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Evolutionary and environmental influences on life history traits in Neotropical microteiid lizards

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ABSTRACT

We examine the life history traits of microteiid lizards (families Alopoglossidae and Gymnophthalmidae), focusing on how environmental variables and female body size influence reproductive traits. We compiled life history data from 34 Neotropical microteiid species. We assess phylogenetic signals and the influence of climatic variables on these traits by employing comparative phylogenetic methods. Our results indicate significant phylogenetic signals in most life history traits, suggesting evolutionary structure within these lizard clades. Clutch size (number of eggs) does not vary within microteiid species such that increasing reproductive investment by increasing clutch size is not an option. We found positive correlations between female body size and egg volume. This finding supports our prediction that lizards with a fixed clutch size will exhibit reproductive compensation by producing larger eggs. Our environmental analyses reveal that less arid conditions favour larger body and egg sizes, while increased precipitation and seasonality positively influence reproductive investment, leading to higher relative clutch mass and larger egg volumes. Conversely, higher mean annual temperatures negatively impact reproductive traits. These findings highlight the adaptive strategies of microteiid lizards in response to diverse and fluctuating environmental conditions, balancing reproductive investment and offspring survival to optimize their success across varying habitats.

Keywords: adaptation; Alopoglossidae; Gymnophthalmidae; ecology; reproduction; Squamata

INTRODUCTION

Life history refers to the changes an organism undergoes from birth to reproduction and death, including traits such as lifespan, growth rate, age at maturity, and reproductive strategies (Ricklefs and Relyea 2016). Due to resource constraints and diverse environmental conditions, organisms may allocate energy disproportionately to specific functions, limiting investment in others (Stearns 1992, Mesquita *et al.* 2016a). Consequently, life history traits can vary among species, populations, or even individuals (Winemiller 1992, Winemiller and Rose 1992). Among squamates, for example, some life history traits remain fixed (no variation), while others show considerable variation within the same species (Howard 1974, Shine 2005).

In reptiles, key life history traits include clutch size, egg size, body size, and clutch mass (Vitt and Price 1982, Dunham and Miles 1985, Dunham *et al.* 1988). Body size significantly influences reproductive characteristics, with studies showing that larger females tend to produce more eggs or have a greater total clutch mass (Blueweiss *et al.* 1978, Vitt 1981, Du *et al.* 2005). Another crucial aspect is relative clutch mass, which estimates the energy females allocate to offspring in a single reproductive event (Tinkle *et al.* 1970, Vitt and Price 1982). Additionally, at least six reproductive strategies are recognized, ranging from short-lived species with small clutches and early reproduction to long-lived species with larger clutches and delayed reproduction (Tinkle *et al.* 1970, Dunham *et al.* 1988, Mesquita *et al.* 2016a, 2016b). In addition, live bearing (viviparity) has independently evolved more often among squamate reptiles than in any other tetrapod group (Blackburn 1982, Shine 1985, Blackburn and Vitt 1992, Pyron and Burbrink 2014).

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Environmental factors, such as climate, significantly influence many life history traits, with evolutionary history also playing a crucial role (Dunham and Miles 1985, Fitch 1985, Brown and Shine 2006, Mesquita *et al.* 2016a). For example, lizard clutch sizes vary across latitudinal gradients, generally increasing at higher latitudes (Mesquita *et al.* 2016a, Meiri *et al.* 2020). However, some lizard species maintain a fixed clutch size of one or two eggs, regardless of local climatic conditions (Losos 2011, Mesquita *et al.* 2016a, Meiri *et al.* 2020). Other factors, such as habitat specialization and foraging mode, also influence reproductive variations. For instance, arboreal, fossorial, and crevice-dwelling lizards tend to have smaller clutches, which allows greater mobility for pregnant females in these environments (Andrews and Rand 1974, Vitt 1981, Ashton 2005). Additionally, a co-evolutionary relationship has been proposed between relative clutch mass and foraging mode, where actively foraging lizards have streamlined bodies and clutches that comprise a relatively low proportion of total body mass. Conversely, sit-and-wait lizards have a stocky body shape and high relative clutch mass (Vitt and Congdon 1978, Huey and Pianka 1981).

Clutch or litter size is one of the most studied life history traits among vertebrates, with squamate reptiles exhibiting a wide range from one to more than 100 offspring (Stearns 1989, Vitt and Caldwell 2013). Among oviparous species, clutch size variation may reflect adaptive responses to climatic factors or female body size. In some cases, producing small clutches might be more advantageous, as carrying large clutches (high relative clutch mass) could compromise females' locomotor performance and foraging success, thereby increasing the risks of predation and extinction (Meiri *et al.* 2013, 2020). An alternative to producing large clutches is to produce small clutches more frequently. However, a high frequency of egg production might be unviable in highly variable or seasonal environments, underscoring that egg production is an adaptive response to environmental variations.

Specific lineages of squamate reptiles exhibit a fixed clutch size, typically producing one or two eggs. This fixed clutch size has evolved independently in various lizard clades, including *Anolis*, gekkonids, dibamids, and microteiids (Shine and Greer 1991). Some studies correlate this reproductive strategy with specific environments, such as forested areas or fossorial habits (e.g. Andrews and Rand 1974, Ashton 2005). Other adaptive strategies have been selected for reptiles with a fixed clutch size. For example, anoles produce a single egg per reproductive episode but may employ accelerated egg production, sequential reproduction, or restricted reproduction to a specific season (Andrews and Rand 1974, Mesquita *et al.* 2015). Additionally, lizards with a fixed clutch size often produce a larger relative clutch mass, compensated for by the production of larger eggs, often accompanied by increased female body size. Studies have reported that relative clutch mass and hatchling size in lizards with a fixed clutch size are comparable with those in lizards with variable clutch sizes (Kratochvíl and Kubička 2007, Meiri *et al.* 2015).

Two lizard clades that exhibit fixed clutch size are Gymnophthalmidae and Alopoglossidae, collectively known as microteiids. These small lizards, ranging from 40 to 150 mm in snout–vent length (SVL), are exclusively distributed in the Neotropical region, spanning from southern Mexico to Argentina, with some species inhabiting Caribbean and Central American islands (Vásquez-Restrepo and Diago-Toro 2023, Oliveira *et al.* 2024, Vásquez-Restrepo *et al.* 2024). They are among the most ecologically diverse lizard families in the Neotropics, with terrestrial, fossorial, semiaquatic, and semiarboreal species (Presch 1980, Pianka and Vitt 2003, Siedchlag *et al.* 2010, Souza *et al.* 2015). Currently, 296 species of gymnophthalmids and 32 species of alopoglossids are recognized (Uetz *et al.* 2024). Our study uses comparative phylogenetic methods to examine reproductive investment in female microteiids, focusing on evolutionary trade-offs between these reproductive traits and body size evolution, and which environmental variables best predict life history patterns in these species. Specifically, we test the following hypotheses: (i) female body size constrains clutch mass, predicting that relative clutch mass and egg volume are associated with female body size; and (ii) climatic variables influence reproductive investment, where more seasonal climates favour the production of smaller clutch masses and multiple clutches during the reproductive season, while more stable climates and mesic vegetation result in higher clutch masses and a single clutch per reproductive season.

MATERIALS AND METHODS

Data collection

We compiled a life history database with information on 34 Neotropical microteiid species distributed across 67 populations (Supporting Information Tables S1 and S2). This database comprises data collected by the authors over the past five decades, supplemented by relevant information from the existing literature. For our study, we considered only reproductive females, discarding young females or nonreproductive adult females from a population. The data collected by the authors involved dissection and direct analysis of lizard gonads. We categorized females as reproductive if they had vitellogenic follicles or eggs in their oviducts. The simultaneous presence of vitellogenic follicles and eggs indicated the potential for producing more than one clutch per reproductive season.

For each population, we recorded six variables: adult female mass (g), SVL (mm) from adult females, female SVL at maturity (based on the SVL of the smallest reproductive female), clutch frequency per year (single or multiple), egg volume, and relative clutch mass (RCM, calculated as the total volume of eggs divided by the mass of adult females). For statistical analyses, we assigned a value of 1 for a single clutch and 2 for multiple clutches. To estimate egg volume, we used the ellipsoid formula:

$$V = \frac{4}{3}\pi\left(\frac{length}{2}\right)^2\left(\frac{width}{2}\right)$$

We calculated the mean for each variable in a population. Additionally, when data were available for more than one population per species, we calculated the mean across populations, providing a unique value for each species.

The database also incorporates characteristics from the capture sites of each population, encompassing climatic data. Climatic data included five variables: (i) annual mean temperature, (ii) temperature seasonality, (iii) annual precipitation, (iv) precipitation seasonality, and (v) aridity index. We downloaded the first four climate variables from the WorldClim database (Hijmans *et al.* 2005), with a spatial resolution of 2.5 arc-minutes. The aridity index (Q) was estimated using the equation from Tieleman *et al.* (2003):

$$Q = \frac{p}{(T_{max} + T_{min})\, x\, (T_{max} - T_{min})} x\, 1000,$$

where p is annual precipitation, T_{max} is the highest monthly mean temperature, and T_{min} is the lowest. We obtained values of T_{max} and T_{min} from the International Water Management Institute (IWMI) World Water and Climate Atlas (available at http://www.iwmi.cgiar.org/WAtlas/Default.aspx). Lower Q values correspond to more arid environments. All climatic variables were log-transformed to normalize their distribution, minimize the effect of outliers, and improve the fit of the linear models.

For species where multiple populations were sampled, we calculated mean values for environmental variables to represent the average conditions experienced by the species. We examined variation in environmental conditions between populations, and overall, the environmental variables were consistent across populations. Any minor variations observed did not significantly affect the overall trends in reproductive investment. The life history database and values of climatic variables are available in the Supporting Information (Tables S1 and S2).

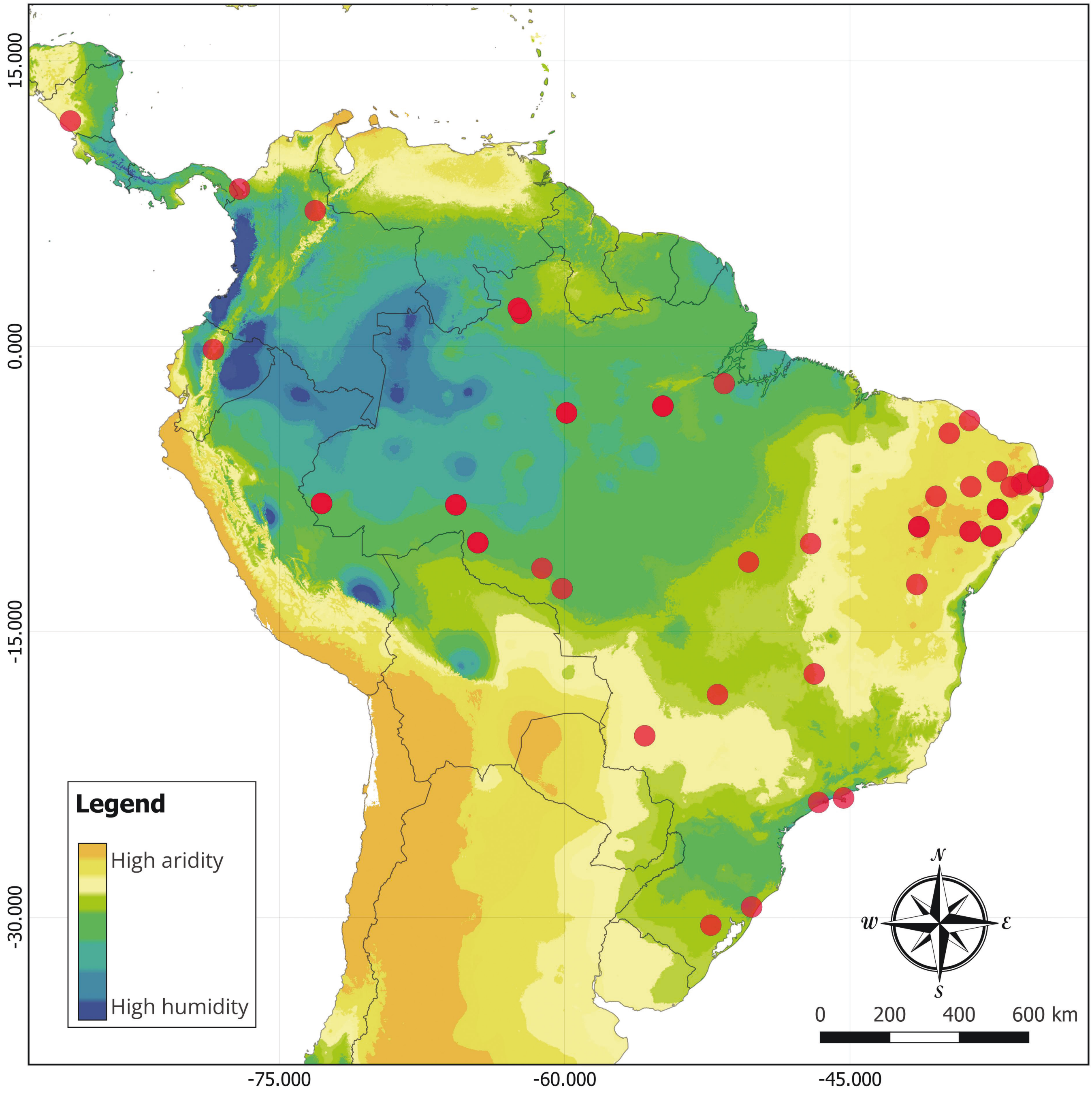

Figure 1. Sampling sites of microteiid lizard (gymnophthalmid and alopoglossid) populations with life history data used in this study.

Historical and environmental effects on life history patterns

We used the time-calibrated tree for squamates proposed by Title *et al.* (2024) and pruned the phylogeny to represent only our sampled species. All molecular methods, details on data processing, and phylogenetic methods are described in Title *et al.* (2024).

To test for phylogenetic signals in each life history trait, we calculated the Bloomberg *K* statistic using the PHYTOOLS package for R (Revell 2012). Values near zero for *K* indicate phylogenetic independence of data, while values near 1 indicate that a given character follows a Brownian motion (BM) evolutionary model (Freckleton *et al.* 2002, Blomberg *et al.* 2003, Losos 2008). $K > 1$ indicates that closely related taxa are more similar than expected in a BM model. Posteriorly, we tested for significance on phylogenetic signal (null hypothesis $K = 0$) by randomizing species names in the phylogeny using likelihood relationship tests (Blomberg *et al.* 2003). We used a 100 pseudo-posterior set of molecular phylogenetic trees (Title *et al.* 2024), pruned to our sampled species containing branch lengths and a matrix containing life history traits for each sampled species. We averaged *K* and *P* values across the set of trees.

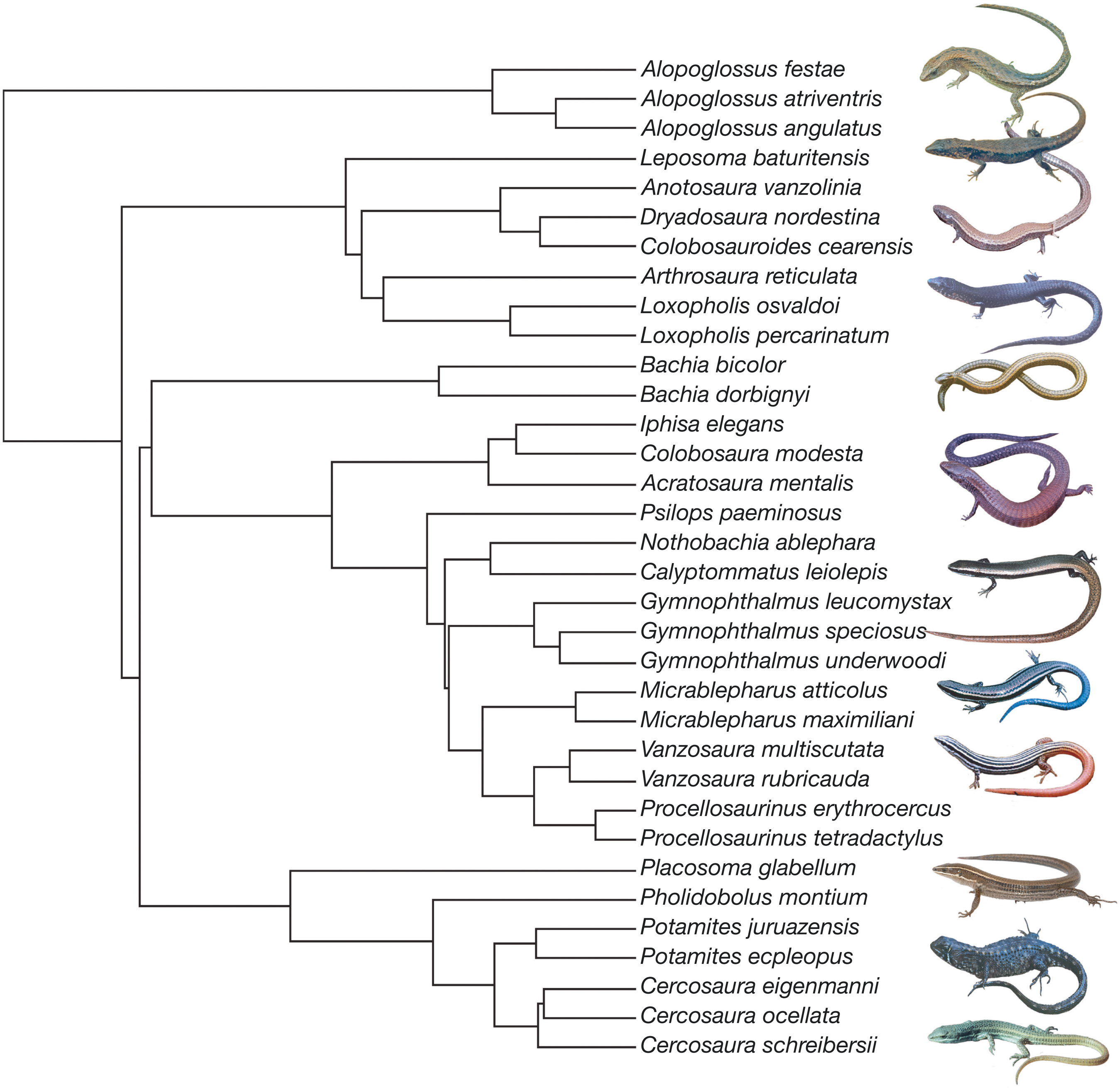

Figure 2. Species with life-history data sampled in this study. The tree is a consensus of molecular phylogenetic trees (Title *et al.* 2024), pruned to our sampled species. Photo credits (listed from top to bottom): *Alopoglossus angulatus* (Laurie Vitt); *Leposoma percarinatum* [substitute for *L. baturitensis*] (Laurie Vitt); *Anotosaura vanzolinia* (Bruno Halluan); *Arthrosaura reticulata* (Laurie Vitt); *Bachia dorbignyi* (Laurie Vitt); *Colobosaura modesta* (Laurie Vitt); *Gymnophthalmus underwoodi* (Laurie Vitt); *Micrablepharus atticolus* (Laurie Vitt); *Vanzosaura rubricauda* (Laurie Vitt); *Pholidobolus montium* (Omar Torres Carvajal); *Potamites ecpleopus* (Laurie Vitt); *Cercosaura schreibersii* (Laurie Vitt).

To test our first hypothesis, we chose to model SVL as the response variable in our analysis because our primary interest lies in understanding how these reproductive traits (RCM and egg volume) influence the evolution of female body size across microteiids, rather than the reverse. Thus, modelling SVL as a response variable allows us to directly assess whether larger females, which may allocate more resources toward egg production (via larger RCM or egg volume), are experiencing selection pressures favouring increased size over evolutionary time. This approach aligns with the hypotheses we laid out in the Introduction and allows us to explore potential evolutionary pathways that would not be captured if SVL were simply treated as a predictor.

To assess the influence of relative clutch mass and egg volume on female body size (SVL) and examine the impact of climatic variables on lizard life history traits, we built ordinary least square (OLS) models. Additionally, we employed phylogenetic regression models using phylogenetic generalized least squares (PGLS) models (Grafen and Hamilton 1989). To construct the PGLS models, we generated covariance matrices based on BM and Ornstein–Uhlenbeck (OU) expectations derived from phylogenetic trees of sampled species obtained from Title *et al.* (2024). In the BM model, trait variance accumulates linearly over time (Cavalli-Sforza and Edwards 1967), while in the OU model, trait variance remains relatively constant over time, with extreme trait values tending to regress to a long-term mean (Lande 1976). Consequently, the BM model describes the evolution of continuous traits under random drift or adaptive evolution, with adaptations randomly following shifting adaptive optima for each lineage. Conversely, the OU model describes trait evolution around an adaptive optimum to which traits are drawn or the evolution of the adaptive optimum itself (O'Meara and Beaulieu 2014). By employing these distinct models, we account for variations in modes of trait evolution, thereby ensuring robustness in our analyses. These models effectively control for the influence of evolutionary history, thereby ensuring data independence. We conducted phylogenetic regressions using the R package CAPER (Orme *et al.* 2013). We performed all statistical analyses in R v.4.3.2 (R Core Team 2021), with a significance level set at 5% to reject null hypotheses.

RESULTS

Life history data from 31 gymnophthalmid and three alopoglossid species distributed across diverse environments in the Neotropical region were analysed (Figs 1, 2). We observed significant phylogenetic signals for all variables analysed except for clutch frequency (Table 1). In addition, we found a significant relationship between female SVL vs. egg volume and RCM (Fig. 3A, B), based both on nonphylogenetic (OLS) and phylogenetic regression models (PGLS BM and PGLS OU), indicating a positive relation between body size and reproductive investment per episode (Table 2).

We found several significant relationships between reproductive and environmental variables (Table 3). Specifically, aridity positively influenced adult female mass (Fig. 3C) and egg volume. Annual precipitation significantly positively affected RCM (Fig. 3D). Precipitation seasonality significantly affected adult female mass negatively in the PGLS BM model, RCM positively in the OLS and OU models, and egg volume negatively across all models (Fig. 3E). Additionally, annual mean temperature negatively impacted clutch frequency (Fig. 3F), RCM (Fig 3G), and egg volume (Fig. 3H). Finally, temperature seasonality negatively affected adult female mass and egg volume. See Table 3 for complete results. In all the models studied, the OU model was the best fit, except for clutch frequency and RCM, where the OLS and BM models, respectively, performed better based on the lowest Akaike information criterion (AIC) values (Table 4).

Table 1. Estimated phylogenetic signal for life history traits in microteiid lizards (Gymnophthalmidae and Alopoglossidae) based on 100 pseudo-posterior molecular phylogenetic trees (Title *et al.* 2024), pruned to our sampled species.

	Average Blomberg's *K*	SD Blomberg's *K*	*P*
Adult female mass	0.644	0.027	**.003**
Adult female SVL	0.718	0.023	**.001**
Female SVL at maturity	0.702	0.023	**.001**
Clutch frequency	0.348	0.015	.237
Relative clutch mass	0.564	0.019	**.009**
Egg volume	0.851	0.030	**.001**

K and *P* values were averaged across the set of trees. Values in bold were statistically significant ($P < .05$).

DISCUSSION

The microteiid lizards (gymnophthalmids and alopoglossids) are known for their ecological diversity, occupying various microhabitats such as fossorial, semi-aquatic, and arboreal environments. Despite this diversity, some biological traits within these groups are phylogenetically conserved (Garda *et al.* 2014, Oliveira *et al.* 2018, Silva-Neta *et al.* 2019). One notable example is their fixed clutch size, with one or two eggs per reproductive episode, depending on the species. Our analysis revealed a phylogenetic signal in nearly all life history traits assessed, except clutch frequency. This finding aligns with other studies suggesting a significant phylogenetic and evolutionary influence on life history traits within lizards (Vitt *et al.* 2003, Vitt and Pianka 2005, Mesquita *et al.* 2016a).

Our results showed a positive relationship between female SVL and egg volume indicating an association between body size and investment per offspring. Lizards with a fixed clutch size often exhibit reproductive compensation by either producing larger eggs or having multiple clutches throughout the year or reproductive season (Kratochvíl and Kubička 2007, Losos 2011, Meiri *et al.* 2012, Mesquita *et al.* 2016a). However, our study revealed an inverse association between female body size and relative clutch mass. We observed a notable consistency when examining relative clutch mass values for each species, with an average of 0.148 ± 0.065. Interestingly, the increase in relative clutch mass does not necessarily coincide with larger female SVL. For instance, some species with high SVL values exhibit low relative

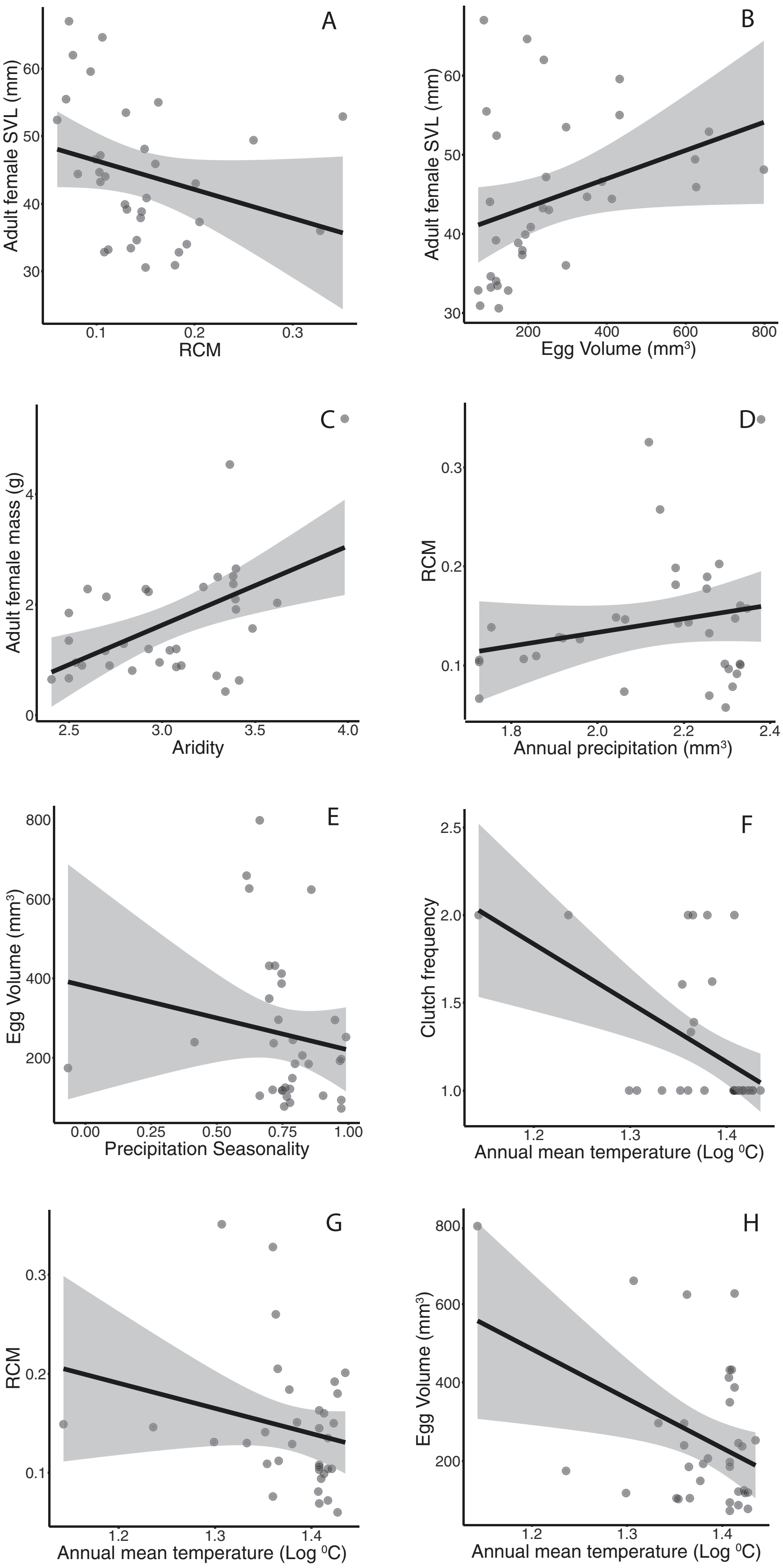

Figure 3. Relationship between the life history traits in microteiid lizards (Gymnophthalmidae and Alopoglossidae) and the significant environmental variables in phylogenetic regression models. A, RCM vs. adult female SVL; B, egg volume vs. adult female SVL; C, aridity vs. adult female mass (note: lower values of the aridity index represent high aridity; see Methods); D, annual precipitation vs. RCM; E, precipitation seasonality vs. egg volume; F, annual mean temperature vs. clutch frequency; G, annual mean temperature vs. RCM; H, annual mean temperature vs. egg volume.

Table 2. Non-phylogenetic (OLS) and phylogenetic regression models (PGLS BM—Brownian motion and PGLS OU—Ornstein–Uhlenbeck) relating variation in life history traits of microteiid lizards (average adult female snout–vent length vs. RCM—relative clutch mass, and egg volume).

Parameter	OLS	PGLS BM	PGLS OU
Coefficient intercept	47.757	16.063	16.084
Coefficient RCM	−71.873	−13.527	−12.587
Coefficient egg volume	.027	.737	.805
P-value intercept	5.66E-14	5.989E-08	5.66E-14
P-value RCM	**.006**	**.004**	**.006**
P-value egg volume	**.003**	**.007**	**.003**
AIC	247.781	237.963	245.781

PGLS parameters were based on 100 pseudo-posterior molecular phylogenetic trees (Title *et al.* 2024), pruned to our sampled species. *K* and *P* values were averaged across the set of trees. Values in bold were statistically significant ($P < .05$).

clutch mass (e.g. *Bachia dorbignyi*, SVL = 67.00, RCM = 0.072), while smaller species may have high relative clutch mass (e.g. *Vanzosaura savanicola*, SVL = 32.02, RCM = 0.196). Species of *Bachia* are elongated for a subterranean existence, having a near snake-like morphology such that any relationship between body size (SVL) and life history traits may differ from other microteiids (Colli *et al.* 1998, Oliveira *et al.* 2024). Our results suggest that various factors, such as biological, environmental, or phylogenetic niche conservatism within taxa, influence each species' investment in relative clutch mass. While not a commonly reported pattern in lizards, a similar phenomenon has been observed in other lizards with a fixed clutch, such as eublepharid geckos (Kratochvíl and Frynta 2006). The distinctive elongated morphology of microteiid lizards, particularly in fossorial species like those of the genus *Bachia*, may account for the absence of a strong statistical relationship between female body size and relative clutch mass in our findings. This morphology probably reflects adaptations to their subterranean lifestyle, which could influence life history traits differently compared with other Gymnophthalmidae. Although exploring this aspect in detail was beyond the scope of our study, it highlights an intriguing avenue for future research. Investigating how body elongation and habitat specialization shape reproductive investment patterns in fossorial lizards could provide valuable insights into the evolutionary pressures acting on these traits within the group.

Furthermore, our data also do not support the idea that reproductive compensation occurs through multiple clutches per reproductive season. At least 70% (24 species) of our sample have a single reproductive episode per season (Supporting Information Table S1). About 11% (four species) have populations with either one or two reproductive episodes per year, and only 17% (six species) showed two clutches per year (Table S1). It is important to note that clutch frequency can be susceptible to sample bias. Quantifying this variable with precision requires long-term studies with adequate sample sizes. In most reproduction studies on squamate reptiles, clutch frequency is typically determined by the simultaneous presence of eggs and vitellogenic follicles in gravid females. However, these studies often do not collect samples year-round, providing only a snapshot of a smaller period of the reproductive season, which could lead to underestimating clutch frequency.

Larger female body size and egg size in less arid environments (lower index values indicate high aridity) can be attributed to several ecological and evolutionary pressures. As we found that female size and egg size are correlated, it is unsurprising that both variables are related to the same climatic variable. Female body and egg size tend to be larger in less arid environments presumably due to the greater availability of resources such as food and water (Pinheiro *et al.* 2002, Vasconcellos *et al.* 2010), which support more extensive growth and development. In these environments, longer growing seasons and stable conditions allow females to grow larger and invest more energy into producing larger eggs (Roff 1992, 2002, Stearns 1992). Notably, certain gymnophthalmid species tend to reproduce during the rainy season, especially those in dry environments. This timing provides optimal conditions for hatching eggs and enhancing the survival of juveniles. Examples include *Anotosaura vanzolinia*, *Calyptommatus leiolepis*, *Colobosauroides cearensis*, *Nothobachia ablephara*, and *Procellosaurinus tetradactylus* (Garda *et al.* 2014, Ramiro *et al.* 2017, Oliveira *et al.* 2018, Silva-Neta *et al.* 2019). Reproductively, larger eggs provide more nutrients to the developing embryo, which is crucial for offspring survival. This strategy of producing fewer but better-provisioned offspring presumably increases the chances of each offspring surviving to maturity (Vitt and Congdon 1978, Thompson and Speake 2002). Furthermore, larger females often have longer lifespans, allowing them to reproduce over a more extended period and take advantage of favourable conditions when they occur (Mendyk 2015, Pearson *et al.* 2016). Moreover, reduced physiological stress from water conservation and heat dissipation enables relatively more energy allocation towards growth and reproduction (Moeller *et al.* 2017, Camacho *et al.* 2023). These factors combine to favour larger body and egg sizes as advantageous adaptations for survival and reproductive success in more mesic environments.

We found that increased annual precipitation is associated with higher RCM in all models, suggesting that females can produce clutches with relatively larger eggs in wetter environments. This phenomenon is not unique to microteiids; many lizard species take advantage of elevated precipitation levels to enhance their reproductive investment, either through larger clutches or through an increased number of clutches produced (Radder and Shine 2007, Huang and Pike 2011, Mesquita *et al.* 2016a). Higher rainfall and humidity during the rainy season serve as regulatory factors in the reproductive cycle of lizards. This correlation is often tied to the increased abundance of seasonal prey and creating more favourable conditions for egg laying and embryo development while reducing the risk of egg desiccation (Andrews and Sexton 1981, Overall 1994, Van Sluys 1995). In environments with more precipitation, the abundance of food and water allows female lizards to attain better nutritional and hydration status, which enables them to invest more energy into reproduction (Padilla Perez *et al.* 2021). In microteiids, this results in higher relative clutch mass with females producing larger eggs or reproducing more frequently. Additionally, the extended and frequent breeding seasons in such environments, combined with reduced physiological stress and improved egg development conditions, further support higher reproductive output (Padilla Perez *et al.* 2021). Consequently, lizards in areas with higher rainfall can afford to allocate more resources to their

Table 3. Non-phylogenetic (OLS) and phylogenetic regression models (PGLS BM—Brownian motion and PGLS OU—Ornstein–Uhlenbeck) relating variation in life history traits of microteiid lizards (F mass—adult female mass, F SVL—adult female snout–vent length, F SVL at mat.—female SVL at maturity, Clutch freq.—clutch frequency per year, RCM—relative clutch mass, and Egg vol.—egg volume) to climatic variables (Aridity index, Annual prec.—annual precipitation, Prec. seas.—precipitation seasonality, Annual temp.—annual mean temperature, and Temp. seas.—temperature seasonality).

Dependent variable	Parameter	OLS				PGLS BM			PGLS OU			
		Est.	SE	*t*	*P*	Est.	SE	*P*	Val.	SE	*t*	*P*
F mass	Intercept	−9.50	8.26	−1.15	.259	−0.13	6.06	.982	−9.50	8.26	−1.15	.259
	Aridity	5.02	1.62	3.11	**.004**	2.94	1.19	**.019**	5.02	1.62	3.11	**.004**
	Annual prec.	−2.81	1.66	−1.69	.102	−2.00	1.21	.109	−2.81	1.66	−1.69	.102
	Prec. seas.	1.65	0.99	1.67	.106	2.74	0.89	**.005**	1.65	0.99	1.67	.106
	Annual temp.	−4.38	3.44	−1.27	.213	−6.10	2.85	**.042**	−4.38	3.44	−1.27	.213
	Temp. seas.	3.57	1.61	2.22	**.034**	2.04	1.17	.091	3.57	1.61	2.22	**.034**
F SVL	Intercept	3.34	108.63	0.03	.976	32.65	69.06	.640	3.48	108.03	0.03	.974
	Aridity	12.68	21.26	0.60	.556	7.89	13.52	.564	12.44	21.14	0.59	.562
	Annual prec.	−17.92	21.85	−0.82	.419	−8.31	13.78	.552	−17.46	21.71	−0.80	.432
	Prec. seas.	−8.03	12.99	−0.62	.541	13.59	10.15	.192	−7.52	12.86	−0.57	.539
	Annual temp.	27.26	45.27	0.60	.552	−13.26	32.55	.687	26.61	45.00	0.59	.561
	Temp. seas.	4.91	21.12	0.23	.818	9.75	13.33	.471	4.94	21.01	0.24	.816
F SVL at mat.	Intercept	113.27	119.20	0.95	.350	89.07	77.47	.260	113.16	118.97	0.95	.350
	Aridity	−6.25	23.33	−0.27	.791	3.27	15.16	.831	−6.29	23.28	−0.27	.789
	Annual prec.	1.11	23.97	0.05	.963	0.78	15.46	.960	1.33	23.91	0.06	.956
	Prec. seas.	−5.50	14.25	−0.39	.702	13.84	11.39	.235	−5.22	14.18	−0.36	.702
	Annual temp.	−23.07	49.67	−0.46	.646	−57.47	36.51	.127	−23.47	49.57	−0.47	.640
	Temp. seas.	−11.47	23.18	−0.49	.625	6.87	14.95	.649	−11.42	23.14	−0.49	.625
Clutch freq.	Intercept	11.71	3.42	3.42	.002	11.02	2.97	.001	11.71	3.42	3.42	.002
	Aridity	−1.07	0.67	−1.59	.123	−0.92	0.58	.124	−1.07	0.67	−1.59	.123
	Annual prec.	0.25	0.69	0.37	.715	0.08	0.59	.891	0.25	0.69	0.37	.715
	Prec. seas.	−0.47	0.41	−1.16	.257	−0.37	0.44	.400	−0.47	0.41	−1.16	.257
	Annual temp.	−3.66	1.43	−2.57	**.016**	−3.57	1.40	**.016**	−3.66	1.43	−2.57	**.016**
	Temp. seas.	−1.26	0.67	−1.89	.069	−1.05	0.57	.076	−1.26	0.67	−1.89	.069
RCM	Intercept	0.79	0.56	1.41	.170	0.49	0.39	.215	0.79	0.56	1.41	.170
	Aridity	−0.12	0.11	−1.10	.279	−0.07	0.08	.401	−0.12	0.11	−1.10	.279
	Annual prec.	0.33	0.11	2.91	**.007**	0.25	0.08	**.004**	0.33	0.11	2.91	**.007**
	Prec. seas.	0.19	0.07	2.88	**.008**	0.10	0.06	.093	0.19	0.07	2.88	**.008**
	Annual temp.	−0.79	0.23	−3.38	**.002**	−0.54	0.18	**.006**	−0.79	0.23	−3.38	**.002**
	Temp. seas.	−0.02	0.11	−0.17	.868	0.00	0.08	.975	−0.02	0.11	−0.17	.868
Egg vol.	Intercept	−1030.60	1349.65	−0.76	.451	104.34	926.00	.911	−1030.60	1349.65	−0.76	.451
	Aridity	700.46	264.13	2.65	**.013**	413.85	181.25	**.030**	700.46	264.13	2.65	**.013**
	Annual prec.	−109.58	271.45	−0.40	.690	−103.69	184.80	.579	−109.58	271.45	−0.40	.690
	Prec. seas.	384.65	161.34	2.38	**.024**	436.85	136.15	**.003**	384.65	161.34	2.38	**.024**
	Annual temp.	−1409.79	562.42	−2.51	**.018**	−1218.97	436.41	**.009**	−1409.79	562.42	−2.51	**.018**
	Temp. seas.	557.03	262.42	2.12	**.043**	284.91	178.71	.122	557.03	262.42	2.12	**.043**

PGLS were based on 100 pseudo-posterior molecular phylogenetic trees (Title *et al.* 2024), pruned to our sampled species. *K* and *P* values were averaged across the set of trees. Values in bold were statistically significant (<0.05).

clutches and more often, enhancing their reproductive success and the survival chances of their offspring.

In all models, higher annual mean temperatures are linked to a decrease in clutch frequency, RCM, and egg volume, indicating that warmer conditions may lead to reduced reproductive output in these species. This negative impact also indicates that these reproductive traits are more pronounced in cooler environments. This relationship was also observed in global-scale studies where lizards from more temperate regions tend to concentrate their clutches in shorter periods, resulting in higher RCM and egg volumes (Mesquita *et al.* 2016a). Environments with lower temperatures lead to a shorter reproductive season. Lizards in these environments often produce fewer but larger clutches, ensuring that offspring are well-provisioned to survive the challenging conditions (Pianka 1970, Mesquita *et al.* 2016a). Higher RCM and larger egg volumes lead to more robust hatchlings,

Table 4. AIC values for non-phylogenetic (OLS) and phylogenetic regression models (PGLS BM—Brownian motion and PGLS OU—Ornstein–Uhlenbeck) relating variation in life-history traits of microteiid lizards (F mass—adult female mass, F SVL—adult female snout–vent length, F SVL at mat.—female SVL at maturity, Clutch freq.—clutch frequency per year, RCM—relative clutch mass, and Egg vol.—egg volume) to climate.

Dependent variable	OLS	PGLS BM	PGLS OU
F mass	89.159	86.777	**84.090**
F SVL	264.397	252.287	**228.130**
F SVL at mat.	270.714	260.102	**233.493**
Clutch freq.	**29.253**	38.231	34.757
RCM	−93.730	**−99.815**	−66.524
Egg vol.	435.737	428.808	**369.507**

Values in bold represent the best models, selected based on the lowest AIC values.

enhancing their chances of survival (Vitt and Congdon 1978, Thompson and Speake 2002). These adaptations may help lizards maximize their reproductive success and offspring viability in colder environments. We also found a negative correlation between clutch frequency and temperature. This result suggests that colder environments result in more than one clutch per reproductive season. While some studies have reported a positive relationship between temperature and lizard clutch frequency (Huang and Pike 2011, Meiri *et al.* 2012, Mesquita *et al.* 2016a), our results indicate a negative relationship. This discrepancy may be attributed to the specific ecological and physiological adaptations of the lizard species we studied, or to the methodological limitations associated with data collection on clutch frequency, which we discussed earlier.

Our results support that greater precipitation and temperature seasonality tends to reduce the mass of adult females, as well as RCM and egg volume. This suggests that more unpredictable and harsh environmental conditions can hinder reproductive success. In contrast, environments that are more stable and experience less seasonal change support larger female body sizes, greater RCM, and increased egg volumes. This indicates that consistent conditions are beneficial for optimal reproductive investment in these lizard species. Furthermore, this result is consistent with the notion that, in seasonal environments, species tend to concentrate reproductive effort in a single season, resulting in high reproductive output when compared with aseasonal environments (Mesquita and Colli 2010, Mesquita *et al.* 2016a). A shorter breeding season results in higher reproductive investment, larger RCM and eggs, and better offspring nutrition. As a consequence, juvenile survival should be enhanced. Temperature seasonality similarly influences these traits by creating optimal periods for growth and reproduction, where lizards can accumulate mass and produce well-provisioned eggs (Colli 1991, Vitt and Colli 1994, Mesquita and Colli 2010). These adaptations ensure that lizards maximize their reproductive success and offspring viability in environments characterized by significant seasonal variations in precipitation and temperature.

Finally, the OU model was the best fit for most traits, except for clutch frequency and RCM. The OU model is widely used to describe traits under stabilizing selection, where extreme values are less favoured, and characteristics tend to be attracted to an optimal value (Lande 1976, Hansen 2013). This model extends the BM model, which assumes that traits evolve randomly, accumulating variation over time (Felsenstein 1985, Pagel 1999). However, the OU model assumes that traits are 'pulled' towards an equilibrium point, representing an adaptation to the environment. In the context of this study, it might be under selective pressure, favouring optimal values in response to environmental conditions.

This modelling choice suggests that microteiid lizards are evolutionarily adapted to certain reproductive strategies, where stabilizing selection favours specific energy investments to enhance reproductive success under different climatic conditions. The use of the OU model, which captures this selection towards an optimal value, implies that the evolution of life history traits in these lizards is shaped by direct selective forces that promote convergence towards strategies that maximize survival in challenging environments (Revell *et al.* 2008, Hansen 2013). Thus, the use of the OU model reinforces the idea that the adaptations observed in microteiids are the result of stabilizing evolutionary pressure, rather than random fluctuations or genetic drift, as suggested by the BM model (Blomberg *et al.* 2003). Therefore, the OU model better captures the interaction between evolutionary history and ecological pressures that shape the reproductive strategies of microteiid lizards (Hansen 1997, Butler and King 2004).

CONCLUSION

Our findings demonstrate significant phylogenetic influences on microteiid life history traits, reinforcing that these traits are evolutionarily conserved in this lineage. We found a positive correlation between female SVL and egg volume and a negative correlation with RCM, suggesting that larger body size enhances reproductive investment. The analysis revealed that milder environments favour higher RCM and larger egg volumes, allowing lizards to allocate more energy to reproduction. This results in fewer but larger and better-provisioned clutches, enhancing offspring survival. Additionally, our study found a relationship between precipitation and temperature seasonality and key reproductive traits, indicating that lizards in seasonal environments invest heavily in reproduction during favourable conditions. These findings underscore lizards' adaptive strategies to thrive in diverse and changing environments, balancing energy allocation, reproductive investment, and offspring survival to ensure their continued success across various habitats.

SUPPLEMENTARY DATA

Supplementary data are available at *Biological Journal of the Linnean Society* online.

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CONFLICT OF INTEREST

None declared.

DATA AVAILABILITY

We include all used data as an Appendix, which is available at the *Biological Journal of Linnean Society* website.

REFERENCES

Andrews R, Rand AS. Reproductive effort in anoline lizards. *Ecology* 1974;**55**:1317–27. https://doi.org/10.2307/1935459

Andrews RM, Sexton OJ. Water relations of the eggs of *Anolis auratus* and *Anolis limifrons*. *Ecology* 1981;**62**:556–62. https://doi.org/10.2307/1937721

Ashton KG. Life history of a fossorial lizard, *Neoseps reynoldsi*. *Journal of Herpetology* 2005;**39**:389–95. https://doi.org/10.1670/148-04a.1

Blackburn DG. Evolutionary origins of viviparity in the Reptilia. I. Sauria. *Amphibia-Reptilia* 1982;**3**:185–205. https://doi.org/10.1163/156853882x00419

Blackburn DG, Vitt LJ. Reproduction in viviparous South American lizards of the genus *Mabuya*. In: Hamlett WC (ed.), *Reproductive Biology of South American Vertebrates*. New York, NY: Springer, 1992, 150–64.

Blomberg SP, Garland T, Ives AR. Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution* 2003;**57**:717–45. https://doi.org/10.1111/j.0014-3820.2003.tb00285.x

Blueweiss L, Fox H, Kudzma V *et al*. Relationships between body size and some life history parameters. *Oecologia* 1978;**37**:257–72. https://doi.org/10.1007/BF00344996

Brown GP, Shine R. Why do most tropical animals reproduce seasonally? Testing hypotheses on an Australian snake. *Ecology* 2006;**87**:133–43. https://doi.org/10.1890/04-1882

Butler MA, King AA. Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *The American Naturalist* 2004;**164**:683–95. https://doi.org/10.1086/426002

Camacho A, Brunes TO, Rodrigues MT. Dehydration alters behavioral thermoregulation and the geography of climatic vulnerability in two Amazonian lizards. *PLoS One* 2023;**18**:e0286502. https://doi.org/10.1371/journal.pone.0286502

Cavalli-Sforza LL, Edwards AWF. Phylogenetic analysis: models and estimation procedures. *Evolution* 1967;**21**:550–70. https://doi.org/10.1111/j.1558-5646.1967.tb03411.x

Colli GR. Reproductive ecology of *Ameiva ameiva* (Sauria, Teiidae) in the cerrado of central Brazil. *Copeia* 1991;**1991**:1002–12. https://doi.org/10.2307/1446095

Colli GR, Zatz MG, Cunha HJ. Notes on the ecology and geographical distribution of the rare gymnophthalmid lizard *Bachia bresslaui*. *Herpetologica* 1998;**54**:169–74.

Du W, Ji X, Shine R. Does body-volume constrain reproductive output in lizards? *Biology Letters* 2005;**1**:98–100. https://doi.org/10.1098/rsbl.2004.0268

Dunham AE, Miles DB. Patterns of covariation in life history traits of squamate reptiles: The effects of size and phylogeny reconsidered. *The American Naturalist* 1985;**126**:231–57. https://doi.org/10.1086/284411

Dunham AE, Miles DB, Reznick DN. Life history patterns in squamate reptiles. In: Gans C, Huey RB (eds), *Biology of the Reptilia, Vol 16, Ecology B, Defense and Life History.* New York: Alan R. Liss, Inc., 1988. 441–522.

Felsenstein J. Phylogenies and the comparative method. *The American Naturalist* 1985;**125**:1–15. https://doi.org/10.1086/284325

Fitch HS. Variation in clutch and litter size in New World reptiles. *Miscellaneous Publications of the Museum of Natural History, University of Kansas* 1985;**76**:1–76.

Freckleton RP, Harvey PH, Pagel M. Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist* 2002;**160**:712–26. https://doi.org/10.1086/343873

Garda AA, Medeiros PHS, Lion MB *et al*. Autoecology of *Dryadosaura nordestina* (Squamata: Gymnophthalmidae) from Atlantic forest fragments in Northeastern Brazil. *Zoologia* 2014;**31**:418–25.

Grafen A, Hamilton WD. The phylogenetic regression. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* 1989;**326**:119–57.

Hansen TF. Stabilizing selection and the comparative analysis of adaptation. *Evolution* 1997;**51**:1341–51. https://doi.org/10.1111/j.1558-5646.1997.tb01457.x

Hansen TF. Adaptive landscapes and macroevolutionary dynamics. In: Svensson E, Calsbeek R (eds), *The Adaptive Landscape in Evolutionary Biology*. Oxford: Oxford University Press, 2013, 205–26.

Hijmans RJ, Cameron SE, Parra JL *et al*. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 2005;**25**:1965–78.

Howard CW. Comparative reproductive ecology of horned lizards (genus *Phrynosoma*) in southwestern United States and northern Mexico. *Journal of the Arizona Academy of Science* 1974;**9**:108–16. https://doi.org/10.2307/40023610

Huang W-S, Pike DA. Climate change impacts on fitness depend on nesting habitat in lizards. *Functional Ecology* 2011;**25**:1125–36. https://doi.org/10.1111/j.1365-2435.2011.01855.x

Huey RB, Pianka ER. Ecological consequences of foraging mode. *Ecology* 1981;**62**:991–9. https://doi.org/10.2307/1936998

Kratochvíl L, Frynta D. Body-size effect on egg size in eublepharid geckos (Squamata: Eublepharidae), lizards with invariant clutch size: Negative allometry for egg size in ectotherms is not universal. *Biological Journal of the Linnean Society* 2006;**88**:527–32. https://doi.org/10.1111/j.1095-8312.2006.00627.x

Kratochvíl L, Kubička L. Why reduce clutch size to one or two eggs? Reproductive allometries reveal different evolutionary causes of invariant clutch size in lizards. *Functional Ecology* 2007;**21**:171–7. https://doi.org/10.1111/j.1365-2435.2006.01202.x

Lande R. Natural selection and random genetic drift in phenotypic evolution. *Evolution* 1976;**30**:314–34. https://doi.org/10.1111/j.1558-5646.1976.tb00911.x

Losos JB. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters* 2008;**11**:995–1003. https://doi.org/10.1111/j.1461-0248.2008.01229.x

Losos JB. *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles.* Berkeley, CA: University of California Press, 2011.

Meiri S, Brown JH, Sibly RM. The ecology of lizard reproductive output. *Global Ecology and Biogeography* 2012;**21**:592–602. https://doi.org/10.1111/j.1466-8238.2011.00700.x

Meiri S, Bauer AM, Chirio L *et al*. Are lizards feeling the heat? A tale of ecology and evolution under two temperatures. *Global Ecology and Biogeography* 2013;**22**:834–45.

Meiri S, Feldman A, Kratochvíl L. Squamate hatchling size and the evolutionary causes of negative offspring size allometry. *Journal of Evolutionary Biology* 2015;**28**:438–46. https://doi.org/10.1111/jeb.12580

Meiri S, Avila L, Bauer AM *et al*. The global diversity and distribution of lizard clutch sizes. *Global Ecology and Biogeography* 2020;**29**:1515–30.

Mendyk RW. Life expectancy and longevity of varanid lizards (Reptilia: Squamata: Varanidae) in North American zoos. *Zoo Biology* 2015;**34**:139–52. https://doi.org/10.1002/zoo.21195

Mesquita DO, Colli GR. Life history patterns in South American tropical lizards. In: Gallegos OH, Cruz FRM, Sánchez JFM (eds), *Reproducción en Reptiles: Morfología, Ecología y Evolución.* México: Universidad Autónoma del Estado de México, 2010, 45–71.

Mesquita DO, Costa GC, Figueredo AS *et al*. The autecology of *Anolis brasiliensis* (Squamata, Dactyloidae) in a Neotropical savanna. *The Herpetological Journal* 2015;**25**:233–44.

Mesquita DO, Costa GC, Colli GR *et al*. Life-history patterns of lizards of the world. *The American Naturalist* 2016a;**187**:689–705. https://doi.org/10.1086/686055

Mesquita DO, Faria RG, Colli GR *et al*. Lizard life-history strategies. *Austral Ecology* 2016b;**41**:1–5.

Moeller KT, Demare G, Davies S *et al*. Dehydration enhances multiple physiological defense mechanisms in a desert lizard, *Heloderma suspectum*. *The Journal of Experimental Biology* 2017;**220**:2166–74. https://doi.org/10.1242/jeb.150367

O'Meara BC, Beaulieu JM. Modelling stabilizing selection: the attraction of Ornstein–Uhlenbeck models. In: Garamszegi LZ (ed.), *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice*. Berlin: Springer, 2014, 381–93.

Oliveira BHS, Queiroz RNM, Cavalcanti LBQ *et al*. Autecology of Neotropical lizard species *Anotosaura vanzolinia* (Squamata, Gymnophthalmidae) in a Caatinga region, north-eastern Brazil. *Herpetological Journal* 2018;**28**:19–26.

Oliveira BHS, Colli GR, Vitt LJ *et al*. Evolution of fossoriality in microteiid lizards. *Zoological Journal of the Linnean Society* 2024;**201**:1–11.

Orme D, Freckleton R, Thomas G *et al*. *Caper: Comparative Analyses of Phylogenetics and Evolution in R. R package version 0.5.2*. 2013. http://CRAN.R-project.org/package=caper (June 2024, date last accessed).

Overall KL. Lizard egg environments. In: Vitt LJ, Pianka ER (eds), *Lizard Ecology: Historical and Experimental Perspectives*. Princeton, NJ: Princeton University Press, 1994, 403.

Padilla Perez DJ, de Carvalho JE, Navas CA. Effects of food intake and hydration state on behavioral thermoregulation and locomotor activity in the tropidurid lizard *Tropidurus catalanensis*. *Journal of Experimental Biology* 2021;**224**:jeb242199. https://doi.org/10.1242/jeb.242199

Pagel M. Inferring the historical patterns of biological evolution. *Nature* 1999;**401**:877–84. https://doi.org/10.1038/44766

Pearson SK, Godfrey SS, Bull CM *et al*. Larger lizards live longer in the group-living *Egernia stokesii*. *Australian Journal of Zoology* 2016;**64**:182–91. https://doi.org/10.1071/zo16024

Pianka ER. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. *Ecology* 1970;**51**:703–20. https://doi.org/10.2307/1934053

Pianka ER, Vitt LJ. *Lizards: Windows to the Evolution of Diversity*. Berkeley, CA: University of California Press, 2003.

Pinheiro F, Diniz IR, Coelho D *et al*. Seasonal pattern of insect abundance in the Brazilian cerrado. *Austral Ecology* 2002;**27**:132–6. https://doi.org/10.1046/j.1442-9993.2002.01165.x

Presch W. Evolutionary history of the South-American microteiid lizards (Teiidae, Gymnophthalminae). *Copeia* 1980;**1980**:36–56. https://doi.org/10.2307/1444132

Pyron RA, Burbrink FT. Early origin of viviparity and multiple reversions to oviparity in squamate reptiles. *Ecology Letters* 2014;**17**:13–21. https://doi.org/10.1111/ele.12168

R Core Team. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. 2021. https://www.R-project.org/.

Radder RS, Shine R. Why do female lizards lay their eggs in communal nests? *The Journal of Animal Ecology* 2007;**76**:881–7. https://doi.org/10.1111/j.1365-2656.2007.01279.x

Ramiro CN, Junior MT, Rodrigues MT. Reproductive biology of three sympatric species of gymnophthalmid lizards from the sand dunes of the middle São Francisco River, Bahia, Brazil. *South American Journal of Herpetology* 2017;**12**:76–88. https://doi.org/10.2994/sajh-d-16-00044.1

Revell LJ. phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 2012;**3**:217–23. https://doi.org/10.1111/j.2041-210x.2011.00169.x

Revell LJ, Harmon LJ, Collar DC. Phylogenetic signal, evolutionary process, and rate. *Systematic Biology* 2008;**57**:591–601. https://doi.org/10.1080/10635150802302427

Ricklefs R, Relyea R. *A Economia da Natureza*. Rio de Janeiro: Guanabara Koogan, 2016.

Roff DA. *The Evolution of Life Histories: Theory and Analysis*. New York, NY: Chapman & Hall, 1992.

Roff DA. *Life History Evolution*. Sunderland, MA: Sinauer Associates, 2002.

Shine R. The evolution of viviparity in reptiles: an ecological analysis. In: Gans C, Billet F (eds), *Biology of the Reptilia*. New York, NY: John Wiley & Sons, 1985, 605–94.

Shine R. Life-history evolution in reptiles. *Annual Review of Ecology, Evolution, and Systematics* 2005;**36**:23–46. https://doi.org/10.1146/annurev.ecolsys.36.102003.152631

Shine R, Greer AE. Why are clutch sizes more variable in some species than in others? *Evolution* 1991;**45**:1696–706. https://doi.org/10.1111/j.1558-5646.1991.tb02675.x

Siedchlag AC, Benozzati ML, Passoni JC *et al*. Genetic structure, phylogeny, and biogeography of Brazilian eyelid-less lizards of genera *Calyptommatus* and *Nothobachia* (Squamata, Gymnophthalmidae) as inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 2010;**56**:622–30. https://doi.org/10.1016/j.ympev.2010.04.027

Silva-Neta AF, Matias CSL, Avila RW. Autecology of the lizard *Colobosauroides cearensis* (Squamata: Gymnophthalmidae) from Brazilian semiarid Caatinga. *Phyllomedusa* 2019;**18**:209–23.

Souza SM, Pellegrino KCM, Nunes PMS *et al*. On the discovery of bisexual populations of the parthenogenetic lizard *Leposoma percarinatum* (Gymnophthalmidae), with insights into the origin of parthenogenesis in *Leposoma*. *South American Journal of Herpetology* 2015;**10**:121–31.

Stearns SC. Trade-offs in life-history evolution. *Functional Ecology* 1989;**3**:259–68. https://doi.org/10.2307/2389364

Stearns SC. *The Evolution of Life Histories*. Oxford: Oxford University Press, 1992.

Thompson MB, Speake BK. Energy and nutrient utilisation by embryonic reptiles. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 2002;**133**:529–38. https://doi.org/10.1016/s1095-6433(02)00188-5

Tieleman BI, Williams JB, Bloomer P. Adaptation of metabolism and evaporative water loss along an aridity gradient. *Proceedings Biological Sciences* 2003;**270**:207–14. https://doi.org/10.1098/rspb.2002.2205

Tinkle DW, Wilbur HH, Tilley SG. Evolutionary strategies in lizard reproduction. *Evolution* 1970;**24**:55–74.

Title PO, Singhal S, Grundler MC *et al*. The macroevolutionary singularity of snakes. *Science* 2024;**383**:918–23. https://doi.org/10.1126/science.adh2449

Uetz P, Freed P, Aguilar R *et al*. *The Reptile Database*. 2024. http://www.reptile-database.org (June 2024, date last accessed).

Van Sluys M. Seasonal variation in prey choice by the lizard *Tropidurus itambere* Tropiduridae in southeastern Brazil. *Ciencia e Cultura* 1995;**47**:61–5.

Vasconcellos A, Andreazze R, Almeida AM *et al*. Seasonality of insects in the semi-arid Caatinga of northeastern Brazil. *Revista Brasileira de Entomologia* 2010;**54**:471–6. https://doi.org/10.1590/s0085-56262010000300019

Vásquez-Restrepo JD, Diago-Toro MF. Alice in Lizardland: exploring the spatiotemporal speciation and morphological evolutionary rates in the highly diverse microteiid lizards (Squamata: Gymnophthalmidae). *Biological Journal of the Linnean Society* 2023;**142**:208–19. https://doi.org/10.1093/biolinnean/blad127

Vásquez-Restrepo JD, Ribeiro-Júnior MA, Sánchez-Pacheco SJ. Once upon a time: exploring the biogeographic history of the largest endemic lizard family in the Neotropics (Squamata: Gymnophthalmidae). *Biological Journal of the Linnean Society* 2024;**143**:blae080.

Vitt LJ. Lizard reproduction: Habitat specificity and constraints on relative clutch mass. *The American Naturalist* 1981;**117**:506–14. https://doi.org/10.1086/283731

Vitt LJ, Caldwell JP. *Herpetology: An Introductory Biology of Amphibians and Reptiles*. London: Academic Press, 2013.

Vitt LJ, Colli GR. Geographical ecology of a neotropical lizard: *Ameiva ameiva* (Teiidae) in Brazil. *Canadian Journal of Zoology* 1994;**72**:1986–2008. https://doi.org/10.1139/z94-271

Vitt LJ, Congdon JD. Body shape, reproductive effort, and relative clutch mass in lizards: Resolution of a paradox. *The American Naturalist* 1978;**112**:595–608. https://doi.org/10.1086/283300

Vitt LJ, Pianka ER. Deep history impacts present-day ecology and biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* 2005;**102**:7877–81. https://doi.org/10.1073/pnas.0501104102

Vitt LJ, Price HJ. Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica* 1982;**38**:237–55.

Vitt LJ, Pianka ER, Cooper WE *et al*. History and the global ecology of squamate reptiles. *The American Naturalist* 2003;**162**:44–60. https://doi.org/10.1086/375172

Winemiller KO. Life-history strategies and the effectiveness of sexual selection. *Oikos* 1992;**63**:318–27. https://doi.org/10.2307/3545395

Winemiller KO, Rose KA. Patterns of life-history diversification in north american fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 1992;**49**:2196–218. https://doi.org/10.1139/f92-242