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# High-elevation females lay larger eggs in the Atlas Day Gecko, *Quedenfeldtia trachyblepharus* (Boettger, 1873)

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## Abstract

Identifying how reproductive investment varies along elevational gradients is a powerful tool for understanding life-history evolution in ectotherms. In taxa with invariant clutch size, reproductive responses to harsh environments are expected to be determined by per-offspring investment (egg provisioning), while at the same time being subject to maternal body size effects. We investigated elevational variation in reproductive traits of the Atlas Day Gecko, *Quedenfeldtia trachyblepharus*, a diurnal high-mountain species endemic to the High Atlas Mountains (Morocco). Maternal body size increased with elevation, indicating larger females at higher sites. Egg mass and egg volume increased with maternal body size, whereas relative clutch mass (RCM) declined with female size. Importantly, high-elevation females produced larger eggs than expected for their body size. Hatchling size and body condition were positively associated with egg traits, but elevation did not explain additional variation in hatchling traits once egg traits were considered. Overall, the differences observed in offspring traits appear to be mediated by maternal egg provisioning, consistent with increased per-offspring investment that may enhance offspring survival in high-elevation environments.

## Key Words

alpine gecko, egg size, hatchling size, High Atlas, maternal size, relative clutch mass

## Introduction

Life-history variation in reptiles reflects natural selection on energy allocation to growth, survival, and reproduction strategies across heterogeneous environments. Along latitudinal and elevational gradients, populations often diverge in maternal investment and in the maternal effects shaping offspring phenotype at birth, consistent with both local adaptation and phenotypic plasticity (Doughty 1996; Bonnet et al. 2000; Kratochvíl and Frynta 2006; Uusi-Heikkilä et al. 2012; Slavenko et al. 2019).

Elevational gradients provide powerful natural experiments because they generate predictable shifts in temperature regimes, season length, food availability, and predation pressure, thereby shaping activity seasons and the time window available for reproduction (Grant and Dunham 1990; Mathies and Andrews 1995; Zamora-Camacho et al. 2013). In response to these environmental shifts, populations are expected to diverge in reproductive traits and strategies (Ballinger 1979; Meiri et al. 2020; Wise and Jaeger 2021). For example, in cold environments, reproductive females may partially buffer

embryos from suboptimal or variable thermal conditions through behavioural thermoregulation and microhabitat selection (i.e., maternal manipulation), thereby influencing developmental trajectories and offspring phenotype (Le Henanff et al. 2013; Feldman et al. 2016). However, these patterns are not universal because elevation integrates multiple ecological dimensions, and reproductive responses are constrained by lineage-specific traits, including transitions to viviparity (Shine 1983; Blackburn 2000). Thus, many oviparous lineages persist in cold environments and may instead adjust nesting behaviour (e.g., Blouin-Demers et al. 2004; Pike et al. 2010), reproductive timing (e.g., Olsson and Shine 1997; Warner and Shine 2007), and egg provisioning (e.g., Deme et al. 2022) to cope with thermal and seasonal limitations.

In oviparous reptiles, female body size often predicts reproductive investment because it constrains abdominal volume and energetic capacity, thereby shaping egg size, clutch size, or both (Bonnet et al. 2000; Kratochvíl and Frynta 2006; Martins et al. 2022; Lourdais et al. 2024). This size dependence is particularly relevant in taxa with invariant clutch size, where the classical offspring size–number trade-off is expressed primarily through egg size rather than clutch size (Goodman 2006; Kratochvíl and Frynta 2006). In geckos (clade Gekkota), egg dimensions and mass can vary among females, populations, and environments, providing a key pathway through which mothers modulate offspring traits (Sakai 2021). Egg size, in turn, is a major determinant of hatchling size and condition, with potential consequences for early energy reserves, growth, and survival (VanDamme et al. 1992; Iraeta et al. 2006; Le Henanff et al. 2013). Understanding how elevation and maternal size jointly shape egg provisioning therefore offers a mechanistic link between environmental gradients and early-life fitness components.

The Atlas Day Gecko, *Quedenfeldtia trachyblepharus* (Boettger, 1873), is a cold-adapted, diurnal gecko whose activity and reproduction are constrained by seasonal thermal conditions in the High Atlas Mountains of Morocco (Bouazza et al. 2016). Early in the activity season, field body temperatures are typically below the preferred range ($T_{pref} \approx 29.5$–$31.5$ °C), whereas individuals reach or remain within $T_{pref}$ mainly in late spring (Bouazza et al. 2016). The species occurs from approximately 1,400 m to > 4,000 m, offering a natural gradient for testing how high-mountain conditions shape variation in maternal traits and egg provisioning. Although elevational divergence in reproductive traits has been documented in several lizard clades (Mathies and Andrews 1995; Iraeta et al. 2006; Rodríguez-Díaz and Braña 2012; Deme et al. 2022), few studies have examined variation in egg and hatchling traits across elevation in oviparous geckos with invariant clutch size.

Here, we examine how maternal body size and elevation of origin jointly relate to reproductive traits in *Q. trachyblepharus*. We quantified egg mass, egg volume, and relative clutch mass (RCM) in females sampled across five elevation classes (1,900–3,000 m) in the High Atlas Mountains and tested whether elevation explains variation in these traits. To link maternal investment to early offspring traits, we also measured hatchling size and body condition after incubation under standardized laboratory conditions. Our main question is whether high-elevation environments are associated with shifts in maternal size and/or per-offspring investment (egg traits), and whether such shifts translate into predictable variation in hatchling traits. We predicted that (i) consistent with Bergmann's rule, females from higher elevations would exhibit larger body size and enhanced body condition. Given the invariant clutch size of geckos, we further predicted that (ii) maternal investment–egg mass, egg volume, and relative clutch mass (RCM) would vary among elevations, reflecting increased per-offspring investment under the shorter activity seasons and thermal constraints characteristic of high-altitude environments.

# Materials and methods

## Study sites and husbandry

From April–June 2014, we captured 51 gravid female Atlas Day Geckos at five sites located at approximately 1,900, 2,100, 2,600, 2,750, and 3,000 m asl in the vicinity of Oukaimeden, High Atlas Mountains, Morocco (Fig. 1). The High Atlas climate is cold temperate, with annual precipitation of approximately 500–600 mm. Mean monthly temperatures range from ~22 °C in the warmest month to ~ – 5 °C in the coldest month, and snowfall occurs mainly between November and March (Bouazza et al. 2016).

Individuals were captured by hand or using a noose while basking during the day. At capture and again at oviposition, we measured snout–vent length (SVL; 0.1 mm, digital calipers; CAD-1, Barcelona, Spain) and body mass (0.001 g, electronic balance; KERN ABS-N, Balingen, Germany). Females were housed individually in plastic terraria (Fauna box; 30 × 20 × 20 cm) with a sand substrate and shelters. The room was maintained at 22 ± 2 °C, and basking heat was provided by a 60 W spotlight placed at one end of each enclosure, creating a thermal gradient of approximately 22–40 °C. Photoperiod was set to 14L:10D; water was provided ad libitum, and females were fed mealworms every two days until oviposition. Post-oviposition mass was recorded within 24 h of laying. Within a few days after oviposition, all females were released at their exact capture sites.

## Egg and hatchling traits

We measured each egg's dimensions (length and width) to the nearest 0.01 mm and weighed them to an accuracy of 0.001 g. For further size measurements of these fragile eggs and subsequent hatchlings, we used imaging software (Inkscape, GNU General Public Licence), with a calibration scale included in each image. Eggs were

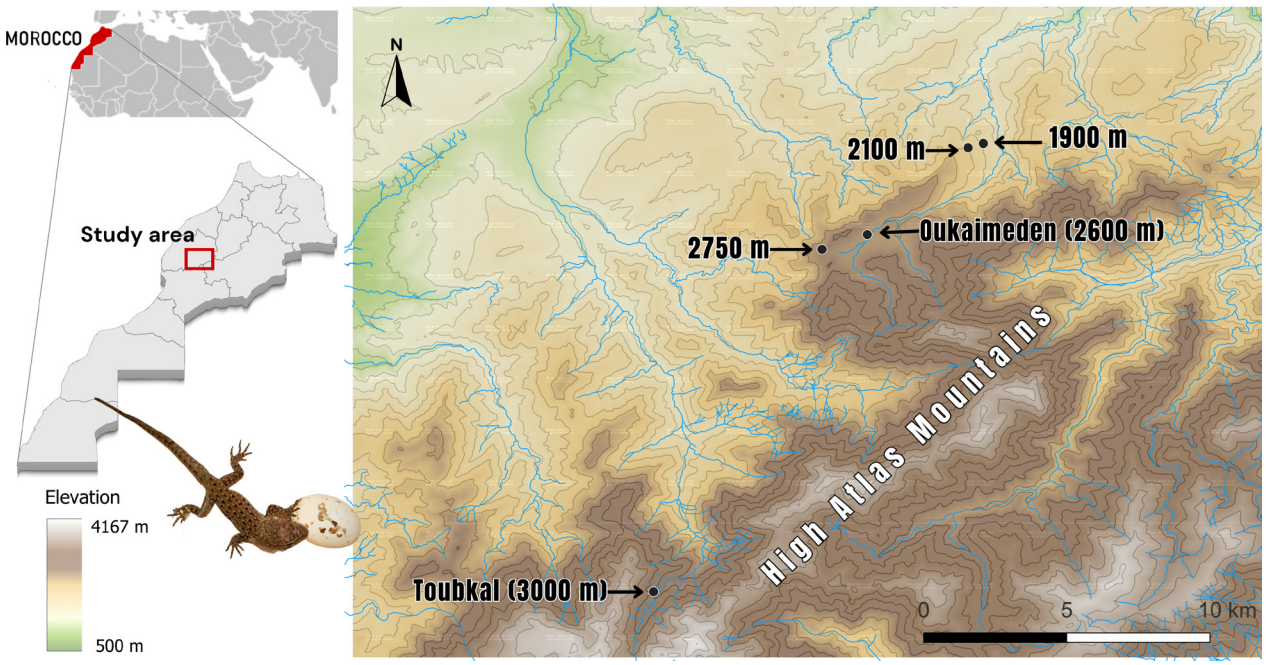


**Figure 1.** Location of the five sampling sites along an elevational gradient (1,900–3,000 m) in the High Atlas Mountains, Morocco.

incubated in moist vermiculite within a temperature-controlled climatic chamber (Pol-eko Aparatura, Wodzisław Śląski, Poland). Two incubation temperatures (24 °C and 29 °C) were initially used to encompass plausible nest temperatures for the species (Bouazza et al., unpublished data) and facilitate comparison with previous studies in lizards (e.g. Le Henanff et al. 2013). However, no eggs hatched at 24 °C; consequently, all hatchling analyses are based solely on eggs incubated at 29 °C. Within 24 h of hatching, we measured hatchling SVL (to the nearest 0.1 mm) and body mass (to the nearest 0.001 g).

Egg volume ($mm^3$) was calculated as $V = (\pi/6) \times L \times W^2$, where $L$ is egg length and $W$ is egg width (Maritz and Douglas 1994). Because females laid a single egg, clutch mass was equivalent to egg mass. Relative clutch mass (RCM, %) was computed as RCM = (egg mass/post-oviposition mass) × 100. Hatchling body condition was estimated as the residuals from a linear regression of ln(hatchling mass) on ln(hatchling SVL).

## Statistical analyses

All analyses were performed in R (R Core Team) using RStudio (v. 4.5.1). Significance was assessed at $\alpha = 0.05$. We inspected response variables and model residuals for normality (Shapiro–Wilk test) and homogeneity of variance (Levene's test), and applied log-transformations when needed. Competing models were compared using Akaike's Information Criterion (AIC) and likelihood-ratio tests. Pearson correlations were used to quantify bivariate relationships among continuous traits (e.g., maternal SVL vs. egg traits).

To test for elevational variation in reproductive and hatchling traits, we fitted linear mixed-effects models with elevation class as a fixed factor, maternal SVL as a covariate for size-dependent traits, and site as a random effect (random intercept). We evaluated the effect of elevation by comparing nested models with and without the elevation term and conducted post hoc pairwise comparisons among elevation classes using Tukey-adjusted tests. For size-adjusted comparisons, we calculated residuals from regressions of egg mass, egg volume, and relative clutch mass (RCM) on maternal SVL.

# Results

## Maternal body size and reproductive output across elevation

Maternal body size and body mass differed among the five elevation classes (Table 1). Female SVL increased with elevation ($r = 0.48$, $p < 0.001$) indicating that females were generally larger at higher sites. Maternal body mass also increased with elevation and this pattern persisted after controlling for maternal size ($r = 0.34$, $p = 0.011$). The smallest gravid female measured 35.7 mm SVL. All ovipositing females produced a single egg (clutch size = 1). Hatching success was 91% at 29 °C, and incubation lasted 42–51 days (mean 45.4 ± 0.47, n = 18).

## Elevational variation in egg traits

Egg mass and egg volume were significantly affected by maternal SVL, with larger females having heavier ($r = 0.62$, $p < 0.001$) and larger eggs ($r = 0.52$, $p < 0.001$). Egg mass and egg volume differed significantly between sampled sites (egg mass: $F_{4,45} = 17.04$, $p < 0.0001$; egg

**Table 1.** Summary of results on the effect of elevation origin on maternal body size and reproductive traits of *Quedenfeldtia trachyblepharus* in the High Atlas of Morocco. Values are mean ± SE (n). Linear mixed effect models with maternal SVL as a covariate were used to remove the effect of maternal body size on reproductive traits. Hatchling traits and incubation time include only eggs incubated at 29 °C. Means with different superscripts differed significantly. Bold font indicates a significant difference.

| Trait | 1,900 m | 2,100 m | 2,600 m | 2,750 m | 3,000 m | Elevation effect |
|---|---|---|---|---|---|---|
| **Gravid female SVL (mm)** | $40.44^{a} \pm 0.57$ (16) | $41.83^{ab} \pm 0.72$ (3) | $41.54^{ab} \pm 0.46$ (17) | $44.32^{b} \pm 0.60$ (13) | $45.02^{b} \pm 0.92$ (2) | $F_{4,47} = 4.03$, ***p* = 0.006** |
| **Gravid female mass (g)** | $1.78^{a} \pm 0.06$ (16) | $1.89^{ab} \pm 0.12$ (3) | $2.05^{ab} \pm 0.07$ (17) | $2.33^{b} \pm 0.08$ (13) | $2.22^{b} \pm 0.04$ (2) | $F_{4,47} = 4.03$, ***p* = 0.006** |
| **Gravid female BC** | $-0.032^{a} \pm 0.024$ (16) | $0.110^{a} \pm 0.073$ (3) | $-0.003^{a} \pm 0.025$ (18) | $0.015^{a} \pm 0.021$ (15) | $0.008^{a} \pm 0.001$ (2) | $F_{4,49} = 1.55$, $p = 0.203$ |
| **Post-oviposition mass (g)** | $1.52^{a} \pm 0.05$ (16) | $1.59^{a} \pm 0.06$ (3) | $1.73^{a} \pm 0.05$ (17) | $1.96^{a} \pm 0.06$ (13) | $2.06^{a} \pm 0.04$ (2) | $F_{4,46} = 1.93$, p = 0.12 |
| **Relative clutch mass (RCM, %)** | $19.22^{ab} \pm 0.48$ (14) | $18.89^{a} \pm 0.62$ (3) | $17.41^{a} \pm 0.45$ (17) | $16.92^{b} \pm 0.39$ (13) | $21.18^{b} \pm 0.11$ (2) | $F_{4,41} = 8.29$, ***p* < 0.001** |
| **Egg mass (g)** | $0.336^{a} \pm 0.008$ (14) | $0.352^{a} \pm 0.010$ (3) | $0.401^{ab} \pm 0.009$ (17) | $0.456^{c} \pm 0.010$ (13) | $0.537^{d} \pm 0.018$ (2) | $F_{4,41} = 14.12$, ***p* < 0.001** |
| **Egg volume ($mm^3$)** | $450.31^{a} \pm 12.08$ (16) | $479.62^{a} \pm 14.73$ (3) | $560.44^{ab} \pm 13.01$ (17) | $628.92^{c} \pm 14.37$ (13) | $717.53^{d} \pm 57.50$ (2) | $F_{4,43} = 10.54$, ***p* < 0.001** |
| **Incubation time (days)** | $46.0^{a} \pm 0.41$ (4) | $45.5^{a} \pm 0.50$ (2) | $45.2^{a} \pm 0.36$ (5) | $44.8^{a} \pm 0.31$ (4) | $43.0^{a}$ (1) | $F_{4,12} = 1.33$, $p = 0.315$ |
| **Hatchling SVL (mm)** | $20.29^{a} \pm 0.54$ (4) | $20.85^{a} \pm 0.61$ (2) | $21.14^{a} \pm 0.49$ (5) | $21.62^{a} \pm 0.44$ (4) | $21.85^{a}$ (1) | $F_{4,11} = 0.443$, $p = 0.775$ |
| **Hatchling body condition (BC)** | $0.012^{a} \pm 0.021$ (4) | $0.028^{a} \pm 0.026$ (2) | $0.054^{a} \pm 0.019$ (5) | $0.071^{a} \pm 0.022$ (4) | $0.10^{a}$ (1) | $F_{4,11} = 1.223$, $p = 0.356$ |

volume: $F_{4,47} = 14.32$, $p < 0.001$), and this difference did not disappear even after the effect of maternal SVL had been removed (Tables 1, 2, Fig. 2A). Egg mass residuals and egg volume residuals were correlated with elevation gradient (egg mass: r = 0.29, $p = 0.04$, egg volume: r = 0.32; $p = 0.02$).

Relative clutch mass (RCM) decreased with maternal SVL (r = – 0.36, p = 0.009) and varied among elevations, as shown by variation in residual RCM among elevation (Tables 1, 2, Fig. 2B). However, RCM residuals did not correlate with the elevational gradient (r = 0.042, p = 0.77).

## Variation in hatchling traits

Hatchling SVL increased with egg mass (r = 0.78, p = 0.0005) and egg volume (r = 0.5, p = 0.03). When maternal SVL and egg traits were included in the same model, the effect of maternal size was only marginal (p = 0.09), suggesting that the relationship between maternal size and hatchling size was largely mediated through egg provisioning. Elevation did not explain additional variation in hatchling SVL (Tables 1, 2).

Hatchling body condition (BC) also increased with egg mass (r = 0.47, p = 0.046) and, more strongly, with egg volume (r = 0.65, p = 0.003). Elevation did not contribute additional explained variance in hatchling body condition (Tables 1, 2).

**Table 2.** Statistical significance of different models for the effect of elevation on maternal body size and reproductive traits of *Quedenfeldtia trachyblepharus* in the High Atlas Mountains of Morocco. Bold font indicates a significant difference.

| Trait | Best model | AIC | $\chi^2$ | p-value |
|---|---|---|---|---|
| Gravid female SVL (mm) | ~ Elevation | 238.19 | 15.77 | **0.003** |
| Gravid female mass (g) | ~ maternal SVL + Elevation | -27.11 | 14.39 | **0.006** |
| Post-oviposition mass (g) | ~ maternal SVL + Elevation | -32.60 | 8.39 | 0.078 |
| Relative clutch mass (RCM, %) | ~ maternal SVL + Elevation | 240.31 | 18.74 | **0.0008** |
| Egg mass (g) | ~ maternal SVL + Elevation | -190.34 | 41.28 | **<0.0001** |
| Egg volume ($mm^3$) | ~ maternal SVL + Elevation | 568.26 | 35.28 | **<0.0001** |
| Incubation time (days) | ~ maternal SVL + Elevation | 81.71 | 4.65 | 0.32 |
| Hatchling SVL (mm) | ~ maternal SVL + Elevation | 43.46 | 2.45 | 0.65 |
| Body condition (BC) | ~ maternal SVL + Elevation | -34.48 | 6.62 | 0.15 |

# Discussion

Our results revealed significant among-population differences in maternal body size, egg size, and relative clutch mass (RCM) in *Quedenfeldtia trachyblepharus* along an elevational gradient. Our finding that high-elevation females produced larger and heavier eggs is consistent with our predictions. These findings also suggest that females increase per-offspring investment in high-elevation populations, likely reflecting environmental differences along the gradient.

Maternal body size increased with elevation, consistent with previous work showing that *Q. trachyblepharus* from higher altitudes tend to have larger body size, because higher elevation habitats provide this alpine gecko with a sort of "refuge" from competition, allowing for greater maternal investment to ensure better body conditions (Comas et al. 2014; Comas 2020). Geographic patterns in lizard body size are often related to local environmental conditions, and factors such as resource abundance may promote larger female body size, aligning with broader patterns linking growth and reproductive investment (Sebens 2003). In lizards, variation in maternal body size is influenced mainly by seasonal limitations of food resources, which can restrict growth (Adolph and Porter 1996; Iraeta et al. 2006). Alternatively, between-population variation in maternal body size may have evolved during adaptive radiation and changing climate conditions in different localities (Angilletta 2009).

Maternal body size is one of the primary traits that directly or indirectly influences life-history traits in organisms, leading to covariation among fitness-related traits, including egg traits (Kratochvíl and Frynta 2006; Slavenko et al. 2019; Wise and Jaeger 2021). In our study, egg mass and egg volume increased with maternal SVL, consistent with the positive association between maternal size and offspring quality reported in geckos and other lizards with fixed clutch size (Goodman 2006; Kratochvíl

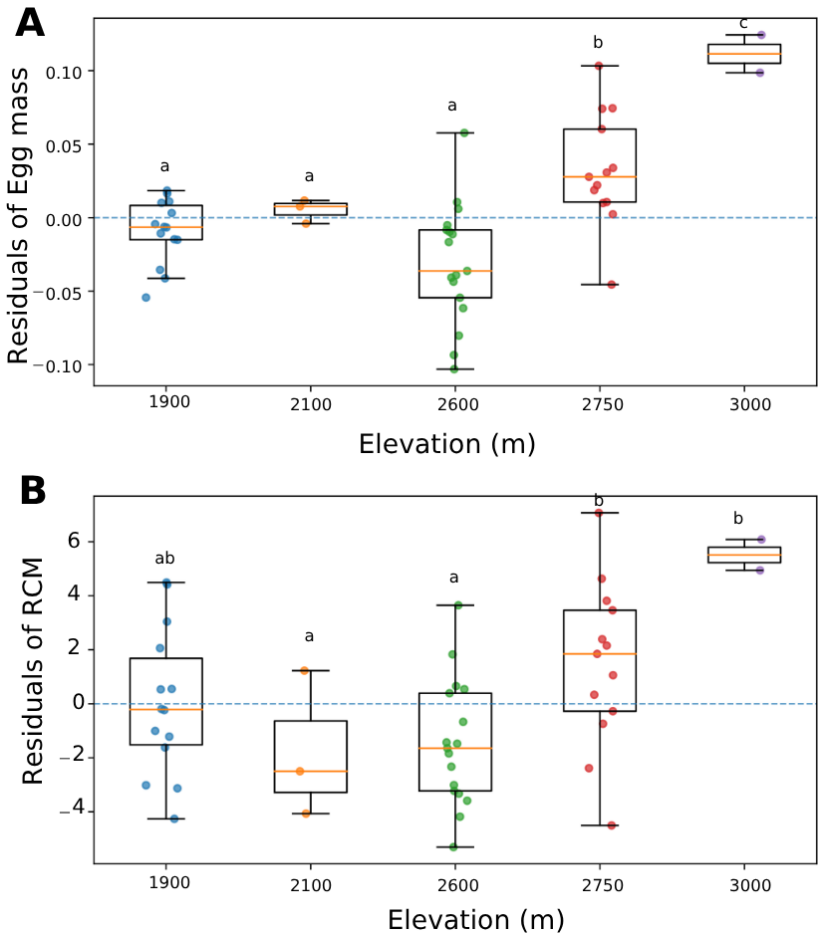


**Figure 2.** Elevational variation in size-adjusted egg traits in *Quedenfeldtia trachyblepharus*. **A.** Residual egg mass; **B.** residual relative clutch mass (RCM). Residuals were calculated from regressions against maternal snout–vent length. Different letters indicate statistically significant differences among elevations based on Tukey's post hoc tests; groups sharing the same letter are not significantly different.

and Frynta 2006; Schwarz and Meiri 2017; Sakai 2021). However, relative clutch mass (RCM) declined with female size, indicating negative allometry in reproductive allocation. This relationship may make female reproductive output susceptible to age because lizards show indeterminate growth (Vitt and Congdon 1978; Shine 1992). In *Q. trachyblepharus*, however, maternal body size is not the only determinant of reproductive traits (egg mass/egg volume/RCM), because among-population differences in reproductive traits persisted after controlling for maternal SVL. Previous studies on lizard species have shown that variation in reproductive output can be site-specific, depending on the size of reproductive females and their energy storage capacity (Roitberg et al. 2013). Therefore, reproductive traits among populations of *Q. trachyblepharus* may be driven by the interplay between intrinsic factors (e.g., body size and age) and extrinsic factors (e.g., local environmental conditions) (Comas et al. 2014; Comas 2020).

As we predicted, females produced larger eggs at higher elevations, and egg traits were key predictors of hatchling phenotype. Hatchling size and body condition were positively associated with egg traits (egg mass and egg volume). Egg size is often a close proxy for the total resources allocated to embryonic development, which may influence neonatal condition (Le Henanff et al. 2013). Similar patterns have been observed in lizards with variable clutch size, where females produce smaller clutches of larger eggs at high elevations (Deme et al. 2022). These results are consistent with the idea that environmental constraints in the Atlas Mountains (e.g., low temperatures and short activity seasons) shift female reproductive allocation per offspring investment (i.e. from offspring quantity to offspring quality), when time for growth is limited and larger offspring gain survival or performance advantages (see Andrews et al. 2000; Uller and Olsson 2010; Le Henanff et al. 2013). In contrast, elevation did not explain additional variation in hatchling SVL or body condition once egg traits were considered, suggesting that elevational effects on hatchlings operate mainly through maternal provisioning rather than direct population differences in hatchling phenotype.

The observed elevational patterns in life-history traits may also be influenced by other biotic and abiotic factors associated with geographic distance between studied populations, beyond temperature directly linked to elevation. Unfortunately, we currently do not have detailed information on biotic factors such as prey availability and

predation pressure for each population. Future work combining nest microclimate monitoring, maternal body condition, and incubation under fluctuating thermal regimes, followed by measurements of post-hatching growth and ecophysiological traits (e.g., early thermal preference and performance), would clarify the mechanisms and fitness consequences of increased egg size at high elevation (see Iraeta et al. 2006).

In conclusion, our findings highlight how maternal size-dependent allocation and elevational context jointly shape reproductive output in a high-mountain gecko. Larger eggs at high elevation, independent of maternal size, underscore the potential importance of maternal provisioning as a pathway linking environmental constraint to offspring traits. However, understanding whether these shifts along elevational gradients are driven only by environmental conditions or reflect genetically based local adaptation requires further investigation.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

All fieldwork complied with Moroccan regulations, and animal collection and handling were authorized by the Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification (HCEFLCD), Rabat, Morocco (permit no. 05-13 HCEFLCD/DLCDPN/CFF), in coordination with the Faculty of Sciences, Cadi Ayyad University (Marrakech).

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The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
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### Author contributions

Conceptualization: OL, AL, AB, GBD. Data curation: AL, AB. Formal analysis: GBD, AB, OL. Investigation: AB, AL. Methodology: AB, GBD, OL. Project administration: EHEM. Resources: EHEM. Software: AB. Supervision: AB. Validation: OL, AB, GBD. Writing - original draft: AL, AB. Writing - review and editing: GBD, OL, AB.

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### Data availability

All data supporting the findings of this study are provided in the main text..