## Introduction

Cognition is defined as the processes by which animals gather, preserve, and use information from their environment through perception, learning, memory, and decision making (Shettleworth (2010)). These cognitive processes underpin several aspects of animals’ ecology such as foraging, mate choice, antipredatory strategies, and/or social behaviours, that are crucial for the survival and reproduction of animals (Dukas (2004)). Particularly, learning - the acquisition of neuronal representations of new information (Dukas (2004)) - is seen as fundamental for coping with environmental changes by enabling individuals to create new associations between events (Dukas (2004); Leal and Powell (2012); Buchanan, Grindstaff, and Pravosudov (2013)). However, the capacity of individuals to acquire new information exhibits natural variation influenced by factors like age, sex, gut microbiota, or the environment where animals develop (Szuran, Zimmermann, and Welzl (1994); Lemaire et al. (2000); Zhu et al. (2004); Joshua J. Amiel and Shine (2012); Joshua Johnstone Amiel, Lindström, and Shine (2014); Carazo et al. (2014); Noble, Byrne, and Whiting (2014); Alemohammad et al. (2022)). The developmental environment, in particular, plays a pivotal role, as the brain is especially susceptible to environmental influences during early stages of development (Zhu et al. (2004)). Hence, investigating the effects of the developmental environment on learning can be essential to understand the evolution of learning and predict animals’ responses towards environmental change. In this sense, prenatal Glucocorticoids (GCs) and prenatal thermal environment are known to play a prominent role in shaping learning abilities in different taxa (see Lemaire et al. (2000); Zhu et al. (2004); Joshua J. Amiel and Shine (2012); Joshua Johnstone Amiel, Lindström, and Shine (2014); O. L. Crino, Driscoll, and Breuner (2014); Abayarathna and Webb (2020)). GCs - hormones related to organisms’ response to stress (Sapolsky, Romero, and Munck (2000)) - exert sustained effects on neural structure and physiology that are associated with animals’ performance on learning tasks (Lemaire et al. (2000); Zhu et al. (2004); O. L. Crino et al. (2014); Farrell et al. (2015); Bebus et al. (2016)). Some studies have demonstrated that prenatal stress and high prenatal GC levels impair with learning (Lemaire et al. (2000); Zhu et al. (2004); Farrell et al. (2015)), while others showed diverse effects depending on factors such as sex or the nature of the learning task (Szuran, Zimmermann, and Welzl (1994); O. L. Crino et al. (2014); Farrell et al. (2015); Bebus et al. (2016)). Similarly, some experiments have shown significant impacts of prenatal temperature on learning in ectotherms (Joshua J. Amiel and Shine (2012); Joshua Johnstone Amiel, Lindström, and Shine (2014); Dayananda and Webb (2017); Abayarathna and Webb (2020)). For instance, high incubation temperatures have been linked with faster learning rates in skinks (Joshua J. Amiel and Shine (2012); Joshua Johnstone Amiel, Lindström, and Shine (2014)), while velvet geckos incubated at temperatures over their natural range learn slower than those incubated within the natural thermal limits (Abayarathna and Webb (2020)). In this vein, the effect of prenatal temperature appears to be linked to alterations in neural structure and metabolic activity (Coomber, Crews, and Gonzalez-Lima (1997); Sakata et al. (2000); Joshua J. Amiel, Bao, and Shine (2017); Beltrán et al. (2021)) that share some similarities with those resulting from prenatal increased stress or GC levels (Lemaire et al. (2000); Zhu et al. (2004); Du et al. (2009)). This suggests that prenatal GCs and temperature can act on the same physiological mechanisms and, thus, both could interact to shape individual variation in learning skills (Noble, Stenhouse, and Schwanz (2018)). Furthermore, GCs can play an pivotal role in determining vertebrate responses to elevated temperatures (Ondi L. Crino et al. (2023)) potentially fostering natural interactions between temperature and GCs. Despite the proximate similarities of prenatal GCs and temperature effects and the potential role of GCs in vertebrates response to elevated temperatures, our understanding of how these two factors interact remains incomplete. In this study, our objective is to explore the interactive effects between prenatal Glucocorticoids (GCs) and the prenatal thermal environment on learning. We utilized two species of skinks, the delicate skink (*Lampropholis delicata*) and the common garden skink (*L. guichenoti*), as model species. We experimentally increased Corticosterone (CORT) - the main GC in birds, reptiles, amphibians, and rodents (Ondi L. Crino et al. (2023)) - levels in the eggs of these two species of skinks and then incubated them at two different temperatures in a 2X2 factorial design. Post-incubation, the juveniles were subjectd to a colour-associative and a reversal task to comprehensively assess their learning abilities. Our hypothesis posits that changes in CORT levels and temperature during early development will induce sustained effects on brain’s morphology and physiology that will ultimately impact learning skills. We predict that individuals exposed to high levels of CORT and/or low temperatures will perform less proficiently in the learning tasks compared to control individuals or those exposed to high temperatures. Additionally, we anticipate that incubation at high temperatures will mitigate the impact of CORT on skink performance, while cold incubation temperatures are expected to enhance the detrimental effects of CORT on learning.

## Methods

### Subjects

*L. guichenoti* and *L. delicata* are small (∼35–55 mm snout-vent length (SVL)), oviparous, and generalist skinks that usually share the same habitat in suburban areas throughout south-eastern Australia (Chapple, Simmonds, and Wong (2011)). They also have similar breeding periods, but with some differences in reproductive output: while *L. delicata* lays 1 to 6 eggs in only one clutch per season, *L. guichenoti* clutches are smaller (1-5 eggs per clutch) but they usually lay two clutches per season (Chapple, Simmonds, and Wong (2011); Chapple et al. (2014)).

### Husbandry

*Breeding colony* – We tested juveniles coming from a breeding colony established in the lab since 2019. There is a total of 270 and 180 adults of *L. delicata* and *L. guichenoti* respectively, housed in big containers (41.5 L x 30.5 W x 21 H cm) with six lizards (2 males and 4 females) per enclosure. Enclosures are provided with non-stick matting, shelter, and several small water dishes. Water is given daily, and they are fed approx. 40 mid-size crickets (*Acheta domestica*) per enclosure three days a week. Crickets are dusted with calcium weekly and multivitamin and calcium biweekly. To ensure a temperature gradient, we employ a heat chord and a heat lamp following a 12 h light:12 h dark cycle. Room temperatures are set to 22-24 Celsius, and warm side of enclosures is usually at 32 Celsius.

*Eggs collection and incubation* – Between mid-October 2022 to the end of February 2023, we provided females with a place to lay the eggs by means of small boxes (12.5 L x 8.3 W x 5 H cm) with moist vermiculite inside, that were placed in one extreme of the communal enclosures (see above). We checked for the presence of eggs in the boxes three days a week. After collection, we measured length and width of eggs with a digital caliper to the nearest 0.1 mm and weight them with a (OHAUS, Model spx123) digital scale ± 0.001g error. Then eggs were treated with CORT or vehicle (see CORT and Temperature manipulation below) and were placed in individual cups (80 mL) with moist vermiculite (12 parts water to 4 parts vermiculite). The cups were covered with cling wrap to retain moisture and left in LATWIT 2X5D-R1160 incubators at two different temperatures (see CORT and Temperature manipulation below) until hatching.

*Hatchlings* – Eggs in the incubator were checked three times a week for hatchlings. After hatchling, we measured juveniles’ SVL and Tail Length (TL) with a rule to the nearest mm and weighted them with a (OHAUS, Model spx123) digital scale ± 0.001g error. We then placed hatchlings in individual enclosures (18.7L x 13.2W x 6.3H cm) and provided them with non-stick matting and a small water dish. During this period, they were sprayed water every day and received 3-6 small *A. domestica* crickets three times a week. All care otherwise follows similar protocols to adults (see above).

Two weeks before we started the training phase (see below), lizards were moved to the experimental arena for acclimatation. The arenas were individual medium size (41 L x 29.7 W x 22 H cm) plastic containers with a shelter (9 L x 6 W x 1.5 H cm) on one of the extremes and a water dish on the other. These new enclosures were placed in two rooms in 7 different racks associated to 7 different CCTV systems (device model DVR-HP210475) that allowed us to record their behaviour during the experiment (see details below). The number of lizards per species and treatment in each rack was counterbalanced to control for any effect of the room or the position of the lizard in the rack. During acclimatation and all the experiment, lizards were fed with only one cricket per day dusted with calcium and multivitamin (see protocol below), and water was supplied *ad libitum*. We provided a temperature gradient by means of a heat cord and heat lamps in a 12 h light: 12 h dark cycle. The rooms temperature was set to between 22-24 Celsius.

### CORT and Temperature manipulation

To test empirically the effect of early environment we manipulated CORT concentration in eggs and incubated them under one of two temperature regimes (‘Cold’ – 23ºC ± 3ºC or ‘Hot’ – 30ºC ± 3ºC) in a 2x2 factorial design ((**FigMethods?**) A). We first allocated eggs to one of two different treatments: CORT treatment, where eggs were topically supplied with 5µL of CORT dissolved in 70% Ethanol and 30% DMSO (vehicle) at a final (10 pg CORT/mL) concentration (CORT treatment); and a Control treatment, where eggs received an equal volume of the vehicle. CORT concentration employed in the CORT treatment represents 2 standard deviations above the mean natural concentration obtained in eggs from both species (non-published data). Then, eggs were incubated in one of the two previously mentioned temperature regimes (‘Cold’ or ‘Hot’) until hatching. The number of eggs per clutch assigned to each hormone and temperature treatment were counterbalanced in both species.

### Learning

To estimate learning skills, we tested skinks’ ability to locate a food reward in a series of behavioural tasks ((**FigMethods?**) B) (see Leal and Powell (2012); Clark et al. (2014)). First, we performed a training phase where lizards had to learn to eat from white 3D-printed PLA ramps (9 L x 4 W x 5 H cm) identical to the ones from the experiment except for the colour (see below). We divided this training phase into three stages: in the first stage, lizards had to eat a small, frozen cricket (*A. domestica*) from an opaque petri dish (3D x 1.6H cm) placed in the middle of their enclosure ((**FigMethods?**) B, Stage 1); in the second stage, the petri dish with the cricket was placed on top of the white 3D printed ramps ((**FigMethods?**) B, Stage 2); and finally, the cricket was left inside a well (3D x 1.75H cm) on the top of the ramp in the third and last stage ((**FigMethods?**) B, Stage 3). Every trial began when we left the feeding block (petri dish, ramp, or both) inside the enclosure and finished one hour later when we took it away. At the end of the experiment, we recorded whether the cricket has been consumed or not. Trial was considered successful if the lizard could locate and consume the reward, while completion of each stage required the lizards to eat the crickets in at least 5 out of 6 trials. This phase lasted 38 days until all the lizards were able to eat from the ramp; only in one case we decided not to use the lizard because its behaviour was not consistent over the course of the training phase. In the next phase, we trained lizards to associate between colour and a food reward (Associative task in (**FigMethods?**) B). The test was like the third stage of the training phase, but here lizards were presented with three feeders that differed in the colour. We placed the food reward (small, frozen, *A. domestica* crickets) inside the wells of the three feeders, covering two of the crickets with 3D-printed lids (3D x 0.5H cm) so prey was only accessible in “the correct” ramp. The food reward was placed in all three wells to avoid lizard using prey chemical cues, and the lids had a series of small holes on the top to allow the release of those chemicals. The colours of the feeders were green, red, and blue, as previous studies demonstrate that squamates can discriminate between these colours (Baden and Osorio (2019)). To control for potential colour preference that could bias our results, we split the subjects into two groups counterbalanced by treatment and species: in one group the correct choice (i.e., the ramp with non-covered cricket) was the blue one in the associative task and red in the reversal (see below), while we did the opposite for the other group. In all trials, the position of the feeders was changed randomly to ensure subjects were using colour rather than spatial cues for the association. Lizards were tested in this task once a day for 35 days. After the colour association phase, we performed a choice reversal task (Reversal task in (**FigMethods?**) B). This task was like the colour association test, except that the attainability of prey was indicated by a different colour, requiring the lizards to form a novel association between the new colour and the food reward. This test was done once a day for 40 days. All trials were done daily between the 6th of March until the 26th of June 2023, beginning at 11 am until 12 pm. Trials in the learning phases (colour associative task and reversal tasks) were recorded with different CCTV systems always using the same camera per individual. Videos were analysed manually using a standard video player (IINA) by PR, who recorded whether the first choice made by each subject was the correct feeder or not. A choice was considered to be made if the head of the lizard was inside the well of one of the ramps. PR was blinded to the treatments of the lizards during the analyses of the video. We considered a trial failed if there was no choice in one hour of recording and those trials were considered as ‘non data’ in the analyses.

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| Experimental design of early environment manipulation (**A**) and learning tasks (**B**). Stages 1-3 indicate the different phases of the habituation process. In the associative and reversal tasks, white lids show the ramps where the food reward was not attainable. |

### Statistical analyses

* We split by species to analyse them separately. We also saw a significant effect of the colour assigned (blue or red) in the preliminary analises, so we decided to split the data by colour as well.

### Results

Originally, we started with 96 lizards, 48 per species and 12 per treatment per species. However, due to natural mortality (n = 11), no completion of the training stage (n = 1), or no motivation during the learning tasks (n = 3; see above), we ended up with a total of 81 lizards. Final sample sizes per treatment and species are disclosed on (**Tabledata?**).

|  | | | Associative task | | | Reversal task | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Specie | Group | Treatment | Mean | 95% CI | p-value | Mean | 95% CI | p-value |
| *L. delicata* | Red | CORT-Cold (n = 5) | **0.104** | **0.06 , 0.151** | **0.000** | **0.045** | **0.018 , 0.072** | **0.001** |
|  |  | Control-Cold (n = 6) | **0.067** | **0.032 , 0.103** | **0.001** | **0.069** | **0.042 , 0.097** | **0.000** |
|  |  | CORT-Hot (n = 5) | **0.074** | **0.033 , 0.115** | **0.000** | **0.053** | **0.025 , 0.081** | **0.000** |
|  |  | Control-Hot (n = 5) | **0.098** | **0.055 , 0.143** | **0.000** | **0.034** | **0.009 , 0.059** | **0.008** |
|  | Blue | CORT-Cold (n = 6) | 0.005 | -0.04 , 0.052 | 0.855 | **0.038** | **0.014 , 0.063** | **0.004** |
|  |  | Control-Cold (n = 6) | 0.003 | -0.042 , 0.049 | 0.881 | **0.057** | **0.032 , 0.083** | **0.001** |
|  |  | CORT-Hot (n = 6) | 0.027 | -0.016 , 0.07 | 0.204 | **0.060** | **0.037 , 0.086** | **0.000** |
|  |  | Control-Hot (n = 5) | 0.047 | 0.002 , 0.095 | 0.042 | **0.059** | **0.031 , 0.088** | **0.000** |
| *L. guichenoti* | Red | CORT-Cold (n = 5) | **0.119** | **0.062 , 0.183** | **0.000** | **0.041** | **0.008 , 0.076** | **0.020** |
|  |  | Control-Cold (n = 4) | **0.104** | **0.045 , 0.169** | **0.002** | **0.085** | **0.042 , 0.134** | **0.002** |
|  |  | CORT-Hot (n = 5) | **0.081** | **0.029 , 0.135** | **0.006** | **0.053** | **0.018 , 0.088** | **0.006** |
|  |  | Control-Hot (n = 5) | **0.080** | **0.028 , 0.136** | **0.006** | **0.074** | **0.038 , 0.113** | **0.001** |
|  | Blue | CORT-Cold (n = 5) | 0.074 | 0.006 , 0.143 | 0.034 | **0.056** | **0.021 , 0.093** | **0.006** |
|  |  | Control-Cold (n = 3) | 0.002 | -0.085 , 0.086 | 0.952 | 0.040 | -0.004 , 0.085 | 0.069 |
|  |  | CORT-Hot (n = 5) | **0.100** | **0.03 , 0.178** | **0.007** | **0.080** | **0.044 , 0.12** | **0.000** |
|  |  | Control-Hot (n = 5) | 0.057 | -0.01 , 0.125 | 0.085 | **0.054** | **0.02 , 0.089** | **0.006** |

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