Maternal investment and early thermal conditions affect performance and antipredator responses

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Running title: Thermal and maternal effects in lizards

Lay summary: Early thermal conditions can interact with maternal resource investment to shape offspring performance and behaviour. While anthropogenic climate change is expected to alter the thermal conditions during development, other anthropogenic factors are likely to impact the resource availability and stress levels of mothers. In this study we found that these two factors can interact together to shape offspring responses, which could have important consequences for wildlife conservation in the face of rapid environmental change.

Abstract: Exposure to increased temperatures during early development can lead to phenotypic plasticity in morphology, physiology, and behaviour across a range of ectothermic animals. In addition, maternal effects are known to be important contributors to phenotypic variation in offspring. Whether the two factors interact to shape offspring morphology and behaviour has been barely explored. This is critical since both incubation temperature and maternal resource investment are likely to change as consequence of altered environmental conditions. Using a fully-factorial design we explored how the manipulation of early thermal environment and yolk-quantity in eggs affected the morphology, performance and antipredator behaviour of two sympatric Australian species (*Lampropholis delicata* and *L. guichenoti*) that differ in a range of life-history traits. We found that juveniles from the hot treatment were larger than those on the cold treatment in *L. guichenoti* but not *L. delicata*. We also found that incubation temperature and maternal investment interacted to shape performance, measured as running speed. Finally, we found that maternal investment impacted antipredator behaviour, with animals from the yolk-reduced treatment incubated under cold conditions resuming activity faster after a simulated predatory attack in *L. delicata*, but not *L. guichenoti*. Our results highlight the importance of exploring the multifaceted role that environments play across generations to understand how different anthropogenic factors will impact wildlife in the future. In addition, our study shows that the responses to different anthropogenic factors can be species-specific.

Keywords: Bayesian multivariate mixed effects models, incubation temperature, *Lampropholis*, morphology, yolk-reduction.

Introduction

Gradual and sudden changes in temperature due to anthropogenic activities pose a challenge to organisms, having important consequences on phenotype and fitness. Ectotherms are especially vulnerable to altered thermal conditions, and exposure to increased temperatures during early development have been shown to lead to phenotypic plasticity in morphology, physiology and behaviour, that can impact fitness in a range of taxonomic groups (Dang et al., 2015; Dayananda & Webb, 2017; Noble et al., 2018; Raynal et al., 2022; Ślipiński et al., 2021; Valenzuela & Lance, 2004). While research has focused mainly on the effects of early life temperature on individual development, little work has addressed the multifaceted role that environments play across generations. Environmental stress (e.g., changes in thermal or resource conditions) experienced by mothers is expected to cascade to affect offspring through maternal effects, and this may interact in complex ways with environments experienced by offspring.

Maternal effects are important contributors to offspring phenotypic variation (Bernardo, 1996; Noble et al., 2014; Wolf & Wade, 2009), and may moderate the effects of the environment experienced during development. Mothers can adjust their reproductive behaviour or differentially invest in energy and resources that are deposited in eggs in response to changes in the environmental conditions they experience (Carter et al., 2018; Huang et al., 2013; Rutstein et al., 2005). For example, nutrient deprived mothers alter their reproductive allocation compared to mothers fed with normal quality food, leading to changes in offspring phenotype and sex (Warner et al., 2007). Similarly, maternal diet can affect hormone deposition in eggs, which is known to influence hatching success, and offspring phenotype and fitness (e.g., Rosenfeld and Roberts 2004; Warner and Lovern 2014; Rutstein et al. 2005; Huang et al. 2013; Carter et al. 2018). Therefore, maternal effects can exacerbate, dampen or counteract negative phenotypic or fitness effects of early life environments experienced by offspring, and may play an important role in explaining the diversity of phenotypic responses observed within and across species (e.g., Noble et al. 2018). Nonetheless, the interaction between maternal and offspring environments on key fitness traits is seldom explored in detail to better understand the multifaceted role environments will have on phenotypic development and fitness. Quantifying such effects is important in an era of climate change because maternal environments will be impacted – among others, their ability to acquire and invest resources in reproduction (McCarty, 2001; McRae et al., 2008).

Maternal and offspring environments that impact upon behaviour are likely to have important consequences in shaping how organisms interact with their environment. Such behavioural changes can have a direct link to fitness (reviewed in Saaristo et al., 2018 in association with chemical contamination). Antipredator responses, including predator escape and refuge seeking, are a case in point since the inability to escape from predatory attacks are inevitably associated with mortality. Thermal developmental conditions and maternal effects are known to affect antipredator strategies. For instance, exposure to high temperatures during early development (e.g., eggs or juveniles) has been shown to affect sprint speed and a range of antipredator behaviours such as predator avoidance and hiding time (Brodie & Russell, 1999; Dalesman & Rundle, 2010; McDonald & Schwanz, 2018; Webb et al., 2001). Similarly, maternal effects can pre-adapt offspring responses to the prevalent predatory conditions by changing egg composition (Sharda et al., 2021). Such effects are likely mediated by changes in morphology (e.g., size, body condition etc), which in turn can influence the antipredator strategies of individuals (Lancaster et al., 2010; Mcghee et al., 2012; Räsänen et al., 2005). Clearly, thermal conditions and maternal effects independently have the potential to influence a range of fitness-related behaviours, however, whether the two interact to shape offspring responses remains unknown.

To test how species with different life-history traits respond to altered development temperatures and maternal resource investment, we measured an integrated set of morphological and behavioural traits related to antipredator responses in two closely related lizard species, *Lampropholis delicata* and *L. guichenoti*. We apply 'phenotypic engineering' methods (Sinervo & Basolo, 1996) to manipulate both maternal investment in eggs and offspring temperature in a fully factorial design. We predicted that: 1) embryos experiencing high temperatures early in development would be smaller in size with longer tails and have reduced performance (e.g., Sanger et al., 2018; Tiatragul et al., 2017). As a result, we expect them to be risk adverse relative to embryos experiencing cold temperatures; 2) lower maternal investment in eggs should exacerbate the effects of temperature; 3) *Lampropholis delicata* will be more strongly impacted by temperature and reduced maternal investment because of the smaller egg size and larger clutches compared to *L. guichenoti*.

Methods

Study species and housing

We used two sympatric skink species. The delicate skink (*Lampropholis delicata*) is a small lizard (max. SVL 51 mm) native to south-eastern Australia (Wilson & Swan, 2010). Females lay a single clutch of 3-6 small eggs each year. It has been used extensively in experiments to explore how different environments affect the morphology and performance of individuals (Bilcke et al., 2006; De Jong et al., 2023; Downes & Hoefer, 2007). In addition, it is an invasive species on some islands (Chapple, 2016; Chapple et al., 2014), which suggests that the species has the potential to respond and become used to novel environmental conditions. The garden skink (*Lampropholis guichenoti*) is a small lizard (max. SVL 48 mm) and widespread across south-eastern Australia (Wilson & Swan, 2010). Females lay one or two clutches of 2-4 large eggs a year. The garden skink has been used in previous studies exploring the effect of rearing temperatures and humidity conditions on offspring phenotypic plasticity (Booth et al., 2000; Qualls & Shine, 1998).

We captured gravid female *L. delicata* and *L. guichenoti* in semiurban parks in Sydney (Australia). Animals were brought to the laboratory at XXX (not reported for blind review) where they were housed in single-species groups of five in indoor terraria (3-4 females – width x length: 40x55 cm) to allow them to lay eggs. Terraria were filled with approximately 8 cm deep of soil, refuge, a water container, and a container full of vermiculite for egg laying. Terraria were heated by a lamp and had a UV lamp for UVA/UVB exposure. The heat lamp was situated at one end to ensure a temperature gradient. Lights were set to a photoperiod of 12:12 h (light/dark). Animals were provided with water every day (both spraying the soil and filling the water container) and with crickets dusted in calcium and multivitamin every second day. Females were kept in the laboratory for around two weeks for egg-laying and were then released at their capture locations.

Experimental design

To explore how incubation temperature and maternal investment interact to affect performance and antipredator behaviour of juveniles, we designed a fully-factorial experiment where eggs of the two skink species were exposed to two levels of temperature [cold (23 ± 3° C) or hot (28 ± 3° C)] and yolk removal (yolk content reduced or a sham-control) to simulate changes in maternal investment in eggs. Incubation temperatures were selected to mimic extreme temperatures measured in natural nests of *L. delicata* (Cheetham et al., 2011).

Enclosures were checked daily for eggs. We randomly allocated one egg from a clutch to each of our four treatments: 23°C sham-control eggs; 23°C yolk reduced eggs; 28°C sham-control eggs; and 28°C yolk reduced eggs. Our design was a partial split-clutch design as it was not possible to allocate eggs from a given clutch to each of the four treatments (i.e., a split-clutch design) given the small clutch sizes of some individuals. Eggs allocated to the yolk reduced treatment were weighed (to the nearest mg), and then pierced with a sterilised insulin syringe to extract part of the yolk. Eggs were weighted again, and the difference in weight pre- and post-extraction was used as an approximation of the percentage of yolk extracted. Following methods in Sinervo, 1990 (Sinervo, 1990) we aimed for around 15% yolk removal (mean =- SD = 12.49% ± 2.64). Control eggs were weighted and pierced with a needle, but we did not remove any yolk. Eggs were then placed in a container filled with four grams of vermiculite dampened with 12 g of water and covered with cling-wrap (Glad Wrap) to avoid dehydration. Each egg was then placed in an incubator at the corresponding temperature.

Measures of morphological traits, performance, and antipredator behaviour

We checked the eggs every day for hatchlings and each hatched lizard was individually housed in terraria (20 x 35 cm) heated by a heat cord. All animals also had UV lighting. Enclosures contained paper as substrate, a water container, and a refuge. All the animals were housed in the same laboratory conditions. Juveniles were feed every second day with crickets.

Juveniles were measured and their behaviour tested when they were 3-5 weeks old. We ensured that there was equal representation from each of the four treatment combinations and species (e.g., eggs in cold treatment had longer incubation times) during each measurement session (groups of 48 per day, see below). Body size and mass can influence performance and behaviour (Baxter-Gilbert et al., 2018; Huey & Hertz, 1984). As such, we measured weight, snout-vent length, tail length and total length at each measurement to control for these during the analysis. Given the small size of hatchlings, we weighed lizards (to the nearest mg) using an Ohaus scale and took a ventral photo of each lizard. From this photo we later measured the snout-vent length (SVL) as the distance (in mm) from the snout to the cloaca, and the tail length as the distance from the cloaca to the tip of the tail using imageJ (Abràmoff et al., 2004).

We set up 12 CCTV cameras with each recording four individual terraria simultaneously. Each week we selected 48 juveniles from the correct age window – a mix of the two species and four treatment combinations. We weighted and photographed the animals, and then placed them randomly across the shelves to avoid any biases associated with the location in the laboratory. The terraria for the assays were opaque to avoid lizards viewing each other which could influence their behaviour. In addition, the terraria were separated from the walking corridors by thick-opaque curtains to avoid the presence of the researchers to influence lizard behaviour. All enclosures had a refuge and a water container. The heat lamp was placed on one side of the enclosure to ensure a thermal gradient of at least 6 degrees between the lamp and the refuge. The same group of animals were housed in these terraria during the 6 days of the trials.

Over the six days animals were under cameras we took three measurements of performance and antipredator behaviour for each animal with one day between subsequent measurements. More specifically, we collected the following behavioural variables:

(1) *Running speed (in seconds)*: We measured running performance as the total time needed to run the one-metre-long straight racetrack. We also recorded burst speed as the fastest 25 cm section (the racetrack had a detector and time tracker every 25cm). For analysis, we used the total time used to cover the full one meter and the fastest time taken to run a 25 cm interval. Fifteen minutes before each performance measure, lizards were placed in an incubator at 28°C to ensure constant body temperature across lizards. After the trial, each animal was placed back in their corresponding terraria. We repeated the running trial 3 times for each individual, on alternate days.

(2) *Activity*: We measured the distance travelled (in cm) as a proxy for the activity level of individuals. To record activity, we removed the refuge and the water container from the terraria to avoid animals hiding. We then switched on the camera and left the animals to behave and move freely in their terrariums for 20 minutes. The distance covered was later calculated using the software EthoVision XT (vers. 12.0).

(3) *Antipredator behaviour*. Immediately after the activity trial, we replaced the refuge. After 30 minutes, we simulated a predatory attack. To do this, we approached the terraria and tapped the animals with a painting brush near the tail until they took refuge. The same person (JZ) performed all the predatory attacks. The only identification in the terraria was the randomly allocated ID number provided to the eggs at the beginning of the experiment such that JZ was blind to the treatment. After the simulated attack, we recorded each lizard's response for 90 minutes. From the videos we calculated (1) the time (in seconds) each lizard took to seek refuge since the first tape in the tail (hereafter "time to hide") (2) the time between the moment the animal took refuge (time to hide) until the animal's head appeared at the entrance and was clearly visible in the videos (hereafter "hiding time", in seconds) and (3) the time elapsed since the animal took refuge (time to hide) to the moment the animal left the refuge to start their normal activity after the predatory attack (hereafter "time to activity"). We consider this to be the moment when the back forelimbs left the refuge. We repeated the activity and antipredator assays three times in alternate days from performance trails.

All trials took place between 9 and 12 am, during the period when activity was the highest. We recorded 22 individuals per species and treatment. We discarded from the analysis any individual that lost their tail during the experiment (n = 5 out of 176) to avoid any bias associated with impaired running ability. The final sample sizes were 22 for hot-control *L. delicata*, and 23:control and 28:yolk-reduced *L. guichenoti*, and 21 for the rest of the combinations.

Statistical analysis

We used Bayesian Multivariate Mixed Effects Models using *rstan* (Team, 2020) in the package *brms* (Bürkner, 2018) to explore whether incubation temperature and maternal investment impacted morphology (tail length, SVL and weight), performance (running speed and activity level) and antipredator behaviour. We also estimated the correlations between the variables measured at the between- and within-individual level. We first checked for normality of the data by visualizing the residuals of intercept only random effects model. To meet the assumptions of normality running speed (both 25 cm burst and 1 m long) was log-transformed for the two species. For all models, we ran four MCMC chains, with each chain being run for 4000 iterations with a warmup of 1000 and used default priors. We retained each sample (thinning of 1) from each chain. We checked that MCMC chains were mixing well by visualising trace plots, checked that all chains had converged ($R_{hat} < 1.01$), and that the effective sample size for each parameter was greater than 1000.

Both species were analysed separately. We ran two separate multivariate mixed models for each species, one with morphological traits, and the other with performance and antipredator behaviour as response variables. We separated morphology from performance and behaviour because the latter variables were measured 3 times allowing us to decompose between and within-individual variation (O'Dea et al., 2022). Missing data resulted from video failures for some assays. Instead of a complete case analysis, we retained missing data and using data augmentation methods during model fitting which can be more powerful than complete case analyses (Noble & Nakagawa, 2021). Models contained fixed effects (explanatory variables) of incubation temperature and maternal investment treatment along with their interaction. We also included individual and clutch identity as random effects (intercepts). In the morphology model, only clutch was added as random effect given that we only had a single measurement for each individual. In the behaviour model, SVL was included as covariate to control for any potential effect of body size on the traits measured. We repeated the behaviour/performance model without SVL as covariate to explore for any indirect effect of temperature and maternal treatments on behaviour that might have been influenced by body size. Most of the performance and antipredator variables showed moderate to high repeatability between the three different measures taken (Table S1). Using the posterior distributions from these models, we derived the key interaction comparison of interest – whether the difference between control and yolk removal treatments was amplified or subdued in response to temperature. In addition, we used the posterior distribution to calculate the overall temperature and maternal investment effect by pooling the posteriors across the second factor. We present the posterior mean and 95% credible intervals (CI) for these parameters of interest. Credible intervals not overlapping zero were considered significant and we calculate and present the probability (pMCMC) of obtaining this effect under a null hypothesis of no effect.

Results

Maternal investment and early thermal environment affected morphology in L guichenoti but not L. delicata

We did not find any effect of temperature, maternal investment, or their interaction on morphology in *Lampropholis delicata* [tail length: (Fig1a), snout-vent-length (SVL, Fig 1b) or weight (Fig 1c) (See Table 1)].

In contrast, maternal investment and temperature treatment interacted to affect weight in *L guichenti* (Table 1). The weight difference between control and yolk removal treatment was larger in the cold incubation temperature compared to the difference under warm incubation temperatures for *L guichenoti* (Table 1). We also found a statistically significant effect of incubation temperature in juvenile size of *L. guichenoti* (Table 1). Generally, individuals coming from eggs incubated at hotter temperatures had longer tails (estimate =

6.347, 95% CI = 9.619– 3.079, Table 1, Fig 1d), larger SVL (estimate = 2.973, 95% CI = 4.715 – 1.241, Table 1, Fig 1e) and were heavier (estimate = 0.112, 95% CI = 0.207– 0.019, Table1, Fig1f) than those hatched from eggs at colder temperatures.

In both species, there was a positive correlation between SVL, tail length and body mass, with individuals with larger bodies also being heavier and having longer tails (Supp Info Table S2).

Impacts of maternal investment on running performance are mediated by early thermal environment in both species

We found a statistically significant interaction between maternal yolk investment and incubation temperature on 25cm burst speed of juvenile *L. guichenoti* (Fig 2d, Table 1). This effect persisted even when controlling for SVL (Table S3). There was a significantly bigger difference in 25 cm burst speed between control and yolk removal eggs in lizards incubated under hot conditions compared to cold conditions (Table 2 – estimate = -0.470, 95% CI: -0.854 – -0.081, pMCMC = 0.018**)**.

Although not significant, we also found a similar interaction between maternal yolk investment and incubation temperature on 1m sprint speed in *L. delicata* (Table 2 & Table S3). However, in contrast to *L. guichenoti*, there was a significantly smaller difference in 1 cm burst speed between control and yolk removal eggs in lizards incubated under hot conditions compared to cold conditions (Table 2 – estimate = 0.335, 95% CI: -0.023 – 0.689, pMCMC = 0.068**)**.

In both species, trials where individuals had a faster burst speed also took shorter to travel the full 1m track (*L. delicata*: within-individual correlation ± SE = 0.42, 95% CI = 0.30–0.54; *L. guichenoti*: within-individual correlation ± SE = 0.51, 95% CI = 0.4–0.61). In addition, individuals that has faster burst speed also tended to run the full 1m faster (*L. delicata*: between-individual correlation = 0.82, 95% CI = 0.63–0.95; *L. guichenoti*: within-individual correlation = 0.95, 95% CI = 0.89–0.99).

Weak evidence that antipredator behaviour is affected by early thermal environment and maternal investment

Antipredator behaviours were weakly integrated with performance measures at the between and within-individual levels for most traits (Table S4). At the between-individual level, there was a strong correlation (r = 0.90, 95% CI: 0.78–0.97) between the hiding time and the time to activity as well as between the time to activity and burst speed (r = 0.32, 95% CI: 0.04 – 0.57) in *L. guichenoti*. At the within-individual level trials lizards with shorter hiding times also resumed their activity faster overall for both species (*L. guichenoti*: r = 0.69, 95% CI: 0.58 – 0.77; *L. delicata*: r = 0.82, 95% CI: 0.73 – 0.88).

Changes in the time to activity after a simulated predatory attack between control and yolk removal eggs depended on temperature in *L. delicata* when controlling for body size (interaction estimate = -1,003.752, 95% CI = -1,988.452– -33.590, pMCMC = 0.044, Table S3). Similar effects were observed when not controlling for body size, but it was not significant (Table 2). Yolk reduced lizards appeared to resume activity faster compared to lizards hatching from control eggs when incubated at cold temperatures whereas there was no difference between control and yolk removed eggs under hot temperatures (Fig. 3b). We did not find strong evidence that other behavioural traits involved in antipredator responses were impacted by temperature, maternal investment, or their interaction in *L. delicata* or *L. guichenoti* (Table 2 & Table S3; Figure 3).

Discussion

Environmental conditions experienced by offspring are expected to interact in complex ways with the environments experienced by their parents. Anthropogenic climate change and other human-associated stressors will simultaneously alter temperatures while impacting other factors such as maternal food availability and stress levels that could affect the maternal investment in eggs. In ectotherms, temperature conditions during early life are known to have important effects on individuals (Noble et al., 2018; Singh et al., 2020; While et al., 2018). but little work has explored the interaction between maternal investment and temperatures; even though there have been suggestions of these factors explaining variation in thermal effects (Noble et al., 2018). Understanding how maternal effects interact with offspring environments to affect development and fitness is important for ascertaining whether climate induced changes are likely to be exacerbated or dampened by impacts in parental generations and help to explain why responses vary so dramatically across populations and species with respect to early thermal conditions. Here we explored whether cold and hot incubation temperatures lead to different responses in morphology, performance and antipredator behaviour in two sympatric skink species (*L. delicata* and *L. guichenoti*), and whether a controlled manipulation in the amount of yolk in eggs moderated such responses. We found that hot incubation temperatures affect morphology, and that temperature interacts with maternal yolk treatment to moderate performance and the associated antipredator responses. The effects observed appear to be species-specific, and possibly the result of different life-history strategies.

Effect of early life thermal conditions and maternal investment on morphology

Contrary to our expectations we found that juveniles of *L. guichenoti* emerging from eggs incubated at hot temperatures were larger and heavier than those reared at cold temperatures, however incubation temperature did not significantly affect morphology in *L. delicata* (see also de Jong et al., 2022). Since we did not find any effect of incubation temperature on body size on the day of hatch in either of the two species (data collected for another study), our results show that the difference in body size between individuals coming from cold and hot incubation regimes in *L. guichenoti* appeared during early juvenile development. Our findings suggest that, rather than a change in metabolic and developmental rates during embryo growth of this species, incubation temperature programmed post-hatching metabolism, potentially affecting feeding and growth rates, as observed in previous studies in lizards exposed to high temperatures (Singh et al., 2020).

We did not find any effect of the maternal investment treatment on body length for either *L. guichenoti* or *L. delicata*, but body mass was affected in *L. guichenoti*. Although we found that individuals of both species hatched smaller from the yolk reduced treatment than from the control (again, data collected for another study, but see also e.g., Warner and Lovern 2014), maternal investment effects on morphology seem to have disappeared by the age of 3-5 weeks. This finding contrasts with previous studies where juveniles from yolk-reduced treatments hatched smaller but also showed slower growth rates than those from control treatments (Warner & Lovern, 2014). Our results are not completely surprising, however, since many of the impacts of incubation conditions on morphological and behavioural traits observed in recently hatched individuals often disappear as the individuals age (McDonald & Schwanz, 2018; Pearson & Warner, 2016). This could also be the case for many maternal effects. In our study, the fact that juveniles of both yolk-reduced and control eggs attain a similar body size a few weeks after hatching suggests that individuals can, to some extent, compensate for the poor start in life by accelerating their growth during the first few weeks, probably by increasing their feeding rates. This might be key, since in a range of species, larger juvenile body size has been associated with better survival (e.g., Einum & Fleming, 2000; Webb et al., 2006), although this relationship is sometimes complex and dependant of other ecological and biological factors (Langkilde & Shine, 2005; Sinervo et al., 1992; Warner & Andrews, 2002).

Effect of early life thermal conditions and maternal investment on performance and behaviour

The growth compensation observed in the analyses of morphology might be associated with changes in the allocation of resources and trade-offs with other fitness-associated traits during development, such as the observed slower running speed of juveniles of *L. delicata* hatched from yolk-reduced eggs and of *L. guichenoti* hatched from yolk-reduced eggs in hot incubation conditions. This result suggests that, even though animals from poor developmental conditions are able to morphologically catch up with individuals from more beneficial early-life conditions, this might come at a cost in performance. This is in accordance with previous studies on *Sceloporus undulatus* showing that clutches with individuals with fast grow rates, but slow runners, had lower survival than slow growing but fast runners (Warner & Andrews, 2002).

Impaired performance was expected to lead to more risk adverse individuals to compensate for a potential increased vulnerability to predators. In contrast to our prediction, antipredator behaviour of *L. guichenoti* was not affected by our treatments. In addition, we found that juvenile *L. delicata* from the yolk-reduced treatments, and especially when reared at cold temperatures, took shorter to resume activity after a simulated predatory attack than those from the control treatment – although this was not a strong effect. Our results show that despite their impaired performance, juveniles from the yolk-reduced treatment leave the refuge quicker than those from the control treatment. This contrasts with previous studies that have found that individuals with perceived higher vulnerability alter their antipredator behaviour to hide for longer to successfully avoid a predatory attack (e.g., Cooper, 2007; Iglesias-Carrasco et al., 2016; Martin & López, 1999). Instead, our results suggest that the benefits of resuming activities, such as basking and feeding, might potentially outweigh the potential survival costs in *L. delicata*, at least in a laboratory setting where real predators are absent. However, from our experiment we cannot know whether the change in antipredator response observed confers a fitness advantage regarding, for example, quicker growth, or instead would lead to costs in terms of increased predation risk in the wild. Further experiments would benefit from studying how incubation temperature and maternal investment interact to affect behaviour, and the consequent fitness payoffs, in a more natural setting.

Species-specific responses

The two skink species studied differed in their morphological, performance and antipredator responses to the incubation temperature and maternal investment. These differences could be in part associated with some life-history traits, such as the size of the egg. Eggs of *L. delicata* are smaller than those of *L. guichenoti*, which might make these eggs more sensitive to small alterations in the incubation environment, strongly impacting the phenotype and behaviour of juveniles, as observed in our study (Thompson et al., 2001). While this result suggests that environmental changes in early thermal environment coupled with reduced maternal investment will impact *L delicata* more negatively compared to *L guichenoti,* we caution over interpretation because phenotypic and behavioural plasticity could provide juveniles with increased environmental tolerance that may confer a fitness benefit in face of climate change (DeWitt et al., 1998; Fox et al., 2019; Yeh & Price, 2004, but see Oostra et al., 2018). The ability to plastically respond to different environmental conditions could also explain *L delicata's* success as an invasive species (see e.g., (Davidson et al., 2011). In contrast, the lack of behavioural responses in *L. guichenoti* could be a sign of the inability of the species to adaptively react to environmental challenges, or rather suggest that in this species the explored behavioural responses might not impose a fitness cost. Since the incubation temperatures used in our experiment overlap with the those occurring in the wild (Cheetham et al., 2011), it will be interesting to explore how more extreme thermal incubation conditions, expected as consequence of anthropogenic climate change, will interact with maternal condition to shape hatchling performance and survival in the future.

Conclusions

We have shown that exploring the complex interaction between offspring and maternal environments is critical to predict how anthropogenic activities will affect individual performance and ultimately fitness. Although maternal yolk investment did not buffer the effects of higher incubation temperature in all the morphological and behavioural traits measured, the general pattern suggests that a reduction in the resources allocated by mothers to eggs exacerbates the response triggered by warmer temperatures. Future research will benefit from studying whether such plastic responses are adaptive in novel environment conditions, whether more extreme temperatures predicted by climate change will exert stronger reactions, and whether species sensitivity depends on species-specific life-history traits.

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Author contribution: MI-C and DN conceived and designed the experiment; MI-C and JZ collected the data; MI-C and DN analysed the data. MI-C drafted the first version of the manuscript; all authors contributed to the draft and gave final approval for publication.

Data availability: Data used in this article can be accessed in https://github.com/daniel1noble/lampro_yolk_behav

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Figures

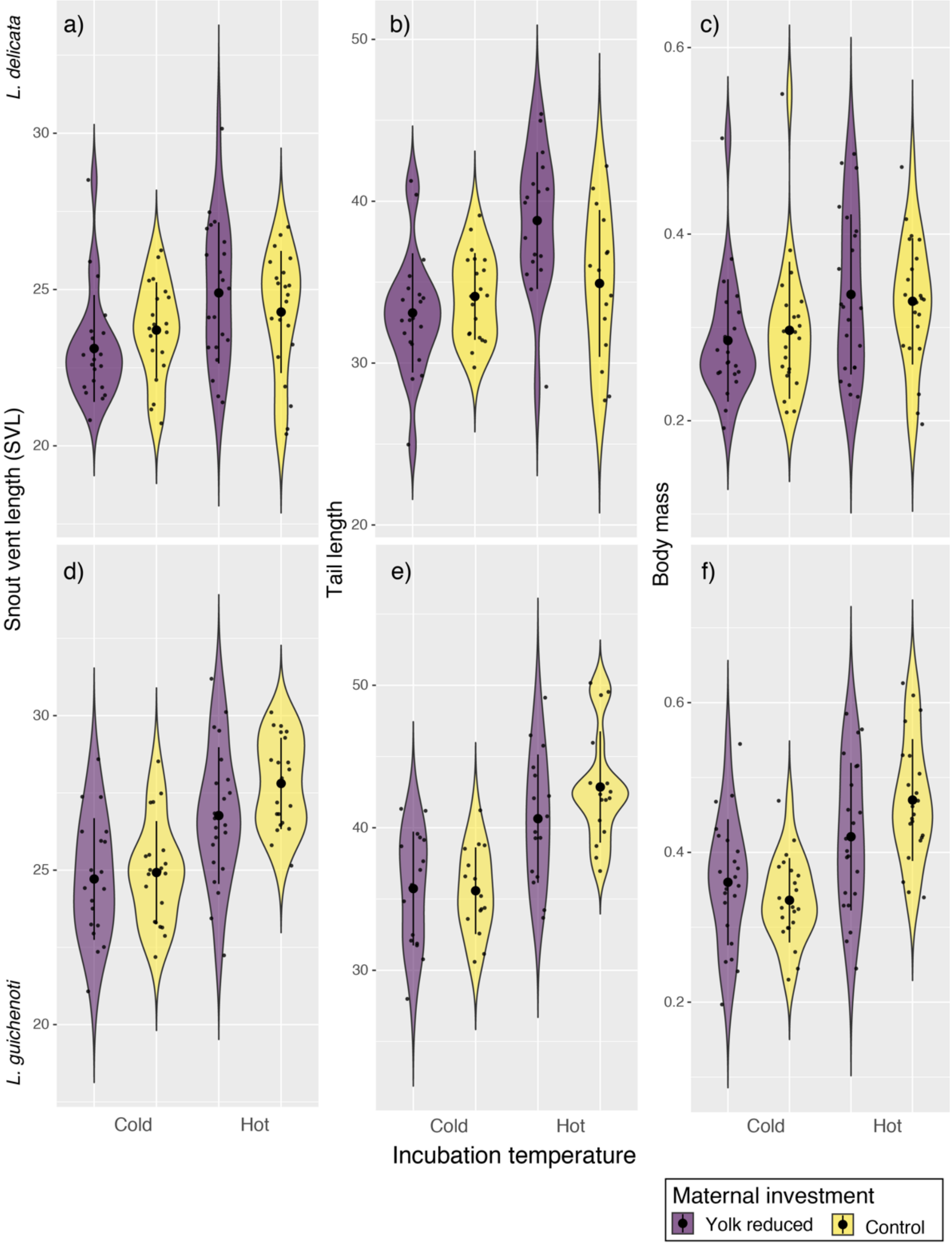

Figure 1. Effect of temperature (cold, 23 °C vs hot, 28 °C) and maternal resource investment (yolk reduced vs control) in morphological traits of *L. delicata* (a, b and c) and *L. guichenoti* (d, e and f).

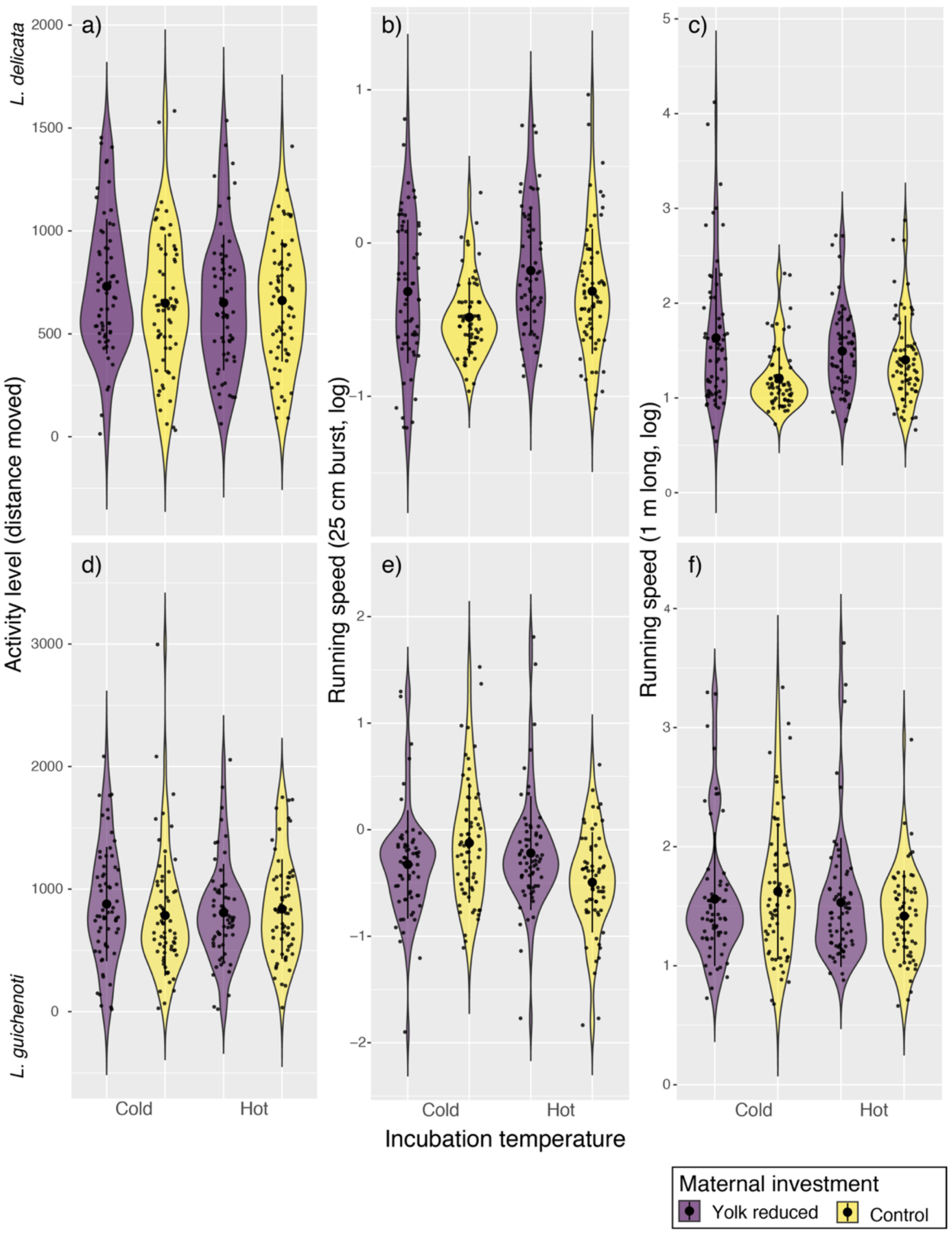

Figure 2. Effect of temperature (cold, 23 °C vs hot, 28 °C) and maternal resource investment (yolk reduced vs control) in lizard performance: distance moved and running speed (25 cm burnst and 1 m). *L. delicata* panels a, b and c, and *L. guichenoti* panels d, e and f. Note: 3 datapoints (raw data > 10s and < 0.01s) in the 25 burst of *L. delicata* were removed for visualization reasons.

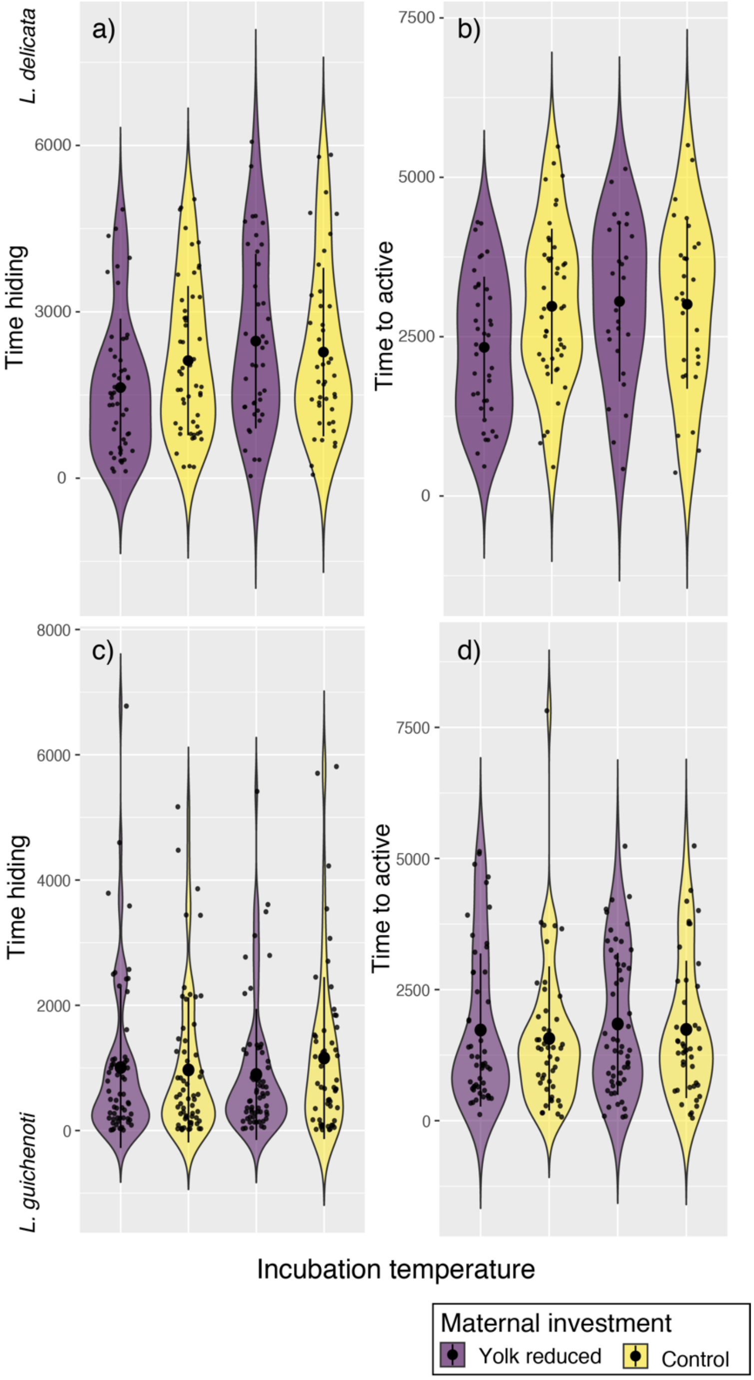

Figure 3. Effect of temperature (cold, 23 °C vs hot, 28 °C) and maternal resource investment (yolk reduced, control) in lizard antipredator behaviour: time hiding (time, in seconds, since the lizard hided in the refuge until the head was visible) and time to active (time before resuming activity). *L. delicata* panels a and b, and *L. guichenoti* panels c and d.

Tables

Table 1– Posterior means and 95% credible intervals for the interaction between temperature (Temp) and maternal investment (Invest) along with the main effects of temperature and maternal investment on morphological traits for *Lampropholis delicata* and *Lampropholis guichenoti*. Main effects are pooled posterior means over each level of the second predictor variable (either temperature or maternal investment treatments depending on the focal variable). Posterior distributions are estimated from a multi-response model that accounts for the correlation between morphological traits. Bold indicates significant effects.

Species	Trait	Term	Estimate	2.5%	97.5%	pMCMC
L. delicata	SVL	Interaction [(C23 - A23) - (C28 - A28)]	-0.198	-1.651	1.288	0.790
		Temp (23-28)	-0.192	-1.327	0.913	0.738
		Invest (C-A)	0.404	-0.663	1.442	0.438
	Weight	Interaction [(C23 - A23) - (C28 - A28)]	0.010	-0.035	0.057	0.665
		Temp (23-28)	-0.006	-0.042	0.031	0.728
		Invest (C-A)	0.002	-0.031	0.038	0.918
	Tail	Interaction [(C23 - A23) - (C28 - A28)]	-2.898	-6.238	0.516	0.089
		Temp (23-28)	-1.299	-4.979	2.128	0.565
		Invest (C-A)	-0.777	-4.348	2.475	0.768
L. guichenoti	SVL	Interaction [(C23 - A23) - (C28 - A28)]	1.324	-0.501	3.124	0.150
		Temp (23-28)	**-2.973**	**-4.715**	**-1.241**	**0.000**
		Invest (C-A)	0.348	-1.394	2.072	0.739
	Weight	**Interaction [(C23 - A23) - (C28 - A28)]**	**0.089**	**0.006**	**0.172**	**0.035**
		Temp (23-28)	**-0.112**	**-0.207**	**-0.019**	**0.012**
		Invest (C-A)	0.014	-0.080	0.108	0.862
	Tail	Interaction [(C23 - A23) - (C28 - A28)]	2.174	-1.420	5.776	0.241
		Temp (23-28)	**-6.347**	**-9.619**	**-3.079**	**0.000**
		Invest (C-A)	0.902	-2.361	4.147	0.627

Table 22 – Posterior means and 95% credible intervals for the interaction between temperature (Temp) and maternal investment (Invest) along with the main effects of temperature and maternal investment on behavioural and performance traits for *Lampropholis delicata* and *Lamprpholis guichenoti*. Main effects are pooled posterior means over each level of second predictor variable. Estimates are from a Bayesian multivariate (multi-response) model not controlling for SVL. See Supplement for model with SVL controlled. Bold estimates are significant and italics indicated effects with less than a 10% chance of being observed.

Species	Trait	Term	Estimate	Q2.5	Q97.5	pMCMC
L. delicata	Time to Activity (s)	*Interaction [(C23 - A23) - (C28 - A28)]*	*-864.379*	*-1,847.746*	*103.120*	*0.080*
		Temp (23-28)	-676.650	-1,696.061	325.761	0.239
		Invest (C-A)	233.230	-826.597	1,216.182	0.731
	Hiding Time (s)	Interaction [(C23 - A23) - (C28 - A28)]	-718.025	-1,631.020	192.257	0.117
		Temp (23-28)	-502.792	-1,406.149	388.546	0.328
		Invest (C-A)	115.504	-810.196	985.614	0.830
	Distance Moved (cm)	Interaction [(C23 - A23) - (C28 - A28)]	35.435	-174.231	252.904	0.748
		Temp (23-28)	33.968	-121.384	187.916	0.660
		Invest (C-A)	-50.048	-204.844	109.218	0.528
	log 1m Speed (cm/s)	*Interaction [(C23 - A23) - (C28 - A28)]*	*0.335*	*-0.023*	*0.689*	*0.068*
		Temp (23-28)	-0.028	-0.405	0.349	0.928
		Invest (C-A)	-0.262	-0.644	0.116	0.233
	log Burst Speed (cm/s)	Interaction [(C23 - A23) - (C28 - A28)]	0.214	-0.178	0.591	0.279
		Temp (23-28)	-0.062	-0.398	0.270	0.737
		Invest (C-A)	-0.095	-0.435	0.238	0.610
L. guichenoti	Time to Activity (s)	Interaction [(C23 - A23) - (C28 - A28)]	-93.237	-1,263.710	1,052.332	0.876
		Temp (23-28)	-42.896	-870.269	778.343	0.929
		Invest (C-A)	133.420	-681.068	951.159	0.750
	Hiding Time (s)	Interaction [(C23 - A23) - (C28 - A28)]	166.056	-694.735	989.883	0.683
		Temp (23-28)	-2.416	-631.727	619.633	0.992
		Invest (C-A)	90.790	-519.904	697.379	0.767
	Distance Moved (cm)	Interaction [(C23 - A23) - (C28 - A28)]	127.921	-185.868	444.379	0.423
		Temp (23-28)	4.077	-249.201	263.186	0.976
		Invest (C-A)	-25.340	-282.031	232.134	0.843
	log 1m Speed (cm/s)	Interaction [(C23 - A23) - (C28 - A28)]	-0.179	-0.549	0.206	0.348

Species	Trait	Term	Estimate	Q2.5	Q97.5	pMCMC
		Temp (23-28)	0.116	-0.198	0.432	0.489
		Invest (C-A)	-0.027	-0.347	0.281	0.878
	log Burst Speed (cm/s)	**Interaction [(C23 - A23) - (C28 - A28)]**	**-0.470**	**-0.854**	**-0.081**	**0.018**
		Temp (23-28)	0.134	-0.327	0.603	0.774
		Invest (C-A)	-0.034	-0.502	0.424	0.953

Supplementary material for

Maternal resources and early thermal conditions affect performance and antipredator responses

Supplementary results

Table S1. Repeatability of the three performance and antipredatory behaviour measures.

	L. delicata			***L. guichenoti***		
	R	l	U	R	l	u
Hiding time	0.2807	0.0222	0.5025	0.2391	0.0612	0.4072
Time to activity	0.0724	0.0001	0.2431	0.2315	0.0307	0.4093
Distance moved	0.2644	0.0406	0.4859	0.4824	0.3425	0.6092
Running velocity 1m	0.4580	0.3128	0.5893	0.5579	0.4339	0.6698
Running velocity 25cm	0.3440	0.2055	0.4812	0.6310	0.5223	0.7294

Table S2. Within-individual correlations between morphological traits estimated from Bayesian multivariate models for morphology in *Lampropholis delicata and L. guichenoti*.

L. delicata

Within-individual correlations in morphological traits

	Estimate	SE	l-95% CI	U-95% CI	Rhat	Bulk_ESS	Tail_ESS

rescor(SVL, Weight)	**0.8**	**0.04**	**0.7**	**0.87**	**1**	**12001**	**10099**
rescor(SVL, Tail length)	**0.53**	**0.09**	**0.33**	**0.7**	**1**	**11828**	**10260**
rescor(Weight, Tail length)	**0.56**	**0.09**	**0.36**	**0.72**	**1**	**12109**	**10709**

L. guichenoti

Within-individual correlations in morphological traits

	Estimate	**Est.Error**	**l-95% CI**	**U-95% CI**	**Rhat**	**Bulk_ESS**	**Tail_ESS**
rescor(SVL, Weight)	**0.69**	**0.06**	**0.55**	**0.8**	**1**	**6372**	**7408**
rescor(SVL, Tail length)	**0.63**	**0.08**	**0.45**	**0.77**	**1**	**5176**	**6727**
rescor(Weight, Tail length)	**0.88**	**0.04**	**0.79**	**0.93**	**1**	**3383**	**6556**

Table 3S3. Posterior means and 95% credible intervals for the interaction between temperature (Temp) and maternal investment (Invest) along with the main effects of temperature and maternal investment on behavioural and performance traits for *Lampropholis delicata* and *Lampropholis guichenoti*. Main effects are pooled posterior means over each level of second predictor variable. Estimates are from a Bayesian multivariate (multi-response) model controlling for SVL (Z-transformed).

Species	Trait	Term	Estimate	Q2.5	Q97.5	pMCMC
L. delicata	Time to activity (s)	**Interaction [(C23 - A23) - (C28 - A28)]**	**-1,003.752**	**-1,988.452**	**-33.590**	**0.044**
		Temp (23-28)	-468.643	-1,589.133	597.340	0.543
		Invest (C-A)	122.220	-1,014.488	1,158.751	0.873
	Hiding time (s)	*Interaction [(C23 - A23) - (C28 - A28)]*	*-896.713*	*-1,803.445*	*24.917*	*0.057*
		Temp (23-28)	-423.236	-1,444.311	558.994	0.544
		Invest (C-A)	62.101	-961.269	1,022.564	0.922
	Distance Moved (cm)	Interaction [(C23 - A23) - (C28 - A28)]	54.939	-174.283	295.328	0.642
		Temp (23-28)	56.787	-120.822	231.572	0.522
		Invest (C-A)	-35.953	-206.360	140.925	0.668
	log 1m Speed (cm/s)	Interaction [(C23 - A23) - (C28 - A28)]	0.312	-0.071	0.692	0.109
		Temp (23-28)	-0.054	-0.439	0.334	0.826
		Invest (C-A)	-0.267	-0.646	0.109	0.198
	log Burst Speed (cm/s)	Interaction [(C23 - A23) - (C28 - A28)]	0.184	-0.206	0.577	0.352
		Temp (23-28)	-0.129	-0.454	0.210	0.457
		Invest (C-A)	-0.098	-0.423	0.223	0.566
L. guichenoti	Time to activity (s)	Interaction [(C23 - A23) - (C28 - A28)]	-105.815	-1,301.414	1,101.039	0.863
		Temp (23-28)	43.518	-893.814	998.022	0.935
		Invest (C-A)	108.002	-750.916	976.971	0.809
	Hiding time (s)	Interaction [(C23 - A23) - (C28 - A28)]	298.455	-574.277	1,159.178	0.499
		Temp (23-28)	-65.151	-808.196	660.997	0.867
		Invest (C-A)	49.173	-628.295	718.879	0.884
	Distance Moved (cm)	Interaction [(C23 - A23) - (C28 - A28)]	130.568	-198.951	467.296	0.440
		Temp (23-28)	8.658	-287.891	299.148	0.943
		Invest (C-A)	-53.818	-323.685	212.532	0.697
	log 1m Speed (cm/s)	Interaction [(C23 - A23) - (C28 - A28)]	-0.135	-0.528	0.265	0.493
		Temp (23-28)	0.024	-0.307	0.358	0.887
		Invest (C-A)	-0.008	-0.318	0.301	0.962

Species	**Trait**	**Term**	**Estimate**	**Q2.5**	**Q97.5**	**pMCMC**
	log Burst Speed (cm/s)	**Interaction [(C23 - A23) - (C28 - A28)]**	**-0.413**	**-0.810**	**-0.006**	**0.046**
		Temp (23-28)	-0.015	-0.483	0.452	0.956
		Invest (C-A)	0.008	-0.432	0.455	0.991

Table 4S4. Posterior means and 95% credible intervals for the between and within-individual correlations among behavioural traits in *Lampropholis delicata* and *Lampropholis guichenoti*. Estimates are from a Bayesian multivariate (multi-response) model. Bold estimates indicate ones where the 95% credible interval does not overlap zero.

Species - level	**Correlation**	**Estimate**	**2.5 % CI**	**97.5 % CI**
L. delicata - Between Individual	cor(Time to Activity (s), Hiding Time(s))	0.29159827	-0.60960494	0.868097048
	cor(Time to Activity (s), Distance Moved (cm))	-0.13655106	-0.72829302	0.620152880
	cor(Hiding Time(s), Distance Moved (cm))	-0.13688198	-0.70275908	0.579493448
	cor(Time to Activity (s), 1m Speed (cm/s))	0.27195884	-0.38825792	0.776064363
	cor(Hiding Time(s), 1m Speed (cm/s))	0.15041240	-0.46974706	0.688090745
	cor(Distance Moved (cm), 1m Speed (cm/s))	0.24238409	-0.13979502	0.628382729
	cor(Time to Activity (s), Burst Speed (cm/s))	0.22520672	-0.46104064	0.762376365
	cor(Hiding Time(s), Burst Speed (cm/s))	0.19915158	-0.42866231	0.739702151
	cor(Distance Moved (cm), Burst Speed (cm/s))	0.26857069	-0.12762202	0.664960881
	cor(1m Speed (cm/s), Burst Speed (cm/s))	**0.82102166**	**0.62546459**	**0.952074963**
L. delicata - Within Individual	cor(Time to Activity (s), Hiding Time(s))	**0.81659503**	**0.73344677**	**0.880468668**
	cor(Time to Activity (s), Distance Moved (cm))	-0.15311562	-0.33138147	0.034234536
	cor(Hiding Time(s), Distance Moved (cm))	-0.07303817	-0.24215358	0.098905974
	cor(Time to Activity (s), 1m Speed (cm/s))	0.07619062	-0.11077008	0.260270547
	cor(Hiding Time(s), 1m Speed (cm/s))	0.01950419	-0.15776967	0.196633984
	cor(Distance Moved (cm), 1m Speed (cm/s))	0.01958401	-0.13491722	0.169922742
	cor(Time to Activity (s), Burst Speed (cm/s))	0.02807736	-0.18700479	0.239544933
	cor(Hiding Time(s), Burst Speed (cm/s))	-0.04548645	-0.24981026	0.159714536
	cor(Distance Moved (cm), Burst Speed (cm/s))	0.01922480	-0.12981225	0.169160469
	cor(1m Speed (cm/s), Burst Speed (cm/s))	**0.42413076**	**0.29703469**	**0.542793049**
L. guichenoti - Between Individual	cor(Time to Activity (s), Hiding Time(s))	**0.90369565**	**0.77529782**	**0.978227159**
	cor(Time to Activity (s), Distance Moved (cm))	-0.45171409	-0.69358613	-0.177708817
	cor(Hiding Time(s), Distance Moved (cm))	-0.29881986	-0.57921282	-0.002829739
	cor(Time to Activity (s), 1m Speed (cm/s))	0.24722197	-0.03334559	0.511867690
	cor(Hiding Time(s), 1m Speed (cm/s))	0.19628177	-0.08423812	0.469426798
	cor(Distance Moved (cm), 1m Speed (cm/s))	-0.03441905	-0.33088469	0.271057143
	cor(Time to Activity (s), Burst Speed (cm/s))	**0.31610099**	**0.03933083**	**0.571799305**
	cor(Hiding Time(s), Burst Speed (cm/s))	0.25109151	-0.02586077	0.510175923
	cor(Distance Moved (cm), Burst Speed (cm/s))	-0.15763758	-0.43004251	0.126905402
	cor(1m Speed (cm/s), Burst Speed (cm/s))	**0.95286559**	**0.89131640**	**0.989537957**
L. guichenoti - Within Individual	cor(Time to Activity (s), Hiding Time(s))	**0.68721300**	**0.58149348**	**0.771981041**
	cor(Time to Activity (s), Distance Moved (cm))	-0.03812672	-0.20063612	0.121080431
	cor(Hiding Time(s), Distance Moved (cm))	0.06659344	-0.08967582	0.221268294

Species - level	Correlation	Estimate	2.5 % CI	97.5 % CI
	cor(Time to Activity (s), 1m Speed (cm/s))	-0.01538997	-0.16973859	0.140063113
	cor(Hiding Time(s), 1m Speed (cm/s))	-0.04596171	-0.19493574	0.108994499
	cor(Distance Moved (cm), 1m Speed (cm/s))	-0.03168564	-0.17659253	0.116113479
	cor(Time to Activity (s), Burst Speed (cm/s))	-0.04886429	-0.21126303	0.117981964
	cor(Hiding Time(s), Burst Speed (cm/s))	-0.02058361	-0.17741319	0.138176209
	cor(Distance Moved (cm), Burst Speed (cm/s))	0.04028649	-0.10947845	0.189531771
	cor(1m Speed (cm/s), Burst Speed (cm/s))	**0.50825642**	**0.39813324**	**0.609206642**