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Spatial learning in captive and wild-born lizards: heritability and environmental effects

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Abstract

Animals raised in captivity go through drastically different life experiences compared with those raised in the wild. The captive environment is usually characterised by highly stable conditions and limited social interactions. Such early developmental environment, alone and interacting with genes, can have long-lasting effects on cognitive performance. By testing pairs of mothers and offspring delicate skinks, *Lampropholis delicata*, we investigated how being raised in a captive environment shapes spatial learning. Additionally, with this design, we were able to evaluate the additive genetic component and strength of genetic effects in this lizard species. Using a Y-maze task, we compared the spatial learning abilities of wild-caught adult female (mothers) delicate skinks, to their captive-born and raised sexually mature offspring. We found that more mothers completed the task and showed shorter latencies compared with offspring who took longer to complete the maze. The offspring performance did not appear to correlate with their mothers' performance, indicating little narrow-sense heritability. Furthermore, offspring performance was neither affected nor predicted by their mothers' performance, indicating a limited overall genetic effect. Our results suggest that early life experiences in a captive environment may have a hindering effect on cognitive performance.

Significance statement

How important are environmental effects compared with genetics on the development of learning abilities in non-human animals? Studying mother-offspring skink pairs, we show that wild-born mothers outperformed their captive-born offspring in a spatial learning task. We further show that offspring performance in the task was neither explained nor predicted by their mothers' performance. We suggest that conditions during early-life stages shape spatial learning more than genetics, and stable captive conditions may have a negative effect on the development of spatial learning.

Introduction

Cognitive abilities (i.e. all mechanisms enabling animals to obtain and use information from their environment; Shettleworth 2010) can be shaped by a variety of environmental factors as well as by genetic inheritance (Dukas 2004).

While this nature-nurture debate in humans has yielded advanced research into epigenetic mechanisms, brain plasticity, and interactions between genes and the environment (Sameroff 2010), our understanding of what determines variations in non-human animal cognition is still somewhat limited (Boogert et al. 2018; Sorato et al. 2018). In order to understand the evolution of cognition, we must understand the degree of heritability of cognitive traits, and whether they offer fitness advantages (Thornton and Lukas 2012). Furthermore, to get better insights into how species react to changes in their environment, we must know the degree to which environmental conditions contribute to shaping cognitive traits.

The genetic basis of cognitive traits has been mostly studied in humans (Croston et al. 2015), showing that 30–80% of variance in intelligence (defined as general cognitive abilities) can be explained by genetic variation (Deary et al. 2009). In

contrast to humans, very little is known about the genetic effects and degree of heritability of cognitive traits in non-human animals (e.g. Boogert et al. 2011; Hopkins et al. 2014). Nevertheless, using artificial selection experiments and quantitative genetics tools, studies have found a genetic basis for variation in cognition in chimpanzees (*Pan troglodytes*) (Hopkins et al. 2014), snails (*Lymnaea stagnalis*) (Orr et al. 2008), fish (*Rhodeus ocellatus*) (Smith et al. 2015), and several species of insects (Dukas 2008). Thus, across taxa, variation in cognitive traits seems to be at least partially determined by genetic variation. However, the extent of these genetic effects, as well as how they interact with different environmental factors, is unclear (Boogert et al. 2011).

In addition to genetics, conditions during early development can have long-lasting effects on cognitive performance as brain and neuronal pathways are still developing (e.g. Fumagalli et al. 2007; Tierney and Nelson 2009). In birds, for example, stressful conditions experienced early in life, such as food deprivation, increased brood size, or exposure to increased stress hormone concentrations, affect brain development and, as a result, song learning (reviewed by MacDougall-Shackleton and Spencer 2012). Similarly, in mammals, prenatal as well as postnatal stress can affect cognitive function throughout life (reviewed by Hedges and Woon 2011). While most studies conclude that developmental stress leads to cognitive deficiencies, some studies find the opposite, with more stressed individuals showing increased cognitive abilities (Pravosudov 2003; Parker et al. 2005). Thus, some 'stressful' conditions may enhance cognition.

Living in complex or changing environments may require increased cognitive abilities for survival, while living in a stable predictable environment may be less cognitively demanding (Kotrschal and Taborsky 2010; Tebbich et al. 2010). Therefore, complex (or enriched) environments can enhance brain development and improve cognitive performance (Pollen et al. 2007; Sale et al. 2009). For example, a single environmental change in food availability early in ontogeny caused a plastic response in cichlid fish *Simochromis pleurospilus*, enhancing their cognitive abilities (Kotrschal and Taborsky 2010).

Cognitive abilities can be further shaped by numerous other factors relating to the individual tested and the testing conditions. Different individual traits such as personality traits (Carere and Locurto 2011), as well as sex (Carazo et al. 2014) and age (Noble et al. 2014) were all found to be linked to differences in cognitive abilities. For example, if sexual selection, or different reproductive strategies, presents different spatial needs for males and females, the sexes may differ in their spatial learning abilities (Jones et al. 2003; Holding et al. 2012). Prior experience and familiarity with the environment can also have a great impact on performance (Paulissen 2008). For example, little brown skinks (*Scincella lateralis*) familiar with their test chamber were able to learn a spatial task while

skinks with no previous experience with the test chamber were not capable of spatial learning (Paulissen 2008). Similarly, mice that were trained on a maze task outperformed mice with no prior experience (Light et al. 2010). Furthermore, the methods used to assess cognitive abilities and their ecological relevance, as well as the individual level of motivation to perform the given task, can greatly influence performance (Paulissen 2008; Matsubara et al. 2017; Shaw 2017).

We studied spatial learning abilities in a lizard, the delicate skink (*Lampropholis delicata*). Spatial learning is a cognitive dimension crucial to survival (Dayananda and Webb 2017), as it can assist in finding mates, escaping predators, and locating food (Holtzman et al. 1999; Carazo et al. 2014). The delicate skink is one of the most common lizards in coastal eastern Australia (Chapple et al. 2011; Wilson and Swan 2010). It is naturally found in moist habitats, such as rainforests and woodlands, but it is also a successful urban invader and is the only Australian lizard that successfully invaded habitats outside of Australia (Chapple et al. 2013). The species was shown to exhibit learning capabilities (Chung et al. 2017; Goulet et al. 2018; Kang et al. 2018) and thus can serve as a good species for this study. By testing pairs of mothers and offspring delicate skink, we aimed to estimate the additive genetic component and the strength of genetic effects on spatial learning in this lizard species. Furthermore, by comparing wild-born individuals and captive-born individuals, we aimed to better understand possible effects of the captive environment on cognitive performance.

Methods

Twenty gravid females (hereafter mothers) were captured in Brisbane, Queensland, Australia (27.4773° S, 152.9840° E) between 29 August and 9 September, 2016. The capture site was an old cemetery, with open and shaded areas with thick layers of leaf litter. They were brought to Monash University in Melbourne, Australia, and individually marked using visual implant elastomer (Northwest Marine Technologies). Lizards were housed individually in plastic containers (19 × 33 × 11 cm) and kept in a constant temperature room (22 ± 1 °C) on a constant day-night cycle (14 h light:10 h dark). Females laid eggs between 27 September and 26 December, 2016. Eggs were incubated under constant temperature (26 ± 0.2 °C). Hatchlings were kept in plastic containers (19 × 33 × 11 cm) either alone or with 1–3 hatchlings from the same clutch (depending on clutch size and hatching success), within the same temperature-controlled room. In cases where mothers had more than one living offspring, one was randomly chosen for the experiment (total of 20 offspring; 11 females and 9 males). Post-laying, mothers were kept in groups of 2–6 in large plastic containers (25 × 20 × 18 cm). Prior to the onset of the experiment, mothers were reassigned to new housing

containers in groups of 2–6 and, if needed, experimental offspring were isolated from their siblings.

Experimental design

Spatial learning abilities were tested using a standard Y-maze (Fig. 1). The Y-maze is a well-known task to measure learning abilities in reptiles (Burghardt 1977; Wilkinson and Huber 2012), and using a shelter as a reward is relevant to this species as it naturally seeks and hides in shelters (Chapple et al. 2011). The study protocol was based on Chung et al. (2017). Lizards were placed at the end of the starting arm, under a transparent holding container, for 5 min of acclimation. After acclimation, the container was removed and the lizard was free to explore the maze for 10 min. The two remaining arms of the maze, the decision arms, each led to an identical shelter (a black plant tube of 125×45 mm; Fig. 1d). At the start of the experiment, each lizard was randomly assigned a 'safe' side. Upon entering the safe shelter (at the end of the safe-side arm), the shelter was gently lifted and placed in the lizard housing container. If the lizard entered the 'unsafe' shelter (at the end of the 'unsafe'-side arm), the shelter was lifted and the lizard was placed back at the starting arm of the maze. Each lizard had up to 25 trials to learn to select the safe side and enter the safe shelter. Trials were considered correct if lizards initially turned into the safe-side arm, did not exit that arm, and entered the safe shelter in it with all four legs. An individual was considered as having learned the location of the safe side if it correctly completed five out of six consecutive trials (hereafter, success criterion (SC)), based on Noble et al. (2014).

At any given trial, if the lizard did not reach the safe shelter by the end of 10 min, it was gently guided into it for reinforcement using a paint brush. All trials were performed with an observer in the room, and it was not possible to record data using blinded methods. Throughout the 10 min in each trial, if
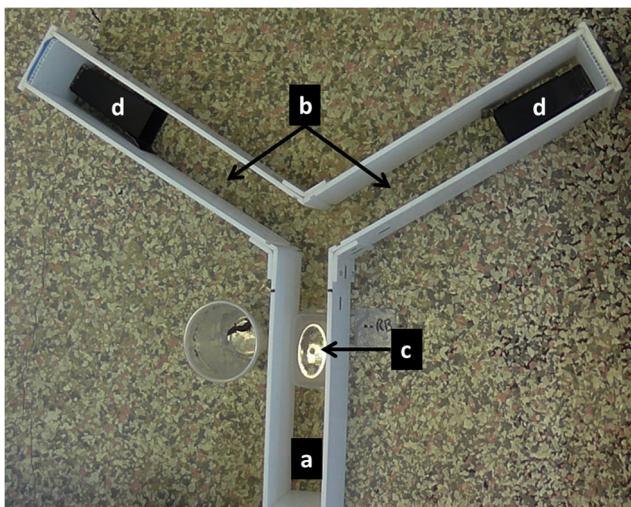

Fig. 1 Standard Y-maze used for the spatial learning task. a The starting arm. b Decision arms. c Acclimation holding container. d Shelter

no movement was detected by the observer for 45 s, lizards were gently tapped on their pelvic girdle with a paint brush to encourage movement. For each trial, the following metrics were recorded: the number of wrong turns—exiting the safe-side arm or turning into the unsafe-side arm from the starting arm and latency to enter the safe shelter—amount of time (including the 5 min of acclimation) that the lizard took to enter the safe shelter. In trials where lizards did not enter the safe shelter, they were given the maximum latency time of 15 min. The last trial a lizard needed to achieve the SC was considered as the number of trials to reach the SC. If a lizard did not reach the SC, it was given 25 as its number of trials.

The experiment ran between 1 and 27 October, 2017, when offspring were 8–11 month old (average age 10 months, median age 10.5 months) and had snout-vent length (SVL) of 30.5–35.5 mm (average SVL 33.1 mm, median 33 mm). At this size and age, they are considered sexually matured young adults (Joss and Minard 1985; Forsman and Shine 1995a; Miller et al. 2017). Lizards were tested up to four times a day with a minimum of 90 min between trials. After every trial, the floor, as well as the shelters and the acclimation holding container, was washed with soap to remove any possible chemical cues. All repetitions were carried out by the same observer. To standardise conditions, prior to each experimental day, lizards were not fed for 24 h.

Statistical analysis

We calculated the probability to reach the SC randomly. Assuming the null probability to complete each trial successfully is 50%, we summed the number of possible combinations to successfully complete five out of six consecutive trials within 25 trials. The expected random probability to reach the SC is the number of successful combinations divided by the total number of possible combinations (2^{25}). We used Fisher's exact test for count data to compare the observed number of individuals that reached the SC and the number of individuals expected at random. In addition, we used a one-sided Fisher's test to compare the number of mothers that reached the SC and the number of offspring that reached it.

To examine differences in performance between mothers and their offspring, we ran generalised linear mixed models (GLMM). We tested lizards' latency to enter the safe shelter (log transformed for normal distribution) and the number of wrong turns (Poisson distribution) as a function of trial number (to test for improvement over time), with group (mothers, male-offspring, and female-offspring) and reaching the SC or not as fixed factors. Lizard ID was included as a random factor.

Prior experience and familiarity with the habitat, in this case the experimental maze, can greatly improve learning abilities (Paulissen 2008). When facing a novel environment, animals are expected to devote time to explore the new habitat in

order to accumulate knowledge about it (Berger-Tal et al. 2014). Thus, to better evaluate learning, we divided the experiment into two phases. First, an exploration phase in which lizards familiarised themselves with the maze, even at the expense of entering a shelter; and second, a learning phase, in which, if learning has occurred, lizards would show improvement over time. We thus fitted a power curve to the plot showing latency to enter the safe shelter as a function of trial number (Fig. 2) and found the maximum point (i.e. the point at which the function derivative equals zero). We used that maximum point as the division point for the two phases. The slope of each individual in the learning phase (i.e. the second phase) was considered as the individual performance estimation. We evaluated the best-fitting model to explain the change in latency to solve the maze over trials using AICc values (Akaike information criterion corrected for small sample sizes), selecting one out of 14 a priori specified models for each phase (exploration and learning; Table 1). The following factors were included in the different models as fixed factors: trial number, group (mothers, male-offspring, and female-offspring), whether or not individuals reached the SC (binary: yes or no), body size (snout to vent length), and safe side

(whether the safe shelter was assigned to the right or left arm of the maze). In addition, lizard ID was included as a random factor.

In order to assess the genetic component of spatial learning in this species, we used three tests. In the first, we tested the narrow-sense heritability by correlating the performance estimation of mothers and their offspring. We used data from all individuals irrespective of if they reached the SC, as similarities between mothers and offspring performance are independent of our pre-determined SC. Individuals' performance estimation was defined as the slope in the latency to enter the safe shelter during their learning phase. Next, we ran eight linear mixed models (see Table 2) with the offspring's performance estimation as the response variable. The following factors were included in the different models as fixed factors: mothers' performance estimation; whether or not mothers reached the SC (binary: yes or no); the offspring number of trials to reach the SC (minimum of five trials and maximum of 25); the offspring sex; and the offspring social experience which is the number of days the offspring was housed with at least one sibling in the same container, or zero in cases only a single egg hatched from its clutch. In addition, lizard ID was

Fig. 2 Mothers and offspring performance in the Y-maze. Latency to enter the safe shelter along the trials for females (a) and offspring (b) that reached the success criterion SC (10 mothers and four offspring; light blue) and those that did not reach the SC (10 mothers and 16 offspring; light red). Vertical lines separate between the exploration and learning phases; and number of wrong turns along the trials for mothers (c) and offspring (d) that reached the SC (light blue) and those that did not reach the SC (light red) (mean and 95% CI)
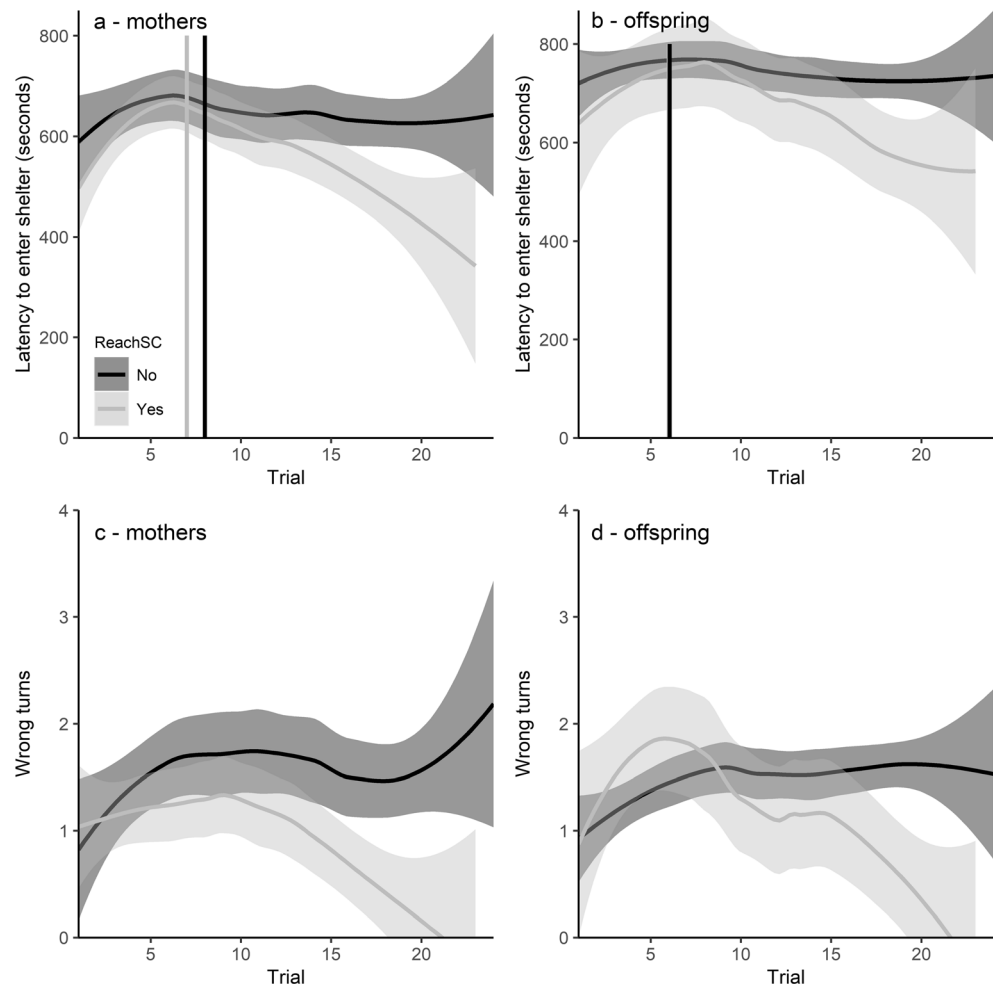
Table 1 Models explaining latency to enter the safe shelter at the first exploration phase (A) and at the second learning phase (B). The following factors were considered: trial number (Trial), group (mothers, male-offspring, and female-offspring), whether the individual reached the success criterion SC or not (Reach SC), body size (snout to vent length), and safe side (whether the safe shelter was assigned to the right or left arm of the maze)

Model	Factors	AICc	ΔAICc	Akaike weights	Cumulative Akaike weights
A) Exploration phase					
1	Trial × group × reach SC	− 725.61	0	1	1
2	Trial × group × reach SC + body size	− 547.3	178.31	0	1
3	Trial × group × reach SC + safe side	− 545.16	180.45	0	1
4	Trial × group × reach SC + body size + safe side	− 491.24	234.37	0	1
5	Trial	− 303.81	421.8	0	1
6	Trial × reach SC	− 297.12	428.49	0	1
7	Trial × reach SC + body size	− 295.22	430.39	0	1
8	Trial + group + reach SC	− 293	432.61	0	1
9	Trial × reach SC + safe side	− 289.29	436.32	0	1
10	Trial × reach SC + body size + safe side	− 284.59	441.02	0	1
11	Trial + group + reach SC + body size	− 284.49	441.12	0	1
12	Trial × group	− 283.65	441.96	0	1
13	Trial + group + reach SC + safe side	− 281.96	443.65	0	1
14	Trial + group + reach SC + body size + safe side	− 269.75	455.85	0	1
B) Learning phase					
1	Trial × group × reach SC	− 1140.29	0	1	1
2	Trial × group × reach SC + body size	− 961.79	178.5	0	1
3	Trial × group × reach SC + safe side	− 959.8	180.49	0	1
4	Trial × group × reach SC + body size + safe side	− 905.7	234.59	0	1
5	Trial × reach SC + body size	− 709.34	430.96	0	1
6	Trial × reach SC	− 706.22	434.07	0	1
7	Trial × reach SC + body size + safe side	− 698.51	441.78	0	1
8	Trial × reach SC + safe side	− 697.98	442.31	0	1
9	Trial + group + reach SC	− 679.4	460.89	0	1
10	Trial	− 674.96	465.34	0	1
11	Trial + group + reach SC + body size	− 670.36	469.93	0	1
12	Trial + group + reach SC + safe side	− 668.35	471.95	0	1
13	Trial × group	− 663.39	476.9	0	1
14	Trial + group + reach SC + body size + safe side	− 655.55	484.75	0	1

included as a random factor. We used AICc model selection to test which model best explains the offspring performance estimation. Finally, we ran a random forest model to test what factors can predict whether an offspring will reach the SC or not. All of the abovementioned factors were considered in the random forest, in addition to the mothers' number of trials to reach the SC, and the offspring performance estimation.

Data availability

The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Results

Mothers performed better than the offspring in the maze task. Ten out of the 20 mothers, compared with only four out of the 20 offspring (three males and one female), reached the SC. Two mothers of the four successful offspring (that reached the SC) reached the SC, while the other two did not. The expected probability of achieving the SC randomly is 0.047, meaning that one out of the 20 should have reached the SC ($0.047 \times 20 = 0.94{\sim}1$). The mothers' observed probability to reach the SC ($10/20 = 0.5$) was significantly higher than expected by chance (Fisher's exact test for count data, odd ratio = 17.65, $p = 0.003$). Offspring's observed probability to reach the SC ($4/20 = 0.2$) was not significantly different from what was expected by chance (odds ratio = 4.58, $p = 0.34$). Mothers were

Table 2 Models explaining offspring performance estimation. The following factors were considered: number of trials of the offspring (the number of trials to reach the success criterion SC or 25 where individuals did not reach it), offspring sex, offspring social experience (the number of days the offspring was housed with at least one sibling in the same container or zero in cases only a single egg hatched from their clutch), mothers' performance estimation, and whether mothers reached the SC (yes or no)

Model	Factors	AICc	ΔAICc	Akaike weights	Cumulative Akaike weights
1	Number of trials	− 127.51	0.00	0.46	0.46
2	Number of trials, sex	− 126.25	1.26	0.24	0.70
3	Number of trials, social experience	− 125.55	1.95	0.17	0.87
4	Number of trials, sex, social experience	− 123.85	3.66	0.07	0.94
5	Number of trials, mother's performance estimation	− 123.03	4.48	0.05	0.99
6	Number of trials, mother's performance estimation, mother reaching SC	− 118.11	9.39	0.00	1.00
7	Number of trials, sex, social experience, mother's performance estimation, mother reaching SC	− 106.57	20.94	0.00	1.00
8	Number of trials, sex, social experience, mother reaching SC	− 117.68	9.82	0.00	1.00

significantly better than offspring in their performance (one-sided Fisher's exact test, odd ratio = 3.85, $p = 0.04$). In addition, mothers were faster to solve the maze, showing significantly shorter latency times to enter the safe shelter than male offspring (mothers 618.7 ± 10.6 s (mean ± SE), male offspring 768.8 ± 13.21; $t = 2.22$, $p = 0.033$). A similar, though non-significant, trend was found between mothers and female offspring (female offspring 695.3 ± 13.14 s; $t = 1.5$, $p = 0.144$). The number of wrong turns, however, did not significantly differ between the mothers and either male or female offspring (mothers 1.3 ± 0.07 wrong turns (mean ± SE), male offspring 1.4 ± 0.08; $z = -0.80$, $p = 0.42$; female offspring 1.4 ± 0.08; $z = -0.75$, $p = 0.45$).

For both phases of the experiment, the exploration phase and the learning phase, the best model explaining lizard's latency to enter the safe shelter included the trial number, the group (mothers, male-offspring, and female-offspring), whether or not the individual reached the SC, and the interaction between the three factors (Table 1). This suggests that there were differences in performance in the maze as trials advanced, between mothers and offspring, and between individuals reaching the SC and the ones that did not. The remaining models show a high ΔAICc (Table 1), suggesting that they are very unlikely to better explain lizards' performance. Body size and safe side assigned to each lizard did not affect lizard's performance.

We did not find a strong genetic component for spatial learning, as offspring performance was not correlated, affected, or predicted by the performance of their mothers. Offspring performance estimation (slope of the learning phase) was not significantly correlated with their mother's performance estimation ($t = 0.88$, $p = 0.39$), indicating little heritability in this trait. Between eight possible models explaining offspring performance estimation (Table 2), the best model only included the offspring's number of trials to reach the SC. The next two best models (ΔAICc < 2 indicating

the model is almost as good as the best model selected) included, in addition to the offspring's number of trials, the offspring sex or the offspring social experience. Together, the three models reached cumulative weight of 87% confidence that one of them is the best approximating model. Mothers' performance was not included in any of the top models. Lastly, a random forest model, used to predict whether an offspring would reach the SC or not, reached 94.74% prediction ability (error rate of 0 for not reaching the SC, error rate of 0.25 for reaching the SC, total error rate of 0.0523). However, the only factors contributing to the prediction power (positive raw importance values in Table 3) were the offspring's number of trials to reach the SC and their performance estimation. This means that the exclusion of either one of these two factors would greatly reduce the accuracy of the model (mean decrease accuracy; Table 3). Similarly, both factors were found to be important for estimating a target variable across all trees (mean decrease Gini; Table 3). Mothers' performance did not help predict offspring performance.

Discussion

We found significant differences in spatial learning between our two groups of mothers and offspring. Mothers were significantly better than offspring in solving the maze and they were faster in doing so (Fig. 2a and b). However, we did not find significant differences in the number of wrong turns throughout the trials (Fig. 2c and d), suggesting that among individuals that did not reach the SC, mothers were not more accurate than offspring. Further, while many cognitive traits were shown to vary with genotype (Dukas 2004), we did not find evidence for genetic influence on variability in spatial learning in the delicate skink. Offspring performance did not correlate with mothers' performance, indicating little additive

Table 3 Relative importance of factors in the random forest model to predict whether an offspring will reach the success criterion SC or not. The following factors were considered: offspring performance estimation, number of trials of the offspring (the number of trials to reach the SC or 25 where individuals did not reach it), offspring sex, offspring social experience (the number of days the offspring was housed with at least one sibling in the same container or zero in cases only a single egg hatched from their clutch), their mothers' performance estimation, their mothers' number of trials to reach the SC, and whether their mothers reached the SC (yes or no). Table presents raw importance of each factor for predicting whether individuals will reach the SC, mean decrease accuracy (decrease in model accuracy), and mean decrease Gini (total decrease in tree node impurity)

Factor	Raw importance for individuals not reaching the SC	Raw importance for individuals reaching the SC	Mean decrease accuracy	Mean decrease Gini
Offspring performance estimation	42.21	41.50	46.69	2.05
Offspring number of trials	53.32	57.11	58.11	2.44
Sex	−2.59	−1.94	−2.50	0.19
Sociality	−7.97	−14.79	−13.93	0.42
Mother performance estimation	−1.25	−7.38	−5.06	0.50
Mother number of trials	0.14	−15.16	−8.19	0.36
Mother reaching SC	2.77	−8.88	−3.01	0.07

genetic component (narrow-sense heritability). Moreover, offspring performance was neither affected (Table 2) nor predicted (Table 3) by their mothers' performance, indicating a limited overall genetic effect. This suggests that rearing environment might have played a more significant role in determining spatial learning abilities. However, we cannot completely rule out the possibility that genetic effects on spatial learning exist in delicate slinks and were simply masked by the different environmental conditions that the offspring experienced compared with their mothers.

Early developmental environment can have long-lasting effects on cognitive performance (Buchanan et al. 2013; Matsubara et al. 2017). Incubation temperature, for example, can affect brain development (Valenzuela and Lance 2004) and has been shown to affect spatial learning abilities post hatching in skinks (*Bassiana duperreyi*; Amiel and Shine 2012) and in geckos (*Amalosia lesueurii*; Dayananda and Webb 2017). In addition, living in a changing or challenging environment often favours increased cognitive abilities, allowing individuals to learn and respond to challenges in their environment more appropriately (Roth et al. 2010; Batabyal and Thaker 2019). For example, mountain chickadees (*Poecile gambeli*) from a higher elevation population with harsher winter climates showed increased spatial memory and outperformed individuals from a milder environment in an associative learning task (Freas et al. 2012). Furthermore, the development of many learning processes is limited to early-life stages (Bronson 1965). For example, Roth and Krochmal (2015) showed that young translocated painted turtles (*Chrysemys picta*) were able to use cues to find paths to a water source in an unfamiliar environment, whereas individuals over the age of four failed in locating a water source.

In our study, the mothers who were wild-born and brought into captivity as adults outperformed their captive-born offspring in a spatial learning task. The offspring were incubated in the lab under controlled constant conditions, whereas their mothers probably experienced changing conditions during their development. Post hatching, the offspring were kept under constant conditions, never having experienced extreme temperatures, dry seasons, starvation periods, or predation pressure—conditions that are likely to have occurred in the mothers' natural habitat. In captive individuals, body size and brain size can be affected by growing up in an impoverished environment (Wiggins et al. 2018), which might explain why, in our experiment, mothers showed better spatial learning performances compared with their offspring. A few studies tested differences in cognitive abilities between captive and wild individuals and showed mixed results; for example, McCune et al. (2019) showed that wild Mexican jays (*Aphelocoma wollweberi*) outperformed captive individuals in a problem-solving task, while Cauchoix et al. (2017) found similar performance in captive and wild great tits (*Parus major*) in a reversal learning task. As the different studies were conducted on different species, and since many potential factors can affect behaviour and cognitive development (diet, stress, motivation to solve the task, etc.), it is impossible to determine the strength and direction of the effect of captive conditions on cognitive development at large. However, our results suggest that perhaps the stable captive environment had a hindering effect on the offspring' spatial learning ability (Thornton and Lukas 2012). Thus, captive conditions and environmental enrichment should be taken into consideration and be accounted for when comparing between different studies.

Other than environmental and genetic effects, mothers and offspring differences in performance could also be attributed to differences in motivation levels or age. Having never experienced predation pressure, offspring may have been less motivated to seek shelter. Nonetheless, offspring were observed using the shelter in their housing containers. The offspring were about 10 months old when tested in the maze and were

considered as young adults (Joss and Minard 1985). Several studies show an increase in cognitive performance from childhood to adulthood (reviewed by Thornton and Lukas 2012). However, the only two studies to test age effects in lizards found no such trends. Both young eastern water skinks (*Eulamprus quoyii*) (Noble et al. 2014) and juvenile blue-tongue lizards (*Tiliqua scincoides scincoides*) (Szabo et al. 2019) show similar learning abilities as adults. Noble et al. (2014) further showed that young eastern water skinks engaged in social learning more than their adult counterparts. Both ours and Noble et al. (2014) studies highlight the significant role early-life experiences may have on cognitive abilities.

Cognitive traits can also be influenced by the individual's sex (Carazo et al. 2014), social environment (Cacioppo and Hawkley 2009), and personality (Carere and Locurto 2011). Sexual dimorphism in spatial performance was demonstrated in many species, with males usually outperforming females (Geary 1995; Jones et al. 2003). For example, more male eastern water skinks were able to learn a spatial learning task than females and they were quicker to learn it (Carazo et al. 2014). Some behavioural sexual dimorphism was also found in delicate skinks (Forsman and Shine 1995b; Michelangeli et al. 2016) and can perhaps result in differences in spatial learning abilities. Michelangeli et al. (2016) showed differences in explorative behaviour between males and females delicate skinks with females being faster explorers (took less time to cross a barrier). This may give females an advantage in the task presented here. Indeed, while mothers were significantly faster in solving the maze than male offspring, there was no significant difference between the mothers and their female offspring, suggesting perhaps that female delicate skinks are better at spatial learning than males. Out of the four offspring to reach the SC in our experiment, there were three males and only one female. However, the female offspring that reached the SC did so within 14 trials, whereas the male offspring that reached the SC took 20–23 trials, and mothers reached the SC within 6–23 trials (mean 16.6, median 18). Thus, differences in performance can vary greatly within each sex and may be more strongly determined by other factors. However, due to the limited number of offspring that reached the SC, and as we only tested wild females, we cannot determine whether there are indeed differences in spatial learning between males and females.

Social isolation usually has a negative effect on cognitive abilities (Volkers and Scherder 2011). In rodents for example, synapse formation may vary based on conditions the individual has experienced and isolation rearing was shown to restrict brain development (Coss 1991; Tromborg and Coss 2015). However, some studies find no effect (Riley et al. 2017) or a positive effect of isolation on cognitive performance

(Wongwitdecha and Marsden 1996). The only study to have tested this in reptiles showed that in a group-living lizard (*Egernia striolata*), spatial learning was not affected by social environment (Riley et al. 2017). In our experiment, two of the offspring reaching the SC never experienced any interaction with another lizard. The other two that reached the SC shared their house bin with one or two siblings their entire lives until isolated from them prior to the experiment. Thus, while we cannot conclude on how group rearing might affect spatial learning in our species due to low sample size, our results do suggest that there is no relationship between spatial learning and social environment in this species. Further research in this area is required to better understand social environment effects on spatial learning. Finally, delicate skinks have been shown to exhibit consistent among-individual variation in activity and exploration (Michelangeli et al. 2016; Moule et al. 2016). However, Chung et al. (2017) found that such personality differences had little effect on the individual's probability to learn an associative learning task, their learning speed or accuracy. Thus, we did not measure inter-individual variation in behaviour in our experiment, though we did account for individual differences in our analysis.

Overall, our results demonstrate that delicate skinks are capable of spatial learning in a Y-maze task. Our results further suggest that rearing conditions and environmental factors outweigh any potential genetic component in the development of this cognitive trait and seem to shape spatial learning performance in this species. Given the importance of early-life environment on cognitive development (Feldman and Eidelman 2009; Salvanes et al. 2013; Davis et al. 2017), our study suggests that the ecological relevance of results from cognitive tests performed on captive-born individuals should be treated with caution. Admittedly, lab experiments offer the opportunity to standardise conditions between individuals and control for contextual factors (Morand-Ferron et al. 2016) and can therefore greatly advance our knowledge of the evolution of cognition. However, captive conditions cannot fully inform us of the selection pressures that act on wild populations (Thornton and Lukas 2012; Matsubara et al. 2017). Thus, the ecological relevance of such experiments may very much depend on the captive conditions, the time spent in captivity, and how closely they mimic the species' natural environment.

Compliance with ethical standards

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

Ethical approval   All animal care and experimental procedures were approved by the Monash University Animal Ethics Committee (BSCI/2016/17, BSCI/2017/33). All applicable international, national, and/or institutional guidelines for the use of animals were followed.

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