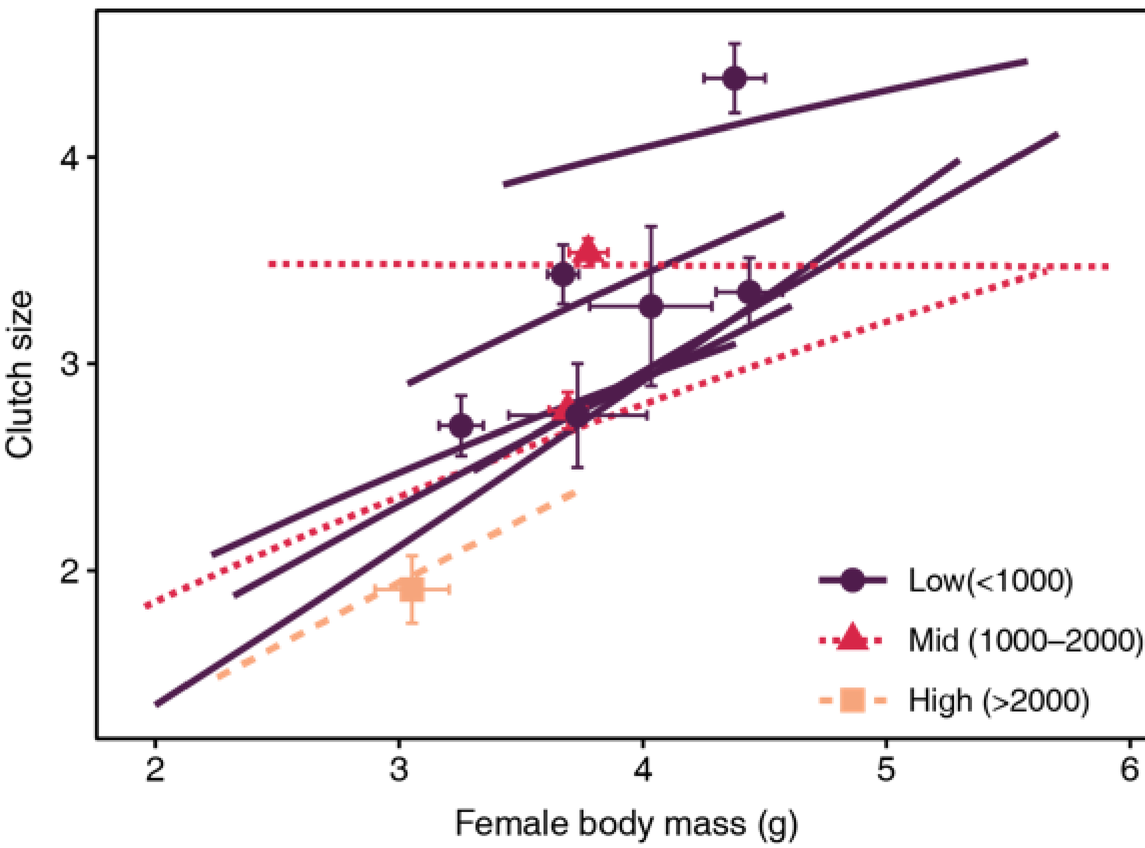

Figure 2

Relationship between clutch size and female body mass (g). Data points presented as mean ± s.e. for each population and were coloured based on their altitude category. Intraspecific clutch size showed a positive relationship with increasing female body mass where lines represent the population-level relationship from the linear mixed-effects model.

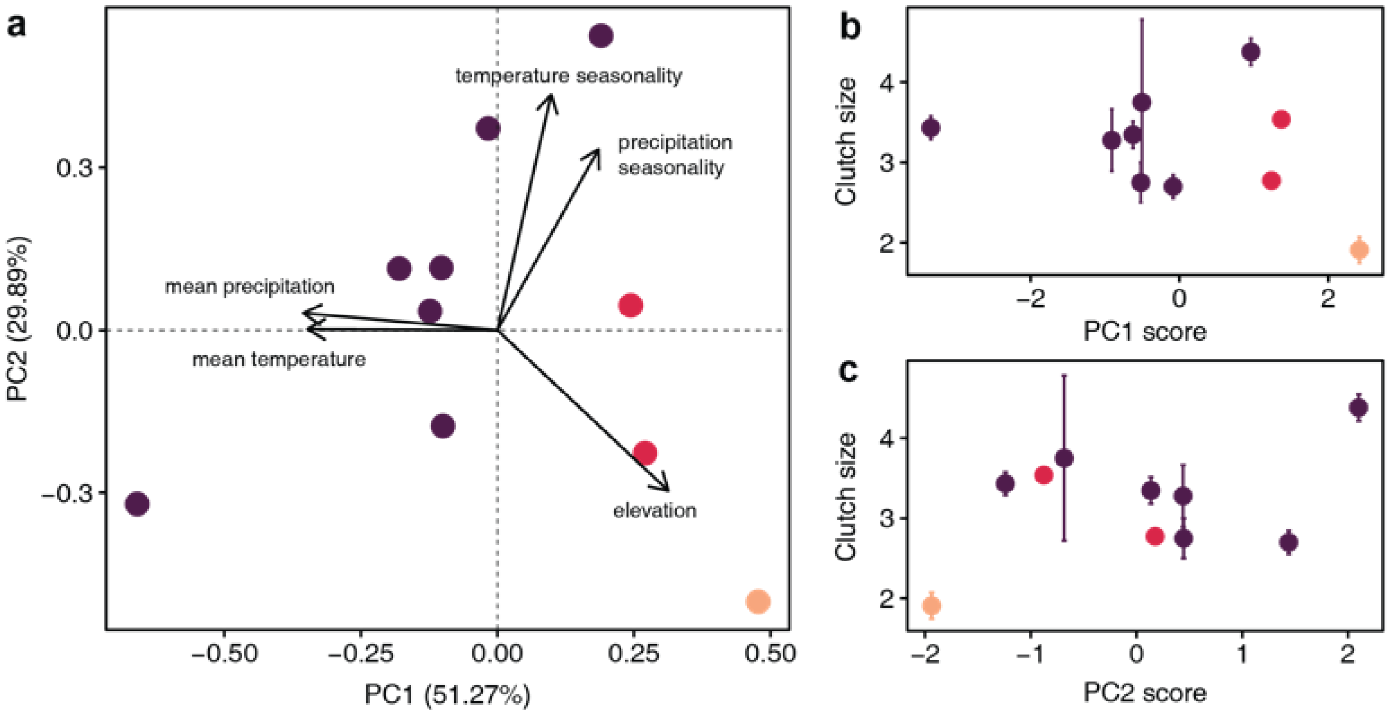

Figure 3

a) Principal component (PC) scatter plot of climatic conditions between populations based on PC1 and PC2 scores, where positive PC1 values indicate higher elevation with lower mean annual temperature and precipitation. Negative PC2 indicates higher elevation with lower temperature and precipitation seasonality. b-c) The relationship between clutch size and PC1 and PC2 score, representing climatic mean or climate seasonality at higher altitude, respectively. Data points presented as a population means ± s.e.

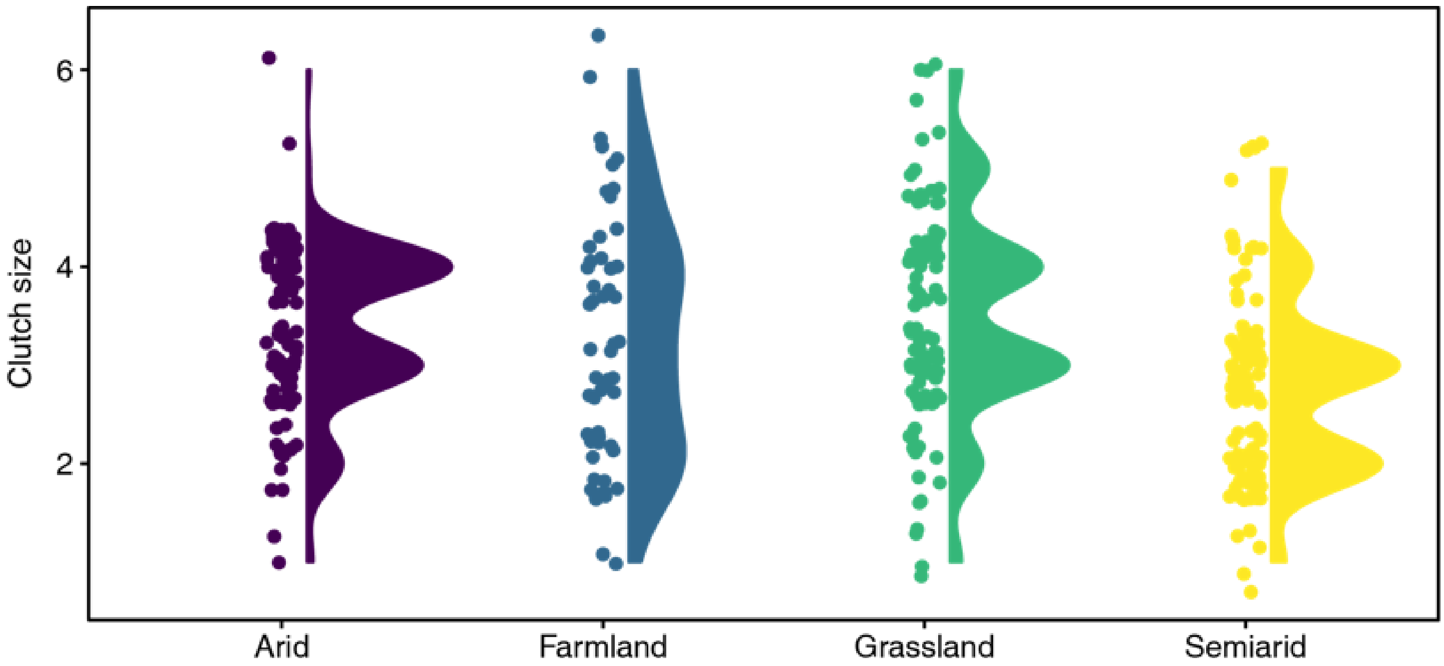

Figure 4

Differences in clutch size produced by female *E. argus* between habitats. Data points represent individual clutch sizes, and the half-violin plot represents the distribution of data points.

Supplementary Files

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