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FEATURED STUDENT RESEARCH PAPER

Effects of early thermal environment on the behavior and learning of a lizard with bimodal reproduction

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Abstract

Early developmental temperatures influence the physiology and behavior of reptiles, with important consequences for their fitness and survival. For example, many viviparous lizards are cold adapted which may restrict their activity times during the reproductive season, increasing their susceptibility to global warming. However, it is unclear if and how lizards with different reproductive modes (oviparity vs. viviparity) can respond to rising temperatures by modifying their life-history traits. We examined the effect of developmental temperatures on hatchling behavior and learning in viviparous and oviparous populations of the lizard *Saiphos equalis* to test whether their reproductive behavior can buffer against rising temperatures. Gravid females from both populations were subjected to current or projected end-of-century (future) thermal environments to evaluate differences in the exploratory, foraging and antipredator behavior, and spatial learning ability of their offspring. We found that viviparous lizards were more exploratory and had a less-pronounced antipredator response than oviparous lizards. Regardless of the mode of reproduction, elevated temperatures reduced the exploratory behavior of hatchling lizards. Elevated temperatures also reduced the foraging efficiency of oviparous, but not viviparous, hatchlings. Finally, future-gestated oviparous hatchlings were more likely to choose the correct refuge and made fewer mistakes in a spatial learning task; however, we found only weak evidence of spatial learning in *S. equalis*. Our results suggest that although global warming is likely to have a negative impact on phenotypic traits, in *S. equalis*, some of these effects may be ameliorated by maternal behavior and/or physiological responses during pregnancy, particularly in viviparous populations.

Significance statement

Computational modeling studies suggest that live-bearing lizards (viviparous) are more vulnerable to global warming compared with egg-laying ones (oviparous). However, there is little experimental evidence showing that viviparous species are indeed at a greater risk of extinction. Using a lizard species that has both oviparous and viviparous populations, we tested the effect of high developmental temperatures (projected for 2100) on the behavior and learning of their offspring. We found that elevated temperatures had a stronger negative effect on egg-laying lizards by producing hatchlings with lower foraging efficiency. Our results suggest that viviparous mothers can ameliorate some of the effects of global warming on their offspring. Moreover, our study suggests that if live bearers are indeed more vulnerable to global warming, it is likely not due to maladaptive behavior in offspring, but rather, to other causes that affect pregnant females.

Keywords Global warming · Foraging performance · Incubation temperature · Spatial learning · Reptile · Viviparity

Introduction

Environmental temperature affects the development, physiology, and behavior of ectotherms such as reptiles, whose temperature regulation mostly depends on external sources (Brattstrom 1979; Huey 1982; Noble et al. 2018). For instance, incubation temperature largely determines embryonic development in chelonians (Deeming and Ferguson 1991; Booth 2000), crocodilians (Webb and Cooper-Preston 1989; Birchard and Marcellini 1996), and squamates (Deeming and Ferguson 1991; Deeming 2004), with important

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consequences for their fitness and survival (Mitchell et al. 2018). The thermal environment that a developing embryo experiences depends mostly on female behavior, conditioned either by the female's thermoregulatory behavior (in viviparous species) or by the location and depth of the nest where the female will lay her eggs (in oviparous species) (Packard et al. 1977). Although most squamates are oviparous, viviparity has independently evolved more than 100 times within this group (Blackburn 2006; Van Dyke et al. 2014).

The repeated convergent evolution of viviparity has been framed by two main hypotheses. The "maternal manipulation" hypothesis states that the stable temperatures provided by females during egg retention result in higher offspring viability (Shine 1995; Pincheira-Donoso et al. 2013). The second hypothesis, the "cold-climate" hypothesis (Sergeev 1940; Shine 2014), states that viviparity evolved via female behavioral thermoregulation (i.e., maternal buffering) to protect embryos from low environmental temperatures (Tinkle and Gibbons 1977; Shine 1985). In fact, viviparity (as an adaptation to cold environments) is associated with low thermal preference and heat tolerance which may increase the sensitivity of viviparous species to elevated temperatures compared with oviparous species (Sinervo et al. 2010; Meiri et al. 2013). These predictions are part of an ongoing debate because some studies have shown that lizards at high latitude and elevation (cold environments) might have a slightly larger "thermal-safety margin" (Sunday et al. 2014) compared with tropical lizards, particularly those from lowlands (Huey et al. 2009). Similarly, in thermally constrained environments (high latitudes or altitudes), lizards might benefit from reasonable warming (Adolph and Porter 1993; Chamaillé-Jammes et al. 2006). For instance, in a long-term study in common European lizards, an increase in female body size, and therefore reproductive output, was correlated with higher temperatures experienced in summer (Chamaillé-Jammes et al. 2006). However, Sinervo et al. (2010) showed that extinction probability in lizards strongly correlates with the magnitude of warming in spring, but not other seasons (Sinervo et al. 2010). This suggests that extinction in this group is driven by energetic deficiency during the reproductive season when the energy demands are highest (Huey et al. 2010). Because the embryo is a life stage particularly vulnerable to environmental stress (e.g., global warming), viviparity has been identified as the main risk factor in exacerbating recent widespread lizard population extinctions (Sinervo et al. 2010; Pincheira-Donoso et al. 2013). However, most of the studies examining this hypothesis are based on computational modeling (Sinervo et al. 2010; Meiri et al. 2013) and there is little experimental evidence that viviparous species are indeed at a greater risk of extinction (but see Wang et al. 2017). Moreover, the findings of these studies are often difficult to interpret or extrapolate because of the phylogenetic and ecological differences between species (Meiri et al. 2013).

Currently, viviparous species are underrepresented in studies testing phenotypic plasticity in behavioral traits of reptiles (Noble et al. 2018). Similarly, although the number of studies testing the effect of incubation temperatures on squamate cognitive ability is increasing (Amiel and Shine 2012; Clark et al. 2014; Dayananda and Webb 2017; Siviter et al. 2017a), all the species tested so far are oviparous and the direction of this effect seems to be species specific. For instance, learning abilities are negatively affected by high incubation temperatures in the velvet *gecko Amalosia lesueurii* (Dayananda and Webb 2017; Abayarathna and Webb 2020) and the bearded dragon *Pogona vitticeps* (Siviter et al. 2017a), while three-lined skinks *Bassiana duperreyi* incubated at warmer temperatures performed better than hatchlings incubated at lower temperatures (Amiel and Shine 2012; Amiel et al. 2014).

In a global-warming scenario, species with low dispersal ability, such as lizards, are more likely to respond through adaptation or behavioral and physiological plasticity (Visser 2008; MacLean and Beissinger 2017). Plastic changes in offspring phenotype, such as a larger body size or a greater sprint speed, should help animals endure changing temperatures and possibly adapt to new environments (Ghalambor et al. 2007; Visser 2008). However, the extent to which lizards with different modes of reproduction are able to respond to climate change by modifying key behavioral and cognitive traits that will later determine their fitness is still unclear. The Australian skink *Saiphos equalis* (Gray 1825), is one of only a handful of species in the world with geographic variation in its reproductive mode (Heulin et al. 1993; Smith and Shine 1997; Fairbairn et al. 1998). The populations inhabiting the Northern Tablelands of New South Wales (NSW) are viviparous; females 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, including the Sydney region, have prolonged uterine egg retention (hereafter 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 days (Smith and Shine 1997). While these oviparous populations have a considerably shorter incubation duration compared with other sympatric oviparous lizards (> 30 days) (Qualls and Shine 1998), it is well known that small differences in the incubation period can have profound effects on hatchling phenotype and fitness (Vince and Chinn 1971; Shine and Olsson 2003; Radder et al. 2008; While et al. 2009). Therefore, *S. equalis* represents a unique opportunity to test specific predictions on the interplay between global warming and reproductive mode, while controlling for relatedness.

Here, we examined the effect of thermal environment during development on exploratory, foraging, and antipredator behavior, and on the spatial learning ability of hatchling lizards from an oviparous and a viviparous population of

S. equalis. Due to the low-temperature preferences of *S. equalis* (Wu et al. 2009), we predicted that elevated temperatures will have a negative impact in most, if not all, of the traits examined in offspring from both populations. However, given that high temperatures during reproduction might have a greater impact on viviparous species (Sinervo et al. 2010; Pincheira-Donoso et al. 2013), we predicted a greater negative effect of elevated temperature on offspring from viviparous populations.

Materials and methods

Animal capture and husbandry

During September and November 2017, we collected gravid female *S. equalis* by hand from two populations: Riamukka State Forest (viviparous, $n = 12$), in northern NSW (31° 20′ S, 151° 39′ E), and greater Sydney (oviparous, $n = 32$), in southern NSW (Winston Hills (33° 46′ S, 150° 59′ E), Willoughby (33° 48′ S, 151° 11′ E), Tempe (33° 55′ S, 151° 08′ E), and Hurstville (33° 58′ S, 151° 05′ E)) (Online resource 1, Table 1). Animals were found under rocks, logs, and in leaf litter. We determined gravidity in females based on appearance and light abdominal palpation of eggs/embryos. We transported all lizards to Macquarie University (Sydney), within 48 h of capture and recorded their weight (± 0.1 g) and body size (snout-to-vent length (SVL) using a transparent ruler to ± 1 mm). Each female was housed in a separate plastic enclosure (200 L × 150 W × 90 mm H) with moist potting soil to a depth of 5 cm. Each cage contained a 100 × 100 mm wooden shelter and a water dish. Animals were fed three times a week with five to six crickets (~ 10 mm) each time. Crickets were dusted with vitamins (aristopet Repti-vite) and calcium (URS Ultimate Calcium) once per week. Females were kept in these conditions for 3 days before they were allocated to one of the thermal environments.

A considerable proportion of the females with whom we started the study turned out not to be gravid and had to be removed from the incubation experiments. In consequence, our final sample size included 11 females from the oviparous Sydney population and 8 females from the viviparous Riamukka population.

Thermal treatments and developmental environments

Gravid females from both populations were evenly and randomly allocated to one of two cycling incubators (PGR15/Growth chamber, Conviron, Melbourne, Australia). The first treatment (hereafter referred as "current") was designed to match the preferred temperatures reported for gravid females of the species (sinusoidal daily curve with mean and standard deviation of 22 ± 1.6 °C; range = 20–25 °C; Online resource 2, Table 1) (Wu et al. 2009). The second treatment (hereafter referred as "future") was set to have a mean increase in temperature of 3 °C (25 ± 1.6 °C; range = 23–28 °C; Online resource 2, Table 1), which corresponds to the expected increase in spring and summer temperatures by 2100 in south-eastern NSW (Dowdy et al. 2015). Female enclosures were checked for eggs twice a day. Eggs were transferred to a 100-mL plastic jar with moist vermiculite (water potential of − 200 kPa). Plastic jars were sealed with cling wrap to prevent desiccation and remained in the same incubators as their mothers until hatching. Temperature inside the incubators was registered every 15 min using Thermocron iButton loggers (DSG1921G, ± 0.5 °C, Maxim Integrated Products/Dallas Semiconductor, Texas, USA). After all females gave birth or oviposited, we released them at their original site of capture.

To minimize observer bias, blinded methods were use when all behavioral data were analyzed. For each hatchling lizard, we measured its weight (± 0.001 g) and body size (SVL ± 0.05 mm) and calculated its body condition index (BCI) using the residuals from a linear regression of $\log_{10}$(mass) on $\log_{10}$(SVL) (Cox et al. 2011). Then, each hatchling was transferred to a separate plastic enclosure (175 × 120 × 80 mm) containing moist potting soil to a depth of approximately 3 cm. Each enclosure contained a 45 × 45 mm ceramic tile shelter and a water dish. Animals were housed in a room (~ 21 °C) with a thermal gradient of 21–34 °C during the day and a 12L:12D light cycle. We fed hatchlings three times a week with five pin-head crickets (~ 3 mm) each time. Crickets were dusted with vitamins twice per week.

Exploratory behavior

Exploratory behavior or "exploration" is defined as the rate at which an individual moves through a novel space and is commonly assayed in a wide range of animal species (Verbeek et al. 1994; Dingemanse et al. 2002; Sih et al. 2004). At 1 week of age, we measured exploratory behavior in hatchling lizards by introducing them to a novel arena. The experimental room was kept at ~ 21 °C which is the approximate preferred body temperature of these lizards in the laboratory (Wu et al. 2009; IB et al., unpublished data). The arena consisted of a plastic container (320 × 220 × 140 mm) with butcher paper as substrate and two black circular containers placed at each end of the arena as refuges (65 mm D × 30 mm H). Each one of the refuges had one entrance on the inner side. We repeated this procedure with different novel arenas at 12 weeks (containing white sand as substrate) and at 20 weeks (containing a thin layer of moist potting soil as substrate). The boxes and the two black circular containers had the same dimensions and orientation as in the first arena.

At the beginning of each trial, we introduced the lizard into the arena within a central, containment refuge. The hatchling was let to habituate within this refuge for 15 min. The trial started when we lifted the central refuge and ran for 60 min. From video recordings, we scored: (i) time spent moving (s) and (ii) number of times they entered a refuge. We analyzed each novel arena independently by combining these two variables using a principal component analysis (PCA). This PCA used the correlation matrix because the variables were on different scales and this approach standardizes the data (Jolliffe 2002). A *varimax* rotation was applied on the PCA to maximize the sum of the variances of the squared loadings (Jolliffe 2002). The PCA was performed using the *principal* function in the package *psych* (Revelle 2017) in the statistical software R (R Core Team 2018). For each novel arena, the two behaviors were highly correlated and positively loaded on a single component (Online resource 2, Table 2). For later analysis, we used the first principal component (PC1) of each arena as our "exploratory score," where a higher value reflects a higher exploratory behavior.

Antipredator behavior

At 1 week of age, we measured the antipredator response of hatchling lizards by simulating a predator attack. The experiments were staged in containers (320 × 220 × 140 mm) with butcher paper as substrate and without refuges in an attempt to observe antipredator behaviors other than fleeing. The experiment took place in a room maintained at ~ 21 °C. Prior to commencing a trial, the body temperature of hatchlings was measured with a handheld infrared thermometer (nearest 0.5 °C) pointed to the lizard's abdomen at a distance of ~ 1 cm. To begin a trial, each hatchling was transferred from its home enclosure to the experimental arena using a wide spoon in order to reduce handling stress. The hatchling was placed in the center of the arena and left to habituate for 30 s. Then, we simulated an attack from a predator by tapping the hatchling's pelvic girdle with a small paintbrush every 5 s, ten times in total. Only one antipredator behavior was observed enough times to be considered for statistical analysis. This behavior consisted of the flipping of the lizard's entire body just after being tapped with the paintbrush. With this behavior, the hatchlings would usually move far away from the paintbrush and then continue running. We refer to this behavior as "jumping." On video recording, we analyzed (i) the proportion of time running; (ii) the number of times the animal was motionless; and (iii) the number of jumps. At the end of the trial, the lizard was gently placed back into its home enclosure and we measured the time it took to hide in the substrate. Lizards that did not hide within 30 s were given the maximum time.

Foraging behavior

At 2 weeks of age, we measured the foraging abilities of hatchling lizards. Hatchlings were fasted for 48 h prior to the trial, which was conducted in the hatchling's home enclosure in a room maintained at ~ 21 °C. We placed five pin-head crickets (~ 5 mm) in the enclosure and video recorded the behavior of hatchlings for 25 min. On video recordings, we quantified (i) the total time spent chasing the crickets; (ii) the number of attacks; (iii) the total time handling the crickets; and (iv) the number of crickets eaten. To quantify the foraging performance of the lizards, these variables were combined using a PCA. The four behaviors were highly correlated and positively loaded on two components that explained 73% of the covariance in the data (Online resource 2, Table 3). The first component explained 37% of the covariance and was positively correlated with the number of crickets eaten and the time handling the crickets. The second component explained 36% of the covariance and was positively correlated with the number of attacks and time spent chasing the crickets.

Spatial learning

We conducted morphological and physiological measurements on our experimental animals that are not included in this study. Because the cognition experiment was relatively long, we decided to conduct after all the other measurements were completed. Furthermore, we trialed other cognitive tasks, such as association tasks, that did not work. Therefore, it was only in week 16 that we evaluated spatial learning ability. For the experiment, three identical circular black plastic refuges (inverted take-away food containers, 100 D × 50 mm H) were placed in line 4 cm apart, at the end of a rectangular arena (450 × 400 × 360 mm) covered with white paper (Online resource 2, Fig. 1). Each refuge had a small entrance, of similar size, but two of them had a transparent barrier obstructing the entrance. We filled the refuges with moist potting mix substrate to provide a suitable refuge for the animals and the transparent barriers had small holes to allow chemical cues to freely flow out of the containers. The experimental arenas were placed in a room at constant temperature (~ 21 °C) and remained in the same position during the whole experiment to allow individuals to use spatial cues in the environment to locate the safe refuge. The butcher paper sheets in the arenas were flipped after every trial and then discarded. Before each trial, we mixed together the substrate from the three refuges to prevent individuals from using familiar chemical cues to locate the correct refuge. The location of the correct refuge was randomly determined for each individual and balanced between experimental groups and stayed the same through the experiment so lizards could learn the location of the open refuge. At the beginning of each trial, we placed the animal under a containment refuge opposite to the three refuges. When the refuge was removed, we chased the lizard with a paintbrush and recorded (i) the first choice made by the animal; (ii) the number of incorrect choices; and, (iii) the time taken to enter the correct refuge. Animals that failed to locate the correct refuge within 2 min were guided to it by slowly orienting their head towards the correct refuge; in some cases, it was necessary to gently push their pelvic girdle with the paintbrush so that lizards ran towards the safe refuge. We ran 3 trials per day for 6 consecutive days. We considered that a lizard had learnt the task if its first choice was the correct refuge in five consecutive trials or in seven out of eight trials.

Statistical analysis

When necessary, model assumptions of normality of residuals and homogeneity of variances were verified graphically and using Shapiro-Wilk's tests and Levene's test, respectively (Zuur et al. 2010). We used linear (LMM) and generalized (GLMM) mixed models to evaluate the effect of thermal environment (current vs. future), population (viviparous vs. oviparous), and their interaction, on our response variables. The selection of predictive variables was done using a stepwise backward elimination, starting from the most complex global model and dropping the fixed effects that were not significant until a minimal adequate model was reached (Harrison et al. 2018). Model selection was based on the corrected Akaike Information Criteria (Sugiura 1978; Burnham and Anderson 2002), and when necessary, the simplest (i.e., most parsimonious) model was chosen. Hatchling sex was not included in the models to avoid overparameterization due to low statistical power. The models were structured as follows:

1. A Gaussian LMM was used to test differences in the *exploratory score* between thermal environments and populations in each experimental arena. All final models included thermal environment and population as fixed effects and mother identity as a random effect to account for the non-independence in the data.
2. To test differences in antipredator behavior between thermal environments and populations, we used a GLMM with a binomial error distribution (for the proportion of time running), a GLMM using a Poisson error distribution ("log" link) (for the number of stops and number of jumps) and a Gaussian LMM (for the time to hide in the substrate). All final models included mother identity as a random effect and thermal environment and population as fixed effects, except for the proportion of time running which included SVL as a covariate as well.
3. A Gaussian LMM was used to test differences in foraging behavior (principal components 1 and 2 independently) between thermal environments and populations. Both models included mother identity as a random effect and thermal environment and population as fixed effects. However, the final model for PC2 included body temperature and the interaction term *population* × *thermal environment* as well.
4. To test for differences in spatial cognitive ability between thermal environments and populations across trials, we used: a binomial GLMM for the probability of choosing the correct refuge (correct = 1, not correct = 0), a GLMM using a Poisson error distribution (log link) for the number of incorrect choices, and a Gaussian GLMM for the time to enter the correct refuge. As random effects in each of these models, we included individual identity, individual identity nested within mother identity, individual identity nested within day, and trial nested within day (Noble et al. 2012). The final model for the time to enter the correct refuge included trial number, population, and thermal environment as fixed effects. However, the final models for the probability of choosing the correct refuge and for the number of incorrect choices included body temperature and the interaction term *population* × *thermal environment* as well.

The R packages "lme4" (Bates et al. 2015), "lmerTest" (Kuznetsova et al. 2017), and "MuMIn" (Bartoń 2018) were used to perform model analyses and calculate 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 Core Team 2018) at a significance level of $\alpha = 0.05$.

Results

Hatching and birthing occurred between early January and mid-February 2018 (Online resource 1, Table 1), and the variation in oviposition or birthing dates within experimental groups was relatively small (coefficient of variation range = 1.42–4.65%). High temperatures reduced the gestation period of females; however, this effect was statistically significant only for oviparous lizards (for oviparous: $\beta = -0.16 \pm 0.05$ (SEM), $Z = -3.24$, $P < 0.01$; for viviparous: $\beta = -0.07 \pm 0.07$, $Z = -1.02$, $P = 0.31$). We consider the lack of significance for viviparous lizards to be an artefact of low statistical power. On average, viviparous females exposed to future temperatures gave birth earlier compared with females exposed to current temperatures (mean ± SD, future = 99.8 days ± 2.6 vs. current = 107.3 days ± 1.5). Likewise, oviparous females exposed to future temperatures oviposited earlier (future = 106.6 days ± 4.9 vs. current = 123.2 days ± 4.3).

Effect of thermal environments on exploratory behavior

Viviparous lizards explored the paper-covered arena significantly more than oviparous lizards (population: $\beta = 0.76 \pm 0.31$ (SEM); $t_{16.16} = 2.45$; $P = 0.02$; Fig. 1a). Regardless of the mode of reproduction, hatchling *S. equalis* gestated under future temperatures explored the paper substrate arena significantly less than offspring from the current thermal environment (thermal environment: $\beta = -0.73 \pm 0.32$; $t_{16.82} = -2.26$; $P = 0.03$; Fig. 1a). Exploratory behavior in the sand-covered arena was low in all groups; therefore, we did not find significant differences between populations ($\beta = 0.004 \pm 0.36$; $P = 0.99$) or thermal environments ($\beta = 0.4 \pm 0.37$; $P = 0.30$; Fig. 1b). Finally, viviparous lizards explored the arena covered with potting soil significantly more often compared with the oviparous population (population: $\beta = 0.81 \pm 0.23$; $t_{17.31} = 2.91$; $P = 0.009$; Fig. 1c). Elevated temperatures did not significantly affect hatchling exploratory behavior in the potting soil arena (thermal environment: $\beta = 0.54 \pm 0.28$; $t_{16.16} = 1.87$; $P = 0.08$; Fig. 1c).

Antipredator behavior

Elevated developmental temperatures did not have any effect on the proportion of time running, number of stops, and number of jumps performed by hatchling *S. equalis* during the simulated attack ($P > 0.5$ for all the measurements). However, viviparous and oviparous hatchlings differed significantly in their antipredator responses (Fig. 2). Compared with oviparous hatchlings, viviparous hatchlings ran for significantly less time (population: $\beta = -0.37 \pm 0.18$; $Z = -2$; $P = 0.04$; Fig. 2b) and stopped significantly more often ($\beta = 0.39 \pm 0.1$; $Z = 3.82$; $P < 0.001$; Fig. 2a) while escaping from the simulated predator. Similarly, the "jump" behavior was observed significantly less frequently in viviparous hatchlings (population: $\beta = -0.76 \pm 0.18$; $Z = -4.14$; $P < 0.001$). Finally, we did not find differences in the time to refuge in the substrate between populations ($P = 0.65$) or thermal environments ($P = 0.18$).

Foraging behavior

Hatchlings from different populations and thermal environments ate similar numbers of crickets and spent a similar amount of time handling them (principal component 1; population ($P = 0.62$), thermal environment ($P = 0.67$)). However, lizards from both populations gestated under the future thermal environment attacked crickets more frequently and chased their prey for longer (principal component 2; thermal environment: $\beta = 1.12 \pm 0.51$; $t_{20.15} = 2.20$; $P = 0.04$; Fig. 3). Interestingly, the effect of elevated developmental temperatures on foraging behavior was stronger in the oviparous population (principal component 2; population × thermal

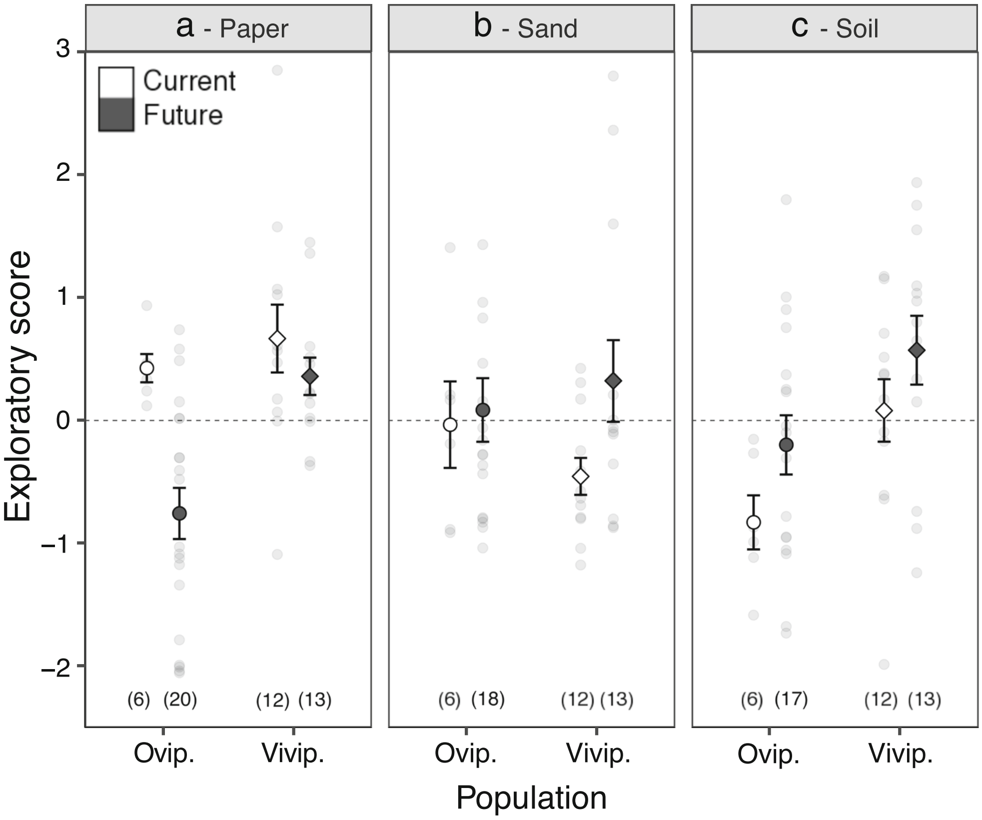


Fig. 1 Exploratory behavior of hatchlings from two populations (oviparous, viviparous) of *Saiphos equalis* subjected to different (current—open symbols vs. future—filled symbols) thermal environments in three different novel arenas (**a** paper, **b** sand, **c** soil). Plotted are means ± standard errors of the mean (SEM) and individual data points (in grey). The number of individuals in each group is indicated in the bottom of the figure

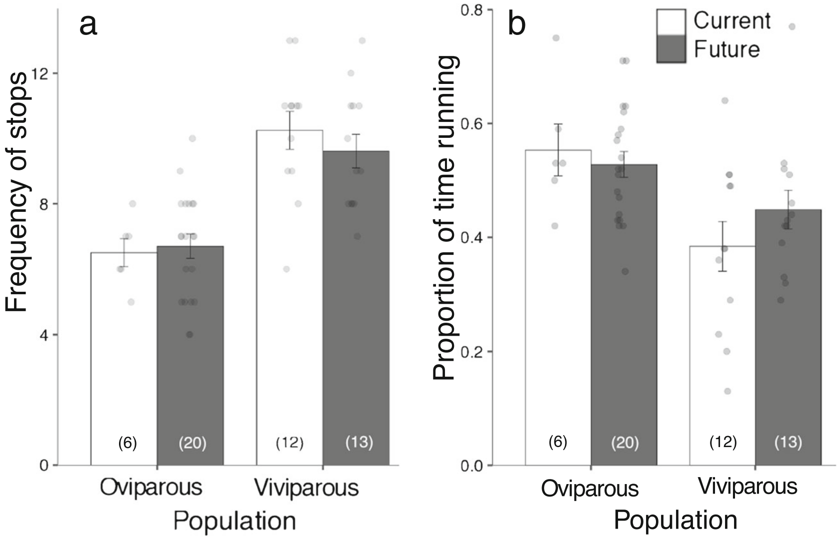


Fig. 2 Effect of early thermal environment (current—white columns vs. future—black columns) on **a** the frequency of stops and **b** the proportion of time running from a simulated predator attack of hatchlings from two populations (oviparous, viviparous) of *Saiphos equalis*. Plotted are means ± standard errors of the mean (SEM) and individual data points (in grey). The number of individuals in each group is indicated in the bottom of each bar

environment, $\beta = -1.68 \pm 0.65$; $t_{12.54} = -2.56$; $P = 0.02$; Fig. 3), meaning that oviparous lizards gestated under future thermal environments attacked the crickets more often and chased them for longer, compared with viviparous lizards from the same treatment.

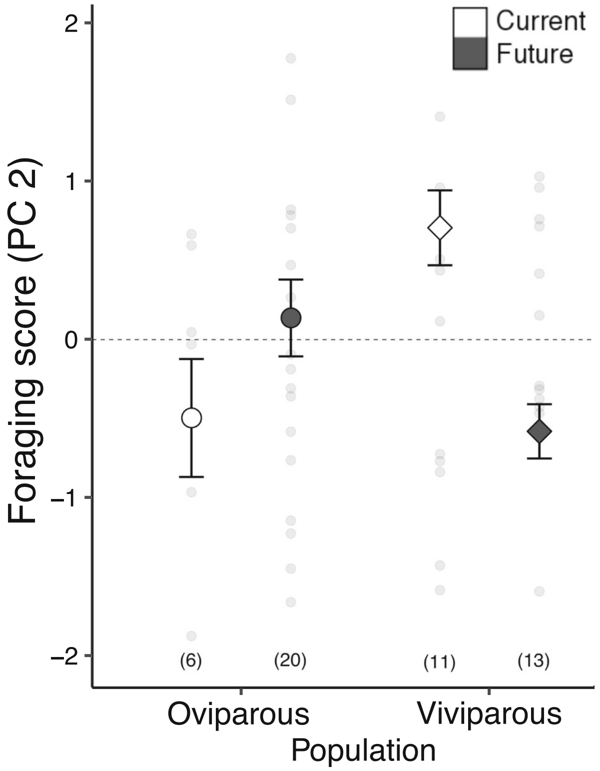
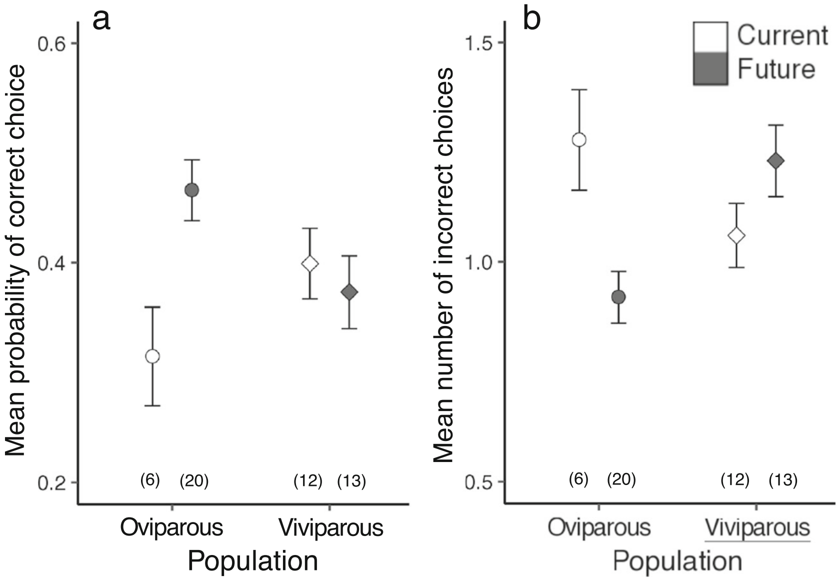


Fig. 3 Effect of early thermal environment (current—open symbols vs. future—filled symbols) on the foraging performance (PC2 from a principal component analysis) of hatchlings from two populations (oviparous, viviparous) of *Saiphos equalis*. Plotted are means ± standard errors of the mean (SEM) and individual data points (in grey). The number of individuals in each group is indicated in the bottom of the Fig. For details, see "Methods"

Spatial cognitive ability

Generally, hatchling lizards showed little evidence of spatial learning in the task used here. Although the number of incorrect choices slightly decreased throughout the trials (trial, $\beta = -0.03 \pm 0.01$; $P = 0.04$), the probability of choosing the correct refuge first did not significantly increase (*trial*, $\beta = 0.03 \pm 0.02$; $P = 0.25$) and the latency to correct choice (trial, $\beta = 0.52 \pm 0.5$; $P = 0.36$) did not significantly decrease during the experiment, as was expected if lizards had learnt the task. In fact, only 9/49 lizards (18%) reached learning criterion. Of these nine animals, four were future-gestated oviparous lizards, four were current-gestated viviparous lizards, and one was a future-gestated viviparous lizard. None of the current-gestated oviparous lizards learnt the task. This pattern was consistent with the overall number of incorrect choices and the overall probability of choosing the safe refuge first (i.e., removing the effect of trial). Future-gestated lizards had a higher probability of choosing the correct option first (thermal environment: $\beta = 0.81 \pm 0.3$; $Z = 2.51$; $P = 0.01$; Fig. 4a). The effect of elevated developmental temperatures was different between populations (population × thermal environment, $\beta = -0.91 \pm 0.42$; $Z = -2.18$; $P = 0.03$; Fig. 4a). Oviparous lizards gestated under future thermal environments had a higher probability of choosing the safe option first compared with viviparous lizards from the same treatment. Likewise, future-gestated lizards made fewer incorrect choices (thermal environment: $\beta = -0.38 \pm 0.14$; $Z = -2.71$; $P = 0.006$; Fig. 4b). The effect of elevated developmental temperatures was different between populations (population × thermal environment, $\beta = 0.53 \pm 0.18$; $Z = 2.91$; $P = 0.003$; Fig. 4b), meaning that future-gestated oviparous lizards made fewer incorrect choices compared with viviparous lizards from the same treatment. Body temperature (T_b) had a marginal effect on the probability of choosing the correct option first (T_b: $\beta = -$

Fig. 4 Effect of early thermal environment (current—open symbols vs. future—filled symbols) on the performance of hatchling lizards from two populations (oviparous, viviparous) of *Saiphos equalis* in a spatial learning task. We scored **a** the probability of choosing the correct refuge in the first attempt and **b** the number of incorrect choices on each trial. Plotted are means ± standard errors of the mean (SEM). The number of individuals in each group is indicated in the bottom of the figure



0.15 ± 0.07; $P = 0.04$) and the number of mistakes (T_b: $\beta = 0.07 \pm 0.03$; $P = 0.05$).

Discussion

In order to predict the vulnerability of lizards to global warming, we need experimental studies that test if and how lizards can respond through adaptation by modifying key life-history traits. Here, we provide experimental evidence suggesting that elevated temperatures affect different traits in viviparous and oviparous populations of *Saiphos equalis*. Elevated developmental temperatures reduced exploratory behavior in oviparous and viviparous hatchling lizards; however, these differences did not persist as the lizards got older. Interestingly, regardless of the thermal environment, viviparous lizards were more explorative and displayed fewer anti-predator behaviors. In a feeding assay, oviparous hatchlings gestated under future temperatures attacked more crickets and chased them for longer than viviparous lizards from the same treatment. Finally, oviparous lizards from the future thermal environment had a higher probability of choosing the safe refuge correctly and made fewer mistakes compared with viviparous lizards from the same treatment. However, we found little evidence of spatial learning in the species, thus it is likely that these results have little to do with differences in cognitive ability between groups.

Elevated temperatures during early embryonic development can affect the activity levels (i.e., exploratory behavior) of new-born squamates (Burger 1989; Qualls and Andrews 1999; Kuznetsova et al. 2017). However, this effect is not consistent across species. For instance, high incubation temperatures increase the activity levels of some lizards (Qualls and Andrews 1999; Li et al. 2017) and snakes (Burger 1989) but have a negative effect on the activity of the gecko *Coleonyx elegans* (Trnik et al. 2011). The negative effect of elevated developmental temperatures on exploratory behavior found in this study in *Saiphos equalis* and by Trnik et al. (2011) in *C. elegans* supports the hypothesis that high incubation temperatures have greater negative effects on lizards that prefer low body temperatures (Sinervo et al. 2010; Pincheira-Donoso et al. 2013), as is the case for these *C. elegans* (Angilletta et al. 1999) and for *S. equalis* (Wu et al. 2009). However, the impact of elevated developmental temperatures on exploratory behavior will largely depend upon the local environment. For instance, more active individuals may disperse (Cote et al. 2010), forage (Pasquier and Grüter 2016), and gather information about their surroundings more rapidly (Bajer et al. 2015) but may experience higher predation risk (Biro et al. 2004). We considered that a reduction in exploratory behavior might have more profound consequences in viviparous *S. equalis*, which, regardless of the thermal environment, were more exploratory than oviparous lizards.

Although the thermal environments affected exploratory behavior in hatchling *S. equalis*, the effect disappeared at 20 weeks of age when tested on the potting soil substrate. Similarly, hot-incubated *Pogona vitticeps* were bolder and explored novel environments more compared with cold-incubated lizards, but the pattern disappeared when tested several months later (Siviter et al. 2017b). These results suggest that the effect of elevated developmental temperatures on hatchling exploratory behavior is transitory (Amiel and Shine 2012). However, it remains unknown how these early differences in exploratory behavior will impact hatchling survival in the short term.

Interestingly, the antipredator behavior experiment showed that, regardless of the thermal environment, viviparous lizards ran significantly less, stopped more, and displayed fewer antipredator behaviors while escaping from a simulated predator. Our results suggest that viviparous lizards experience lower predation pressure which does not select for strong antipredator responses. This is further supported by the fact that: (i) predator density (e.g., birds) is lower in montane regions of Australia (Leach et al. 2018); (ii) viviparous hatchlings were more exploratory; and (iii) viviparous hatchlings have lower escape speed and endurance performance (IB et al., unpublished data). Unexpectedly, thermal environments did not affect the antipredator behavior of hatchling *S. equalis* as has been reported in other squamates (Elphick and Shine 1998; Burger 1998; Downes and Shine 1999). It is possible that our protocol to elicit antipredator behaviors in this species is not the most reliable representation of a predatory attack in the wild. Since the natural history and behavior of *S. equalis* remain poorly studied, we lack a repertoire of antipredator behaviors against their natural predators.

Regardless of the population, hatchling lizards gestated under elevated temperatures attacked the crickets more frequently and spent more time chasing their prey. This effect was stronger in oviparous lizards, meaning that even though they ate the same quantity of crickets, future-gestated oviparous lizards attacked and chased the crickets significantly more compared with future-gestated viviparous lizards. This suggests a reduced foraging efficiency in oviparous *S. equalis* gestated under elevated temperatures. There is increasing evidence showing the effects of elevated developmental temperatures on foraging performance in squamates; however, the direction of the effect appears to be species specific. For instance, hot incubation temperatures increased foraging efficiency in pine snakes *Pituophis melanoleucus* (Burger 1991) and bearded dragons *Pogona vitticeps* (Siviter et al. 2019) but had the opposite effect on veiled chameleons *Chamaeleo calyptratus* (Ballen et al. 2015). For chameleons, as well as for *S. equalis*, a reduced foraging performance can have profound consequences in their growth rate (Houston and McNamara 2014) and vulnerability to predators (Downes 2001; Biro et al. 2004).

We found little evidence of spatial learning in the task presented to hatchling *S. equalis.* Only 18% of the lizards reached the established learning criterion. One plausible explanation for these findings is that, due to their semi-fossorial habits, *S. equalis* does not rely primarily on visual cues during spatial navigation (Day et al. 1999), as is the case in fossorial mammals (Mittelstaedt and Mittelstaedt 1980). However, the fact that some lizards learnt the task suggests that they must use other mechanisms, such as egocentric strategies, to locate the safe refuge (LaDage et al. 2012). The difficulty of creating appropriate experimental setups while controlling for chemical cues is perhaps one of the reasons why no other study has explored learning abilities in fossorial squamates (Schwenk 1995).

Although future-gestated oviparous lizards had an overall higher probability of choosing the correct refuge and made fewer mistakes compared with future-gestated viviparous lizards, it is likely that these results have little to do with significant differences in cognitive ability between groups. An increased spatial learning ability has a positive impact on the survival of hatchling lizards in the wild (Dayananda and Webb 2017); however, performance in *S. equalis* was no different from chance (50% correct choices) and future-gestated oviparous lizards performed only slightly better than current-gestated oviparous lizards (Fig. 4). Therefore, it is likely that the differences we found in this experiment have little, if any, ecological relevance for the survival of lizards in the wild. Further studies are needed to understand the effect of high developmental temperatures on cognitive ability in *S. equalis,* perhaps using other spatial learning tasks such as mazes (Day et al. 1999; Wilkinson et al. 2007) or escape tasks (Holtzman et al. 1999; LaDage et al. 2012), which have been successfully used in reptiles before.

Our results on foraging and learning experiments suggest that viviparous *Saiphos equalis* have either reduced phenotypic plasticity or that viviparous females are somehow buffering the negative effects of elevated temperatures on their offspring. The most likely way viviparous females can buffer the effect of elevated temperatures is by behavioral thermoregulation (Beuchat 1986; Shine and Harlow 1993). We did not measure soil temperature at different depths and/or female depth under the soil during the gestation period, thus we cannot exclude this explanation. However, it is unlikely that soil temperatures change considerably in the 5-cm-deep enclosures in which females were kept. Another possibility is that the differences in phenotypic plasticity observed in hatchlings were due to prenatal maternal effects (Fox and Mousseau 1998; Sheriff and Love 2013), which have been proposed as an important source of adaptive (or maladaptive) variation (Marshall and Uller 2007; Love and Williams 2008). The partially shelled eggs from the oviparous population of *S. equalis* might change the interaction between the embryos and their environment (Stewart et al. 2010; Laird et al. 2019). Similarly, the gene expression profile in the placenta of viviparous and oviparous populations is significantly different, particularly in genes important for uterine remodeling, respiratory gas and water exchange, and immune regulation (Foster et al. 2020). Therefore, although the origin of viviparity in *S. equalis* is relatively recent (Smith et al. 2001), it is possible that their simple placenta could act, to some degree, as a means to protect offspring from hormonal diffusion from the mother (Welberg and Seckl 2001), as has been described in viviparous *Sceloporus* lizards (Painter et al. 2002).

This study suggests that both populations of *S. equalis* will be affected by future global warming. However, contrary with our predictions, we found that high developmental temperatures had a stronger effect on oviparous *S. equalis.* This does not necessarily mean that these populations will be more vulnerable in a global warming scenario. First, nest selection by females can protect the offspring of oviparous lizards from elevated temperatures (Telemeco et al. 2009). Second, the oviparous population of *S. equalis* used in this study has a considerably shorter incubation duration (5–7 days) compared with other sympatric oviparous lizards (> 30 days) (Smith and Shine 1997; Qualls and Shine 1998); thus, it is not possible to measure the relative advantage of a long incubation period or a developed eggshell (Hallmann and Griebeler 2015). Third, we are aware that *population* and *mode of reproduction* are confounding factors in our study, and therefore, it is difficult to make generalizations on the effect of climate change in other viviparous and oviparous species. However, this comparison is still interesting and provides us with important information on the vulnerability of lizards to climate change with respect to reproductive behavior. Finally, we are aware of the limitations we can draw from our sample size; however, some of the effect sizes that we report here are large (Cohen's $d > 0.8$) and highly significant ($P \leq 0.01$), showing that there is a strong effect of thermal environments on *S. equalis* behavior.

Predicting organismal vulnerability to global warming is challenging because extensive biological information—often non-existent—is required to generate robust estimates. Our results show that the viviparous population of *S. equalis* were no less plastic in their phenotypic responses to changes in developmental temperatures. In fact, changes in the early thermal environment affected oviparous *S. equalis* more strongly, suggesting some buffering effect from viviparous females on the phenotype of their offspring. Some authors have suggested that lizards from high latitudes or altitudes, which are frequently viviparous, might be less vulnerable to climate warming compared with tropical lizards (Adolph and Porter 1993; Chamaillé-Jammes et al. 2006; Sunday et al. 2014). However, the vulnerability of viviparous lizards to global warming might be higher during reproduction when rising temperatures will restrict their activity more compared with oviparous lizards (Sinervo et al. 2010; Pincheira-Donoso et al. 2013; Wang et al. 2017). Therefore, the challenge of maintaining optimal temperatures for female physiological processes (e.g., homeostasis, growth) while maintaining a stable environment for the embryo, could make viviparous lizards more vulnerable to extinction (Beuchat 1988; Pincheira-Donoso et al. 2013; Wang et al. 2017).

We provide new insights into the extent to which lizards with different reproductive mode can modify key behavioral and cognitive traits that ultimately affect fitness, in response to global warming. Although the differences in the reproductive physiology of our two populations of *S. equalis* are not as large as other viviparous and oviparous species, our results suggest that the higher vulnerability of viviparous lizards to global warming is not due to a limited plastic response in offspring phenotype, but more likely due to other factors that affect pregnant females.

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Data availability statement The datasets generated during the current study (raw data and R script code) are available through the Open Science Framework (OSF; https://osf.io/9zhmq/).

Author contributions Conceptualization: MJW and IB. Methodology: IB, VD, and RL. Formal analysis: IB. Resources: IB and MJW. Data curation: IB. Writing—original draft: IB, VD, and RL. Writing—review and editing: IB and MJW. Visualization: IB. Supervision: IB and MJW. Funding acquisition: IB and MJW.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures were in accordance with the ethical standards of the institution or practice at which the studies were conducted. Collection of animals was approved by the New South Wales National Parks and Wildlife Service, Office of Environment and Heritage (OEH; License No. SL101962). The experiments were approved by the Macquarie University Animal Ethics Committee (ARA 2017-029).

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