

A global test of the cold-climate hypothesis for the evolution of viviparity of squamate reptiles

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Funding information

China Scholarship Council; National Science Foundation, Grant/Award Number: DBI-1349865 and IOS-1038016; National Natural Science Foundation of China, Grant/Award Number: 31720103904 and 31525006; The Strategic Priority Research Program of the Chinese Academy of Sciences, Grant/Award Number: XDPB0202

Editor: Daniel Pincheira-Donoso

Abstract

Aim: The evolution of viviparity in squamate reptiles has attracted considerable scientific attention since the beginning of last century. The cold-climate hypothesis posits that cold regions favor viviparity (and therefore the incidence of viviparous squamates is increased in these regions) because viviparous females can use thermoregulatory behavior to shorten embryonic developmental time and to reduce exposure of embryos to stressful temperatures. However, a rigorous global-scale test of the impact of viviparity on the developmental time and viability of embryos is still absent. Recently developed biophysical models and climate databases enable us to conduct a mechanistic test of this hypothesis.

Location: Global.

Time period: Summer.

Major taxa studied: Squamata.

Methods: We integrated global climate data, a biophysical model, and developmental functions to quantify the effects of temperature on embryo developmental time, developmental viability, and energy consumption of oviparous versus viviparous embryos. To examine the accuracy of our predictions, we calculated the percentage of squamate reptiles that were viviparous in each region and assessed developmental temperature of gravid females, latitude and elevation as predictors for the percentage of squamate reptiles.

Results: Compared with oviparous embryos, viviparous embryos develop faster in cold regions, and experience similar embryonic developmental viability. Across most latitudes and elevations, the total energetic cost of development is lower for viviparous embryos than for oviparous embryos. Cold regions contain a higher proportion of viviparous species than do hot regions. By comparing the distribution pattern of viviparity and temperature effects on embryonic development, we found that shortened development time provided the strongest benefit of viviparity.

Main conclusions: Our global and biophysical model based comparison generally supports the cold-climate hypothesis. Moreover, viviparity in cold climates appears beneficial primarily by shortening developmental time.

KEYWORDS

biophysical model, cold-climate hypothesis, developmental time, developmental viability, embryo, energy consumption, reproductive mode, squamate, thermoregulation, viviparity

1 | INTRODUCTION

Squamate embryos complete development either within eggs that are exposed to external environmental conditions (oviparity) or inside a female's body (viviparity). Taxonomic and phylogenetic evidence indicates that oviparity is ancestral in squamates (Neill, 1964; Weekes, 1935), and that viviparity has evolved independently more than 108 times (Blackburn, 2006). A recent large-scale phylogenetic analysis suggests an early evolution of viviparity and detects multiple reversions to oviparity in squamates (Pyron & Burbrink, 2014), but their conclusion of a viviparous squamate ancestor has been questioned (e.g. Blackburn, 2015; Griffith et al., 2015; King & Lee, 2015; Shine, 2015; Wright, Lyons, Brandley, & Hillis, 2015). Regardless, transitions from oviparity to viviparity clearly have occurred frequently in reptiles.

The evolution of viviparity in squamates has been a hot topic since the beginning of last century (reviewed by Shine, 2014; Tinkle & Gibbons, 1977). Classical comparative studies demonstrate that there are relatively more viviparous species than oviparous species in cold climates, for example, at high latitudes or elevations (Duellman, 1965; Greene, 1970; Sergeev, 1940; Shine, 2014; Tinkle & Gibbons, 1977). The 'cold-climate hypothesis' was proposed to explain the evolution of viviparity and is the prevailing hypothesis (Hodges, 2004; Lambert & Wiens, 2013; Qualls & Andrews, 1999; Rodriguez-Diaz & Braña, 2012; Shine, 1985). This hypothesis posits that cold regions favor the evolution of viviparity, because viviparous females using thermoregulatory behavior will shorten the developmental time of their embryos as well as reduce the risk that their (immobile) embryos will be exposed to extreme or lethal temperatures (Neill, 1964; Packard, Tracy, & Roth, 1977; Sergeev, 1940; Shine & Bull, 1979).

Some alternative hypotheses have also been proposed. The climatic predictability hypothesis (CPH) suggests that egg retention enables a female to postpone oviposition until conditions are optimal for egg-laying (Tinkle & Gibbons, 1977), whereas the maternal manipulation hypothesis (MMH) suggests that viviparity could not only facilitate embryonic development and survival, but also improve offspring fitness by modifying developmentally sensitive phenotypic traits (Shine, 1995). Nonetheless, viviparity is not necessarily adaptive in unpredictable or seasonal climates, which is inconsistent with the predictions of both the CPH and MMH (Feldman et al., 2015). A recent study based on phylogenetic regressions showed that not only low temperatures but also oxygen deprivation played an important role in the evolution of viviparity (Pincheira-Donoso et al., 2017). Other environmental factors (e.g. moisture and predators), as well as biological and ecological attributes of species (e.g. arboreal or burrowing habits, restriction to aquatic or xeric environments, and venomousness) have also been explored as potential causes of the evolution of viviparity or egg retention (a potential intermediate step from oviparity to viviparity) (Neill, 1964; Packard et al., 1977; Sergeev, 1940; Shine & Bull, 1979). However, these factors appear less likely to favor egg retention – a critical evolutionary stage – than do temperature and oxygen (Andrews, 2002; Pincheira-Donoso et al., 2017; Shine, 2014; Shine & Bull, 1979).

Numerous field and laboratory studies have tested the following assumptions of the cold-climate hypothesis: (a) gravid females provide

a higher developmental temperature than does soil; (b) this temperature difference accelerates development of internal embryos; and (c) earlier hatching promotes survivorship of hatchlings (Demarco, 1992; Parker & Andrews, 2007; Shine, 1983). These studies have estimated nest temperature and maternal body temperature as well as reaction norms of embryos. For example, because females behaviorally regulate temperature, gravid lizards averaged 7°C warmer than local nest temperatures, thereby shortening developmental times relative to those of eggs in nests (Shine, 1983). When reared at the same constant temperature, lizards exhibiting viviparity or extended egg retention have shorter total embryonic developmental time (TEDT, from ovulation to hatching; Demarco, 1992). Reptiles from higher latitudes and elevations have more advanced embryonic stages at oviposition (or viviparity as the extreme; Braña, Bea, & Arrayago, 1991; Rodriguez-Diaz & Braña, 2012). Therefore, viviparity at high latitudes and elevations may confer advantages for relatively rapid development and enhanced fitness of offspring (Qualls & Andrews, 1999; Parker & Andrews, 2007; Shine, 1983).

Recent work has used phylogenetic comparative methods to continue testing the cold-climate hypothesis at broader taxonomic and geographic scales. These integrative studies found that transitions from oviparity to viviparity are consistently associated with colonization of cold climates (e.g. sites with low mean temperature during the egg-laying season or in spring) in some lizard lineages (e.g. *Liolaemus* and *Phrynosomatidae* lizards; Lambert & Wiens, 2013; Pincheira-Donoso, Tregenza, Witt, & Hodgson, 2013; Pincheira-Donoso et al., 2017) as well as in some snakes (Feldman et al., 2015). Furthermore, these analyses also suggest that viviparity evolves in cooler climates, viviparous lizards and snakes inhabiting warm climates represent secondary invasions of these environments, and the retention of viviparity in these climates may be a result of phylogenetic conservatism (Feldman et al., 2015; Lambert & Wiens, 2013). Viviparous lineages in cold climates experience climatic instability but have fewer competitors, which are thought to promote extinction and speciation rates, respectively, leading to higher turnover (lineage replacement through time) of livebearing lineages, but lower net diversification rates (Lambert & Wiens, 2013; Lynch, 2009; Pyron & Burbrink, 2014).

Broadly, the cold-climate hypothesis is well, although not comprehensively, supported. The evidence is especially less clear in the field and laboratory tests. For example, limited data on incubation and gestation periods do not suggest that developmental times are shorter in high latitude viviparous species than sympatric oviparous species (Tinkle & Gibbons, 1977). Also, mean temperatures of gravid viviparous females and of nest sites are similar in some lizards (Andrews & Rose, 1994). Although phylogenetic analyses provide overwhelming support for the cold-climate hypothesis, these studies have relied on air temperatures (rather than body temperature per se) as indicators of environmental conditions faced by adults and embryos, and have not considered the developmental rate and viability of embryos. Therefore, the mechanistic (e.g. physiological and behavioral) links between cold climate and viviparity are still missing.

In this study, we combine global climate data, biophysical (mechanistic) models (Buckley, 2008; Kearney, Isaac, & Porter, 2014) and

embryonic temperature functions to conduct an embryo-based test of the cold-climate hypotheses at a global scale. Note that our model (non-phylogenetic) estimates only the relative fitness of oviparous versus viviparous squamates, not their evolutionary origins. Specifically, we first use a biophysical model to calculate developmental temperatures of embryos in oviparous and viviparous squamates, and then quantify the effects of temperature on the developmental time, developmental viability and embryonic energy consumption to evaluate geographic patterns of the relative fitness of oviparous versus viviparous modes of reproduction. We use *Sceloporus* lizards as models for our analyses: *Sceloporus* includes both viviparous and oviparous species (Lambert & Wiens, 2013), and these lizards have been well studied and have often been used in biophysical studies (Adolph & Porter, 1993; Angilletta, 2001; Buckley, 2008; Levy et al., 2015). If the cold-climate hypothesis is correct, then viviparous embryos in cold climate will have a shorter development, higher viability and lower energy expenses than do oviparous embryos. Moreover, we use a regression analysis to quantify three covarying predictors of the proportion of viviparity: temperature, latitude, and elevation (Feldman et al., 2015; Qualls & Andrews, 1999; Shine, 1983). We use a spatial regression to control for similarities in the proportion of viviparity due to spatial proximity.

2 | METHODS

2.1 | Basic assumptions

For approximately the first third of incubation (Andrews & Mathies, 2000), oviparous and viviparous embryos are inside their mother and thus experience similar environments (assuming females select similar body temperatures). But thereafter, they will be exposed to different environments until final hatching, and so we thus focused on this later period. We assumed that viviparous embryos have no 'placental' connections with their mothers: embryos use energy only from yolks to fuel development. This assumption is reasonable because most viviparous squamates ovulate large yolked eggs and have placentae with little complexity (type I placentae), which involves little modification (only eggshell reduction) from basic oviparity (Blackburn, 1993; Stewart, 1992; Thompson et al., 1999; Weekes, 1935). We also assumed oviparous females lay their eggs at 5-cm depth in sandy soil, and that both oviparous and viviparous females could use this same depth burrows for thermoregulation during overnight retreats or when avoiding excessive heat on the ground surface. These assumptions are reasonable: 5 cm is a common depth for lizard nests (Angilletta, Sears, & Pringle, 2009; Ryberg, Hill, Lay, & Fitzgerald, 2012; Shine, 1999; Taylor, 2004; Warner & Shine, 2008; Webb, Pike, & Shine, 2008). Thus, we used maternal body temperature (see below) and substrate temperature (sandy soil) (at 5-cm depth) as the developmental temperature of viviparous embryos and oviparous embryos, respectively.

2.2 | Developmental temperature

We extracted global microclimate data from the 'microclim' dataset [0.2° resolution (represents 22.264 km at equator); Kearney et al.,

TABLE 1 Climate variables derived from the 'microclim' dataset

Variable	Variable name in code
Longitude	lon
Latitude	lat
Air temperature 1 cm above ground in 0% shade	TA1cm_sun
Air temperature 1 cm above ground in 100% shade	TA1cm_shade
Air temperature 120 cm above ground	TA120cm
Wind speed 1 cm above ground	V1cm
Solar radiation	SOLR
Substrate temperature at 0 cm in 0% shade	D0cm_sun
Substrate temperature at 0 cm in 100% shade	D0cm_shade
Substrate temperature at -5 cm in 0% shade	D5cm_sun
Substrate temperature at -5 cm in 100% shade	D5cm_shade
Zenith angle	ZEN

2014]. This dataset is based on long-term average macroclimates (downscaled) and contains gridded hourly estimates of typical microclimatic conditions at high resolution for the globe. Hourly estimates used here were for a 24-h period on the middle day of each month. We used only data for June for the Northern Hemisphere and for December for the Southern Hemisphere: relatively high temperatures and rates of embryonic development typically occur during these months at most latitudes and elevations (Adolph & Porter, 1993). Data were extracted and analysed in R 3.4.1 (R Core Team, 2016; mainly with the library 'RNetCDF'). Table 1 shows variables extracted from the 'microclim' dataset.

We estimated hourly developmental temperatures of oviparous and viviparous species for grid cells spanning global land areas (except Antarctica). Because nest-site selection (especially canopy vegetation cover) will affect developmental temperature (Morjan, 2003; Muth, 1980; Pike, Webb, & Shine, 2010; Warner, Jorgensen, & Janzen, 2010), we considered two extreme scenarios for oviparous species: females laying eggs in open areas (0% shade) versus in full shade (100%). To calculate developmental temperatures of viviparous species, we began by using a biophysical model (Buckley, 2008) that translates environmental factors onto operative temperatures. We calculated operative temperatures of females on the ground (in 0% shade and 100% shade) and in nests (5-cm depth in 0% shade and 100% shade), respectively. Viviparous females were allowed to thermoregulate within the range of these four potential operative temperatures. We assumed these gravid females thermoregulate as close to their thermal optimum (32°C in Beuchat, 1986) as possible during the day, but that their body temperatures would conform to nest temperature (in 100% shade) during the night.

Gravid females of viviparous species often leave their retreats during the day for at least a few hours to forage (Shine, 1980), and sites with limited 'foraging hours' are unlikely to enable successful hatching. Thus, we calculated hours per day when operative temperatures above ground (in 0% shade or 100% shade) were within the range of

preferred temperatures (29.4–39.3°C, central 80% of field body temperatures; Levy, Buckley, Keitt, & Angilletta, 2016). We assigned a developmental failure to viviparous species at sites where females could not forage for at least 2 hr per day.

2.3 | Developmental time

We used an empirical function (Equation 1) to calculate the developmental rate of embryos (D , percentage of embryonic development accomplished per hour) as a function of hourly developmental temperature (T) (Telemeco et al., 2017). Embryos were assumed to suspend development when temperatures were below the developmental zero temperature (15.9°C). We calculated developmental rate as a linear function of developmental temperature when it was above the developmental zero temperature (Telemeco et al., 2017):

$$\begin{cases} T \leq 15.9, & D=0 \\ T > 15.9, & D = \frac{-0.024545 + 0.001545 \times T}{24} \end{cases} \quad (1)$$

Then we summed developmental rate over 24 hr as the daily development. Finally, we calculated developmental time as the inverse of daily development.

2.4 | Developmental viability

We used an empirical function (Equation 2) (with minor modification from Levy et al., 2015) to calculate the proportional developmental viability (*success*) of embryos (Telemeco et al., 2017). Developmental viability was calculated as a nonlinear function of minima (T_{\min}) and maxima (T_{\max}) of developmental temperature through 24 h:

$$\begin{cases} T_{\min} < 25 \ \& \ T_{\max} < 44, & \text{success} = \frac{e^{(-2.18733 + 0.14268 \times T_{\min})}}{1 + e^{(-2.18733 + 0.14268 \times T_{\min})}} \\ T_{\min} \geq 25 \ \& \ T_{\max} < 44 & \text{success} = 0.8 \\ T_{\max} \geq 44 & \text{success} = 0 \end{cases} \quad (2)$$

If daily minimum temperature was less than 25°C while maximum temperature was less than 44°C, developmental viability was a function of minimum temperature; but if the daily minimum was higher than 25°C while the daily maximum was less than 44°C, developmental viability equaled 0.8. If the daily maximum exceeded 44°C (a temperature that causes embryo mortality, Levy et al., 2015), development failed (developmental viability = 0). In addition, we assumed developmental failure if the calculated developmental time exceeded 100 days, as developmental times at least this long are rare in the literature (Andrews, Mathies, Qualls, & Qualls, 1999; Tinkle & Gibbons, 1977).

2.5 | Energy consumption

We also used an empirical function (Equation 3) to calculate embryonic energy consumption (MR, metabolic rate per hour; Telemeco et al., 2017) as an exponential function of developmental temperature (T) and the Boltzmann constant (k):

$$\text{MR} (J/h) = e^{21.44} * e^{\left(\frac{-8.74901 \times 10^{-20} J}{k \times T}\right)} \quad (3)$$

Then we summed hourly energy metabolism over 24 hr as the daily energy consumption. Finally, we multiplied daily energy consumption by developmental time to get total energy consumption during development. We assumed a developmental failure if the embryonic energy consumption was higher than 10 kJ, which is about 5 times the average energy consumption during development (Robert & Thompson, 2000).

2.6 | Sensitivity analysis

Some of the necessary parameters of the biophysical model lizard (Supporting Information Table S1.1) are not widely available for most species. *Sceloporus* lizards are an exception in this regard, and this genus includes both oviparous and viviparous species and is widely spread across latitudes and elevations in North America. Therefore, *Sceloporus* lizards are an ideal biophysical 'model lizard', at least for North American species. Nonetheless, interspecific variation in body size and thermal optima of gravid lizards may affect heat balance of gravid females, and therefore their body temperatures as well as embryonic development and success. We examined sensitivity to body size by rerunning the above analysis using the snout-vent length (SVL) and body mass of smaller (*Scincella modesta*, a small skink; Ma, Sun, Li, Sha, & Du, 2014) and larger (*Morelia spilota*, a large snake; Ayers & Shine, 1997) squamates. The results suggested that differences in body size do not change the general patterns (Supporting Information Figure S1.1–S1.6). The preferred body temperature of *Sceloporus* shows little geographic and interspecific variation (Buckley, Ehrenberger, & Angilletta, 2015). Moreover, although preferred body temperature differs among squamates, the mean preferred body temperature of lizards is close to 32°C (Qu, Li, Gao, Xu, & Ji, 2011). Assuming a constant preferred body temperature across geography allows us to explore the implications of geographic gradients in environmental temperature without confounding variation in preferred temperatures. We also examined sensitivity to thermal optima of gravid females by rerunning the above analyses with both lower (e.g. of *Lacerta vivipara*; Le Galliard, Le Bris, & Clobert, 2003) and higher (e.g. of *Podarcis muralis*; Braña, 1993) preferred temperatures. The results suggested that variation in thermal optima of gravid females does not substantively change geographic patterns (Supporting Information Figure S1.7–S1.12).

2.7 | Realistic distribution and spatial regression analysis

To examine the robustness of our predictions to the realistic distribution of squamates, we downloaded species' distribution shapefiles from the IUCN Red List Spatial Data (<http://www.iucnredlist.org/>) and a reference table of squamate reproductive modes from the literature (Pyron, 2015). Then we extracted in R (library 'raster') a list of species presented in each 1° × 1° grid cell (in the WGS84 projection; 1° represent 111.32 km at equator) and calculated the percentage of species that were viviparous. Estimates are approximate because shapefiles and viviparity data were available for only 2,922 of approximately 9,882 squamate species. We then did spatial regression analysis (R

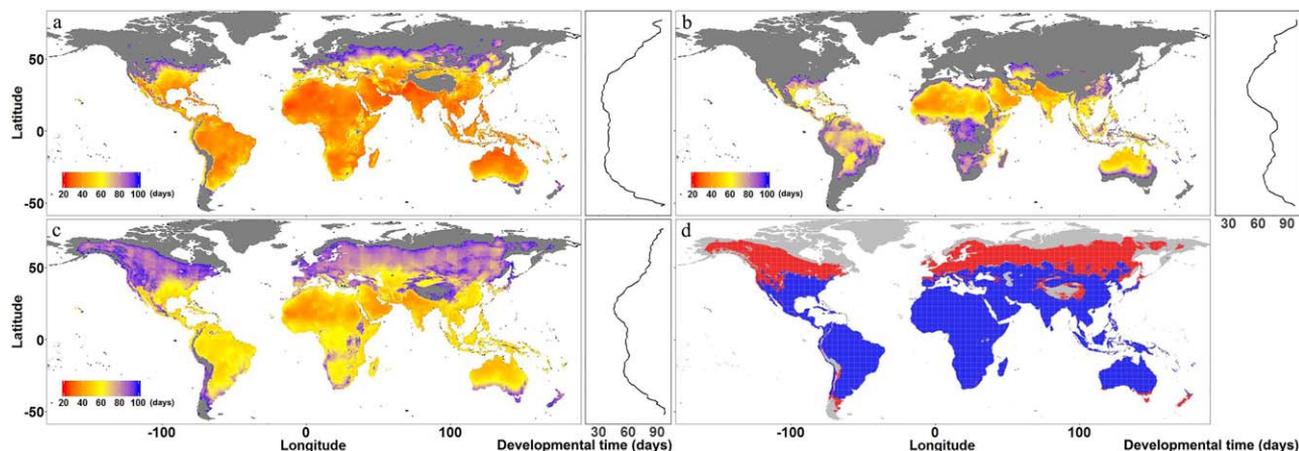


FIGURE 1 Developmental time varies geographically for (a) ‘oviparous’ eggs laid in 0% shade (–5 cm in sand); (b) ‘oviparous’ eggs laid in 100% shade (–5 cm in sand) and (c) ‘viviparous’ embryos. In (d), we depict areas where shorter developmental time is experienced by ‘viviparous’ (red) versus ‘oviparous’ (blue) embryos. We excluded sites where potential foraging times are less than 2 hr per day (for viviparity only) and where developmental time exceeds 100 days (gray). Sites where ‘viviparous’ and ‘oviparous’ embryos are equal are in gray. We depict mean values of each metric across latitudinal bands

library ‘spdep’; Kissling & Carl, 2008) between the percentage of viviparous species and three response variables: developmental temperature of gravid females, latitude and elevation (models were run on a subset: 5,000 out of 25,815 sites). We first developed neighborhoods with threshold distances of 400, 800, or 1,500 km, which were selected from by examining correlograms. Then we used R to fit a basic linear model, a spatial simultaneous autoregressive (SAR) lag model, a SAR error model, and a SAR mixed (lag + error) model. Spatial autocorrelations of residuals were evaluated with Moran’s *I* tests. We then used Akaike’s information criterion (AIC) to evaluate model fit.

3 | RESULTS

3.1 | Developmental time

Developmental time for both reproductive modes generally increases with (absolute) latitude and elevation (Figure 1a–c). However, viviparous species can occupy a relatively large range of latitudes and elevations that enable hatching within 100 days. In cold regions (high latitudes and elevations), viviparous species have a shorter developmental time than do oviparous species, whereas in hot regions (low latitudes and elevations), oviparous species that lay their eggs in open areas have the shortest developmental time. Eggs of oviparous species laid in open areas could generally hatch within 100 days in a larger range of latitudes and elevations, and have shorter developmental times, than would eggs of oviparous species laid in full shade. Thus, in cold regions viviparous species have a development-time advantage: but in hot regions, oviparous species have this advantage (Figure 1d).

3.2 | Developmental viability

Developmental viability for both reproductive modes generally decreases with (absolute) latitude and elevation (Figure 2a–c). Oviparous embryos hatch only if laid in sunny spots at high latitudes and

elevations, but only in shady spots at low latitudes and elevations. Viviparous embryos could develop at most latitudes and elevations: the viable area for viviparous embryos approximates that of a combination of oviparous embryos laid in sun or in shade. Overall, neither viviparity or oviparity has an obvious advantage for the developmental success in most areas of the world (Figure 2d).

3.3 | Energy consumption

Embryos of viviparous species spend less energy during development than do oviparous embryos across most regions globally (Figure 3d). For oviparous species, energy consumption increases in cold regions, even though the low temperatures lower hourly metabolic rate. Estimated consumption sometimes exceeds 5 times the average energy consumption (1.7–2.0 kJ) of embryos of *Sceloporus undulatus* (Angilletta, Winters, & Dunham, 2000). Eggs laid in open areas could hatch in a larger range of latitudes and elevations and have a lower developmental energy consumption in cold regions than eggs laid in full shade (Figure 3a,b). Viviparous species have an advantage over oviparous species in terms of minimizing embryonic energy consumption throughout the globe (Figure 3c,d).

3.4 | Realistic distribution and spatial regression analysis

An analysis of geographic patterns of the relative incidence of viviparity reveals a clear and well-known pattern (see Introduction), namely, that the percentage of viviparity increases with latitude and elevation (Figure 4). In the spatial regression analysis, the spatial SAR mixed (lag + error) model performed the best and had the lowest spatial autocorrelation and the highest model fit (Table 2). In this model, latitude predicted percentage of viviparity better than did developmental temperature or elevation.

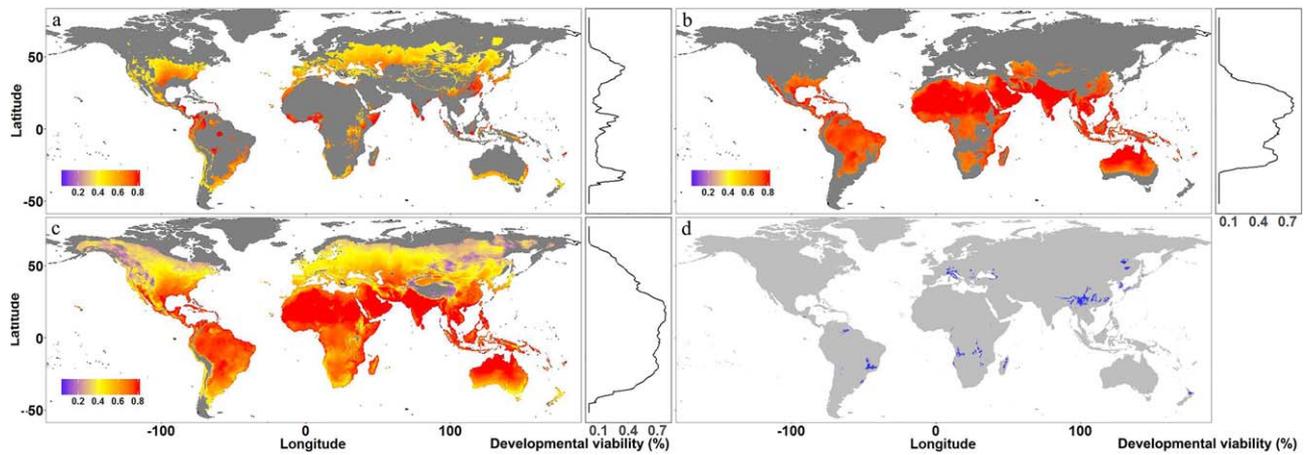


FIGURE 2 Developmental viability varies geographically for (a) ‘oviparous’ eggs laid in 0% shade (–5 cm in sand); (b) ‘oviparous’ eggs laid in 100% shade (–5 cm in sand) and (c) ‘viviparous’ embryos. In (d), we depict areas where higher developmental viability is experienced by ‘viviparous’ (red) versus ‘oviparous’ (blue) embryos. We excluded sites where potential foraging times are less than 2 hr per day (for viviparity only) and where developmental time exceeds 100 days (gray). Sites where ‘viviparous’ and ‘oviparous’ embryos are equal are in gray. We depict mean values of each metric across latitudinal bands

4 | DISCUSSION

4.1 | Main conclusions

This analysis adds support for the cold-climate hypothesis (Andrews, 2000; Feldman et al., 2015; Hodges, 2004; Lambert & Wiens, 2013; Shine & Bull, 1979), but does so from a new perspective: specifically, it identifies mechanistic connections between cold climate and viviparity. Our comparisons suggest that viviparity is not only advantageous in cold regions (high latitudes and elevations), but can also be advantageous in hot regions (low latitudes and elevations) at least in terms of developmental viability and energy consumption. Nevertheless, viviparous embryos had longer developmental times than did oviparous embryos in hot regions. This analysis of developmental times accords with the well-known and observed distribution of oviparity and

viviparity (Figure 4), such that viviparity is relatively common in cold areas but not in relatively warm regions. The spatial regression analysis suggests that latitude predicts viviparity percentage better than do developmental temperature or elevation (Table 2).

4.2 | Developmental time

Compared with oviparous embryos, viviparous embryos develop faster in cold regions but slower in hot regions (Figure 1). This shift reflects geographic patterns of nest temperatures and of maternal body temperatures. Nest temperatures decrease (and development times increase) with latitude and elevation if – as our model assumes – females always lay their eggs at the same depth and degree of shading (Doody et al., 2006). In contrast, viviparous females in our model were given the chance to thermoregulate within four locations (surface or

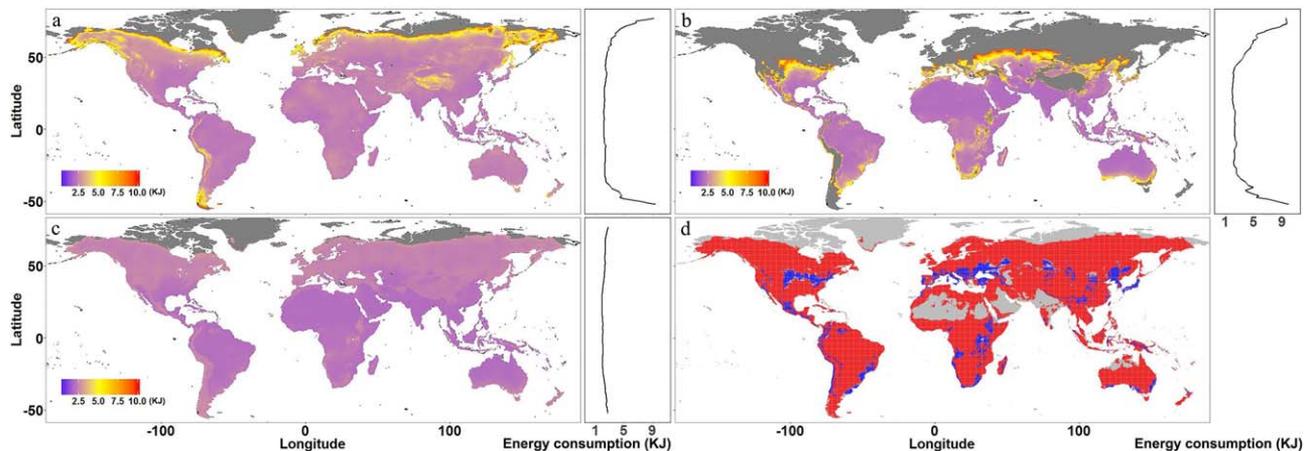


FIGURE 3 Embryonic energy consumption varies geographically for (a) ‘oviparous’ eggs laid in 0% shade (–5 cm in sand); (b) ‘oviparous’ eggs laid in 100% shade (–5 cm in sand) and (c) ‘viviparous’ embryos. In (d), we depict areas where less energy consumption happens for ‘viviparous’ (red) versus ‘oviparous’ (blue) embryos. We excluded sites where potential foraging times are less than 2 hr per day (for viviparity only) and where energy consumption exceeds 10 kJ (gray). Sites where ‘viviparous’ and ‘oviparous’ embryos are equal are in gray. We depict mean values of each metric across latitudinal bands

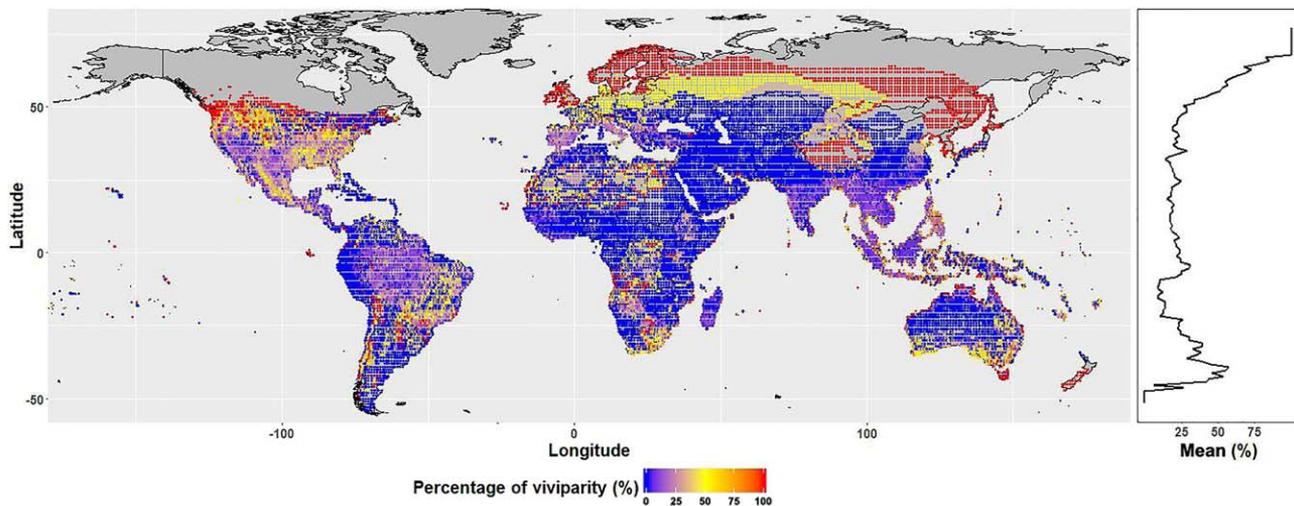


FIGURE 4 The percentage of viviparous squamate species increases with increasing latitude (colors indicate the percentage of viviparous species)

burrow, in full sun or full shade). In cold regions, gravid females could thus use behavior to select relatively warm microhabitats and simultaneously warm their embryos; whereas in hot regions, viviparous females would stay in the shade or retreat to burrows when surface operative temperatures were too hot (Andrews, 1997; Mathies & Andrews, 1996). These choices made by mothers determine the developmental time of their embryos relative to the developmental time of eggs laid in the soil. Previous studies have suggested that viviparous females thermoregulating in cold climates could increase developmental temperature and thus shorten the developmental time (Li, Qu, Hu, & Ji, 2009; Parker & Andrews, 2007; Shine, 1983). But the side effect that viviparous females may lengthen developmental times in hot environments by seeking shade or burrows has been often overlooked.

4.3 | Developmental viability

The cold-climate hypothesis suggests higher developmental viability is a potential benefit associated with viviparity at high latitudes and elevations (Shine & Bull, 1979; Tinkle & Gibbons, 1977): by thermoregulating, viviparous females in cold climates could protect their embryos from extreme cold temperatures (Sergeev, 1940; Tinkle & Gibbons, 1977). However, if given the opportunity to lay eggs in either open

areas or 100% shade, oviparous species can achieve a developmental viability of embryos as high as that of viviparous species in most regions (Figure 2). This may be because we assume embryos of both reproductive modes experience the same minimum temperature at cold area and do not consider 'thermoregulation' of viviparous females at night. In our model, viviparous females spent the night at the same depth (5 cm) as did eggs laid by oviparous females. Nevertheless, the thermal environments and the thermoregulatory behaviors of squamates at night are largely unknown (but see Huey, 1982). Potentially, gravid females may dig deeper to get warmer during cold nights, even though this takes additional energy (Seymour, 1973; Vleck, 1979); or, if available, females might use rodent burrows or hide underneath rocks as economical options (Davidson, Lightfoot, & McIntyre, 2008). In hot regions, however, viviparous females could thermoregulate to protect their embryos from extreme high temperatures and thus achieve developmental viability as high as that of oviparous eggs laid in full shade.

4.4 | Energy consumption

Across most latitudes and elevations, viviparous embryos are predicted to use less energy during development than do oviparous embryos (Figure 3). This is because viviparous embryos experience higher

TABLE 2 Spatial regression analysis between percentage of viviparous species and three response variables: developmental temperature of gravid females, latitude and elevation

Model	Observed [estimate (SE)]							AIC	<i>I</i>
	Temperature	Latitude	Elevation	Temp*Lat	Temp*Ele	Lat*Ele	Temp*Lat*Ele		
Basic linear model	-2.54 (0.19)	2.19 (0.13)	0.01 (0.00)	-0.08 (0.01)	-0.00 (0.00)	-0.00 (0.00)	0.00 (0.00)	45,627.28	.520
SAR lag model	-1.16 (0.15)	1.18 (0.11)	0.01 (0.00)	-0.04 (0.00)	-0.00 (0.00)	-0.00 (0.00)	0.00 (0.00)	43,139.51	.211
SAR error model	-2.11 (0.24)	2.12 (0.17)	0.01 (0.00)	-0.08 (0.01)	-0.00 (0.00)	-0.00 (0.00)	0.00 (0.00)	43,217.29	.215
SAR mixed model	-0.37 (0.25)	1.03 (0.34)	0.02 (0.00)	-0.01 (0.01)	-0.00 (0.00)	-0.00 (0.00)	0.00 (0.00)	43,072.49	.210

Note. Basic linear model, spatial simultaneous autoregressive (SAR) lag model, SAR error model and SAR mixed (lag + error) model were fitted. Spatial autocorrelation of model residuals was evaluated with Moran's *I* tests, with larger absolute values of *I* indicating higher spatial autocorrelation. The fit of models was evaluated with Akaike's information criterion (AIC), with lower AIC indicating better fit of models.

developmental temperature than oviparous embryos do; and higher developmental temperature shortens developmental time more than enough to compensate for increased daily energy consumption. A similar effect of developmental temperature on the total energy consumption during development has previously been found (Angilletta et al., 2000). However, this result may not add substantial support to the cold-climate hypothesis because oviparous females could keep the energy consumption of their embryos as low as viviparous ones by laying eggs in open areas. Furthermore, even for eggs laid in shady areas, embryos could develop without spending 'too much' cumulative energy (not exceeding 5 times the average energy consumption (1.7–2.0 kJ) of embryos of *S. undulatus*) in most regions where squamates exist (see Figure 4). According to our model's predictions, embryonic energy consumption during development remains relatively constant in most regions, regardless of reproductive mode. Thus, energy should not be a limiting factor in the evolution of reproductive modes, at least from the embryo's perspective. Furthermore, our assumption that viviparous females have no 'placental' connections with their embryos will not affect model interpretations, because viviparous embryos spend less energy than do oviparous embryos during development (do not 'need' extra energy supply from gravid females). Interestingly, we found that energy consumption becomes high at high latitudes and elevations due to greatly lengthened developmental time, even though developmental temperatures there are low (Andrews, Qualls, & Rose, 1997; Angilletta et al., 2000; While et al., 2015). Consequently, thermoregulating viviparous females in cold areas could not only shorten embryonic developmental time and thus provide offspring with more time to prepare for winter (relative to oviparous embryos), but also hatch with a higher residual energy content (assuming eggs initially have the same energy content).

4.5 | Limits of the model and future directions

To make our model both simple and general, we excluded potential geographic variation in several factors that can be explored in the future. Although oxygen concentration was recently suggested to play a role in the evolution of viviparity (Pincheira-Donoso et al., 2017), we did not incorporate it into our model, because a clear mechanistic connection between atmosphere oxygen and embryonic development is currently unavailable. We fixed the timing of reproduction, but phenological shifts in that timing with latitude and elevation could buffer the impact of global temperatures (Levy et al., 2016; Radchuk, Turlure, & Schtickzelle, 2013). We assumed fixed patterns (geographic, reproductive mode) of the thermal sensitivity of development or of metabolism, but these could potentially vary. However, embryonic thermal sensitivity varies little in *Sceloporus* (Angilletta, Zelic, Adrian, Hurliman, & Smith, 2013; Buckley et al., 2015), and the mean preferred body temperature (32.8°C) of lizards is close to our assumption of 32°C (Qu et al., 2011). Finally, females might use behavior to compensate for climate variation. For example, oviparous females in hot areas might lay their eggs in deeper sites, and viviparous females might shift their depth when inactive (Doody et al., 2006; Refsnider & Janzen, 2012; Telemeco, Elphick, &

Shine, 2009) or shift from open to shaded habitats for nesting, but their ability to buffer thermal conditions is limited (Telemeco et al., 2017). Our global spatial regression analysis suggests that latitude best predicts the proportion of viviparity. However, we cannot determine whether this would hold for an analysis focused on a local area having a large range of elevations. Further studies could incorporate phenological, spatial, physiological and behavioral variance across populations and species into analyses to evaluate whether and how such shifts affect the relative advantages of viviparity and oviparity. Also, a complete understanding of selective pressures on reproductive modes must include impacts on energetics and survival of mothers.

ACKNOWLEDGMENTS

We thank Rory Telemeco for providing physiological functions used in our model. We thank Rory Telemeco and Michael Sears for suggestions about the biophysical model and thermoregulating rules. We thank Michael Kearney and Ofir Levy for suggestions about the 'microclim' dataset. We thank Sima Bouzid and Matt McElroy for helping to improve R code. L.M. was supported by an internship from China Scholarship Council, L.B.B. (DBI-1349865) and R.B.H. (IOS-1038016) by grants from the National Science Foundation, and W.D. by National Natural Science Foundation of China (31720103904, 31525006) and The Strategic Priority Research Program of the Chinese Academy of Sciences (XDPB0202).

DATA ACCESSIBILITY

R scripts are deposited in the Dryad repository: <https://doi.org/10.5061/dryad.tm06r>.

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REFERENCES

- Adolph, S. C., & Porter, W. P. (1993). Temperature, activity, and lizard life histories. *The American Naturalist*, 142(2), 273–295.
- 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.
- 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.
- Andrews, R. M. (2002). Low oxygen: A constraint on the evolution of viviparity in reptiles. *Physiological and Biochemical Zoology*, 75(2), 145–154.
- Andrews, R. M., & Mathies, T. (2000). Natural history of reptilian development: Constraints on the evolution of viviparity. *Bioscience*, 50, 227–238.
- Andrews, R. M., Mathies, T., Qualls, C. P., & Qualls, F. J. (1999). Rates of embryonic development of *Sceloporus* lizards: Do cold climates favor the evolution of rapid development? *Copeia*, 1999(3), 692–700.

- Andrews, R. M., Qualls, C. P., & Rose, B. R. (1997). Effects of low temperature on embryonic development of *Sceloporus* lizards. *Copeia*, 1997(4), 827–833.
- Andrews, R. M., & Rose, B. R. (1994). Evolution of viviparity - Constraints on egg retention. *Physiological Zoology*, 67, 1006–1024.
- Angilletta, M. J. (2001). Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). *Ecology*, 82, 3044–3056.
- Angilletta, M. J., 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.
- Angilletta, M. J., Winters, R. S., & Dunham, A. E. (2000). Thermal effects on the energetics of lizard embryos: Implications for hatchling phenotypes. *Ecology*, 81, 2957–2968.
- Angilletta, M. J., Zelic, M. H., Adrian, G. J., Hurliman, A. M., & Smith, C. D. (2013). Heat tolerance during embryonic development has not diverged among populations of a widespread species (*Sceloporus undulatus*). *Conservation Physiology*, 1, 1–9.
- Ayers, D. Y., & Shine, R. (1997). Thermal influences on foraging ability: Body size, posture and cooling rate of an ambush predator, the python *Morelia spilota*. *Functional Ecology*, 11(3), 342–347.
- Beuchat, C. A. (1986). Reproductive influences on the thermoregulatory behavior of a live-bearing lizard. *Copeia*, 1986(4), 971–979.
- Blackburn, D. G. (1993). Chorioallantoic placentation in squamate reptiles - Structure, function, development, and evolution. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, 266(5), 414–430.
- Blackburn, D. G. (2006). Squamate reptiles as model organisms for the evolution of viviparity. *Herpetological Monographs*, 20, 131–146.
- 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.
- Braña, F. (1993). Shifts in body temperature and escape behavior of female *Podarcis muralis* during pregnancy. *Oikos*, 66(2), 216–222.
- Braña, F., Bea, A., & Arrayago, M. J. (1991). Egg retention in lacertid lizards - Relationships with reproductive ecology and the evolution of viviparity. *Herpetologica*, 47, 218–226.
- Buckley, L. B. (2008). Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. *The American Naturalist*, 171(1), E1–E19.
- Buckley, L. B., Ehrenberger, J. C., & Angilletta, M. J. (2015). Thermoregulatory behaviour limits local adaptation of thermal niches and confers sensitivity to climate change. *Functional Ecology*, 29, 1038–1047.
- Davidson, A., Lightfoot, D., & McIntyre, J. (2008). Engineering rodents create key habitat for lizards. *Journal of Arid Environments*, 72, 2142–2149.
- Demarco, V. (1992). Embryonic-development times and egg retention in 4 species of sceloporine lizards. *Functional Ecology*, 6(4), 436–444.
- Doody, J. S., Guarino, E., Georges, A., Corey, B., Murray, G., & Ewert, M. (2006). Nest site choice compensates for climate effects on sex ratios in a lizard with environmental sex determination. *Evolutionary Ecology*, 20, 307–330.
- Duellman, W. E. (1965). *A biogeographic account of the herpetofauna of Michoacan, Mexico*. Lawrence: University of Kansas Press.
- Feldman, A., Bauer, A. M., Castro-Herrera, F., Chirio, L., Das, I., Doan, T. M., ... Meiri, S. (2015). The geography of snake reproductive mode: A global analysis of the evolution of snake viviparity. *Global Ecology and Biogeography*, 24(12), 1433–1442.
- Greene, H. W. (1970). Mode of reproduction in lizards and snakes of the Gomez Farias Region, Tamaulipas, Mexico. *Copeia*, 1970(3), 565–568.
- Griffith, O. W., Blackburn, D. G., Brandley, M. C., Van Dyke, J. U., Whittington, C. M., & Thompson, M. B. (2015). Ancestral state reconstructions require biological evidence to test evolutionary hypotheses: A case study examining the evolution of reproductive mode in squamate reptiles. *Journal of Experimental Zoology Part B-Molecular and Developmental Evolution*, 324, 493–503.
- Huey, R. B. (1982). Temperature, physiology, and the ecology of reptiles. In C. Gans & F. H. Pough (Eds.), *Biology of the Reptilia* (Vol. 12, pp. 25–91). London, UK: Academic Press.
- Hodges, W. L. (2004). Evolution of viviparity in horned lizards (*Phrynosoma*): Testing the cold-climate hypothesis. *Journal of Evolutionary Biology*, 17(6), 1230–1237.
- Kearney, M. R., Isaac, A. P., & Porter, W. P. (2014). microclim: Global estimates of hourly microclimate based on long-term monthly climate averages. *Scientific Data*, 1, 140006.
- King, B., & Lee, M. S. Y. (2015). Ancestral state reconstruction, rate heterogeneity, and the evolution of reptile viviparity. *Systematic Biology*, 64, 532–544.
- Kissling, W. D., & Carl, G. (2008). Spatial autocorrelation and the selection of simultaneous autoregressive models. *Global Ecology and Biogeography*, 17, 59–71.
- Lambert, S. M., & Wiens, J. J. (2013). Evolution of viviparity: A phylogenetic test of the cold-climate hypothesis in *phrynosomatid* lizards. *Evolution*, 67(9), 2614–2630.
- Le Galliard, J. F., Le Bris, M., & Clobert, J. (2003). Timing of locomotor impairment and shift in thermal preferences during gravidity in a viviparous lizard. *Functional Ecology*, 17, 877–885.
- Levy, O., Buckley, L. B., Keitt, T. H., & Angilletta, M. J. (2016). Ontogeny constrains phenology: Opportunities for activity and reproduction interact to dictate potential phenologies in a changing climate. *Ecology Letters*, 19(6), 620–628.
- Levy, O., Buckley, L. B., Keitt, T. H., Smith, C. D., Boateng, K. O., Kumar, D. S., & Angilletta, M. J. (2015). Resolving the life cycle alters expected impacts of climate change. *Proceedings of the Royal Society B: Biological Sciences*, 282(1813), 20150837.
- Li, H., Qu, Y. F., Hu, R. B., & Ji, X. (2009). Evolution of viviparity in cold-climate lizards: Testing the maternal manipulation hypothesis. *Evolutionary Ecology*, 23, 777–790.
- Lynch, V. J. (2009). Live-birth in vipers (Viperidae) is a key innovation and adaptation to global cooling during the Cenozoic. *Evolution*, 63(9), 2457–2465.
- Ma, L., Sun, B. J., Li, S. R., Sha, W., & Du, W. G. (2014). Maternal thermal environment induces plastic responses in the reproductive life history of oviparous lizards. *Physiological and Biochemical Zoology*, 87, 677–683.
- Mathies, T., & Andrews, R. M. (1996). Extended egg retention and its influence on embryonic development and egg water balance: Implications for the evolution of viviparity. *Physiological Zoology*, 69(5), 1021–1035.
- Morjan, C. L. (2003). Variation in nesting patterns affecting nest temperatures in two populations of painted turtles (*Chrysemys picta*) with temperature-dependent sex determination. *Behavioral Ecology and Sociobiology*, 53(4), 254–261.
- Muth, A. (1980). Physiological ecology of desert iguana (*Dipsosaurus dorsalis*) eggs - Temperature and water relations. *Ecology*, 61(6), 1335–1343.
- Neill, W. T. (1964). Viviparity in snakes: Some ecological and zoogeographical considerations. *The American Naturalist*, 98(898), 35–55.
- Packard, G. C., Tracy, C. R., & Roth, J. J. (1977). Physiological ecology of reptilian eggs and embryos, and evolution of viviparity within class

- Reptilia. *Biological Reviews of the Cambridge Philosophical Society*, 52, 71–105.
- Parker, S. L., & Andrews, R. M. (2007). Incubation temperature and phenotypic traits of *Sceloporus undulatus*: Implications for the northern limits of distribution. *Oecologia*, 151(2), 218–231.
- Pike, D. A., Webb, J. K., & Shine, R. (2010). Nesting in a thermally challenging environment: Nest-site selection in a rock-dwelling gecko, *Oedura lesueurii* (Reptilia: Gekkonidae). *Biological Journal of the Linnean Society*, 99, 250–259.
- 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, 1238–1246.
- Pincheira-Donoso, D., Tregenza, T., Witt, M. J., & Hodgson, D. J. (2013). The evolution of viviparity opens opportunities for lizard radiation but drives it into a climatic cul-de-sac. *Global Ecology and Biogeography*, 22, 857–867.
- Pyron, R. A. (2015). Advancing perspectives on parity-mode evolution. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 324(6), 562–563.
- Pyron, R. A., & Burbrink, F. T. (2014). Early origin of viviparity and multiple reversions to oviparity in squamate reptiles. *Ecology Letters*, 17, 13–21.
- Qu, Y. F., Li, H., Gao, J. F., Xu, X. F., & Ji, X. (2011). Thermal preference, thermal tolerance and the thermal dependence of digestive performance in two *Phrynocephalus* lizards (Agamidae), with a review of species studied. *Current Zoology*, 57, 684–700.
- Qualls, C. P., & Andrews, R. M. (1999). Cold climates and the evolution of viviparity in reptiles: Cold incubation temperatures produce poor-quality offspring in the lizard, *Sceloporus virgatus*. *Biological Journal of the Linnean Society*, 67, 353–376.
- R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Radchuk, V., Turlure, C., & Schtickzelle, N. (2013). Each life stage matters: The importance of assessing the response to climate change over the complete life cycle in butterflies. *Journal of Animal Ecology*, 82, 275–285.
- Refsnider, J. M., & Janzen, F. J. (2012). Behavioural plasticity may compensate for climate change in a long-lived reptile with temperature-dependent sex determination. *Biological Conservation*, 152, 90–95.
- Robert, K. A., & Thompson, M. B. (2000). Energy consumption by embryos of a viviparous lizard, *Eulamprus tympanum*, during development. *Comparative Biochemistry and Physiology Part A: Molecular, and Integrative Physiology*, 127, 481–486.
- Rodriguez-Diaz, T., & Braña, F. (2012). Altitudinal variation in egg retention and rates of embryonic development in oviparous *Zootoca vivipara* fits predictions from the cold-climate model on the evolution of viviparity. *Journal of Evolutionary Biology*, 25(9), 1877–1887.
- Ryberg, W. A., Hill, M. T., Lay, D., & Fitzgerald, L. A. (2012). Observations on the nesting ecology and early life history of the Dunes Sagebrush Lizard (*Sceloporus arenicolus*). *Western North American Naturalist*, 72, 582–585.
- Sergeev, A. (1940). Researches in the viviparity of reptiles. *Moscow Society of Naturalists (Jubilee Issue)*, 1–34.
- Seymour, R. S. (1973). Physiological correlates of forced activity and burrowing in the spadefoot toad, *Scaphiopus hammondi*. *Copeia*, 1973(1), 103–115.
- Shine, R. (1980). "Costs" of reproduction in reptiles. *Oecologia*, 46(1), 92–100.
- Shine, R. (1983). Reptilian viviparity in cold climates: Testing the assumptions of an evolutionary hypothesis. *Oecologia*, 57(3), 397–405.
- Shine, R. (1985). The evolution of viviparity in reptiles: An ecological analysis. In C. Gans, & F. Billet (Eds.), *Biology of the Reptilia* (Vol.15, pp. 605–694). New York, NY: Wiley.
- Shine, R. (1995). A new hypothesis for the evolution of viviparity in reptiles. *The American Naturalist*, 145(5), 809–823.
- Shine, R. (1999). Egg-laying reptiles in cold climates: Determinants and consequences of nest temperatures in montane lizards. *Journal of Evolutionary Biology*, 12(5), 918–926.
- 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.
- Shine, R. (2015). The evolution of oviparity in squamate reptiles: An adaptationist perspective. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 324(6), 487–492.
- Shine, R., & Bull, J. (1979). The evolution of live-bearing in lizards and snakes. *The American Naturalist*, 113, 905–923.
- Stewart, J. R. (1992). Placental structure and nutritional provision to embryos in predominantly lecithotrophic viviparous reptiles. *American Zoologist*, 32(2), 303–312.
- Taylor, J. E. (2004). Reproduction in sympatric lizards: Comparison of two species of *Ctenotus* (Scincidae) in south-eastern Australia. *Australian Journal of Zoology*, 52(6), 649–666.
- Telemeco, R. S., Elphick, M. J., & Shine, R. (2009). Nesting lizards (*Bassiana duperreyi*) compensate partly, but not completely, for climate change. *Ecology*, 90, 17–22.
- Telemeco, R. S., Fletcher, B., Levy, O., Riley, A., Rodriguez-Sanchez, Y., Smith, C., ... 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.
- Thompson, M. B., Speake, B. K., Stewart, J. R., Russell, K. J., McCartney, R. J., & Surai, P. F. (1999). Placental nutrition in the viviparous lizard *Niveoscincus metallicus*: The influence of placental type. *Journal of Experimental Biology*, 202, 2985–2992.
- Tinkle, D. W., & Gibbons, J. W. (1977). The distribution and evolution of viviparity in reptiles. *Miscellaneous Publications Museum of Zoology University of Michigan*, 154, 1–55.
- Vleck, D. (1979). The energy cost of burrowing by the pocket gopher *Thomomys bottae*. *Physiological Zoology*, 52(2), 122–136.
- Warner, D. A., Jorgensen, C. F., & Janzen, F. J. (2010). Maternal and abiotic effects on egg mortality and hatchling size of turtles: Temporal variation in selection over seven years. *Functional Ecology*, 24, 857–866.
- Warner, D. A., & Shine, R. (2008). Maternal nest-site choice in a lizard with temperature-dependent sex determination. *Animal Behaviour*, 75, 861–870.
- Webb, J. K., Pike, D. A., & Shine, R. (2008). Population ecology of the velvet gecko, *Oedura lesueurii* in south eastern Australia: Implications for the persistence of an endangered snake. *Austral Ecology*, 33, 839–847.
- Weekes, H. C. (1935). A review of placentation among reptiles with, particular regard to the function and evolution of the placenta. *Proceedings of the Zoological Society of London*, 105(3), 625–645.
- While, G. M., Williamson, J., Prescott, G., Horvathova, T., Fresnillo, B., Beeton, N. J., ... Uller, T. (2015). Adaptive responses to cool climate promotes persistence of a non-native lizard. *Proceedings of the Royal Society B: Biological Sciences*, 282(1803), 20142638.

Wright, A. M., Lyons, K. M., Brandley, M. C., & Hillis, D. M. (2015). Which came first: The lizard or the egg? Robustness in phylogenetic reconstruction of ancestral states. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 324, 504–516.

BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Ma L, Buckley LB, Huey RB, Du W-G. A global test of the cold-climate hypothesis for the evolution of viviparity of squamate reptiles. *Global Ecol Biogeogr.* 2018;00: 1–11. <https://doi.org/10.1111/geb.12730>