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Effects of reproductive condition on body mass and thermal ecology in the female Mesquite Lizard, *Sceloporus grammicus*, in a population from central Mexico

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Abstract

Reproductive condition influences ecophysiological traits in viviparous female lizards, which may have various effects on their fitness. In this study, the effects of reproductive condition on body mass and thermal ecology were evaluated in females from a central Mexico population of *Sceloporus grammicus*. Sampling was conducted during pregnancy and postpartum periods, recording body mass, snout-vent length (SVL), body temperature, and substrate and air temperatures. The data were analyzed using linear mixed and general linear models to evaluate differences between reproductive conditions. The study included repeated measurements from recaptured individuals, allowing intra-individual comparisons across reproductive conditions. After controlling for body size, pregnant females had a significantly higher body mass than postpartum females. Despite this higher mass, pregnant females had a significantly lower body temperature than postpartum females. These results suggest that changes in body mass and thermal ecology are associated with the reproductive condition of *S. grammicus* females.

Key Words

body mass, physiology, pregnancy, reproductive stage, thermoregulation

Introduction

Reptile reproduction involves significant energetic costs that can be reflected in ecophysiological changes in individuals (Muñoz Nolasco 2015; Stellatelli et al. 2024). In viviparous lizards, pregnancy can affect locomotor ability, thermoregulation, behavior, and escape success (Altamirano Álvarez et al. 2015). For example, pregnant females modify their thermoregulatory behavior to maintain optimal temperatures during gestation (Angilletta et al. 2000). However, this behavior may result in pregnant females thermoregulating at lower, higher, or similar body temperatures compared with non-pregnant females, depending on the species and environmental conditions (Woolrich-Piña et al. 2006).

Body mass during pregnancy, however, has consistent, direct effects on females because the embryonic load substantially increases the female's mass, reduces locomotor capacity, limits activity time, and increases vulnerability to predation, thereby affecting survival (Domínguez-López et al. 2018; Suárez-Varón et al. 2024). In this way, the reproductive condition of females is associated with changes in body mass and adjustments in thermal ecology (Andrews et al. 1997; Angilletta et al. 2000; Woolrich-Piña et

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al. 2006), reflecting the energetic and physiological costs of reproduction (Domínguez-López et al. 2018).

Sceloporus grammicus is a lizard with a broad distribution in Mexico (Maciel Mata 2005), found at elevations ranging from 100 to 4,400 m above sea level (m a.s.l.; Domínguez Godoy 2021). These lizards are found in diverse habitats, such as pine-oak forests, shrublands, deserts, and urban areas (Hernández et al. 2024). Some interpopulation variations in reproductive cycles have been documented. For example, in central Mexico, reproduction is seasonal and asynchronous, as males exhibit testicular activity at the end of spring and beginning of summer, whereas females undergo vitellogenesis and ovulation during the summer and early autumn, with births occurring in spring (Guillette and Casas-Andreu 1980; Andrews et al. 1997). *Sceloporus grammicus*, a viviparous species with a gestation period of more than 6 months, is an ideal model for analyzing two contrasting reproductive stages in females: during pregnancy and after birth.

Although previous studies have documented differences in body temperature between pregnant and non-pregnant females in *Sceloporus* (Beuchat 1986; Andrews and Rose 1994), studies in *S. grammicus* have generally compared independent groups of females and shown that pregnant females maintain lower body temperatures than non-pregnant females (Andrews et al. 1997; Woolrich-Piña et al. 2006). However, non-pregnant females may include individuals in different reproductive states (e.g., females that did not reproduce during that season and postpartum females), whereas little is known about thermal changes occurring immediately before and after parturition in free-living females under natural conditions. Additionally, *S. grammicus* inhabits different elevations, suggesting that thermal ecology and physiology may vary among populations across elevational gradients (Lemos-Espinal and Ballinger 1995; González-Morales et al. 2021). Therefore, evaluating females before and after parturition in a high-elevation population, including partially repeated measurements from the same individuals, may provide additional insight into how reproductive condition is associated with thermoregulation and body condition.

In this study, capture-mark-recapture was used to compare the body mass and thermal ecology of pregnant and postpartum *S. grammicus* females from a population in central Mexico. The hypothesis that reproductive condition influences body mass and thermal ecology in females was tested. Pregnant and postpartum females were predicted to differ in body mass and thermoregulatory strategy due to the ecophysiological costs associated with reproduction.

Materials and methods

The study area is located on a property of the Universidad Autónoma del Estado de México in El Cerrillo Piedras Blancas, Toluca de Lerdo, Estado de México, México (19.41181°N, 99.70067°W, datum WGS84, 2605 m a.s.l.). The area has an annual average temperature of 12.8 °C and a subhumid temperate climate with summer rains, and its vegetation is composed of grasslands (Álvarez-Lopeztello et al. 2016). At this site, *S. grammicus* utilizes seedbeds (structures used to cultivate different plant species) as sites to perch, feed, and find shelter.

Females were captured on two dates in 2025: 26 March, corresponding to the end of pregnancy, and 7 May, during the postpartum period. The reproductive condition of females was determined by abdominal palpation (Hernández-Gallegos et al. 2003). Captured females were marked with a unique combination of cauterized scales on the lower jaw, which allowed identification of recaptured individuals (Ekner et al. 2011). For each captured female, body mass was recorded using a Pesola® scale (precision 0.5 g), and snout-vent length (SVL) was measured with a plastic ruler (to the nearest 1 mm). Additionally, a contact thermometer (Fluke model 51 II) was used to measure three temperatures for each female: (1) body temperature (T_b), recorded by inserting the probe 5 mm into the cloaca; (2) substrate temperature (T_s), measured directly on the substrate at the location where the lizard was first observed; and (3) shaded air temperature (T_a), measured immediately above the same location at approximately the observer's chest height. The probe was shaded by the observer's body to avoid direct solar radiation. T_b was recorded within the first 30 seconds of capture; individuals measured after this interval were excluded from the thermal analysis. T_b was measured only in active females, defined as individuals outside their shelters exhibiting behaviors such as thermoregulation, feeding, or perching. To evaluate whether variation in body mass could occur independently of female reproductive condition, adult males at the same locality in March and May 2026 were additionally included as a seasonal reference for comparison with females using identical measurement protocols. Because thermal measurements from males were obtained only from inactive individuals, these data were not directly comparable with those from active females and therefore were not included in the thermal analyses.

Body mass was analyzed using a linear mixed model (LMM) with a normal distribution. Body mass was used as the dependent variable, reproductive condition (pregnant females, postpartum females, male-March, and male-May) and sex as fixed factors, and SVL as a covariate (Harrison et al. 2018). Pairwise comparisons among groups were performed using Tukey-adjusted estimated marginal means. Because body mass can vary with body size, whether including SVL as a covariate improved the model fit was assessed. To do this, a model with SVL and one without this covariate were compared using the Akaike information criterion (AIC; Akaike 1974). The model with the lowest AIC value was considered to have the best fit to the data, and an AIC difference > 2 (ΔAIC > 2) relative to the other model was considered to indicate substantially greater support for that model (Burnham and Anderson 2002). Individual identity was used as a random effect to

control for the non-independence of observations derived from recaptures in both reproductive stages. The models were fitted using restricted maximum likelihood (REML) to obtain unbiased estimates of the variance components. Statistical inference for the fixed effects was evaluated with *t*-tests using Satterthwaite's approximation and the package lmerTest (Kuznetsova et al. 2017) in R v. 4.4.2 (R Core Team 2021).

A general linear model (LM) was used to examine the influence of T_a and T_s on the T_b of females. Because only one female had all three temperatures recorded during both reproductive stages, the data did not support a repeated-measures design; therefore, random effects were not included. Reproductive condition was included as a fixed factor in the linear model, with T_a and T_s as covariates and their interaction, to assess differences in thermoregulatory strategies between reproductive stages. To assess potential collinearity between T_a and T_s, variance inflation factors (VIFs) were calculated, with values < 5 indicating acceptable collinearity (O'brien 2007). After centering the temperature covariates, problematic collinearity was not detected (VIF: T_a = 2.01, T_s = 1.99). Model assumptions were evaluated through visual inspection of residuals. All analyses were conducted in R using the package lme4 for fitting linear mixed models (Bates et al. 2015) and lmerTest (Kuznetsova et al. 2017). Differences between reproductive stages were estimated from marginal means using the package emmeans (Lenth 2022). Effects were considered significant at $p < 0.05$.

Results

During pregnancy, 28 females were captured, whereas during the postpartum stage, 23 females were captured, of which 32% were recaptured (n = 9). In 2026, 13 adult males were captured in March and 14 in May, of which five males were recaptured in May, representing 38.5%. The LMM showed that body mass increased significantly with SVL ($\beta \pm$ SE = 0.26 ± 0.02, df = 67.63, t = 9.67, $p < 0.001$, Table 1, Fig. 1). The model that included SVL showed the lowest AIC value and a better fit (AIC = 241.00) compared with the model without SVL (AIC = 300.04). Because the difference in AIC between models was > 2 (ΔAIC = 59.04), the model with SVL was selected for further analyses. After accounting for SVL and intra-individual variability, reproductive condition had a significant effect on body mass, with pregnant females being, on average, 3.60 g (± 0.28 SE) heavier than postpartum females ($p < 0.001$, Table 1, Fig. 1).

Model predictions indicated that this difference was maintained across the entire range of SVL (Fig. 1). Consistently, estimated marginal means of body mass adjusted for SVL confirmed higher body mass in pregnant females compared with postpartum females (t = 12.75, df = 46.75, $p < 0.0001$, Fig. 2). Male body mass did not differ significantly between sampling months (t = –0.11, df = 40.9, p = 0.99, Fig. 2).

Table 1. Results of the linear mixed model evaluating the effects of reproductive condition, sex, and snout-vent length (SVL) on body mass in the Mesquite Lizard, *Sceloporus grammicus*. Regression coefficients (β), standard errors (SE), t-statistics, and p-values for fixed effects are presented.

Fixed effect	β	SE	df	t	p-value
Intercept	–10.72	1.66	66.99	–6.52	< 0.001
Pregnant	3.60	0.28	46.75	12.75	< 0.001
Male March	1.51	0.39	71.78	3.87	< 0.001
Male May	1.55	0.38	71.86	4.07	< 0.001
Snout-vent length (mm)	0.26	0.02	67.63	9.67	< 0.001

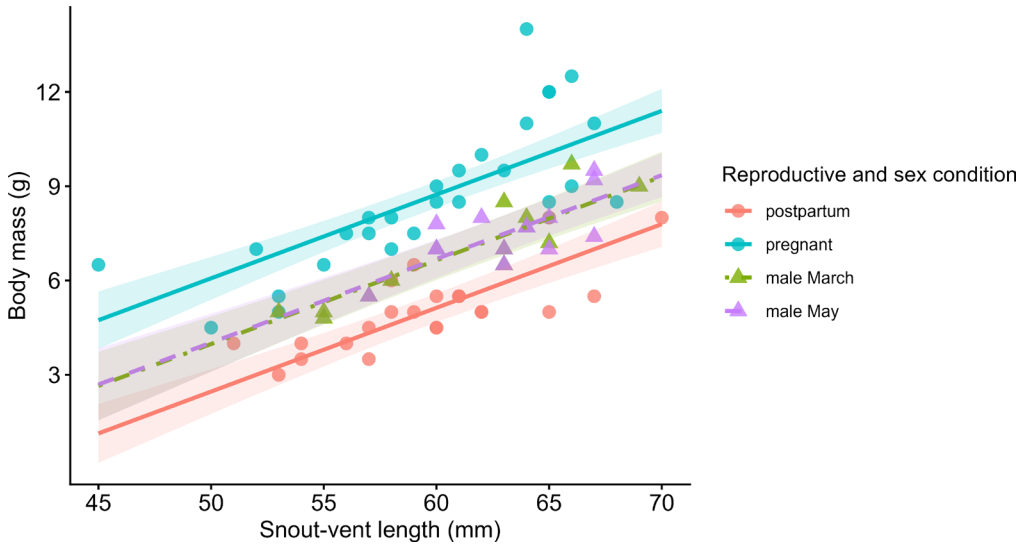


Figure 1. Relationship between snout-vent length (SVL) and body mass in pregnant females, postpartum females, and adult males of the Mesquite Lizard, *Sceloporus grammicus*. Points represent individual observations, lines depict predictions from the linear mixed model, and shaded areas indicate 95% CI.

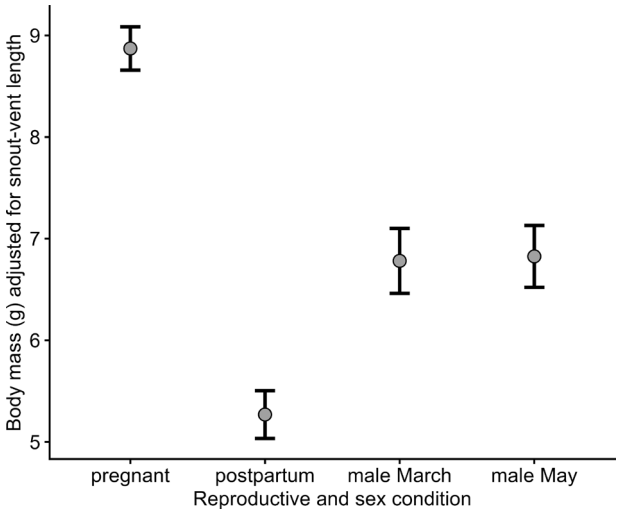


Figure 2. Body mass adjusted for snout-vent length (SVL) in pregnant females, postpartum females, and adult males of the Mesquite Lizard, *Sceloporus grammicus*. Points represent estimated marginal means, and error bars indicate ± 1 SE.

In the analysis of thermal ecology, the LM showed that T_b was influenced by reproductive condition and its interaction with environmental variables. In postpartum females, T_b increased with the T_s, whereas in pregnant females, T_b showed a stronger relationship with T_a (Table 2, Fig. 3). On average, pregnant females ($\bar{X}$ = 30.0 °C) had a body temperature 2.6 °C lower than that of postpartum females ($\bar{X}$ = 32.6 °C). When T_b was compared between pregnant and postpartum females, while statistically controlling for T_s and T_a, consistent differences between reproductive conditions were observed (Fig. 4). Estimated marginal means indicated that postpartum females had a significantly higher T_b than pregnant females (t = 3.56, df = 19, p = 0.02, Fig. 4).

Table 2. Effects of reproductive condition and air (T_a) and substrate (T_s) temperatures on body temperature (T_b) in females of the Mesquite Lizard, *Sceloporus grammicus*. Parameter estimates from the linear model evaluating the influence of reproductive condition and air and substrate temperatures on the body temperature of pregnant and postpartum female Mesquite Lizard, *Sceloporus grammicus* are presented. Regression coefficients (β), standard errors (SE), t-statistics, and p-values are presented for the main effects and interaction terms. The intercept represents the expected body temperature of postpartum females at average air and substrate temperatures.

	β	SE	t	p-value
Intercept	32.15	0.65	49.39	< 0.001
Pregnant	–2.62	0.88	–2.99	0.008
T_a	–0.27	0.36	–0.74	0.469
T_s	0.80	0.51	1.57	0.135
Pregnant * T_a	1.50	0.57	2.64	0.017
Pregnant * T_s	–2.27	0.77	–2.96	0.009

Discussion

The results of this study indicate that reproductive condition significantly influences body mass and thermal ecology in female *S. grammicus*. These findings are consistent with previous studies in lizards showing that females exhibit changes associated with reproductive stage, supporting the hypothesis that pregnancy represents a significant physiological cost reflected in differences in body mass and modifications in thermoregulatory strategy compared with the postpartum stage (Andrews et al. 1997; Domínguez-López et al. 2018).

Pregnant females had greater body mass compared with postpartum females, even after statistically controlling for body size. Adult males used as a seasonal

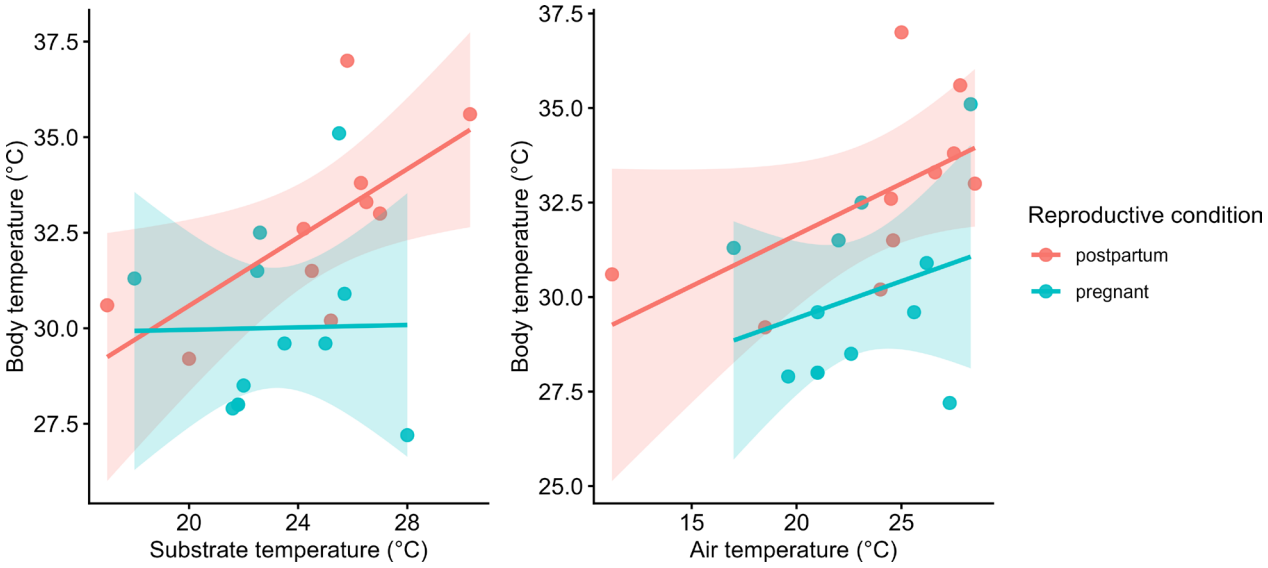


Figure 3. Relationship between body temperature (T_b), and substrate (T_s) (left graph), and air (T_a) temperatures (right graph) in pregnant and postpartum female Mesquite Lizard, *Sceloporus grammicus*. Lines represent linear fits, and shading represents 95% confidence intervals. Statistical inferences are based on the full linear model.

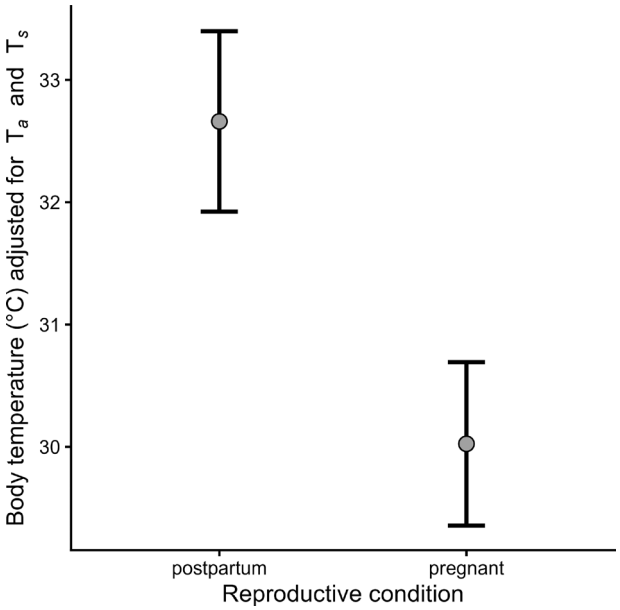


Figure 4. Adjusted body temperature (T_b) of pregnant and postpartum female Mesquite Lizard, *Sceloporus grammicus*, estimated from a linear model that includes substrate (T_s) and air (T_a) temperatures as covariates. Points represent estimated marginal means, and error bars indicate ± 1 SE.

reference did not exhibit detectable differences in body mass between the periods corresponding to female pregnancy (March) and the postpartum stage (May). Although these males were sampled during the following reproductive season, they were collected at the same locality and in the same months. Consequently, the lack of seasonal variation in male body mass provides additional support for the interpretation that the decline observed in females is associated with reproductive condition rather than with seasonal variation at the population level. In this species, the gestation period lasts more than 6 months, beginning in autumn, with births occurring in spring (Sánchez Manjarrez 2024). In *S. grammicus* and most other viviparous sceloporines, embryos are most developed in March. Late pregnancy is usually the period when a female attains her maximum body mass, as each embryo experiences an increase of up to 268% in mass during gestation (Méndez de la Cruz et al. 1988). Although the greater body mass of pregnant females can be attributed to embryonic load, this increase was not associated with a higher T_b. Instead, pregnant females had a lower T_b compared with postpartum females, suggesting that differences in T_b between reproductive conditions are more likely explained by changes in thermoregulatory behavior during pregnancy than by the increase in body mass itself. However, increased body mass and greater vulnerability to predators during pregnancy may also restrict habitat use and reduce the ability of females to reach their preferred T_b. Currently, the frequency of predation in this study population is unknown, but preliminary analyses showed no significant differences in the frequency of caudal regeneration between pregnant and postpartum females (23.3% and 37.5%, respectively; $X^2 = 1.28$, df = 1, $p = 0.25$). However, some females may have lost their tails during pregnancy or between sampling events, making it difficult to determine the exact timing of tail loss. Increased body mass has previously been associated with reduced locomotor performance (Stellatelli et al. 2024); thus, these results suggest that female *S. grammicus* may use strategies to balance reproductive success and survival. For example, in *Crotaphytus collaris* and *Sceloporus virgatus*, pregnant females have developed behavioral mechanisms that compensate for the reduction in locomotor performance associated with body mass gain during gestation (Shine 2003; Domínguez-López et al. 2018). Future studies are needed to determine whether pregnant females in this population of *S. grammicus* have specific behavioral characteristics, such as spending more time thermoregulating or foraging (Domínguez-López et al. 2018), which may allow them to compensate for the additional mass of their offspring, especially during the final stages of pregnancy.

With respect to thermal ecology, the T_b of pregnant females in this study (30.0 °C at 2,605 m a.s.l.) was similar to that reported for a population in Mexico City, Mexico, at approximately 2,240 m a.s.l. (30.42 °C; Woolrich-Piña et al. 2006) and was lower than that reported for a population in the Estado de México at 3,400 m a.s.l. (31.9 °C; Andrews et al. 1997). These differences suggest that thermal ecology in *S. grammicus* may vary among populations across elevational gradients (Lemos-Espinal and Ballinger 1995; González-Morales et al. 2021). Similarly, the recorded T_b was lower than that recorded for females of *Sceloporus jarrovi* with the same reproductive status (32 °C; Beuchat 1986; Mathies and Andrews 1997). The results indicate that the relationships between T_b and environmental temperatures differed between reproductive conditions. The T_b of pregnant females was more strongly related to T_a, whereas postpartum females were mainly thigmothermic. This pattern differs from that reported by Woolrich-Piña et al. (2006), who observed a tendency toward thigmothermy in pregnant females. These discrepancies may be explained by differences in habitat type and climatic conditions between locations, variations that can influence the strategies employed by lizards to thermoregulate. Furthermore, the results indicate that pregnant females had a significantly lower temperature (30.0 °C) compared with postpartum females (32.6 °C). This pattern is consistent with studies of other viviparous species of the genus *Sceloporus*, in which pregnant females thermoregulate at a lower T_b than postpartum females (Smith and Ballinger 1994; Mathies and Andrews 1997). A previous study (Woolrich-Piña et al. 2006) found that the body temperature of pregnant female *S. grammicus* (30.42 °C) was significantly lower than the body temperature of non-pregnant females (31.68 °C). Woolrich-Piña et al. (2006) suggested that pregnant females exhibit passive thermoregulation because the increase in body mass makes them more vulnerable to predators. However, this strategy does not appear to apply to pregnant females

from the study population, in which a stronger relationship between T_b and T_a was found. This change in thermoregulatory strategy suggests that gestation involves changes in habitat use, thermal microenvironments, and predation pressure or is associated with the locomotor limitations of pregnancy. Additionally, it is possible that pregnant females of *S. grammicus* thermoregulate at lower temperatures to avoid negative effects on the development of their offspring because it has been documented that higher temperatures result in lighter and smaller offspring (Mathies and Andrews 1997). Laboratory experiments evaluating temperatures selected by pregnant and postpartum females in controlled thermal gradients, as well as their influence on offspring phenotype, could test this hypothesis and provide a better understanding of the mechanisms underlying thermal physiology in relation to reproductive condition. When considered together with previous studies on *S. grammicus*, these findings highlight the importance of accounting for both intra- and interpopulation variation when evaluating the costs and compensatory mechanisms associated with reproduction.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

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

K.N.C.-M., G.G.-G., and O.H.-G. designed the study. All authors contributed with the field sampling. E.O.-H, G.S.-V., G.G.-G., and O.H-G. performed the analyses. All authors contributed to the interpretation of the results. K.N.C.-M., E.O.-H, G.S.-V., and O.H.-G., wrote the article. All authors read and approved the final version.

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Data availability

All of the data that support the findings of this study are available in the main text.