Behavioral Thermoregulation by Mothers Protects Offspring from Global Warming but at a Cost

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ABSTRACT

Thermal conditions during embryonic development affect offspring phenotype in ectotherms. Therefore, rising environmental temperatures can have important consequences for an individual's fitness. Nonetheless, females have some capacity to compensate for potential negative consequences that adverse developmental environments may have on their offspring. Recent studies show that oviparous reptiles exhibit behavioral plasticity in nest site selection, which can buffer their embryos against high incubation temperatures; however, much less is known about these responses in viviparous reptiles. We subjected pregnant viviparous skinks, *Saiphos equalis*, to current or projected midcentury (2050) temperatures to test (i) how elevated temperatures affect female thermoregulatory and foraging behavior; (ii) whether temperatures experienced by females during pregnancy negatively affect the morphology, performance, and behavior of hatchlings; and (iii) whether behavioral thermoregulation during pregnancy is costly to females. Females from the elevated temperature treatment compensated by going deeper belowground to seek cooler temperatures and eating less, and they consequently had a lower body mass relative to snout-to-vent length (condition estimator) compared with females from the current thermal treatment. The temperatures experienced by females in the elevated temperature treatment were high enough to affect foraging and locomotor performance but not the morphology and growth rate of hatchlings. By seeking cooler temperatures, mothers can mitigate some of the effects of high temperatures on their offspring (e.g., reduced body size and growth). However, this protective behavior of females may come at an energetic cost to them. This study adds to growing evidence of lizards' vulnerability to global warming, particularly during reproduction when females are already paying a substantial cost.

Keywords: climate change, viviparity, thermoregulation, developmental plasticity, reptile.

Introduction

Given the rapid rate at which human-induced climate change is occurring (Parmesan and Yohe 2003; Selwood et al. 2015), it is important to predict how organisms will be affected by changes in their environment (Deutsch et al. 2008; Sunday et al. 2014). When faced with a novel challenging environment, species will most likely respond via four mechanisms: (i) shifting their distribution ranges to maintain appropriate niches, (ii) genetic adaptation to keep pace with a rapidly changing environment, (iii) plastic physiological and/or behavioral adjustments, or (iv) extinction (Visser 2008; Gilbert and Miles 2017). Ectotherms are of particular interest for studies on the impacts of climate change because their body temperature strongly depends on the environment (Huey and Stevenson 1979; Angilletta et al. 2002). Moreover, the early temperatures that a developing embryo experiences, whether it is inside the female's body (viviparity) or at a nest site selected by the female (oviparity), are perhaps the most influential environmental variable impacting the development of ectotherms (Huey and Stevenson 1979; Somero 2004). Thus, studying the impact of climate warming on the reproductive behavior and physiology of ectotherms will allow us to predict their risk of extinction (Sinervo et al. 2010; Pincheira-Donoso et al. 2013; López-Alcaide et al. 2017).

Several costs are associated with reproduction in squamate reptiles (Shine 1980; Schwarzkopf 1994). Females incur significant behavioral and physiological changes during pregnancy, such as reduced locomotor performance (Schwarzkopf and Shine 1992; Olsson et al. 2000) and increased basking behavior (Shine 1980; Beuchat 1986), that might reduce their time available to forage (Gregory et al. 1999; Sears and Angilletta 2015) and increase their vulnerability to predators (Downes and Bauwens 2002). Although most of these costs are likely to occur equally in oviparous and viviparous species, viviparous females are more heavily burdened (i.e., have higher relative clutch masses; Qualls and Shine 1998*b*; Recknagel and Elmer 2019) and carry this burden for a longer period of time (e.g., viviparous females are affected by pregnancy about a month longer than oviparous females in the bimodally reproductive lizard *Zootoca vivipara*; Recknagel and Elmer 2019). Therefore, the costs of reproduction are expected to be higher

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for live-bearers than for egg layers (Qualls and Shine 1998*a*), constituting, for instance, an increase in maternal metabolism of 29% in the skink *Eulamprus tympanum* (Robert and Thompson 2000).

Ectotherms living at high latitude and elevation, which are commonly viviparous, might benefit from moderate warming (e.g., increased body size and growth rates; Chamaillé-Jammes et al. 2006; Moore et al. 2018). This is supported by the fact that compared with tropical species, ectotherms living at high latitude and elevation experience warm air temperatures that are lower than their maximum heat tolerance (i.e., these species have a larger thermal-safety margin; Deutsch et al. 2008; Sunday et al. 2014). Nonetheless, the extinction probability of viviparous lizards is strongly correlated with the magnitude of warming in spring but not other seasons (Sinervo et al. 2010). This suggests that the extinction risk of this group is driven by energetic deficiency during the reproductive season when energy demands are highest (Beuchat 1988; Huey et al. 2010). The challenge of maintaining optimal temperatures for sufficient time for female physiological processes (e.g., digestion, maintenance) while maintaining a stable environment for the embryo could make viviparous species more vulnerable to extinction (Mathies and Andrews 1997; Sinervo et al. 2010; Wang et al. 2017). Currently, it is difficult to test these hypotheses because there is little experimental evidence showing whether and how viviparous species can overcome rising air temperatures.

Although shifts in geographic distribution may allow some species to ameliorate the impacts of global warming, this is typically not an option for smaller, less mobile taxa, such as most reptiles, or montane species facing an elevation limit (Buckley and Kingsolver 2012; Huey et al. 2012; but see Barrows et al. 2020). These species are more likely to respond to altered thermal environments through adaptation or behavioral and physiological plasticity (Visser 2008). For instance, female reptiles can modify embryos' thermal environment through behavioral plasticity in thermoregulation or nest site selection (Shine and Harlow 1996; Doody et al. 2006; López-Alcaide et al. 2017). Similarly, developmental plasticity in offspring phenotype, such as a larger body size or a greater sprint speed, can help reptile species respond to changing temperatures and ultimately be favored by natural selection (West-Eberhard 2005; Ghalambor et al. 2007).

The Australian three-toed skink, *Saiphos equalis* (Gray 1825), is a relatively small (approximately 80-mm snout-to-vent length [SVL]) nocturnal and fossorial species. *Saiphos equalis* inhabits cool environments, where it is commonly observed under sun-warmed rocks and logs during the day (Gray 1825; Wu et al. 2009) and foraging on the surface at night (I. Beltrán, personal observation). This is one of only three reptile species known to exhibit geographic variation in reproductive mode (Heulin et al. 1993; Smith and Shine 1997; Fairbairn et al. 1998). Viviparous populations from the Northern Tablelands of New South Wales (NSW), Australia, give birth to fully developed hatchlings inside a membrane from which they emerge within a couple of days. The populations from the northern and central coast of NSW have prolonged uterine egg retention (commonly referred to as "oviparous"; Bustard 1964; Smith and Shine 1997). These oviparous populations lay shelled eggs that will continue developing outside the female's body for approximately 5–7 d (Smith and Shine 1997).

In *S. equalis*, elevated developmental temperatures shorten the gestation period, do not affect hatchling sex ratio, but do produce smaller and slower hatchlings with impaired foraging ability (Beltrán et al. 2020*a*, 2020*b*). However, in these previous studies, housing conditions limited the ability of viviparous females to lower their body temperature by behavioral thermoregulation. Thus, it remains unclear whether females can adjust their thermoregulatory behavior to buffer offspring from elevated temperatures (Doody et al. 2006; Telemeco et al. 2009; Refsnider and Janzen 2012).

We examined the effect of projected midcentury (2050) temperatures predicted under a global warming scenario on (i) the thermoregulatory and foraging behavior of pregnant female *S. equalis*, (ii) key morphological and behavioral life-history traits (SVL and body mass, growth rate, thermal preference, foraging success, and locomotor performance) of their offspring, and (iii) female body condition after parturition. We hypothesized that pregnant females would compensate for high environmental temperatures by selecting deeper (and therefore cooler) sites for the development of embryos (Shine 1983). We did not predict a negative impact of projected temperatures on hatchling phenotype. However, we predicted that by selecting deeper sites for thermoregulation, females would reduce their time available to forage (Gregory et al. 1999). Thus, we predicted that maintaining females under higher temperatures would be costly and would reduce their body condition.

Methods

Animal Collection and Husbandry

The ovulation dates for viviparous *Saiphos equalis* are unknown; however, ovulation most likely occurs during the austral spring (mid to late October; M. Thompson, University of Sydney, personal communication). In early November 2018, we collected 22 viviparous female *S. equalis* in the early stages of pregnancy from Riamukka (31°20′S, 151°39′E) and Enfield (31°18′S, 151°55′E) State Forests in the Northern Tablelands of NSW. Animals were found under rocks and logs. We scored lizards as pregnant on the basis of appearance and light abdominal palpation of embryos and transported all lizards to Macquarie University, Sydney, within 72 h of capture. For each lizard, we measured SVL (with a ruler to the closest ± 1 mm) and mass (± 0.1 g). Each female was housed in a separate plastic enclosure (320 mm L × 22 mm W × 140 mm H) with moist potting mix soil to a depth of 8 cm and a heating cable to heat one side of each enclosure to approximately 30°C. Each cage contained a 100 × 100-mm ceramic tile as shelter and a water dish. Females were kept in these conditions for 5 d, during which time they were fed six crickets every other day (~5 mm in total length). Crickets were dusted with vitamins (Aristopet Repti-vite) and calcium (URS ultimate calcium) once.

To later determine the position of the females in the substrate, we attached a passive integrated transponder (PIT) tag (0.07 g; HT950 PIT tag, Bio-Equip, Shanghai) to each lizard. The small body size of this species restricted us from inserting the tags under their skin; instead, we glued the PIT tag to the dorsal surface of

the lizard using fast-drying superglue (UHU ultrafast superglue). After gluing the tag to the lizard, we gently held it in place for 1 min to allow the glue to dry. We then placed the lizard in a small enclosure and allowed the glue to dry for 2 h. We then moved females back to their enclosure, where they were kept in these conditions for 3 d before they were allocated to one of the thermal treatments.

Thermal Treatments and Developmental Environments

For the experimental treatments, we transferred the pregnant females to cylindrical transparent enclosures (200 mm H × 120 mm D). Each enclosure was covered with black cardboard and contained a water dish and potting soil to a depth of 18 cm (fig. A1). Once in these enclosures, pregnant females were randomly and evenly allocated to one of two cycling incubators (PGR15 growth chamber, Conviron, Melbourne). The first incubator, hereafter referred to as "current," mimicked the cycling soil temperature to which pregnant females are exposed under the rocks where they are observed thermoregulating (table A1). These temperatures were recorded in the field every hour from November 2017 to January 2018 using Thermochron iButton loggers (DSG1921G, ±0.5°C, Maxim Integrated Products, San Jose, CA). The second incubator, hereafter referred to as "future," resembled the temperatures of a global warming scenario of +1.5°C (greenhouse gas concentration scenario: Representative Concentration Pathway 4.5).

The interaction between the soil and the fluctuating air temperatures inside the incubators ensured that a temperature gradient at different depths was created within each enclosure. Soil temperatures inside females' enclosures were registered at different depths (0, 60, 120, 180 mm) every hour between the start of the experiment and parturition using iButton loggers (fig. 1). The relative humidity within the enclosures was maintained at approximately 60% by regularly spraying the soil with water.

A considerable proportion (45%) of the females with whom we started the study turned out not to be pregnant and had to be removed from the experiments. Consequently, our final sample

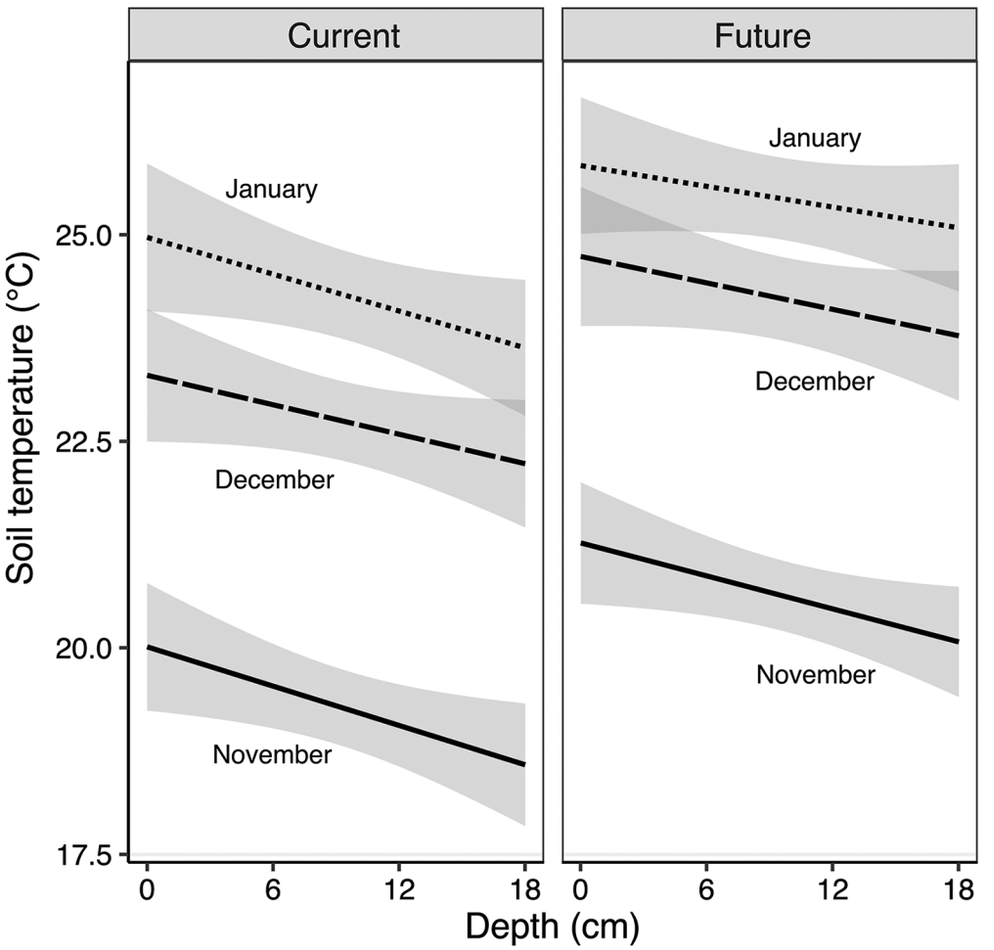

Figure 1. Soil temperatures recorded in the current (n = 12) and future (n = 16) thermal treatments at different depths and across months. Shaded areas correspond to 95% confidence intervals.

size included five females in the current thermal environment and seven females in the future thermal environment.

Female Foraging Behavior and Thermoregulatory Behavior

To evaluate the impact of different thermal treatments on female foraging behavior and thermoregulatory behavior, we followed a protocol that coincided with scheduled animal husbandry as follows: We removed the black cardboard covering the enclosure and measured the depth at which the female's body midpoint was observed under the soil with a ruler (± 0.5 cm). If the females were not observed, we used a PIT tag reader (Halo microchip scanner, St. Saviour, Guernsey, Channel Islands; 1–2-cm measurement deviation) to locate their position below the substrate and then measured the depth. Then we estimated foraging behavior by counting the number of crickets the female ate since the last husbandry session. Finally, new crickets were added to each female's enclosure to bring the total to seven crickets. This procedure was performed once a day, three times per week until parturition, ensuring a similar number of observations in the morning (0900–1100 hours) and in the afternoon (1500–1800 hours).

Change in Female Body Condition

We calculated the female body condition index using the residuals from a linear regression of $\log_{10}$(mass) on $\log_{10}$(SVL) (Cox et al. 2011; Sion et al. 2021). After parturition (late January 2018), females were transferred back to the original enclosures (320 mm × 220 mm × 140 mm) and kept in a room at 20°C. Females were kept in these conditions and then released at their original point of capture. The change in body condition of females was measured at three different stages: start of experiment, after parturition, and before release.

Hatchling Morphology and Growth

For each newborn lizard, we measured mass (± 0.01 g) and calculated SVL (± 0.05 mm) according to digital photographs using the software ImageJ 2.0 (National Institutes of Health, Bethesda, MD; https://imagej.nih.gov/ij/). We repeated these body measurements every 4 wk for 3 mo to track differences in growth rate between thermal treatments.

Hatchlings were kept individually in plastic enclosures (175 mm × 120 mm × 80 mm) containing soil to a depth of 3 cm, a 45 × 45-mm ceramic tile shelter, and a water dish. One side of the enclosure was placed on a timer-controlled heating cable to create a thermal gradient of 20°–34°C during the day, dropping to 20°C at night. Animals were exposed to a 12L:12D light cycle. We fed hatchlings three times a week with five pinhead crickets (~5 mm in total length), with crickets dusted with vitamins and calcium once a week.

Hatchling Thermal Preference

We measured the thermal preferences of all hatchlings in a thermal gradient 1 wk after they hatched. The gradient, consisting of six rectangular runways (each 900 mm × 45 mm), was placed in a temperature-controlled room (~20°C). The bottom of each runway was covered with 5 mm of potting mix for the lizards to move and bury themselves. A linear temperature gradient ranging from 8° to 40°C was created by placing wide heating tape (BriskHeat, Columbus, OH) on one end of the runway and a recirculating chiller bath (Haake F3-C, Munich) on the other end. The arena was insulated with Styrofoam to minimize temperature fluctuations. Hatchlings were deprived food for 48 h before being placed in a runway to ensure that they were postabsorptive. On the morning (~0800 hours) before the measurements were taken, a single lizard was placed in one of the six runways and allowed to habituate for at least 5 h. Animals were chosen haphazardly, and the researcher measuring body temperature was blind to the animal's thermal treatment. After habituation, the body temperature of each lizard was measured every 30 min over 8 h (1300–2100 hours) using a thermocouple thermometer (± 0.1°C; Omega HH912T, Norwalk, CT). Body temperature was measured by gently placing the thermocouple under the lizard at the midpoint of the body (validated by Wu et al. 2009). We calculated the mean preferred body temperature for each individual lizard across the 16 measurements.

Hatchling Foraging Success

When hatchling lizards were 2 wk of age, we measured their foraging success. Hatchlings were fasted for 48 h before the trial, which was conducted in the hatchling's home enclosure in a room maintained at ~20°C. We placed five pinhead crickets (~5 mm) in the enclosure and recorded video of the behavior of hatchlings for 30 min. Using the software BORIS (Friard and Gamba 2016), we quantified (i) latency to emerge from the substrate, (ii) total time spent chasing crickets, (iii) number of attacks on crickets, (iv) total time handling the crickets, and (v) number of crickets eaten. To quantify the foraging ability of the lizards, these variables were combined using a principal component analysis (PCA). The five behaviors were highly correlated and positively loaded on two components (table A2). The first component explained 33% of the variance and was positively correlated with the number of attacks and the time spent chasing the crickets. The second component explained 30% of the variance and was positively correlated with the latency to forage and the number of crickets eaten and negatively correlated with the handling time.

Hatchling Sprint Speed and Acceleration

When hatchling lizards were 3 wk of age, we measured their sprint speed and acceleration in a racetrack (800 mm × 50 mm) covered with a thin layer of substrate (~2 mm). The room was kept at ~20°C, which is approximately the preferred body temperature of these lizards in the laboratory (see "Results"). Before each trial, we recorded the lizard's body temperature. Then we placed the hatchling on the racetrack, let it habituate for 3 min under an opaque cup, and then chased the animal along the track by touching the base of its tail with a paintbrush. Each animal was tested three times, with at least a 30-min rest between trials. Trials were recorded with a slow-motion camera (Sony FDR-AX700 at

250 frames per second). For each trial, researchers were blind to the thermal treatment of the animal being tested. We determined the average and maximum speed (m/s) and average and maximum acceleration (m/s^2) of the animals over 20 and 80 cm using the software Tracker (Open Source Physics, Boston, MA; https://physlets.org/tracker/). To estimate these variables in each video, the snout of the animal was used as a reference point and was manually tracked frame by frame. Because all speed and acceleration measurements were highly correlated, they were combined using a PCA. The variables positively loaded on two components (table A3). The first component explained 42% of the variance and was positively correlated with the average speed and acceleration over 20 and 80 cm. The second component explained 37% of the variance and was positively correlated with the maximum speed and acceleration over 20 and 80 cm.

Statistical Analyses

Model assumptions of normality and homogeneity of variance of residuals were verified visually and using a Shapiro-Wilk's test and Levene's test, respectively (Zuur et al. 2010). The effect of predictors on our response variables were tested using linear mixed models (LMMs) unless stated otherwise.

Soil temperatures recorded by each data logger were averaged to obtain a mean value for every hour of the day (24 h) for each month (November–January). We analyzed the effect of thermal treatment (current vs. future), month, depth, and the interaction (thermal treatment × depth) on soil temperatures. To account for the daily variation in temperature, we used harmonic modeling. This type of analysis is commonly used to model fluctuations in temperature data and other biological phenomena (Fischer and Paterson 2014; Akinnubi and Adeniyi 2017). These models use sine and cosine curves, whose frequencies are multiples of each other (harmonics), to better explain the variation in the data. Using very few harmonics in the regression will produce a model with low fit, but adding too many harmonics will produce a model that overfits the data. In the model, we included the first and second harmonics of a curve (period $[T] = 24$ h) with sine ($\sin(\pi/T \times \text{time})$)and cosine ($\cos(\pi/T \times \text{time})$) components. As random terms in the model, we included the time of day and the position (depth) of each temperature logger nested within female identity (enclosure). This model was used to predict the soil temperatures corresponding to the depth at which females were observed between November and January.

We tested the effect of thermal treatment (current vs. future), month (November–January), and their interaction (thermal treatment × month) on female thermoregulatory behavior. Foraging behavior was analyzed using a generalized LMM using a Poisson error distribution (log link). For both models, female identity and date of measurement were included as random terms, and husbandry schedule (morning vs. afternoon) was included as a covariate. Likewise, we analyzed the effect of thermal treatment (current vs. future), stage (start of experiments, postpartum, and end of experiments), and their interaction (thermal treatment × stage) on female body condition. This model included clutch size as a covariate and female identity as a random term.

We analyzed the effect of the thermal treatment (current vs. future) on each measured trait of hatchling *S. equalis* using LMMs as described below.

SVL and mass. SVL was log transformed to fit model assumptions. Egg mass was included as covariate in the model for SVL. Likewise, SVL was included as covariate in the model for hatchling mass. Both models included mother identity as random term.

Growth rate. We tested the effect of thermal treatment, time (weeks since hatching), and their interaction (thermal treatment × time) on SVL- and mass-related growth rate. Both models included month and hatchling identity nested within mother identity as random terms.

Thermal preferences. This model included hatchling SVL as covariate and mother identity as random term.

Foraging success (principal components 1 and 2 independently). Both models included body temperature and SVL as covariates and mother identity as random term.

Locomotor performance (principal components 1 and 2 independently). We used the data from all trials and accounted for within-individual variation (Careau and Wilson 2017) instead of estimating an overall maximum or average value per individual. For both models, body temperature and SVL were used as covariates; trial number and hatchling identity nested within mother identity were used as random terms.

Hatchling sex was not included in the models to avoid issues with statistical power and because incubation treatments do not affect the sex ratio in this species (Beltrán et al. 2020*a*). The selection of predictive variables was done by a manual step-by-step backward-elimination process, starting from the most complex global model and dropping the fixed terms that were not significant until a minimal adequate model was reached (Harrison et al. 2018). In each step, we evaluated the overall model quality by checking the distribution of residuals, R^2, and the variance inflation factors (Bolker et al. 2009; Zuur et al. 2010). Model selection was based on corrected Akaike information criteria (Burnham and Anderson 2002; Bolker et al. 2009), and when necessary, the simplest (i.e., most parsimonious) model was chosen. The R packages mgcv (Wood 2011) and lme4 (Bates et al. 2015) were used to perform model analyses; lmerTest (Kuznetsova et al. 2017) and MuMIn (Bartoń 2018) were used to calculate the corresponding *P* values of the fixed effects in the mixed models and in model selection, respectively. All analyses were carried out using the statistical software R (R Development Core Team 2018) at a significance level of $\alpha = 0.05$.

Results

Soil Temperatures in Thermal Treatments across Months at Different Depths

Soil temperatures differed between thermal treatments (table 1, pt. A; fig. 1). The future thermal treatment had, on average, an increase in soil temperature of 1.3°C compared with the current thermal treatment. Similarly, soil temperatures increased by approximately 4.9°C between November and January (Australian

Table 1: Outcome of the mixed models evaluating differences in soil temperatures, thermoregulatory and foraging behavior, and change in body condition of pregnant female *Saiphos equalis* subjected to different thermal environments (current vs. future)

Response variable, fixed term	Estimate	SE	df	t or z	P
A. Soil temperatures:					
Intercept	19.877	.100	13.393	198.070	<.001**
Thermal treatment (future)	1.340	.099	4.388	13.540	<.001**
Month (Dec.)	3.529	.069	1,624.689	51.240	<.001**
Month (Jan.)	4.885	.070	1,626.848	69.970	<.001**
Depth	−.062	.006	14.746	−10.500	<.001**
B. Female thermoregulatory behavior:					
Intercept	2.748	.635	31.180	4.330	<.001**
Thermal treatment (future)	1.822	.765	26.289	2.380	.025*
Month (Dec.)	1.445	.689	133.489	2.100	.038*
Month (Jan.)	2.671	.761	103.981	3.510	.001**
Husbandry schedule (afternoon)	1.425	.401	34.571	3.560	.001**
Thermal treatment × month (future × Dec.)	−1.935	.835	230.342	−2.320	.021*
Thermal treatment × month (future × Jan.)	−1.769	.944	225.615	−1.870	.062
C. Female foraging behavior:					
Intercept	1.447	.138	NA	10.470	<.001**
Thermal treatment (future)	−.200	.088	NA	−2.270	.023*
Month (Dec.)	−.433	.171	NA	−2.540	.011*
Month (Jan.)	−.550	.200	NA	−2.750	.006**
Thermal treatment × month (future × Dec.)	.281	.113	NA	2.480	.013*
Thermal treatment × month (future × Jan.)	.077	.160	NA	.480	.629
D. Female body condition:					
Intercept	.145	.046	10.409	3.170	.010**
Thermal treatment (future)	−.048	.021	9.000	−2.270	.049*
Stage (postpartum)	−.122	.021	22.000	−5.780	<.001**
Stage (end of experiments)	−.129	.021	22.000	−6.120	<.001**
Clutch size	−.011	.012	9.000	−.880	.400

Note. NA = not applicable.
*$P < 0.05$.
**$P < 0.01$.

summer months). Soil temperatures decreased with depth by approximately 0.06°C/cm (table 1, pt. A; fig. 1).

Female Foraging and Thermoregulatory Behavior

The initial mass (mean: 5.7 g; SEM: 0.16 g; range: 4.6–6.7 g) and SVL (mean: 83.7 mm; SEM: 1.0 mm; range: 78–89 mm) of mothers did not differ between thermal treatments. Females from the future thermal treatment were observed at greater depths compared with females from the current thermal treatment (table 1, pt. B; fig. 2*A*). Regardless of thermal treatment, females were observed deeper in December and January compared with November (table 1, pt. B). Interestingly, females from the current thermal treatment moved deeper as the temperatures increased from November to January, whereas females from the future thermal treatment remained at similar depths throughout the experiment (table 1, pt. B; thermal treatment × month). Although females from the future thermal treatment went deeper in the substrate, possibly to compensate for the high environmental temperatures, the predictions of our model showed that these females experienced higher body temperatures compared with females from the current thermal environment (fig. 2*B*).

Females from the future thermal treatment ate significantly fewer crickets than females from the current thermal treatment (table 1, pt. C; fig. 3*A*). Regardless of thermal treatment, females ate fewer crickets in December and January compared with the number of crickets eaten in November (table 1, pt. C). Interestingly, females from the current thermal treatment ate more crickets in November but fewer in December, while females from the future thermal treatment ate fewer crickets constantly throughout the experiment (table 1, pt. C; thermal treatment × month).

Change in Female Body Condition

Although the body condition of females from both thermal treatments was reduced throughout the experiment, females from the future treatment had an overall lower body condition (table 1, pt. D; fig. 3*B*).

Hatchlings

Birthing success was 100% in the future treatment (14 lizards), while 4 of 17 (23.5%) lizards from the current treatment died after birth. Thus, our initial sample sizes were $n = 13$ for the current

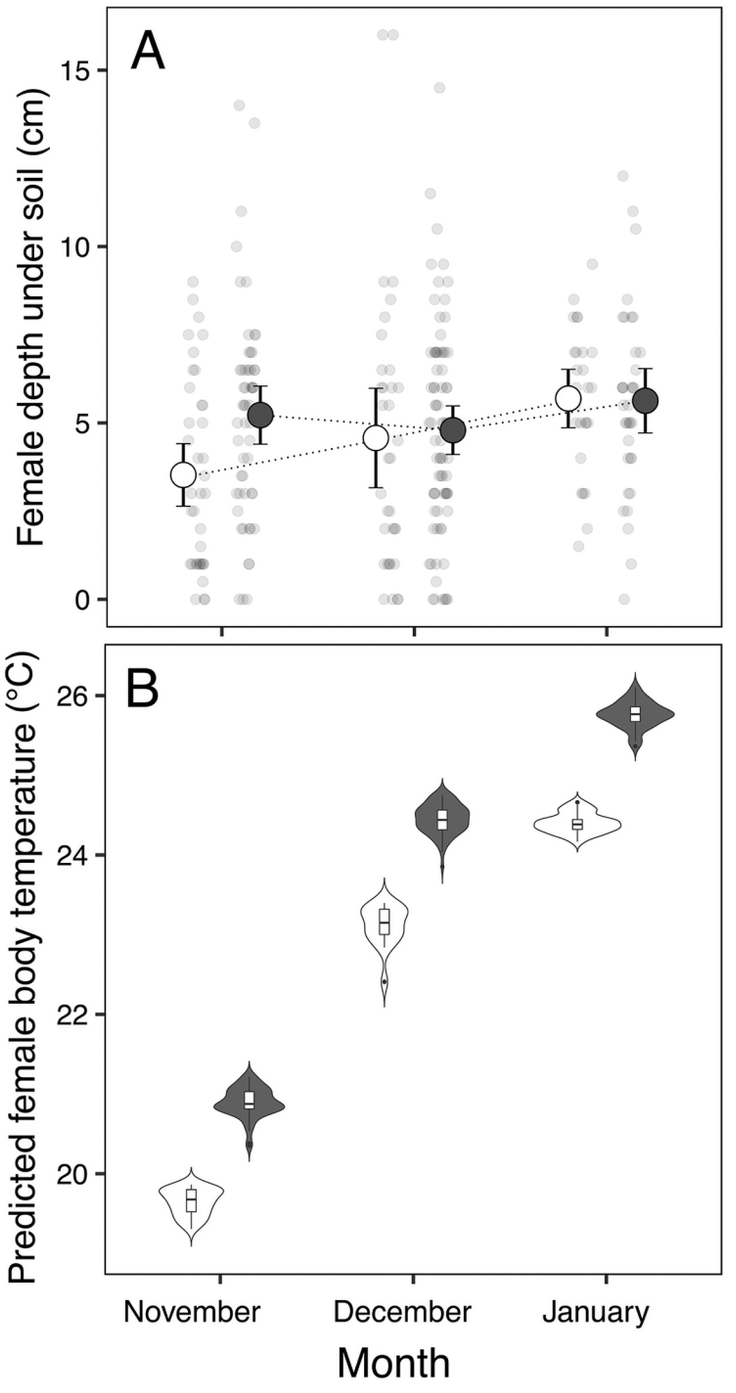

Figure 2. Effect of current (white; $n = 5$) and future (gray; $n = 7$) thermal treatments on the thermoregulatory behavior (*A*) and predicted body temperature (*B*) of pregnant female *Saiphos equalis*. In *A*, data points plotted in light gray correspond to repeated measurements of the depth at which the females were observed under the soil. Error bars indicate 95% confidence intervals.

treatment and $n = 14$ for the future treatment. However, different thermal treatments did not affect SVL (mean: 28.9 mm; SEM: 0.3 mm; range: 25.4–31.7 mm), body mass (mean: 0.3 g; SEM: 0.006 mm; range: 0.19–0.37 g), and growth rate of hatchling *Saiphos equalis*. Similarly, hatchlings from both treatments preferred similar body temperatures ($P > 0.1$ for all measurements; table A4).

Hatchlings from the future treatment emerged faster from the substrate but ate fewer crickets and handled their prey for longer (principal component 2: $\beta = -1.1 \pm 0.29$, $t = -3.69$, df $= 23$, $P = 0.001$; fig. 4*A*). However, hatchlings from both thermal treatments spent similar amounts of time attacking and chasing crickets (principal component 1: $P = 0.18$).

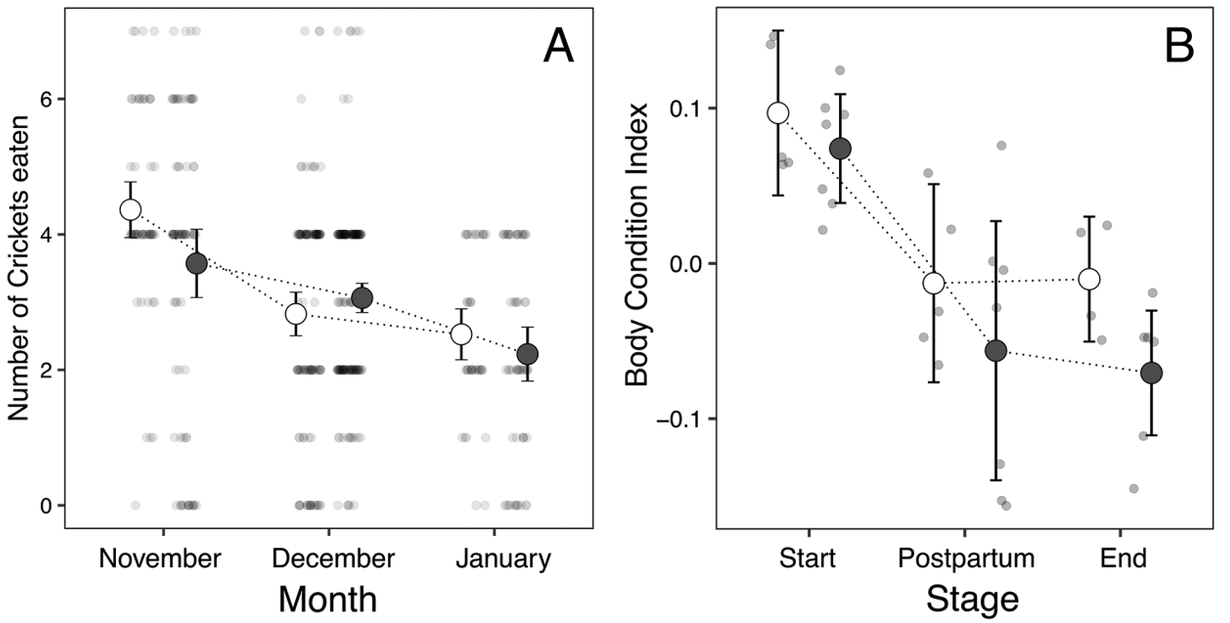

Figure 3. Effect of current (white; $n = 5$) and future (gray; $n = 7$) thermal treatments on the foraging behavior (*A*) and the body condition (*B*) of pregnant female *Saiphos equalis*. In *A*, data points plotted in light gray correspond to repeated measurements of the number of crickets eaten by females in the experiment. Error bars indicate 95% confidence intervals.

Future- and current-incubated hatchling lizards had similar maximum speed and acceleration values (principal component 2: $P > 0.5$). However, hatchlings from the future treatment had a slightly lower average speed and acceleration (principal component 1: $\beta = -0.82 \pm 0.37$, $t = -2.24$, df $= 8.9$, $P = 0.048$; fig. 4*B*) compared with hatchlings from the current treatment.

Discussion

Future climate will affect the phenotype, and possibly the survival, of ectotherms (Huey et al. 2012; Seebacher et al. 2015). Oviparous species may be able to compensate for the effect of high temperatures on their offspring by selecting appropriate nest sites. However, much less is known about the behavioral responses of viviparous females to mitigate these effects on their progeny and whether these responses have any associated costs. Here, we show that female lizards (*Saiphos equalis*) alter their thermoregulatory and foraging behavior in response to high temperatures, possibly to protect their offspring from the negative effects of elevated developmental temperatures. In fact, high temperatures did not affect hatchling body size, growth rate, or thermal preference but produced hatchlings with lower foraging and locomotor performance, suggesting that the protective effect may not be complete. Finally, this buffer effect may have some costs, since females exposed to elevated temperature had poorer body condition.

Overall, females from the future thermal environment selected deeper (i.e., cooler) substrate compared with females from the current thermal environment. Future-incubated females chose significantly lower temperatures in November but then kept a stable body position relative to soil depth during the rest of the experiment, implying that they maintained a stable body temperature. Conversely, females from the current thermal environment moved deeper as environmental temperatures were rising. Behavioral thermoregulation is perhaps the most important way in which viviparous females control the developmental environment of their offspring (Bull 1980; Beuchat 1988). Female decisions can alter the phenotype and posthatching success of their offspring and play an important role as a behavioral response to global warming (Refsnider and Janzen 2012; Du and Shine 2015). Thus, females from the future thermal environment likely selected deeper places in the substrate to achieve lower, more suitable temperatures for embryonic development (Beuchat 1986; Shine and Harlow 1993). In fact, female behavioral thermoregulation could be responsible for the absence of an effect of high developmental temperatures on the body size, growth rate, and thermal preference of hatchling *S. equalis* in this study. For instance, a female *S. equalis* selecting an average depth of 15 cm would experience an approximate reduction in soil temperature of 1°C (given a reduction rate of 0.06°C/cm) compared with a female buried just below the surface. Minor changes in developmental temperatures can have significant consequences on offspring phenotype (Deeming 2004; Booth 2006; Noble et al. 2018), including *S. equalis* (Beltrán et al. 2020*a*). However, considering our low statistical power, further studies are needed to understand the effect of high developmental temperatures on the life-history traits of *S. equalis*.

The predicted soil temperature values derived from the body position of females in the substrate showed that, overall, future-incubated females experienced higher soil temperatures (1.2°–1.4°C) than current-incubated females. This increase in soil temperatures experienced by females affected the foraging success and

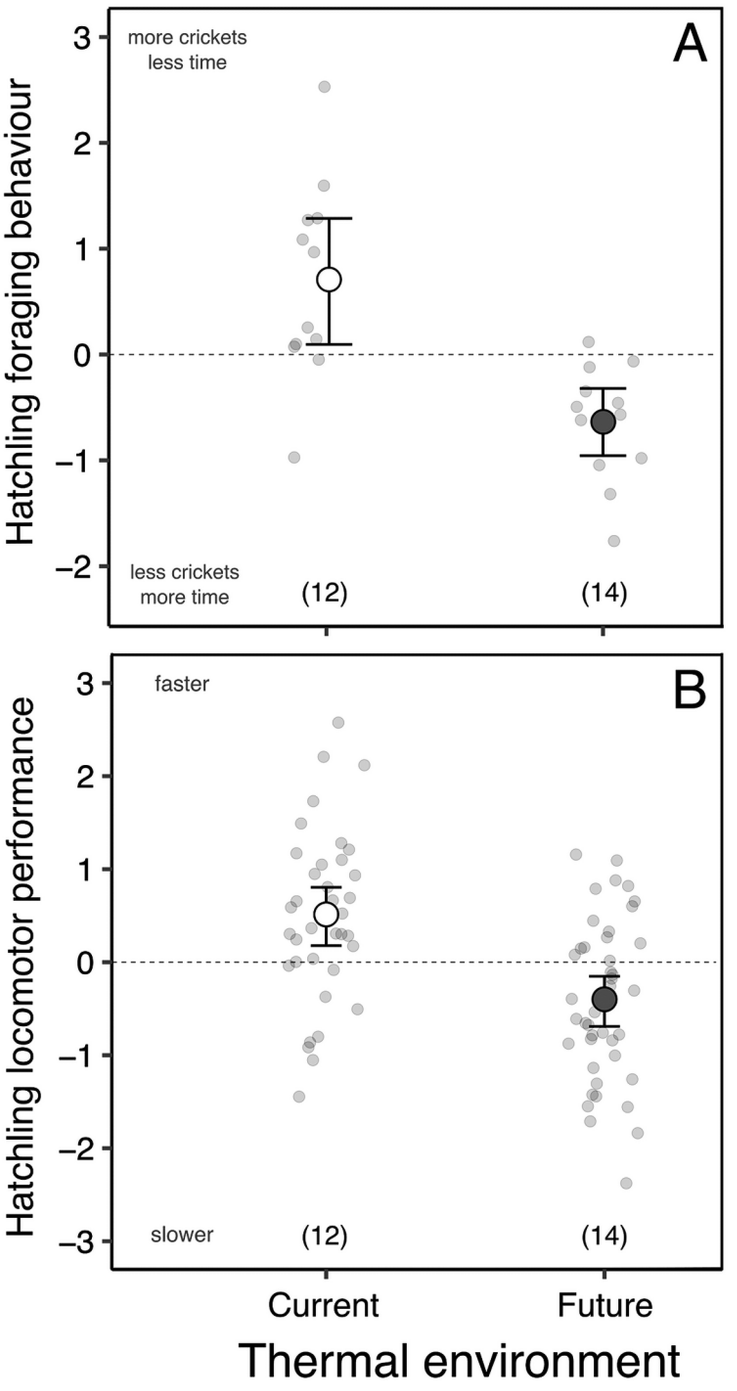

Figure 4. Effect of different early thermal treatments (current vs. future) on the foraging behavior (indexes from second principal component; *A*) and the locomotor performance (indexes from first principal component; *B*) of hatchling *Saiphos equalis*. Data points plotted in light gray correspond to repeated measurements on the experimental animals. Error bars indicate 95% confidence intervals. Sample sizes are indicated at the bottom of the figure.

locomotor performance of hatchling *S. equalis*. Early stages of development (November), in which neurulation and organogenesis take place in reptiles (Andrews 2004), are crucial for the viability of embryos and are highly sensitive to changes in incubation temperature (El Mouden et al. 2000; Andrews 2004). In contrast, later stages of development (December and January) mostly correspond to the embryo's growth and are less sensitive to changes in temperature (Andrews 2004; Virens and Cree 2019). In these later stages, however, we did not find differences in female depth, which could explain the similar body size and growth rate of hatchlings

from different treatments. Importantly, future-gestated hatchlings ate fewer crickets, took longer to catch their prey, and had lower average sprint speed and acceleration. Nonetheless, the reduced foraging and locomotor performance of future-gestated hatchlings may affect their fitness and survival in the wild (Nagy 2000; Downes 2001; Houston and McNamara 2014). Our results suggest that although females could mitigate some of the negative effects of incubation temperature, such as the reduction in body size and growth rate, this protective effect is limited.

The reliability of our measurements on female thermoregulatory behavior depends on the detection accuracy (1–2 cm) of the PIT tag readers. However, we are confident in the validity of these results because (i) the error due to the reader measurements should be spread evenly across females and thermal treatments and (ii) we obtained very similar results when analyzing only the data where the female was observed (although the estimates change significantly; table A5). Nonetheless, we acknowledge that ideally, the temperatures that embryos experienced during their development should be measured by attaching temperature loggers on females (Robert et al. 2006; Vickers and Schwarzkopf 2016).

Elevated temperatures affected the foraging behavior of pregnant females. Overall, females from the future thermal treatment ate fewer crickets compared with females from the current thermal treatment. Interestingly, current-incubated females slowly reduced their food intake as their pregnancy progressed (and as they were choosing deeper thermoregulation sites), while females from the future thermal treatment maintained a lower food intake throughout the experiment. Thus, the imbalance between thermoregulatory and foraging behavior (Shine 1980; Gregory et al. 1999; Weiss 2001) was more noticeable for females from the future thermal treatment, whose metabolic rate and therefore energy expenditure were probably accelerated by high temperatures (Huey and Slatkin 1976; Wu et al. 2009). Accordingly, females from the future thermal treatment had a reduced body condition (proxy for stored energy; Naulleau and Bonnet 1996) compared with females from the other treatment. Although little is known about the behavior of *S. equalis* during winter, it most likely hibernates (I. Beltrán, personal observation). Low food reserves before hibernation can lead to increased female mortality over winter (Madsen and Shine 1992; Brown and Weatherhead 1997), thus leaving few females available to reproduce in the next season (Olsson and Shine 1997; Litzgus et al. 2008) and compromising population viability (Hoare et al. 2006; Reading 2007).

Providing females with plenty of food is likely not representative of the conditions that these lizards experience in the wild. However, controlling this variable allowed us to explore the effect of thermal environment without the confounding factor of food intake, for which both quality and quantity are known to interact with thermoregulatory behaviors in some ectotherms (Pulgar et al. 2003; Gilbert and Miles 2016). Further research could incorporate more sophisticated factorial designs, including the use of more treatment chambers to avoid pseudoreplication, to evaluate the effects of temperature and food supply on female behavioral and physiological responses. Finally, mixed effects models can deal with low sample sizes without providing biased estimates or increasing the type I error rates (false positives; Cnaan et al. 1997; Bolker et al. 2009), and most of the effect sizes we report here are large (Cohen's $d > 0.8$) and highly significant ($P \leq 0.01$). Nonetheless, given that our sample sizes are small, we acknowledge that it is difficult to make generalizations about the effect of climate change in other lizard species.

Females in the wild could select deeper thermoregulation sites, which may buffer offspring from elevated temperatures (Doody et al. 2006; Telemeco et al. 2009). In fact, burrow systems are predicted to buffer the direct effects of climate warming on the body temperature of lizards (Moore et al. 2018). It is also possible that in the wild, females may find another way to adjust their body temperature without necessarily moving farther below the surface. Females could change their pattern of activity, for instance, by being active later at night (Menzel et al. 2006; Levy et al. 2019), adjusting their nesting sites (Telemeco et al. 2009; Refsnider and Janzen 2012), or retreating to shaded areas where temperatures are cooler (Kearney et al. 2009). Moreover, it is even possible that climate warming may broaden the suitable thermal conditions and thus activity times for crepuscular and nocturnal squamates, such as *S. equalis* (Moreno-Rueda et al. 2009; Kearney 2013). Finally, our results suggest that behavioral changes in the times allocated to forage and thermoregulate during pregnancy can have important energetic costs; however, it is less well understood how climate change will affect the availability of cool microhabitats, such as burrows and vegetation structure, for ectotherms (Kearney and Porter 2009; Basson et al. 2017; Refsnider et al. 2018). Further research should be directed to evaluate how widespread behavioral and physiological responses are within ectotherms, as well as how effective they are in mitigating the effects of global warming.

A recent study has suggested the possibility of facultative oviparity in viviparous females of *S. equalis* (Laird et al. 2019). Although Dollo's law of irreversibility states that complex traits, once lost, cannot reevolve (Dollo 1893; Lee and Shine 1998), the recent origin of viviparity in *S. equalis* (Smith et al. 2001) might represent a state of reproductive lability that confers a selective advantage for the species (Laird et al. 2019). While this hypothesis is merely based on a laboratory observation, it suggests that females could avoid the burden of viviparity by laying shelled eggs in earlier stages of development (Recknagel et al. 2018). This would give time for females to build up more energetic reserves before hibernation (Bauwens and Verheyen 1985; Feriche et al. 2016); however, it is unknown whether this would be advantageous for the developing embryo, since viviparity evolved in *S. equalis* likely to protect embryos from cold soil temperatures (Shine 1983; Smith and Shine 1997).

The most recent report of the IPCC (2018) shows how an average increase in air temperature of 1.5°C will be a significant threat to both human and natural environments. Wildlife scientists, in particular those studying ectotherms, have tested the impacts of global warming on diverse offspring phenotypic traits. While oviparous species may be able to compensate for the effect of global warming by behavioral plasticity in nest site selection, much less is known about these responses in viviparous species. Our study suggests that viviparous lizards can mitigate some of

the negative effects of global warming on the development of their offspring. However, our results also show that this protective effect is only partial, and females might incur a cost to their body condition.

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APPENDIX

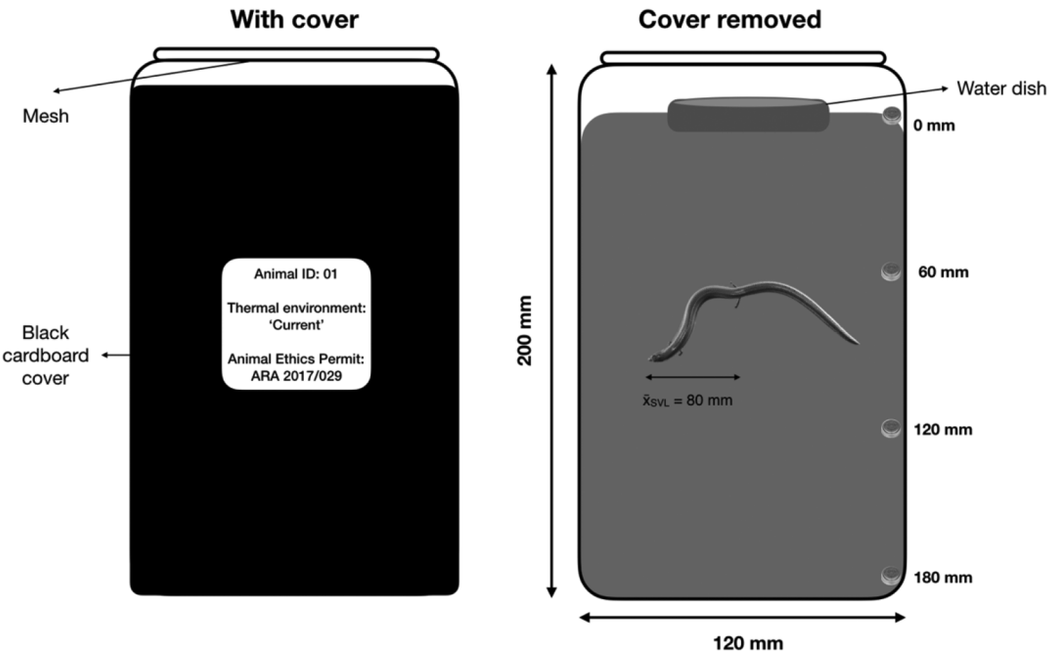

Figure A1. Schematic representation of the cylindrical enclosures where pregnant female *Saiphos equalis* were kept during the thermal treatment experiments. Soil temperatures inside the enclosures were registered at different depths (0, 60, 120, and 180 mm) every hour between the start of the experiment and parturition. A color version of this figure is available online.

Table A1: Settings for the temperature (°C) in the incubators

	Current incubator			Future incubator		
Hour	Nov.	Dec.	Jan.	Nov.	Dec.	Jan.
1	16.1	20.3	21.3	17.6	21.8	22.8
2	15.4	19.5	20.5	16.9	21	22
3	14.9	18.7	19.7	16.4	20.2	21.2
4	14.4	18.1	19.1	15.9	19.6	20.6
5	14	17.5	18.5	15.5	19	20
6	13.6	16.9	17.9	15.1	18.4	19.4
7	13.2	16.4	17.4	14.7	17.9	18.9
8	13	16.2	17.2	14.5	17.7	18.7

Table A1 (*Continued*)

	Current incubator			Future incubator		
Hour	Nov.	Dec.	Jan.	Nov.	Dec.	Jan.
9	13.4	16.4	17.4	14.9	17.9	18.9
10	14.3	17.3	18.3	15.8	18.8	19.8
11	15.7	19	20	17.2	20.5	21.5
12	17.4	20.9	21.9	18.9	22.4	23.4
13	19.3	22.8	23.8	20.8	24.3	25.3
14	20.8	24.8	25.8	22.3	26.3	27.3
15	22.1	26.5	27.5	23.6	28	29
16	23	27.8	28.8	24.5	29.3	30.3
17	23.2	28.4	29.4	24.7	29.9	30.9
18	22.6	28.1	29.1	24.1	29.6	30.6
19	21.7	27.1	28.1	23.2	28.6	29.6
20	20.8	25.9	26.9	22.3	27.4	28.4
21	19.7	24.6	25.6	21.2	26.1	27.1
22	18.7	23.4	24.4	20.2	24.9	25.9
23	17.7	22.3	23.3	19.2	23.8	24.8
24	16.9	21.3	22.3	18.4	22.8	23.8

Note. The photoperiod was 13L : 11D, and the relative humidity was constant at 70%. The temperatures in the current incubator were recorded in the field every hour from November 2017 to January 2018 using Thermochron iButton loggers.

Table A2: Component loadings from the principal component analysis (PCA) for the experiment on foraging success in hatchling viviparous *Saiphos equalis* gestated under different thermal treatments

Behavior	Loadings for PC1	Loadings for PC2	Communalities
Latency	−.23	.6	.42
Time spent chasing crickets	.88	−.15	.54
No. attacks	.92	−.06	.85
Time handling crickets	.04	−.77	.59
No. crickets eaten	−.03	.73	.54
Variance explained by each component (%)	33	30	…
Cumulative explained variance (%)	…	…	63

Note. The PCA for the foraging assay consisted of five behaviors: latency to emerge from substrate, total time spent chasing crickets, number of attacks, total time handling crickets, and number of crickets eaten.

Table A3: Component loadings from the principal component analysis (PCA) for the experiment on sprint speed and acceleration in hatchling viviparous *Saiphos equalis* gestated under different thermal treatments

Behavior	Loadings for PC1	Loadings for PC2	Communalities
Average speed over 20 cm	.93	.08	.87
Average speed over 80 cm	.91	.11	.83
Average acceleration over 20 cm	.90	.26	.87
Average acceleration over 80 cm	.90	.13	.82
Maximum speed over 20 cm	.11	.89	.80
Maximum speed over 80 cm	.17	.79	.66
Maximum acceleration over 20 cm	.16	.87	.79
Maximum acceleration over 80 cm	.15	.83	.70
Variance explained by each component (%)	42	37	…
Cumulative explained variance (%)	…	…	79

Note. The PCA for the performance assay contained eight variables: average speed over 20 cm, average speed over 80 cm, average acceleration over 20 cm, average acceleration over 80 cm, maximum speed over 20 cm, maximum speed over 80 cm, maximum acceleration over 20 cm, and maximum acceleration over 80 cm.

Table A4: Outcome of the mixed models evaluating differences in body size, body mass, mass-related growth rate, SVL-related growth rate, and preferred body temperature of hatchling *Saiphos equalis* born under different thermal environments (current vs. future)

Response variable, fixed term (reference level)	Estimate	SE	df	*t*	*P*
Body size:					
Intercept	28.385	1.159	22.702	24.490	<.001**
Thermal treatment (future)	.537	1.035	8.055	.520	.620
Egg mass	.411	1.733	18.651	.240	.820
Body mass:					
Intercept	−.064	.126	23.318	−.510	.616
Thermal treatment (future)	.021	.017	7.742	1.260	.243
SVL	.012	.004	23.563	2.710	.012*
Growth rate (mass):					
Intercept	.312	.029	5.765	10.740	<.001**
Time (no. weeks since hatching)	.155	.012	2.319	13.070	.0032*
Thermal treatment (future)	−.013	.027	9.987	−.500	.628
Thermal treatment × time	−.011	.006	73.151	−1.880	.065
Growth rate (SVL):					
Intercept	30.580	1.117	3.103	27.380	<.001**
Time (no. weeks since hatching)	3.913	.542	2.152	7.220	.015*
Thermal treatment (future)	−1.232	.714	11.038	−1.730	.112
Thermal treatment × time	.060	.196	73.749	.310	.759
Preferred body temperature:					
Intercept	4.290	12.381	23.000	.350	.730
Thermal treatment (future)	.592	.978	23.000	.600	.550
SVL	.552	.422	23.000	1.310	.200

Note. SVL = snout-to-vent length.
*$P < 0.05$.
**$P < 0.01$.

Table A5: Outcome of the linear mixed model evaluating differences in the thermoregulatory behavior of gravid female *Saiphos equalis* subjected to different thermal environments (current vs. future)

Fixed term (reference level)	Estimate	SE	df	*t*	*P*
Intercept	.212	.994	36.763	.210	.832
Thermal treatment (future)	3.304	1.166	29.921	2.830	.008**
Month (Dec.)	3.257	1.059	109.301	3.080	.003**
Month (Jan.)	4.761	1.384	109.988	3.440	<.001**
Time measured (afternoon)	2.528	.682	108.505	3.710	<.001**
Thermal treatment × month (future × Dec.)	−4.121	1.404	109.985	−2.930	.004**
Thermal treatment × month (future × Jan.)	−3.671	1.659	109.917	−2.210	.029*

Note. In contrast with the model shown in part B of table 1, which uses all of the data, this model includes only the observations in which females were seen through the plastic enclosures.
*$P < 0.05$.
**$P < 0.01$.

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