OXFORD

Evolution Letters, 2025, **0**(XX), 1–12
https://doi.org/10.1093/evlett/qraf043
Letter

Live birth in lizards: A process-based model for the roles of temperature, behavior, and life-history

Guillermo Garcia-Costoya[1], Saúl F. Domínguez-Guerrero[2,3], Lutz Fromhage[4], Matthew E. Gifford[5], Eric A. Riddell[6], Michael L. Logan[1]

[1]Department of Biology and Program in Ecology, Evolution, and Conservation Biology, University of Nevada, Reno, NV, 89557, USA
[2]Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, 06511, USA
[3]Yale Institute for Biospheric Studies, Yale University, New Haven, CT, 06511, USA
[4]Department of Biological and Environmental Science, University of Jyvaskyla, Jyvaskyla, Finland
[5]University of Central Arkansas, 201 Donaghey Ave., LSC 180, Conway, AR 72035, USA
[6]Department of Biology, University of North Carolina – Chapel Hill, Chapel Hill, NC, 27599, USA

Corresponding author: Department of Biology and Program in Ecology, Evolution, and Conservation Biology, University of Nevada, Reno, Reno, NV, 89557, USA. Email: ggarciacostoya@unr.edu

Abstract

Life-history traits evolve to optimize fitness trade-offs across an organism's life cycle. Potentially to mediate the trade-off between survival and fecundity, multiple animal groups have independently evolved live birth (viviparity), including at least 70 transitions in lizards alone. In lizards, viviparity is thought to evolve as a mechanism to improve embryonic development in cold climates (cold climate hypothesis, or CCH), possibly at the expense of the mother's survival. Past comparative studies often align with the CCH's predictions, but they usually treat core features of the hypothesis as implicit and, most importantly, infer process from pattern rather than testing causal mechanisms. To address this, we developed a process-based model that integrates behavior, thermal physiology, life history, and climate to predict optimal gestation length in lizards globally. We generated a comprehensive trait database of 89 lizard populations that vary in parity mode, and we used ecophysiological modelling to test our model's predictive power. Our model produced accurate predictions, strongly supporting the hypothesis that cold climates favor the evolution of viviparity in lizards and revealing the ecological contexts and underlying mechanisms by which this life history strategy evolves.

Keywords: climate, life history, lizards, oviparity, thermoregulation, viviparity

Introduction

Life-history traits evolve to optimize fitness trade-offs occurring over an organism's life cycle (Fromhage et al., 2024; Stearns, 1989). One pervasive life history trade-off is that between survival and fecundity (Gilbert & Manica, 2010). An organism can allocate more resources towards parental care to enhance its current fecundity, but this can negatively impact its survival, compromising future reproductive success. This trade-off is thought to mediate the evolution of animal reproductive strategies, including the transition between oviparity (egg laying) and viviparity (birthing live young; Blackburn, 1999; Kalinka, 2015; Wourms & Lombardi, 1992). Viviparity can be demanding on the mother (Foucart et al., 2014; Hussain et al., 2024; Whittington et al., 2022) and potentially diminish her chances of survival, yet it can also enhance her fecundity by offering protection and favorable developmental conditions to embryos (Shine, 2002; Figure 1). Viviparity has independently evolved at least 150 times in vertebrates (Blackburn, 1999), with the majority of these occurrences (~70) in lizards (Blackburn, 2015), making this group an ideal model for understanding the mechanisms driving evolutionary transitions between parity modes (Shine, 2014).

Live birth in lizards has been proposed to have evolved as a mechanism to enhance offspring viability via maternal manipulation of the environment experienced by embryos (the "maternal manipulation hypothesis" or MMH; Shine, 1995). This process has been posited to occur most often in environments in which temperatures are too cold for effective incubation (the "cold climate hypothesis" or CCH; Shine, 1983, 2014; Shine & Bull, 1979). The CCH posits that a female's ability to behaviorally thermoregulate (i.e., maintain a preferred range of body temperatures by actively moving between thermal microsites) during gestation allows embryos to experience a warmer, and thus more favorable, thermal regime for development than if they were to be laid as eggs in a nest (Shine & Harlow, 1993; Figure S1). As a consequence, cold environments should favor females with longer gestation times (Andrews, 1997) and, if the selective pressure is sufficiently strong (or sustained), females that give birth to "live" young. This is perhaps most likely to occur via gradual increases in gestation length through selection for increased progesterone production in these environments (Blackburn, 1995;

Received June 4, 2025; revisions received October 10, 2025; accepted October 13, 2025

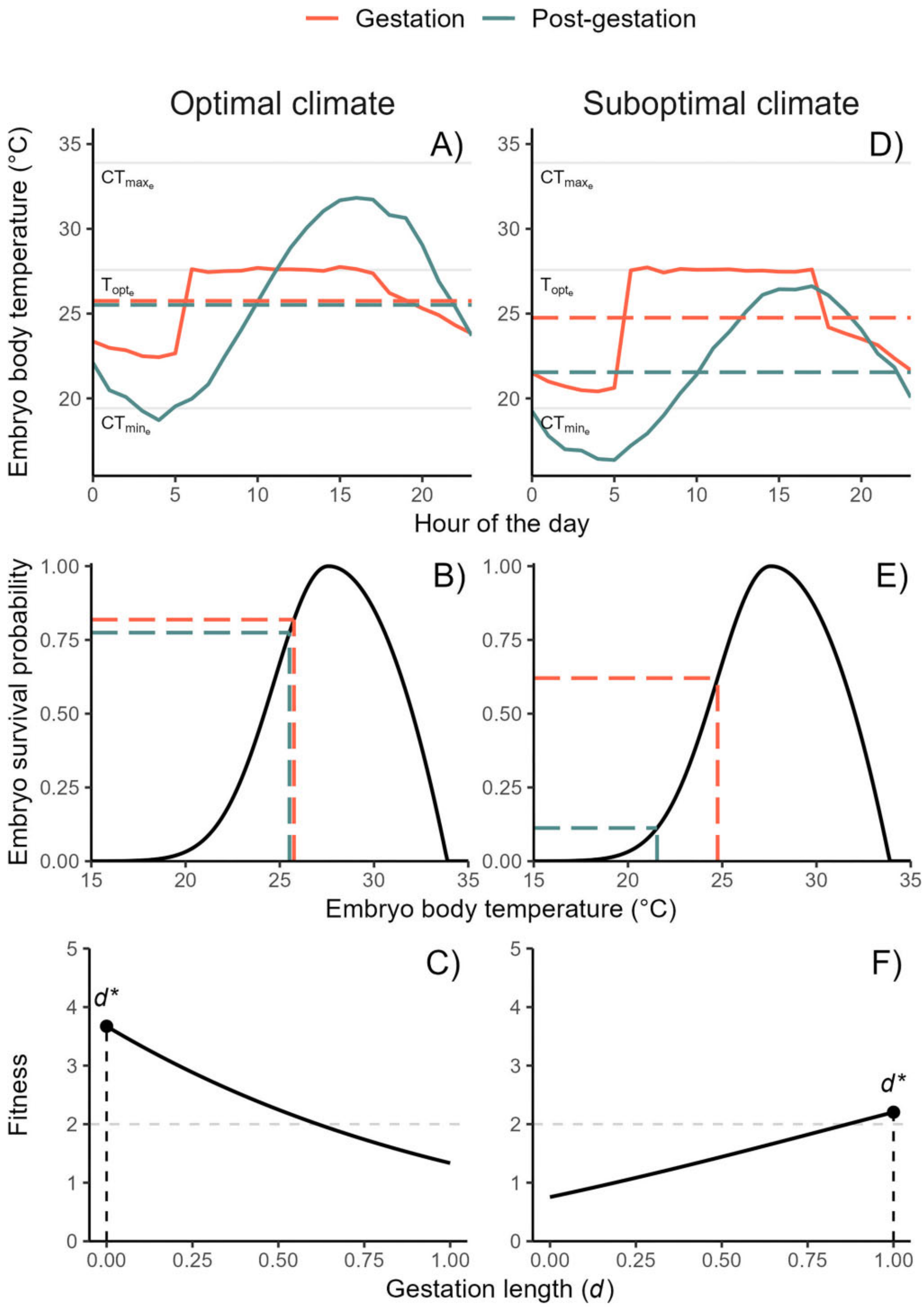

Figure 1. Key features of the cold climate hypothesis for the evolution of viviparity. A) In an optimal climate for embryonic development, the body temperatures that the embryo will experience during gestation (red) and post-gestation (in a nest; dark blue) are both close to the embryo's thermal optimum (T_{opt_e}, central gray solid line) and within its critical thermal limits (CT_{min_e} and CT_{max_e}, bottom and top gray solid lines respectively). As a result, in an optimal climate, there is little difference in embryo survival probability between gestation and incubation (B; black curve is the thermal sensitivity of embryo survival) and this should favor a strategy of laying eggs early in embryonic development (C; d^* is the percentage of total embryonic development at which laying eggs in a nest would maximize fitness—accounting for both embryonic and adult survival). In a suboptimal climate (D; in this case, cold), the embryo can only experience favorable temperatures during gestation when the adult female is behaviorally thermoregulating. As a result, the probability of embryo survival would be substantially smaller during incubation than during gestation (E), and this should favor a strategy of laying eggs late in embryonic development or giving birth to live young ($d^* = 1$).

Stewart, 2021). Support for the CCH primarily stems from phylogenetic and comparative studies that examine the geographic distribution of species of one or the other parity mode in relation to major abiotic variables (Hodges, 2004; Lambert & Wiens, 2013; Ma et al., 2018; Zimin et al., 2022).

While previous studies exploring the evolution of viviparity in squamate reptiles generally find support for the CCH, their conclusions have not been universally accepted for several reasons. First, broad-scale climate indices are often used to characterize local thermal environments without considering how lizards attenuate macroclimate via thermoregulatory behavior. The realized body temperatures of individuals in a given population may not be reflected by broad-scale climatic variables, and indeed, a capacity of gestating females to behaviorally thermoregulate is a core assumption of the CCH itself (Shine & Harlow, 1993). Second, even though the CCH implies the presence and key impact of life-history trade-offs on the strength and form of selection on gestation length, these trade-offs are not considered in comparative studies. Possibly to help alleviate the demands of carrying embryos for long periods of time, viviparity in lizards is associated with a key set of life-history adaptations (Alencar et al., 2024; Domínguez-Guerrero et al., 2022, 2024). As such, an explicit consideration of life history traits and trade-offs is required to understand the mechanisms underlying the evolution of viviparity and to comprehensively assess the validity of the CCH. Lastly, and perhaps most importantly, the nature of phylogenetic comparative studies requires that biological processes be inferred from patterns observed on evolutionary trees. This approach, while valuable, produces fundamentally correlative results that leave implicit the evolutionary processes that led to the patterns observed (Cale et al., 1989; Olson & Arroyo-Santos, 2015). Taken together, these limitations imply that progress can be made in understanding the evolutionary drivers of viviparity by modeling and testing microevolutionary processes that occur at the population level.

Here, we developed a process-based mathematical model that predicts the optimal gestation length of a lizard population as a function of that population's thermal physiology across ontogeny and life history traits while accounting for behavioral thermoregulation in local climates. If our model accurately describes the processes that lead to the evolution of live birth, then it should predict substantially longer gestation lengths in viviparous species compared to oviparous ones. We assessed the accuracy of our model by comparing its predictions against a comprehensive database comprising 89 lizard populations from around the world. Our model produced accurate predictions for a large majority of populations, strongly supporting the hypothesis that cold climates favor the evolution of live birth in lizards and revealing important processes driving this key evolutionary innovation.

Methods

Model structure

We modeled a lizard species that can lay eggs at any point during embryonic development. The proportion of development at which laying occurs (d) is bounded $0 \leq d \leq 1$, with $d = 0$ equating to a species laying as early as possible during development, and $d = 1$ to a species laying when embryonic development is complete (live birth). We define the optimal strategy as d^* such that:

$$d^* = \arg\max_{d} f(d) \tag{1}$$

Where f is the fitness of strategy d, and d^* is the d that maximizes f. Further, d partitions development between gestation (before d, when a female is carrying embryos, indicated by the subindex g) and post-gestation periods (after d if $d < 1$, when eggs are laid, indicated by the subindex p). We define f(d) as:

$$f(d) = P + F \tag{2}$$

Where P is the expected reproductive success during a current breeding season, and F is the expected reproductive success summed across future breeding seasons. We can further decompose P and F as:

$$P = \left(S_{ag} \cdot (1 - C)\right)^{d} \cdot N \cdot \left(S_{eg}\right)^{d} \cdot \left(S_{ep}\right)^{1-d} \tag{3}$$

$$F = \left(S_{ag} \cdot (1 - C)\right)^{d} \cdot \left(S_{ap}\right)^{1-d} \cdot \gamma \tag{4}$$

Where S is the survival probability over the entire period of embryonic development, the subindexes a and e indicate the adult or embryo stages, respectively. As such, S_{ag} and S_{eg} are the female and the embryos' survival probability during gestation, respectively, while S_{ap} and S_{ep} are the female and the embryos' survival probability post-gestation, respectively. C is the cost of carrying embryos (discussed below), N is the clutch/litter size and γ is a parameter modulating the species' average expected future reproductive success ($\gamma \geq 0$). Since survival at a given life and reproductive stage is considered over the entire embryonic developmental period, raising it to the power of d and 1–d allows the estimation of survival over the gestation and post-gestation periods, respectively. In equations 3 and 4, S is determined by the thermal performance curve (TPC) function defined by (Deutsch et al., 2008):

$$TPC = S(T) = \begin{cases} e^{-\left(\frac{T - T_{opt}}{2 \cdot \left(-\frac{CT_{min} - T_{opt}}{4}\right)}\right)^{2}} & \text{if } T < T_{opt} \\ 1 - \left(\frac{T - T_{opt}}{T_{opt} - CT_{max}}\right)^{2} & \text{if } T > T_{opt} \end{cases} \tag{5}$$

Where CT_{min} and CT_{max} are the critical thermal minimum and maximum (if $T < CT_{min}$ or $T > CT_{max}$, then $S = 0$), and T_{opt} is the thermal optimum (if $T = T_{opt}$, then $S = 1$), all traits that are assumed to differ between adults and embryos. Further, T in equation 5 indicates average body temperature experienced by either adult or embryo during or post-gestation. During gestation we assume that 1) adults and embryos experience the same average body temperature (T_g) as the latter is contained within the former, and 2) the adult behaviorally thermoregulates in the context of local microclimatic variation to maintain its embryos as close as possible to the embryos' T_{opt} and between the embryo's CT_{min} and CT_{max}. During the post-gestation period we assume that adults and embryos experience different average body temperatures (T_{ap} and T_{ep}, respectively). First, for T_{ap}, we assume that adults also thermoregulate but in this case attempt to maintain themselves as close as possible to their own T_{opt} and between their CT_{min} and CT_{max}. For the embryo, we assume that, due to the limited ability of an embryo contained within an egg to thermoregulate, T_{ep} is approximately equal to the temperature of the soil at a given shade coverage and depth. We subjected both nest depth and shade coverage to sensitivity analyses (see "Ecophysiological modeling" below). Finally, we define C as:

$$C = d \cdot \alpha \cdot \frac{N \cdot Z_e \cdot S_{eg}}{Z_a} \tag{6}$$

Where Z_e and Z_a are the maximum embryonic mass and the mean adult female mass, respectively, and α is an embryonic carrying cost parameter. Z_e is defined as the mass a hatchling would assume if $T_g = T_{ep} = T_{opt}$ (i.e., the mass a hatchling would assume if incubated in optimal conditions). Thus, this cost is defined by the mass-specific production (the ratio between total offspring mass—NZ_e—and Z_a), weighted by the survival probability of the embryo during gestation. Mass-specific production is a metric often used to describe a species' position along the fast-slow life-history continuum (Domínguez-Guerrero et al., 2022; Meiri et al., 2012, 2020). Further, α modulates the degree to which this ratio affects the adult. We bound this parameter $0 \leq \alpha \leq 1$ such that $\alpha = 0.5$ would reduce the cost of carrying embryos of a given total mass by 50%. C can be defined for the entire development period but sets the cost for only the gestational period when weighed by d. Z_e is weighed by the embryo's survival probability to account for the fact that a lengthened gestation will likely lead to larger embryos and therefore a greater mass carried by the mother per unit time. See Table S1 for all parameter definitions and nomenclature.

Database on lizard thermal physiology, life-history, and natural history

We constructed a database of characteristics of lizard populations that would allow us to obtain population-specific predictions of d^*. To that end, we acquired data on 1) thermophysiological traits, 2) life-history, 3) behavior, 4) depth and shade cover of nests in the wild, and 5) reproductive phenology.

We obtained thermal physiology data of lizards at the embryonic stage from Pettersen et al., 2023) and from the Reptile Development Database (RDD; Noble et al., 2018). We obtained estimates of embryonic T_{opt} from Pettersen et al. (2023) who estimate it as the temperature maximizing hatching success under a constant temperature incubation regime. Following their methodology, we filtered the RDD to include only records of hatching success measured at constant temperatures. We then calculated embryonic CT_{min} and CT_{max} as the temperatures below and above embryonic T_{opt}, respectively, at which hatching success declined to 10%. Next, we obtained adult thermal physiology data from Buckley et al. (2022) and Domínguez-Guerrero et al. (2022). In Buckley et al. (2022), these traits were estimated by fitting the same TPC equation we use here to data examining the thermal sensitivity of sprint speed. In Domínguez-Guerrero et al. (2022), T_{opt} was estimated using thermal preference assays in combination with separate measurements of CT_{min} and CT_{max}. All traits were measured in both males and females (not necessarily during the breeding season) and were associated with geographic information for each population (latitude, longitude, and elevation). Third, we obtained data on life-history traits, activity, and behavior from SquamBase (Meiri, 2024). Finally, we combined these data for each population, retaining only those for which the minimum data to fit our model were available.

Next, for each population with sufficient data to fit our model, we performed two literature searches to obtain information on nesting conditions and the timing of embryonic development. For nesting conditions, we searched on Google Scholar using the species name followed by "nest" or "oviposition." We only examined the first 10 results per search after our initial efforts revealed that papers were rarely relevant beyond the first 10 returns. We obtained information from all articles that reported the depth or shade cover over nests in the wild for the focal population or a population of the same species living at a similar latitude and elevation. For the timing of embryonic development, we performed another population-specific search on Google Scholar using the species name followed by either "reproduction," "reproductive phenology," or "life cycle." Once more, we examined the first 10 results and focused on demographic studies of the exact populations or those of the same species in the closest possible location. We considered embryonic development to begin in the earliest month, when eggs were first observed in the oviducts, and to end in the latest month, when hatchlings were regularly encountered. If no information was available for a given species, we obtained information for the most closely related species available and from a population that was geographically closest to the population of interest (<200 km in all cases).

Ecophysiological modelling

We used the R package "NicheMapR" to simulate the average monthly body temperatures experienced during gestation (by both adults and embryos, T_g) and post-gestation by adults and embryos independently (T_{ap} and T_{ep}). First, we used the "micro_global" function to simulate microclimates at the geographic location (latitude, longitude, and elevation) of each population for every hour of every day of the year within the period when embryonic development occurs in nature for each population. We did this for a simulated 10-year period informed by historical climate data while assuming flat ground (no significant slope or aspect effects) and using NicheMapR's default parameters for surface albedo and soil moisture composition.

Second, we used the "ectotherm" function to estimate T_g and T_{ap}. This function simulates a distribution of body temperatures a lizard would achieve by behaviorally thermoregulating in the context of its available microclimatic variation to maximize biological function while accounting for its shape, mass, thermophysiological traits (CT_{min}, $T_{opt,}$ and CT_{max}) and behavioral tendencies. In all cases, we limited the depth a lizard could burrow in the soil to 10 cm. We used behavioral data from SquamBase to determine whether the species was typically diurnal, nocturnal, or cathemeral, and whether it could climb to thermoregulate. We specified that the species could not climb if it was classified in SquamBase as exclusively terrestrial, fossorial, or cryptic, and limited climbing to a height of two meters in all other cases. Assuming that gestating females adjust thermoregulatory behavior to optimize embryonic development, we generated two body temperature distributions of adults: one for gestation (to infer T_g) and one for post-gestation (to infer T_{ap}). For the first, we set the corresponding parameters of "ectotherm" to the T_{opt}, CT_{min}, and CT_{max} of embryos but for the second, we set these parameters to the values for the adult. In all cases, we simulated body temperature distributions for all days and hours for which we generated microclimatic data and used NicheMapR's default value for the solar absorptance of lizard skin.

Third, we used the output of "micro_global" to estimate the temperature experienced by the embryo post-gestation (T_{ep}). Due to the general inability of lizard embryos to meaningfully alter the temperature they experience via behavioral thermoregulation (Cordero et al., 2018), we assumed that the body temperature of embryos post-gestation would match that of the surrounding soil. Thus, we estimated T_{ep} as the average predicted soil temperature at a given depth and shade cover for all days and hours for which we generated microclimatic data. For populations with sufficient available information, we parameterized T_{ep} at the average depth and shade cover at which that population is known to nest. In all other cases, we modeled soil temperature at 0, 5, 10, and 15 cm below ground and under 0%, 50%, and 100% shade. Finally, we used the output of "micro_global" to estimate a reference value for environmental temperature matching that is used in macroevolutionary studies of the evolution of viviparity in lizards. To this end, we obtained monthly estimates of air temperature at a height of two meters above ground level under shade, a metric similar to the ambient temperature measurements from weather stations used in macroclimatic databases.

Testing the model

We fit our model using the information we assembled from preexisting databases and literature searches to obtain a prediction of optimal gestation length (d^*) for all populations during the period of embryonic development. To compare predictions across populations and species, we first fit the model with $\alpha = 0.5$ and $\gamma = 2$ as default values. For populations for which we had information on nesting conditions in the wild, we fit the model using embryo body temperatures post-gestation (T_{ep}) at the depth and shade at which that population is known to nest. For populations for which we did not have nesting information, we set the default nest depth to 5 cm (the most frequent nesting depth among species for which we had information) and 50% shade coverage. To obtain a unique population-specific prediction, we averaged the estimated d^* across all months during which embryonic development occurs in each population. Lastly, we tested the sensitivity of the model across all combinations of the following parameter values: $\alpha = 0, 0.25, 0.5, 0.75$, and 1, $\gamma = 0, 1, 2, 5$, and 10, nest depth = 0, 5, 10, and 15 cm, nest shade = 0%, 50% and 100%. For nest variables, we only conducted sensitivity analyses in populations for which empirical estimates were not available.

Statistical analysis

We explored the impact of thermoregulatory behavior and nesting conditions on the thermal regimes experienced by lizard embryos across reproductive stages by implementing a linear mixed-effects model (LMM). Using this model, we investigated how average body temperatures (simulated through ecophysiological modeling) were influenced by reproductive stage, parity mode, and other population characteristics. The model's equation was:

$$T = \beta + \beta_1 G + \beta_2 P + \beta_3 V + \beta_4 L + \beta_5 E + \beta_6 V + \beta_7 GV + \beta_8 PV + 1|S \tag{7}$$

Where T, the response variable, is the mean simulated body temperature for a population. β indicates the intercept, which we set to the simulated average air temperature at the reference height at the population's geographic location, assuming the species is oviparous. G, P, and V are indicator variables representing the gestation stage, post-gestation stage, and whether a species is viviparous. As such, β_{1-3} characterize the effects of thermoregulatory behavior during gestation, nest conditions post-gestation, and parity mode on embryo body temperatures, and $\beta_{7,8}$ indicate interactive effects. To quantify the effect of post-gestation nesting conditions, we used T_{ep} from the depth and shade coverage at which a population typically nests, if data were available. If data were missing, we used T_{ep} at a 5 cm nest depth and 50% shade cover. The model also accounted for the effects of absolute latitude (L) and elevation above sea level (E) on T and incorporated species (S) as a random effect.

Second, we explored how our model's predictions (d^*) were influenced by the geographic location and life-history characteristics of populations. To do so, we implemented a generalized linear mixed effects model (GLMM) with a quasi-binomial error structure:

$$d^* = \beta + \beta_1 L + \beta_2 E + \beta_3 M + \beta_4 LE + \beta_5 LM + \beta_6 EM + \beta_7 LEM + 1|S \tag{8}$$

As with the previous model, β indicates the intercept of the relationship and β_{1-3} the effects of absolute latitude (L), elevation (E), and mass-specific production (M). We assumed a quasi-binomial error structure and incorporated species as a random effect. Lastly, to estimate d^*, we used T_{ep} at empirically estimated nest depths and shade cover if available, and a depth of 5 cm and 50% coverage if not, and set $\alpha = 0.5$ and $\beta = 2$ in all cases.

Third, we investigated how our model's output was influenced by the conditions experienced by embryos during development. Specifically, we constructed a model to test how d^* was influenced by the absolute difference between the embryo's thermal optimum (T_{opt_e}) and the temperature experienced by the embryo post-gestation (T_{ep}):

$$d^* = \beta + \beta_1 \left(\left| T_{opt_e} - T_{ep} \right| \right) + 1|S \tag{9}$$

As with the previous model, we employed a GLMM assuming a quasi-binomial error structure, incorporated species as a random effect, used estimates of d^* assuming $\alpha = 0.5$, $\gamma = 2$, and T_{ep} from the depth and shade coverage at which a population typically nests if data were available (and 5 cm nest depth and 50% coverage if data were missing). All data preparation and analysis were conducted in R (R Core Team, 2025).

Results

Database on lizard natural history, thermal physiology, and life history

While we obtained some information on lizard thermal physiology at the embryonic stage (Table S2, Figure S1), these data were insufficient to determine whether embryonic thermophysiological traits could be predicted from adult data (Figure S2). As a result, for model validation purposes, we assumed that embryonic thermophysiological traits were equal across all populations and set these values to the average across all species for which data were available ($CT_{min} = 19.41°C$, $T_{opt} = 27.57°C$, $CT_{max} = 33.83°C$). Next, for the adult stage, after eliminating populations for which we did not have the minimum data necessary to apply our model, we obtained a database of 89 lizard populations (66 oviparous, 23 viviparous) representing 79 species (56 oviparous, 23 viviparous) distributed across the globe (Figure 2, Table S8). Our literature searches yielded information on nesting conditions for 15 populations and the timing of embryonic development for 84 populations (Figure S3, Table S8). We were unable to include snakes in our database and subsequent analysis due to the lack of sufficient data necessary to apply our model to this group.

Ecophysiological modeling

Our ecophysiological modeling revealed that, during months when embryonic development occurs, and regardless of parity mode, behavioral thermoregulation during gestation and nest conditions post-gestation enable embryos to experience a significantly warmer temperature regime than would be inferred if only air temperatures were considered (Figure 3). On average, lizard embryos experience a 6.05°C warmer environment during gestation (LMM, $\beta = 0.77$, df = 182.63, t = 12.8, $p < 0.001$) and a 4.4°C warmer environment post-gestation (LMM, $\beta = 0.846$, df = 182.63, t = 14.1, $p < 0.001$) compared to air temperature-based predictions. Viviparous and oviparous species did not differ in the extent to which nest conditions would increase the temperatures experienced by embryos with respect to air temperature (LMM, β = -0.008, df = 182.76, t = -0.072, p = 0.943). In contrast, during gestation, embryos of viviparous species experience a significantly warmer environment with respect to air temperature than their oviparous counterparts (LMM, $\beta = 0.77$, df = 182.6, t = 6.518, p = <0.001), with viviparous and oviparous

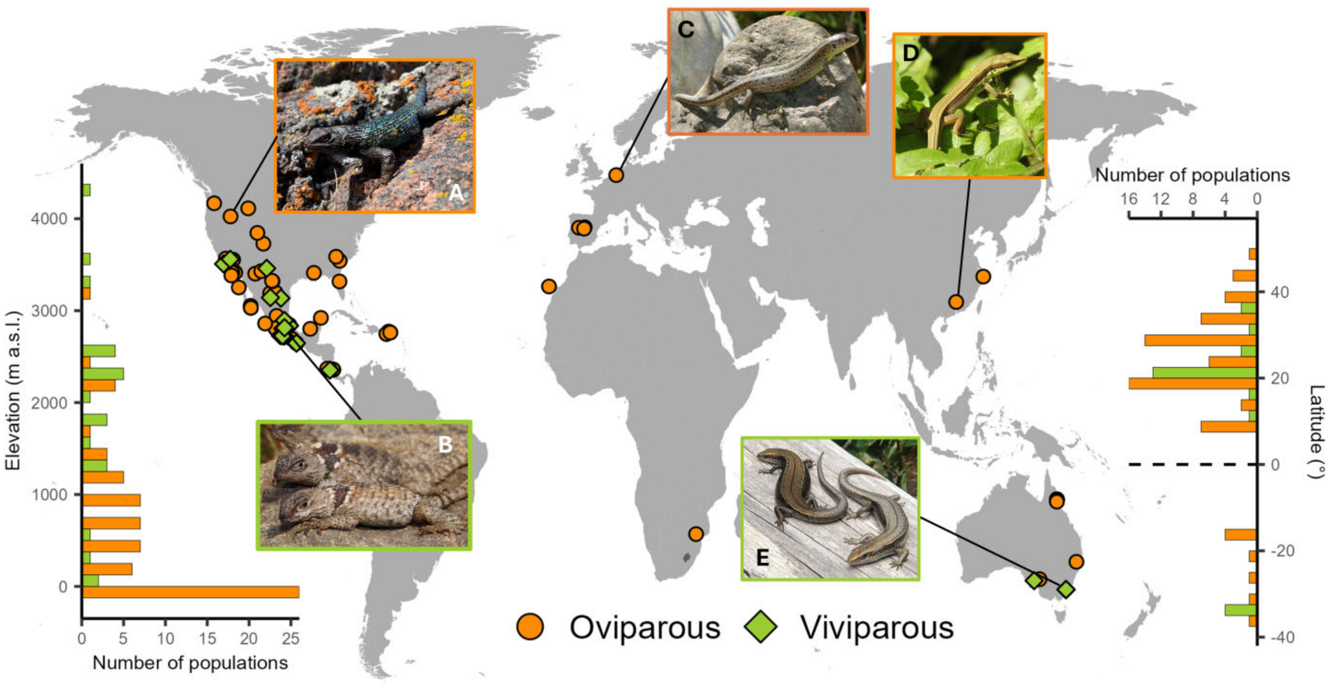

Figure 2. Global, latitudinal, and elevational distributions of all lizard populations for which we had sufficient data to fit our model (including photos of representative species, A: *Sceloporus occidentalis*, B: *Sceloporus mucronatus*, C: *Lacerta agilis*, D: *Takydromus septentrionalis*, E: *Pseudemoia entrecasteauxii*). Viviparous species are more common than oviparous species at high elevations (left histogram). While there is little discernible pattern across latitude (right histogram), it should be noted that viviparous species are comparatively rare and the majority of populations in our data set occur between 10 and 35 °N in the Northern and Western Hemisphere. Image credit to Guillermo Garcia Costoya (A), Saúl Domínguez-Guerrero (B) and iNaturalist users posting under a Creative Commons License (C-E).

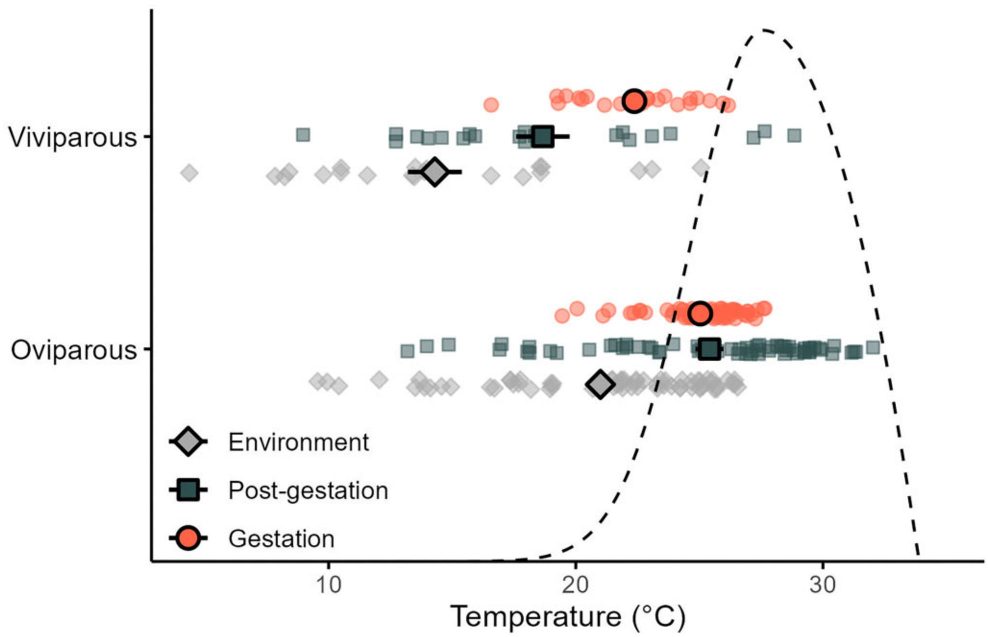

Figure 3. Behavioral thermoregulation by gestating females enhances embryo fitness to a greater extent in viviparous species than in oviparous species. The average body temperatures predicted by our model to be experienced by embryos during gestation (red circles) and post-gestation (blue squares) are more similar in oviparous compared to viviparous species because oviparous species live in environments (gray diamonds; calculated as air temperature at a height of 2 m above ground) that provide incubation temperatures closer to the thermal optima of embryos (dashed line is the average thermal performance curve for embryos which was based on empirically estimated thermal optima and critical thermal limits of hatching success). Transparent points indicate averages of individual populations whereas solid points with black borders indicate the averages of all populations (error bars represent standard error).

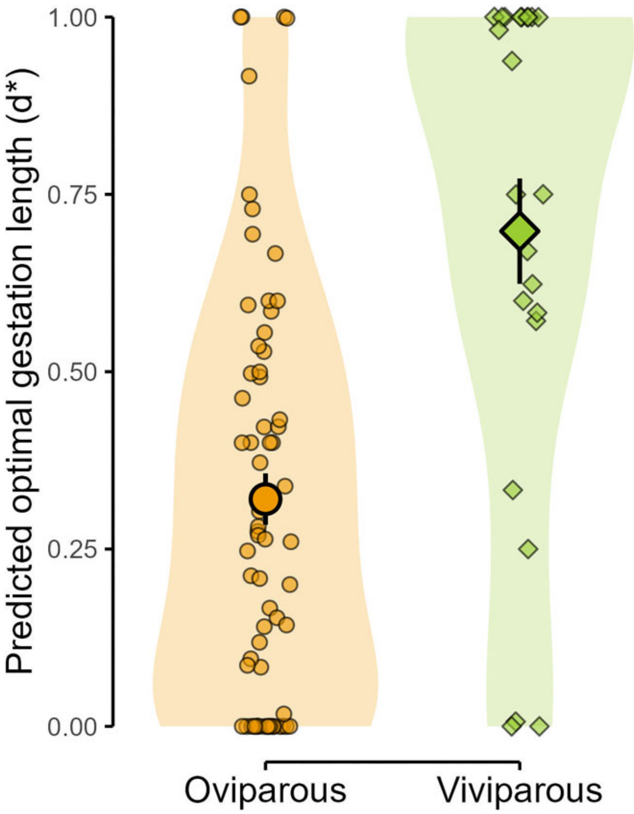

Figure 4. Our model predicted that viviparous lizard species (small green diamonds = individual populations; large green diamond = average across populations) should, on average, have longer gestational periods (d^*) than oviparous species (small orange circles = individual populations; large orange circle = average across populations; error bars represent standard error).

species warming their embryos by 8.1 and 4°C above ambient on average, respectively (Tables S3 & S4). Lastly, we found that nest depth and shade cover affected T_{ep}, with different combinations of these variables leading to average differences of up to 8.8°C (Figure S4, Table S5).

Testing the model

Under default parameter settings, mean d^* for oviparous and viviparous species was 0.32 ± 0.29 (mean ± standard deviation) and 0.7 ± 0.36, respectively. Out of 66 oviparous populations, 3 (4.5%) had a d^* of 1, 13 (19.6%) had a d^* between 0.5 and 0.99, and 50 (75.7%) had a d^* between 0 and 0.49. Out of 23 viviparous populations, 9 (39.1%) had a d^* of 1, 9 (39.1%) had a d^* between 0.5 and 0.99, and 4 (21.7%) had a d^* between 0 and 0.49 (Figure 4, Table S8). Model predictions were sensitive to both α and γ, with larger values of both leading to a decrease in d^*. The negative effect of g on d^* was greater in oviparous than viviparous species, and in both cases the greatest decrease in d^* occurred when γ changed from 0 to 1 (i.e., when future reproduction was possible; Figure S5).

We examined the effects of absolute latitude, elevation, and mass-specific production (MSP) on d^* and found that elevation and the interaction between latitude and elevation (but not latitude on its own) had significant effects on d^* (GLMM, Latitude $\beta = 0.49$, $Z = 1.35$, $p = 0.18$; Elevation $\beta = 1.45$, $Z = 3.58$, $p = <0.001$; Latitude x Elevation $\beta = -0.91$, $Z = -2.21$, $p = 0.026$, Figure 5A & 5B, Table S6). In contrast, MSP was significantly and negatively correlated with d^* (GLMM, $\beta = -0.77$, $Z = -2.06$, $p = 0.04$; Figure 5C, Table S6). To understand the influence of nest conditions on our model's predictions, we tested whether d^* depended on the absolute difference between T_{ep} and the embryonic T_{opt}. We found that this difference had a positive and significant effect on d^* (GLMM, $\beta = 0.41$, $Z = 4.64$, $p < 0.001$; Figure 5D, Table S7), indicating that greater d^* was predicted for populations where T_{ep} was both much cooler and much warmer than the embryonic T_{opt}. Similarly, we found that d^* was differentially sensitive to nest depth and shade depending on the general climate experienced by a population. In populations living in cooler-than-average environments, d^* was positively correlated with both nest depth and shade coverage (Figure 5E). For populations living in warmer-than-average environments, d^* was positively correlated with nest depth when under shade but negatively correlated when nests were exposed (Figure 5F).

Discussion

In squamate reptiles, and lizards specifically, viviparity is thought to evolve as a strategy to improve embryonic development in cold climates (cold climate hypothesis, or CCH; Andrews, 2000; Shine, 1983). Although the CCH has been supported by comparative studies that infer microevolutionary processes from macroevolutionary patterns (Hodges, 2004; Lambert & Wiens, 2013; Ma et al., 2018; Zimin et al., 2022), previous research has not fully accounted for behavioral thermoregulation or the roles of life-history, physiology, and local climatic variation, and thus, causal mechanisms remain unexplained. To address these gaps, we developed and validated a process-based model that predicts a lizard population's optimal gestation length, given the population's features and its local environment. Our model accurately predicted that viviparous populations should have longer gestational periods than oviparous populations and revealed that maternal thermoregulatory behavior in local thermal environments, physiological trait variation across life stages, and factors like egg carrying costs and nesting behavior likely function as important agents of selection that ultimately lead to the evolution of live birth in lizards. The model we present here formalizes the phenomenon of viviparity in lizards, providing a valuable framework for understanding how life-history trade-offs mediate adaptation to thermal environments.

The accuracy of our model validation indicates that our model coo the key processes that lead to the evolution of viviparity in lizards. Our results provide strong support for the CCH, indicating that extended gestation (including live birth) is an optimal strategy at the cooler temperatures typical of higher latitudes and elevations. However, our model also revealed that, in principle, lengthened gestation and/or viviparity should evolve in warm environments if incubation temperatures tend to be above the embryo's thermal optimum and gestating females can cool their embryos through behavioral thermoregulation. Strictly speaking, then, our model supports the "maternal manipulation hypothesis" (Shine, 1995), which states that viviparity should evolve as an adaptation to any thermal environment, not just cold ones, where maternal behavioral thermoregulation enhances embryonic fitness. Regardless, our validation rarely predicted the presence of viviparity in real populations from tropical lowland environments, probably because 1) most lizard nests are underground and are therefore buffered from stressfully hot temperatures, and 2) relatively simple changes in nesting behav-

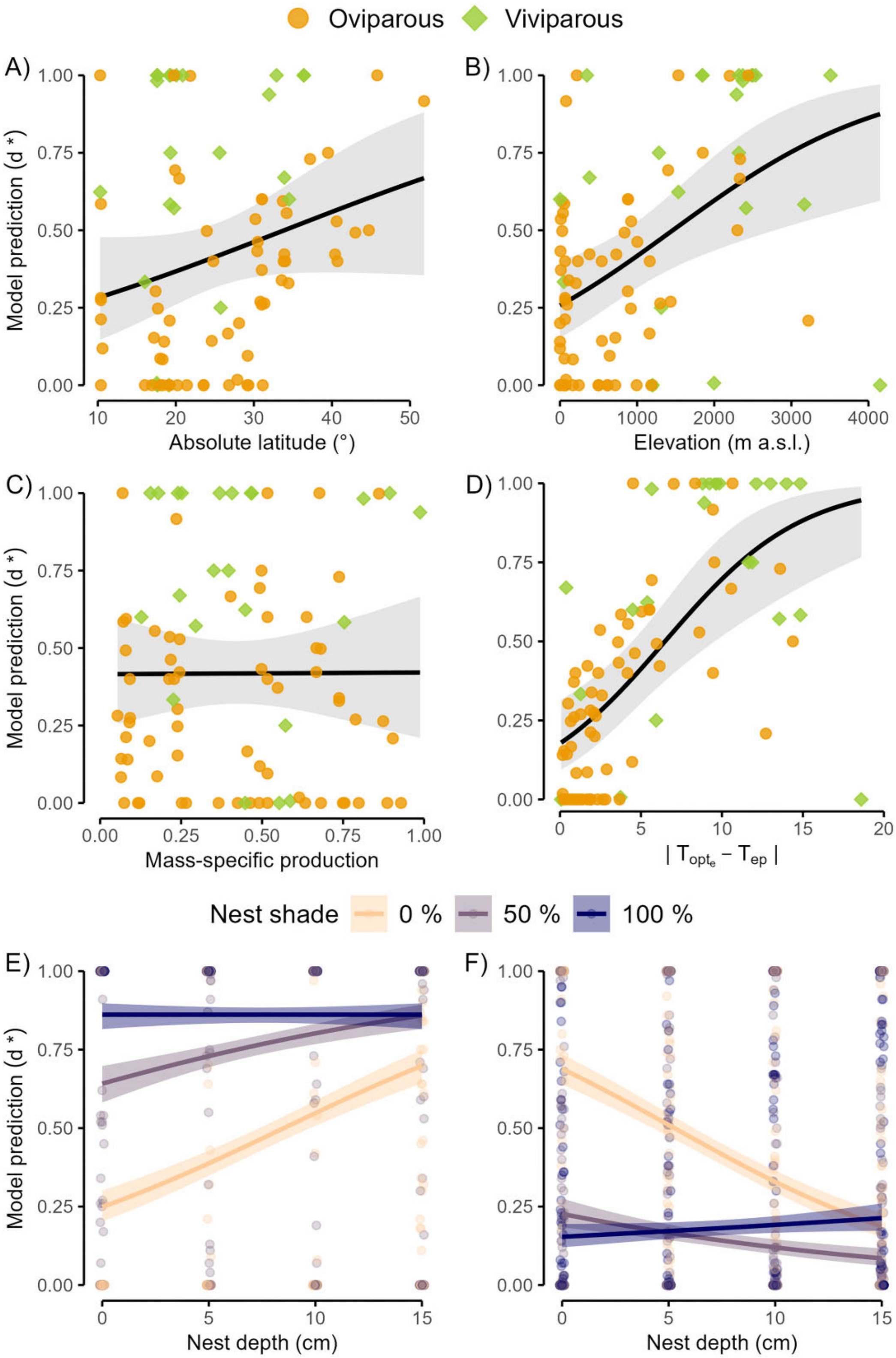

Figure 5. Relationship between our model's average prediction of optimal gestation length (d^*) during months of the year when embryonic development is known to occur and absolute latitude from the equator (A), elevation above sea level (B), mass-specific production (C; the ratio between the adult mass and the product of hatchling mass and clutch size), the absolute difference between embryonic thermal optima (T_{opt_e}) and incubation temperatures (T_{ep}; D), and nesting conditions for populations living in cooler (E) and warmer than average climates (F) with respect to average air temperature. For panels A-D, points represent population-specific estimates of d^* for oviparous (orange circles) and viviparous (green diamonds) populations with the embryonic carrying cost parameter (α) set to 0.5, and average and expected future reproductive success (γ) to 2. Also, for panels A-D, when available, nest depth and shade were used to estimate d^*, otherwise d^* was estimated under default parameter values (depth = 5 cm, shade = 50%). For panels E and F, points represent population-specific estimates of d^* at a given nest depth and shade cover (color-coded from 0% to 100% shade). In all panels, solid lines represent the best-fit line of a generalized linear mixed-effects model with a quasi-binomial error structure, and the shaded areas indicate the 95% confidence intervals around the prediction. Latitude, elevation, mass-specific production, and the relationships between nest conditions and local climate all influenced the predicted gestation length output by our model.

ior (small modifications of nest shade cover or depth) can protect embryos from heat stress (Angilletta Jr. et al., 2009; Telemeco et al., 2017). In nature, embryo development appears to be more limited by cold than by hot incubation temperatures. Nonetheless, this pattern could change as habitats warm under climate change, potentially leading to selection for egg retention at low latitudes and elevations, especially in cases where there is minimal plastic or genetic capacity, or environmental opportunity, to adjust nesting behavior. However, we urge caution in extrapolating this conclusion to suggest that anthropogenic warming will result in the evolution of viviparity. With the exception of the only two lizard genera with mix-parity modes (*Saiphos*; Laird et al., 2019, *Zootoca*; Recknagel et al., 2018), most species may lack the standing genetic variation to evolve viviparity within the time frame of contemporary climate change.

Our findings underscore the importance of accurately characterizing the local thermal regimes that lizard populations experience in the wild to understand the evolution of viviparity. Accounting for behavioral thermoregulation and nest conditions produced estimates that differed substantially from those obtained from commonly used macroclimatic variables. For example, our approach predicted that behavioral thermoregulation improves the conditions for embryonic development to a much greater degree in viviparous compared to oviparous species. While this is an implicit prediction of the CCH, it has not been explicitly tested in prior studies. Additionally, while some previous studies examining the CCH considered nest conditions (e.g., Telemeco et al., 2017), most assumed they are constant (e.g., Ma et al., 2018). Our approach revealed that nest depth and shade cover can substantially influence predicted incubation temperatures, and thus the likelihood that lengthened gestation will be favored by selection.

In addition to behavioral thermoregulation and nest conditions in local environments, variation in life-history traits significantly influenced our model's predictions. At a given latitude and elevation, populations with comparatively lower mass-specific reproductive investment were predicted to have longer gestation periods. This finding aligns with previous research, which shows that the higher reproductive costs associated with viviparity generate selection for larger adult body size and/or smaller litter sizes (Domínguez-Guerrero et al., 2022, 2024). These adaptations may help mitigate the trade-off between adult survival and fecundity by reducing the costs associated with prolonged embryo retention in harsh environments. Indeed, our model predicted that reduced embryonic carrying costs should favor extended gestation, especially in species with multiple breeding seasons.

While our model predicted that gestation length should be longer in viviparous species on average, there was variation around the mean prediction, with a few viviparous species (e.g., *Phrynosoma taurus, P. sherbrookei*) predicted to lay eggs at only a fraction of embryological development and some oviparous species (e.g., *Anolis tropidolepis, Lacerta agilis*) predicted to retain embryos for the entire or nearly all of development. The fact that our model did not perfectly predict parity mode across all species in our validation is not surprising. For example, there is evidence that some of the oviparous species our model predicts should retain eggs through most or all of development actually do so in the wild (e.g., *Sceloporus spinosus;* Calderón-Espinosa et al., 2006). In some cases, there may simply be physical constraints on reproductive systems that make viviparity unlikely even if the strategy would be optimal (e.g., the case of *A. tropidolepis* mentioned above; (Andrews & Mathies, 2000)

Another consideration is that our model's predictions were based on contemporary thermal environments, yet these environments may not represent the ancestral environments within which parity strategies evolved (Derrickson & Ricklefs, 1988; Recknagel et al., 2021). Phylogenetic reconstructions of some of the groups we examine here show that evolutionary transitions from oviparity to viviparity occurred when global climates were cooling (Hodges, 2004; Lambert & Wiens, 2013; Leaché & Linkem, 2015; Recknagel et al., 2021). While the ancestral character state of amniotes might have been viviparity (Jiang et al., 2023), most studies agree that, in squamate reptiles, viviparity is most often a derived character state from oviparity with reversals from viviparity to oviparity being rare or nonexistent (Guillette et al., 1980; King & Lee, 2015; but see Esquerré et al., 2019; Pyron & Burbrink, 2014). Thus, a species could have evolved viviparity in a past cool climate that then changed, or populations could have subsequently dispersed to a geographic region with a different local climate and yet been unable to re-evolve oviparity even though it would now be the optimal strategy. Alternatively, once viviparity evolved in a cold climate, it may offer an advantage in warm climates, particularly in cases where post-gestation embryo mortality is severe, and maternal manipulation can mitigate this risk. This dynamic may play a role in the tropical forest populations in our study, for whom viviparity might be retained as a mechanism to reduce the susceptibility of nests to flooding, disease (Blackburn, 1999), or predation (DeSana et al., 2020; Huang & Wang, 2009; Pike et al., 2016). Nonetheless, our results suggest that it might be worth re-examining previously published phylogenetic results aimed at understanding the evolution of viviparity. While environmental temperature seems to play a crucial role, it is possible that life-history traits in the ancestor of a clade affect the probability of viviparity evolving. For instance, our model suggests that decreased reproductive costs favor the evolution of live birth such that, all else remaining equal, lineages whose ancestors had lower offspring-to-mass ratios should be more likely to evolve viviparity.

Including other biophysical variables, such as oxygen availability or water vapor pressure, may have also influenced model predictions. Through viviparity, a pregnant female not only can improve the thermal regime experienced by the embryo but also enhance its oxygen supply (Andrews, 2002; Leibold et al., 2022; Pincheira-Donoso et al., 2017; Telemeco et al., 2022; Watson & Cox, 2021; Watson et al., 2014). Similarly, the lower water vapor pressure at high elevations may increase evaporative water loss, leading to selection for extended gestation (García-Collazo et al., 2012). While our model reveals that suboptimal thermal environments alone can explain selection for prolonged gestation, we cannot rule out oxygen or water vapor pressure as additional sources of selection favoring the evolution of viviparity in high-elevation lizards.

Our model validation was fundamentally limited by the availability of physiological, ecological, and life-history data. The data required to parameterize our model were rarely available for populations outside of North America or for snakes, leading to an overrepresentation of North American phrynosomatid lizards. While our model's accurate predictions for lizards across diverse habitat types suggests broad applicability, the geographic and taxonomic bias of our test must be accounted for when considering its validity. Further, and importantly, we were forced to treat embryonic thermal traits as constant across species. This assumption may not be completely unrealistic, considering that developmental constraints (Andrews & Mathies, 2000; Cordero et al., 2018; Monasterio et al., 2011) and shielding from natural selection via parental care (Logan et al., 2019; Muñoz, 2022) might lead to limited variation in embryonic thermal traits compared to adults. However, some evidence suggests that embryonic thermal physiology might co-adapt with that of the adult to the overall climatic conditions at a site (Andrews & Schwarzkopf, 2012), and this could generate embryonic trait variation. Nonetheless, much additional research is required to quantify the extent to which thermal physiology varies across species, populations, and ontogeny, and how this variation influences the evolution of parity mode.

Our model represents a significant advance in our understanding of the processes that contribute to the evolution of viviparity in lizards, mathematically formalizing a phenomenon that has been studied for over a century (Shine, 2014). Beyond its descriptive value, our model also holds promise as a forecasting tool, as it can predict not only the optimal gestation length but also the fitness associated with a given strategy. For populations in which our model produces accurate predictions for gestation length in contemporary climates, it could be integrated with climate forecasting tools to predict population viability into the future, helping to explain how life history trade-offs interact with climate to shape the evolution of reproductive strategies.

Data and code availability

The code and data required to reproduce all analyses are available on GitHub (https://github.com/ggcostoya/viviparity-model), and archived on Dryad (https://doi.org/10.5061/dryad.q83bk3jwq).

Supplementary material

Supplementary material is available online at *Evolution Letters*.

Author contributions

G.G.C. and M.L.L. conceived the project. G.G.C. led model development and data analysis with feedback from all authors. G.G.C. and S.D.G. assembled the trait database. G.G.C. wrote the first manuscript draft, and all authors contributed to its revision.

Funding

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

Conflict of interest

The authors declare no conflicts of interest.

Acknowledgements

The authors would like to thank Amanda Pettersen, Daniel Noble, Adam Leaché, Alex Gunderson, Noa Ratia, Christopher Halsch, José F. García, Jennifer Heppner, and the EvolDoers discussion group at the University of Nevada, Reno, for helpful discussions and comments on the manuscript.

References

Alencar, L. R. V., Schwery, O., Gade, M. R., Domínguez-Guerrero, S. F., Tarimo, E., Bodensteiner, B. L., Uyeda, J. C., & Muñoz, M. M. (2024). Opportunity begets opportunity to drive macroevolutionary dynamics of a diverse lizard radiation. *Evolution Letters*, 8, 623. https://doi.org/10.1093/evlett/qrae022.

Andrews, R. M. (1997). Evolution of viviparity: Variation between two sceloporine lizards in the ability to extend egg retention. *Journal of Zoology*, *243*(3), 579–595. https://doi.org/10.1111/j.1469-7998.1997.tb02803.x

Andrews, R. M. (2000). Evolution of viviparity in squamate reptiles (Sceloporus spp.): A variant of the cold-climate model. *Journal of Zoology*, 250(2), 243–253. https://doi.org/10.1111/j.1469-7998.2000.tb01075.x

Andrews, R. M. (2002). Low Oxygen: A Constraint on the Evolution of Viviparity in Reptiles. *Physiological and Biochemical Zoology*, *75*(2), 145–154. https://doi.org/10.1086/339388.

Andrews, R. M., & Mathies, T. (2000). Natural History of Reptilian Development: Constraints on the Evolution of Viviparity. *Bioscience*, 50(3), 227–238. https://doi.org/10.1641/0006-3568(2000)050%255B0227:NHORDC%255D2.3.CO;2

Andrews, R. M., & Schwarzkopf, L. (2012). Thermal performance of squamate embryos with respect to climate, adult life history, and phylogeny. *Biological Journal of the Linnean Society*, *106*(4), 851–864. https://doi.org/10.1111/j.1095-8312.2012.01901.x

Angilletta, M. J., Jr., Sears, M. W., & Pringle, R. M. (2009). Spatial dynamics of nesting behavior: Lizards shift microhabitats to construct nests with beneficial thermal properties. *Ecology*, *90*(10), 2933–2939. https://doi.org/10.1890/08-2224.1.

Blackburn, D. G. (1995). Saltationist and punctuated equilibrium models for the evolution of viviparity and placentation. *Journal of Theoretical Biology*, *174*(2), 199–216. https://doi.org/10.1006/jtbi.1995.0092.

Blackburn, D. G. (1999). Viviparity and oviparity: Evolution and reproductive strategies. In *Encyclopedia of reproduction*. (Vol. 4, pp. 994–1003). Academic Press.

Blackburn, D. G. (2015). Evolution of viviparity in squamate reptiles: Reversibility reconsidered. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 324(6), 473–486. https://doi.org/10.1002/jez.b.22625.

Buckley, L. B., Huey, R. B., & Kingsolver, J. G. (2022). Asymmetry of thermal sensitivity and the thermal risk of climate change. *Global Ecology and Biogeography*, *31*(11), 2231–2244. https://doi.org/10.1111/geb.13570

Calderón-Espinosa, M. L., Andrews, R. M., & Cruz, F. R. M. de la. (2006). Evolution of egg retention in the Sceloporus spinosus group; Exploring the role of physiological, environmental and phylogenetic factors. *Herpetological Monographs*, *20*(1), 147–158. https://doi.org/10.1655/0733-1347(2007)20%255B147:EOERIT%255D2.0.CO;2

Cale, W. G., Henebry, G. M., & Yeakley, J. A. (1989). Inferring Process from Pattern in Natural Communities. *Bioscience*, 39(9), 600–605. https://doi.org/10.2307/1311089

Cordero, G. A., Telemeco, R. S., & Gangloff, E. J. (2018). Reptile embryos are not capable of behavioral thermoregulation in the egg. *Evolution & Development*, 20(1), 40–47. https://doi.org/10.1111/ede.12244

Derrickson, E. M., & Ricklefs, R. E. (1988). Taxon-Dependent Diversification of Life-History Traits and the Perception of Phylogenetic Constraints. *Functional Ecology*, 2(3), 417–423. https://doi.org/10.2307/2389415

DeSana, A., Fargevieille, A., & Warner, D. A. (2020). Survival of lizard eggs varies with microhabitat in the presence of an invertebrate nest predator. *Evolutionary Ecology*, 34(4), 483–499. https://doi.org/10.1007/s10682-020-10058-w

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Pro-*

ceedings of the National Academy of Sciences, *105*(18), 6668–6672. https://doi.org/10.1073/pnas.0709472105

Domínguez-Guerrero, S. F., Esquerré, D., Burress, E. D., Maciel-Mata, C. A., Alencar, L. R. V., & Muñoz, M. M. (2024). Viviparity imparts a macroevolutionary signature of ecological opportunity in the body size of female Liolaemus lizards. *Nature Communications*, *15*(1), 4966. https://doi.org/10.1038/s41467-024-49464-x

Domínguez-Guerrero, S. F., Méndez-de la Cruz, F. R., Manríquez-Morán, N. L., Olson, M. E., Galina-Tessaro, P., Arenas-Moreno, D. M., Bautista- del Moral, A., Benítez-Villaseñor, A., Gadsden, H., Lara-Reséndiz, R. A., Maciel-Mata, C. A., Muñoz-Nolasco, F. J., Santos-Bibiano, R., Valdez-Villavicencio, J. H., Woolrich-Piña, G. A., & Muñoz, M. M. (2022). Exceptional parallelisms characterize the evolutionary transition to live birth in phrynosomatid lizards. *Nature Communications*, *13*(1), 2881. https://doi.org/10.1038/s41467-022-30535-w.

Esquerré, D., Brennan, I. G., Catullo, R. A., Torres-Pérez, F., & Keogh, J. S. (2019). How mountains shape biodiversity: The role of the Andes in biogeography, diversification, and reproductive biology in South America's most species-rich lizard radiation (Squamata: Liolaemidae). *Evolution; International Journal of Organic Evolution*, *73*(2), 214–230. https://doi.org/10.1111/evo.13657

Foucart, T., Lourdais, O., DeNardo, D. F., & Heulin, B. (2014). Influence of reproductive mode on metabolic costs of reproduction: Insight from the bimodal lizard Zootoca vivipara. *Journal of Experimental Biology*, *217*(22), 4049–4056. https://doi.org/10.1242/jeb.104315

Fromhage, L., Jennions, M. D., Myllymaa, L., & Henshaw, J. M. (2024). Fitness as the organismal performance measure guiding adaptive evolution. *Evolution; International Journal of Organic Evolution*, *78*(6), 1039–1053. https://doi.org/10.1093/evolut/qpae043

García-Collazo, R., Villagrán-Santa Cruz, M., Morales-Guillaumin, E., Meza Lázaro, R. N., & Méndez-de la Cruz, F. R. (2012). Egg retention and intrauterine embryonic development in Sceloporus aeneus (Reptilia: Phrynosomatidae): implications for the evolution of viviparity. *Revista Mexicana De Biodiversidad*, *83*(3), 802–808. https://doi.org/10.7550/rmb.33595

Gilbert, J. D. J., & Manica, A. (2010). Parental Care Trade-Offs and Life-History Relationships in Insects. *The American Naturalist*, *176*(2), 212–226. https://doi.org/10.1086/653661

Guillette, L. J., Jones, R. E., Fitzgerald, K. T., & Smith, H. M. (1980). Evolution of Viviparity in the Lizard Genus Sceloporus. *Herpetologica*, *36*(3), 201–215.

Hodges, W. L. (2004). Evolution of viviparity in horned lizards (Phrynosoma): Testing the cold-climate hypothesis. *Journal of Evolutionary Biology*, *17*(6), 1230–1237. https://doi.org/10.1111/j.1420-9101.2004.00770.x

Huang, W., & Wang, H.-Y. (2009). Predation Risks and Anti-Predation Parental Care Behavior: An Experimental Study in a Tropical Skink. *ethol*, *115*(3), 273–279. https://doi.org/10.1111/j.1439-0310.2008.01596.x

Hussain, R., Recknagel, H., & Elmer, K. R. (2024). Higher locomotor costs of pregnancy in viviparous compared to oviparous common lizards (Zootoca vivipara). *Ecology and Evolution*, *14*(8), e70171. https://doi.org/10.1002/ece3.70171

Jiang, B., He, Y., Elsler, A., Wang, S., Keating, J. N., Song, J., Kearns, S. L., & Benton, M. J. (2023). Extended embryo retention and viviparity in the first amniotes. *Nature Ecology & Evolution*, *7*(7), 1131–1140. https://doi.org/10.1038/s41559-023-02074-0

Kalinka, A. T. (2015). How did viviparity originate and evolve? Of conflict, co-option, and cryptic choice. *BioEssays*, *37*(7), 721–731. https://doi.org/10.1002/bies.201400200

King, B., & Lee, M. S. Y. (2015). Ancestral State Reconstruction, Rate Heterogeneity, and the Evolution of Reptile Viviparity. *Systematic Biology*, *64*(3), 532–544. https://doi.org/10.1093/sysbio/syv005

Laird, M. K., Thompson, M. B., & Whittington, C. M. (2019). Facultative oviparity in a viviparous skink (Saiphos equalis). *Biology Letters*, *15*(4), 20180827. https://doi.org/10.1098/rsbl.2018.0827

Lambert, S. M., & Wiens, J. J. (2013). Evolution of Viviparity: A Phylogenetic Test of the Cold-Climate Hypothesis in Phrynosomatid Lizards. *Evolution; International Journal of Organic Evolution*, *67*(9), 2614–2630. https://doi.org/10.1111/evo.12130

Leaché, A. D., & Linkem, C. W. (2015). Phylogenomics of Horned Lizards (Genus: Phrynosoma) Using Targeted Sequence Capture Data. *Copeia*, *103*(3), 586–594. https://doi.org/10.1643/CH-15-248

Leibold, D. C., Gastelum, J. A., VandenBrooks, J. M., & Telemeco, R. S. (2022). Oxygen environment and metabolic oxygen demand predictably interact to affect thermal behavior in a lizard, Sceloporus occidentalis. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, *337*(7), 739–745. https://doi.org/10.1002/jez.2630

Logan, M. L., van Berkel, J., & Clusella-Trullas, S. (2019). The Bogert Effect and environmental heterogeneity. *Oecologia*, *191*(4), 817–827. https://doi.org/10.1007/s00442-019-04541-7

Ma, L., Buckley, L. B., Huey, R. B., & Du, W.-G. (2018). A global test of the cold-climate hypothesis for the evolution of viviparity of squamate reptiles. *Global Ecology and Biogeography*, *27*(6), 679–689. https://doi.org/10.1111/geb.12730

Meiri, S. (2024). SquamBase—A database of squamate (Reptilia: Squamata) traits. *Global Ecology and Biogeography*, *33*(4), e13812. https://doi.org/10.1111/geb.13812

Meiri, S., Avila, L., Bauer, A. M., Chapple, D. G., Das, I., Doan, T. M., Doughty, P., Ellis, R., Grismer, L., Kraus, F., Morando, M., Oliver, P., Pincheira-Donoso, D., Ribeiro-Junior, M. A., Shea, G., Torres-Carvajal, O., Slavenko, A., & Roll, U. (2020). The global diversity and distribution of lizard clutch sizes. *Global Ecology and Biogeography*, *29*(9), 1515–1530. https://doi.org/10.1111/geb.13124

Meiri, S., Brown, J. H., & Sibly, R. M. (2012). The ecology of lizard reproductive output. *Global Ecology and Biogeography*, *21*(5), 592–602. https://doi.org/10.1111/j.1466-8238.2011.00700.x

Monasterio, C., Shoo, L. P., Salvador, A., Siliceo, I., & Díaz, J. A. (2011). Thermal constraints on embryonic development as a proximate cause for elevational range limits in two Mediterranean lacertid lizards. *Ecography*, *34*(6), 1030–1039. https://doi.org/10.1111/j.1600-0587.2010.06905.x

Muñoz, M. M. (2022). The Bogert effect, a factor in evolution. *Evolution; International Journal of Organic Evolution*, *76*(S1), 49–66. https://doi.org/10.1111/evo.14388

Noble, D. W. A., Stenhouse, V., Riley, J. L., Warner, D. A., While, G. M., Du, W.-G., Uller, T., & Schwanz, L. E. (2018). A comprehensive database of thermal developmental plasticity in reptiles. *Scientific Data*, *5*(1), 180138. https://doi.org/10.1038/sdata.2018.138.

Olson, M. E., & Arroyo-Santos, A. (2015). How to Study Adaptation (and Why To Do It That Way). *The Quarterly Review of Biology*, *90*(2), 167–191. https://doi.org/10.1086/681438

Pettersen, A. K., Feiner, N., Noble, D. W. A., While, G. M., Uller, T., & Cornwallis, C. K. (2023). Maternal behavioral thermoregulation facilitated evolutionary transitions from egg laying to live birth. *Evolution Letters*,7, 351. https://doi.org/10.1093/evlett/qrad031

Pike, D. A., Clark, R. W., Manica, A., Tseng, H.-Y., Hsu, J.-Y., & Huang, W.-S. (2016). Surf and turf: Predation by egg-eating snakes has led to the evolution of parental care in a terrestrial lizard. *Scientific Reports*, *6*(1), 22207. https://doi.org/10.1038/srep22207

Pincheira-Donoso, D., Jara, M., Reaney, A., García-Roa, R., Saldarriaga-Córdoba, M., & Hodgson, D. J. (2017). Hypoxia and hypothermia as rival agents of selection driving the evolution of viviparity in lizards. *Global Ecology and Biogeography*, *26*(11), 1238–1246. https://doi.org/10.1111/geb.12626

Pyron, R. A., & Burbrink, F. T. (2014). Early origin of viviparity and multiple reversions to oviparity in squamate reptiles. *Ecology Letters*, *17*(1), 13–21. https://doi.org/10.1111/ele.12168

R Core Team. (2025). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/. Date accessed March 11, 2025.

Recknagel, H., Kamenos, N. A., & Elmer, K. R. (2018). Common lizards break Dollo's law of irreversibility: Genome-wide phylogenomics support a single origin of viviparity and re-evolution of oviparity. *Molecular Phylogenetics and Evolution*, *127*, 579–588. https://doi.org/10.1016/j.ympev.2018.05.029

Recknagel, H., Kamenos, N. A., & Elmer, K. R. (2021). Evolutionary origins of viviparity consistent with palaeoclimate and lineage diversification. *Journal of Evolutionary Biology*, *34*(7), 1167–1176. https://doi.org/10.1111/jeb.13886

Shine, R. (1983). Reptilian viviparity in cold climates: Testing the assumptions of an evolutionary hypothesis. *Oecologia*, *57*(3), 397–405. https://doi.org/10.1007/BF00377186

Shine, R. (1995). A New Hypothesis for the Evolution of Viviparity in Reptiles. *The American Naturalist*, *145*(5), 809–823. https://doi.org/10.1086/285769

Shine, R. (2002). Reconstructing an Adaptationist Scenario: What Selective Forces Favor the Evolution of Viviparity in Montane Reptiles? *The American Naturalist*, *160*(5), 582–593. https://doi.org/10.1086/342815

Shine, R. (2014). Evolution of an Evolutionary Hypothesis: A History of Changing Ideas about the Adaptive Significance of Viviparity in Reptiles. *Journal of Herpetology*, *48*(2), 147–161. https://doi.org/10.1670/13-075

Shine, R., & Bull, J. J. (1979). The Evolution of Live-Bearing in Lizards and Snakes. *The American Naturalist*, *113*(6), 905–923. https://doi.org/10.1086/283444

Shine, R., & Harlow, P. (1993). Maternal thermoregulation influences offspring viability in a viviparous lizard. *Oecologia*, *96*(1), 122–127. https://doi.org/10.1007/BF00318039

Stearns, S. C. (1989). Trade-Offs in Life-History Evolution. *Functional Ecology*, *3*(3), 259–268. https://doi.org/10.2307/2389364

Stewart, J. R. (2021). Developmental morphology and evolution of extraembryonic membranes of lizards and snakes (Reptilia, Squamata). *Journal of Morphology*, *282*(7), 973–994. https://doi.org/10.1002/jmor.21266

Telemeco, R. S., Fletcher, B., Levy, O., Riley, A., Rodriguez-Sanchez, Y., Smith, C., Teague, C., Waters, A., Angilletta Jr, M. J., & Buckley, L. B. (2017). Lizards fail to plastically adjust nesting behavior or thermal tolerance as needed to buffer populations from climate warming. *Global Change Biology*, *23*(3), 1075–1084. https://doi.org/10.1111/gcb.13476

Telemeco, R. S., Gangloff, E. J., Cordero, G. A., Rodgers, E. M., & Aubret, F. (2022). From performance curves to performance surfaces: Interactive effects of temperature and oxygen availability on aerobic and anaerobic performance in the common wall lizard. *Functional Ecology*, *36*(10), 2544–2557. https://doi.org/10.1111/1365-2435.14147

Watson, C. M., & Cox, C. L. (2021). Elevation, oxygen, and the origins of viviparity. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 336(6), 457–469. https://doi.org/10.1002/jez.b.23072

Watson, C. M., Makowsky, R., & Bagley, J. C. (2014). Reproductive mode evolution in lizards revisited: Updated analyses examining geographic, climatic and phylogenetic effects support the cold-climate hypothesis. *Journal of Evolutionary Biology*, *27*(12), 2767–2780. https://doi.org/10.1111/jeb.12536

Whittington, C. M., Van Dyke, J. U., Liang, S. Q. T., Edwards, S. V., Shine, R., Thompson, M. B., & Grueber, C. E. (2022). Understanding the evolution of viviparity using intraspecific variation in reproductive mode and transitional forms of pregnancy. *Biological Reviews*, *97*(3), 1179–1192. https://doi.org/10.1111/brv.12836

Wourms, J., P., & Lombardi, J. (1992). Reflections on the Evolution of Piscine Viviparity1. *American Zoologist*, *32*(2), 276–293. https://doi.org/10.1093/icb/32.2.276

Zimin, A., Zimin, S. V., Shine, R., Avila, L., Bauer, A., Böhm, M., Brown, R., Barki, G., de Oliveira Caetano, G. H., Herrera, Castro, F., Chapple, D., G., Chirio, L., Colli, G. R., Doan, T. M., Glaw, F., Grismer, L. L., Itescu, Y., Kraus, F., LeBreton, M., … Meiri, S. (2022). A global analysis of viviparity in squamates highlights its prevalence in cold climates. *Global Ecology and Biogeography*, *31*(12), 2437–2452. https://doi.org/10.1111/geb.13598

Received June 4, 2025; revisions received October 10, 2025; accepted October 13, 2025