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ORIGINAL PAPER

Effects of incubation temperatures on learning abilities of hatchling velvet geckos

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Abstract

Stressful environments in utero can have a profound influence on cognitive functions and learning ability. In lizards, thermal environments experienced by embryos can shape a range of traits, including sex, body size, and locomotor performance, which may influence fitness. Recent studies suggest that incubation temperatures may also influence brain development and learning ability of some lizard species. Therefore, predicted increases in nest temperatures of lizards may not only affect hatchling morphology and performance, but could also affect their learning ability. To investigate how incubation temperatures influence cognitive abilities of hatchlings, we incubated eggs of the velvet gecko, *Amalosia lesueurii*, under two fluctuating temperature regimes. The warm treatment mimicked the thermal profiles of currently used partly shaded communal nests (mean = 24.3 °C, range 18.4–31.1 °C), and the hot treatment simulated thermal profiles that could be experienced in sun-exposed nests in 2050 (mean = 28.9 °C, range 19.1–38.1 °C). At age three to four weeks, we measured the ability of hatchlings to locate an open shelter in a Y-maze choice test. Both hot and warm-incubated hatchlings successfully learned the task, but hatchlings from the warm-temperature treatment learned the task faster, and made fewer mistakes in the first five trials than hot-incubated hatchlings. These patterns were consistent for hatchlings from two geographic locations, suggesting that thermally stressful conditions in utero may alter the learning abilities of hatchling lizards. Because learning ability can affect the survival of hatchling velvet geckos, future increase in nest temperatures may have wide reaching impacts on populations.

Keywords Reptile cognition · Developmental plasticity · Heatwave · Y-maze · Learning

Introduction

Cognition, the process by which animals acquire, process, store and recall information in order to make behavioural decisions (Rowe and Healy 2014; Shettleworth 2001), is an important trait that can affect how individuals cope with novel or changing environments (Sol et al. 2008, 2005; Wright et al. 2010). In the face of rapid change, the ability to rapidly learn new behaviours may enable individuals to avoid novel predators, track shifting resources, exploit novel foods, and cope with complex environments (Dukas 2004). Thus, individuals with enhanced cognitive abilities are predicted to have higher fitness, although demonstrating this linkage in wild populations is difficult (Morand-Ferron et al. 2016).

While flexible behaviours may help individuals to cope with environmental challenges, changing environments can in turn modify cognitive abilities via developmental plasticity, and such shifts are not always adaptive (Chevin et al. 2010; West-Eberhardt 2003). For example, stressful conditions experienced in utero can have detrimental effects on brain development, memory, spatial learning, and cognitive function in a wide range of species (Markham and Koenig 2011; McEwen et al. 2012; Schoech et al. 2011). While most of this research has focused primarily on mammals, there is a growing body of evidence that environments experienced by early life stages of ectotherms can influence the cognitive abilities of later life stages (Arenas and Farina 2008; Groh et al.

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2004; Tautz et al. 2003). Given the rapid pace of current anthropogenic change, an understanding of how changes in developmental environments will influence cognitive traits of ectotherms, and the ecological consequences of such changes, may enable better forecasts of species persistence under future warming (Carlo et al. 2018; Levy et al. 2015).

In most lizards, females abandon their eggs after oviposition, and mothers do not care for offspring after birth. This lack of parental care makes lizards good model organisms for investigating how developmental environments influence the cognitive abilities of offspring (Noble et al. 2018). Most lizards lay eggs inside shallow nests, and embryos may experience thermal spikes during summer heatwaves (Hall and Warner 2018; Shine and Elphick 2001). In years with prolonged and more intense heatwaves, it is likely that the nests of some lizard species will experience higher-than-average temperatures (Angilletta et al. 2013; Telemeco et al. 2017). While there is a wealth of studies demonstrating that incubation temperatures can have strong and often persistent effects on the morphology, behaviour, and locomotor performance of neonatal reptiles (Deeming and Ferguson 1991; Deeming 2004; Noble et al. 2018; While et al. 2018), only recently have investigators begun to examine how incubation temperature affects learning behaviour.

For example, a study on hatchling three-lined skinks (*Bassiana duperreyi*) found that lizards from a 22 ± 7.5 °C incubation treatment made fewer mistakes in a task where they had to locate an open shelter whilst being chased than lizards from a 16 ± 7.5 °C incubation treatment (Amiel and Shine 2012). In a follow up study, in which the skinks had to locate a food reward in a Y-maze equipped with local cues, eggs incubated at 24 ± 7.5 °C produced hatchlings that were faster learners, and made fewer mistakes, than hatchlings from eggs incubated at 18 ± 5 °C (Amiel et al. 2014). Using the same incubation treatments, researchers also found that only the hot incubated skinks could complete an instrumental learning task (Clark et al. 2014). In bearded dragons, egg incubation temperatures affected the social learning ability of adults. After watching a demonstrator open a door, lizards from a 27 ± 3.0 °C incubation treatment opened the door faster than lizards from a 30 ± 3.0 °C treatment (Siviter et al. 2017). In a recent study on velvet geckos *Amalosia lesueurii*, hatchlings were placed in a rectangular arena containing two identical shelters, one of which was open, and the other was closed. The hatchlings were chased with a paintbrush (to simulate a predatory attack) until they entered the open shelter. Hatchlings from a 27 °C treatment (range 14–37 °C) were slower learners than lizards from a 23.2 °C (range 10–33 °C) treatment (Dayananda and Webb 2017). However, this study did not examine the number of mistakes made by geckos, so the question of whether incubation influenced speed of learning, or accuracy, remains open.

While the above studies demonstrate that lizards are adept learners, the discordant effects of incubation temperature on lizard learning behaviour (warmer incubation temperatures produce ‘better’ learners in some species, but not in others) hampers our ability to predict how higher nest temperatures may influence the cognitive abilities of hatchlings. Furthermore, most studies have tested individuals from a single population, so it is unclear whether the observed patterns necessarily translate to other populations within the species’ geographic ranges. Nest temperatures can vary across latitude and altitude in wide ranging lizard species (Doody et al. 2006), so we might expect to see variation in developmental reaction norms of traits between populations (Angilletta 2009; Noble et al. 2018).

In this study, we investigated whether incubation temperatures affect the cognitive abilities of hatchling velvet geckos *Amalosia lesueurii* from two populations; one from Nowra, near the most southern part of its geographic range in New South Wales, and another from Dharawal National Park, 100 km further north. To facilitate comparisons with previous studies on lizards, we scored the learning ability of hatchlings in a Y-maze, a well-established method in both the animal behaviour and psychological literature (Burghardt 1977; Macphail 1982; Wilkinson and Huber 2012).

Materials and methods

Collection and maintenance of pregnant females

We collected gravid female velvet geckos from two study sites located near Nowra, approximately 170 km south of Sydney, and Dharawal National Park, approximately 70 km south of Sydney, in late spring 2016. Females were transported to the University of Technology Sydney and were housed inside identical plastic cages (Sistema NZ 2.0 L, 220 × 150 × 60 mm, with ventilated lid) in a constant temperature room (23 °C) with a 12:12 light cycle. Each cage contained a white plastic half-pipe shelter (80 mm × 40 mm) and a water dish, with a layer of moist vermiculite to prevent eggs from desiccating. Cages were placed on timer-controlled heating cables set to 32 °C, which created a thermal gradient (23–32 °C) inside the cages during daylight hours, falling to 23 °C at night. We fed geckos crickets twice weekly and ensured that they had a constant supply of water. Each morning and afternoon, one of us (TA) checked all the cages for newly oviposited eggs, and sprayed the vermiculite to maintain a moist substrate. After females laid eggs, we recorded their body mass, and released them at their exact site of capture during suitable weather conditions.

Egg incubation experiment

On the day of egg laying, one of us (TA) recorded the mass of each egg (to nearest 0.01 g) and measured the maximum length and width of each (to nearest 0.01 mm) with Vernier callipers. Each egg was placed singly inside a 100 mL glass jar filled with moist vermiculite (water potential of 200 kPa), and was covered with plastic food wrap to reduce water loss. Nearly all females laid two eggs, so we placed one egg from each clutch into the 'warm' incubator, and the other into the 'hot' incubator (Panasonic MIR 154, 10 step functions). We incubated 84 eggs in the warm incubation treatment and 81 eggs in the hot incubation treatment. We programmed incubators to mimic the cycling temperatures seen inside natural nests, with intermittent heatwaves. For example, in summer 2017–2018, mean temperatures recorded inside 14 communal nests from Morton National Park varied from 23.3 °C in shaded nests to 26.9 °C in sun-exposed nests (Cuartas and Webb, unpublished data). Temperature cycles in the warm treatment mimicked those recorded inside partly shaded communal nests (mean = 24.3 °C, range 18.4–31.1 °C). Thermal cycles of the hot treatment (mean = 28.9 °C, range 19.1 °C–38.1 °C) mimicked the potential future nest temperatures that might occur in sun-exposed nests in 2050 if air temperatures increase by 2–3 °C as predicted by climate models (Dowdy et al. 2015).

Maintenance of hatchling geckos

Once hatchlings emerged from eggs, we housed them individually as described above for females, except that cages had a paper substrate and lacked vermiculite. We fed hatchlings with five pinhead crickets twice weekly, and cleaned their cages at weekly intervals.

Learning task

We tested the learning ability of 16 hot-incubated hatchlings (Dharawal $n = 10$, Nowra $n = 6$) and 33 warm-incubated hatchlings (Dharawal = 13, Nowra $n = 20$). Hatchlings were tested at age three to four weeks (mean age = 27 d ± 7.2 SD) from 14 February to 24 March 2017. We used a Y-maze constructed of opaque plastic arms (33 × 10 × 5 cm) to test the lizard's ability to learn the location of an open shelter during a simulated predatory attack (by a paintbrush). We used this approach to ensure that lizards were sufficiently motivated to learn the task (Burghardt 1977). Each arm contained an identical shelter constructed of a white PVC half pipe (65 × 55 × 25 mm, Fig. 1). One shelter was closed, while the other was open; we positioned shelters such that lizards could not see the entrance to the shelter until they had reached it. Because lizards may use position or local cues to navigate (Day et al. 1999), we provided local visual cues by placing coloured paper flooring inside each arm. Geckos have excellent colour vision, but lack the ability to see red; thus, the floor colours were either solid blue, or blue with orange stripes. To control for colour and positional biases, we randomly allocated geckos into four groups, and each group had a different position and colour combination (Table 1). These combinations remained constant for each individual throughout the trials. Lizards also had access to external landmark cues (objects in the room) which remained constant throughout the trials. While lizards could have used any combination of cues to locate the open shelter, we were not interested in which cues they used; rather, we were interested whether incubation temperature affected the ability of lizards to locate a novel shelter in a biologically relevant task that simulated a predatory attack. In this situation, lizards that failed to learn the location of the 'safe' refuge would be exposed to predators, and thus, more likely to be killed.

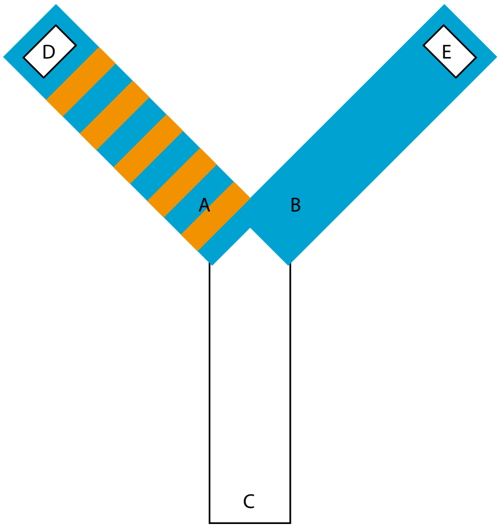

Fig. 1 Diagram of the Y-maze used for the learning trials with hatchling velvet geckos. The position of the open shelter (D), and closed shelter (E), and the coloured floor of the two arms (A and B), remained constant for each individual throughout the trials. At the start of the trial, each gecko was placed under a plastic shelter at the release point (C). Each gecko was allocated to one of four groups, and each group had a different combination for the position of the open shelter (left or right), or solid blue floor (left or right), as explained in Table 1

We ran two trials per day for five consecutive days for each hatchling (10 trials). To begin the test we placed the hatchling at the base of the empty arm (location C, Fig. 1) under a plastic cover. One of us (TA) then removed the cover, and gently tapped the lizard on the tail with a paintbrush to simulate a predatory attack. TA was blind to the treatment (incubation or group) and only tapped the lizard on the tail if it stopped running. Hatchlings that did not locate the correct shelter within 2 min were directed to the

Table 1 Position of the open and closed shelters and the composition of the colour for the floor allocated for four different groups of hatchlings

	Sample size	Open shelter	Closed shelter	Striped floor	Solid floor
Group 1	14	Left	Right	Left	Right
Group 2	14	Right	Left	Left	Right
Group 3	11	Left	Right	Right	Left
Group 4	10	Right	Left	Right	Left

correct shelter with the paintbrush, and were allowed to hide under the shelter for 30 s before they were removed from the maze. For each trial, we recorded: (1) time taken to reach the open shelter; (2) number of mistakes (lizard chose incorrect arm). The raw data is available in the electronic supplementary materials accompanying this article. After completing the trials, we released the hatchlings to the sites where their mothers were captured.

Statistical analysis

To assess whether incubation treatment and population influenced the learning abilities of geckos, we carried out separate two-factor repeated measures ANOVAs, with incubation treatment and population as fixed factors, and number of mistakes in each of the 10 trials, and time taken to complete the task in each trial, as the dependent variables. Mauchley's tests indicated that the assumption of sphericity was violated for 'mistakes' ($\chi^2_{(44)} = 262.31$, $p = 0.001$, $\epsilon = 0.47$), and also 'time to complete task'($\chi^2_{(44)} = 129.10$, $p = 0.001$, $\epsilon = 0.63$), so we used Greenhouse–Geisser estimates for F-tests (Howell 2002). To explore whether local cues (Table 1) influenced learning, we used a two-factor repeated measures ANOVA, with incubation treatment and group as fixed factors, and number of mistakes as the dependent variable. Mauchley's test indicated that the assumption of sphericity was violated ($\chi^2_{(44)} = 262.31$, $p = 0.001$, $\epsilon = 0.47$) so we used Greenhouse–Geisser estimates for F tests.

Results

Number of mistakes

Plots of the number of mistakes versus trial number showed that the number of mistakes declined rapidly with trial number, indicating that the geckos learned the task (Fig. 2). A repeated measures ANOVA showed a significant effect of trial number ($F_{4.2,\ 190.3} = 33.37$, $p = 0.0001$), a significant interaction between trial number and incubation treatment ($F_{4.2,\ 190.3} = 3.47$, $p = 0.0001$), a non-significant interaction between trial number and population ($F_{4.2,\ 190.3} = 1.37$, $p = 0.20$), and a significant interaction between trial number, incubation treatment and population ($F_{4.2,\ 190.3} = 2.56$, $p = 0.037$). To interpret the significant three-way interaction, we plotted data for each population separately. In warm and hot-incubated Nowra lizards, the number of mistakes made by lizards declined as the number of trials progressed, and reached a minimum in trial six (Fig. 2a). In Dharawal lizards, warm-incubated lizards made few mistakes after the fourth trial, whereas hot-incubated lizards made few mistakes after the sixth trial (Fig. 2b). Overall, the main effects (between-subject effects) were not significant for incubation treatment ($F_{1,45} = 0.82$, $p = 0.37$), population ($F_{1,45} = 0.17$, $p = 0.68$), or the interaction between incubation and population ($F_{1,45} = 1.56$, $p = 0.22$). That is, the total number of mistakes made by geckos in the 10 trials was similar among treatments (means ± SD, Nowra: warm = 14.7 ± 7.67, hot = 14.0 ± 2.97; Dharawal: warm = 13.0 ± 5.16, hot = 17.4 ± 6.83).

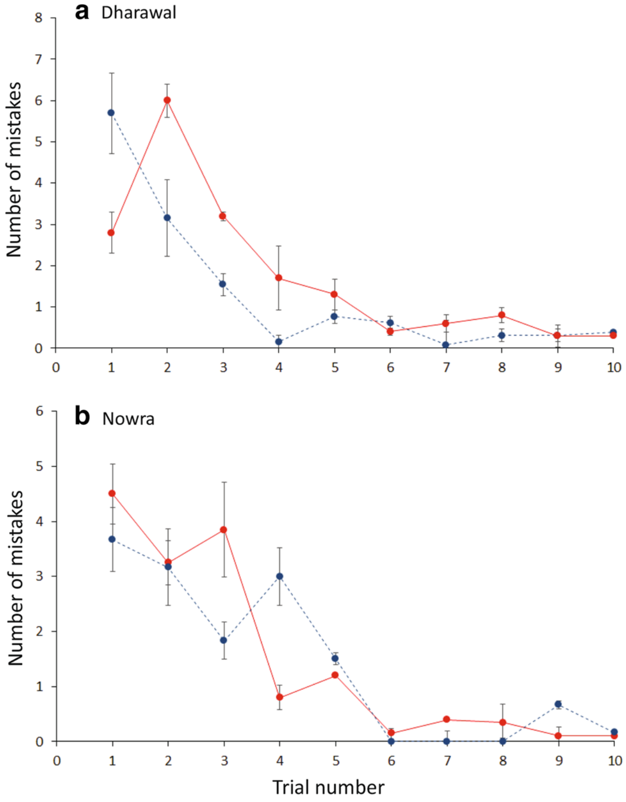

Fig. 2 The number of mistakes made by hatchling velvet geckos versus the trial number for hot-incubated (red solid line) and warm-incubated lizards (blue dotted line) from **a** Dharawal, **b** Nowra. Graphs show means ± standard errors (color figure online)

Time to complete learning task

Plots of the time taken to complete the learning task versus trial number showed a decrease in completion times with trial number (Fig. 3). A repeated measures ANOVA showed a significant effect of trial number ($F_{5.6,\ 253.3} = 45.40$, $p = 0.0001$), a significant interaction between trial number and incubation treatment ($F_{5.6,\ 253.3} = 7.15$, $p = 0.0001$), a significant interaction between trial number and population ($F_{5.6,\ 253.3} = 2.71$, $p = 0.017$), and a significant interaction between trial number, incubation treatment and population ($F_{5.6,\ 253.3} = 3.52$, $p = 0.003$). To interpret the significant interaction terms, we plotted data for each population separately. Plots of trial number versus completion times showed that in both populations, warm-incubated lizards completed some, but not all, trials faster than hot-incubated lizards (Fig. 3). Overall, the main effects (between-subject effects) were significant for incubation treatment ($F_{1,\ 45} = 10.18$, $p = 0.003$), but were not significant for population ($F_{1,\ 45} = 0.02$, $p = 0.89$), or the interaction between incubation and population ($F_{1,\ 45} = 1.31$, $p = 0.26$). That is, in both populations, warm-incubated geckos completed the trials faster than hot-incubated geckos (mean time to complete 10 trials ± SD, Nowra: warm = 279.2 ± 95.1, hot = 399.5 ± 65.5; Dharawal: warm = 307.0 ± 83.3, hot = 363.7 ± 91.6).

To disentangle further the effects of incubation treatment on learning ability, we plotted the sum of completion times from all 10 trials versus the sum of mistakes. There was a significant positive linear relationship between the number of mistakes and time ($r = 0.72$, $n = 49$, $p < 0.0001$); as expected, geckos that made more mistakes took longer to complete the trials. An analysis of covariance (ANCOVA), with the number of mistakes as a covariate, and time as the dependent variable, showed that the slopes of the relationship between mistakes and time were parallel ($F_{1,\ 45} = 0.30$, $p = 0.59$). However, when the number of mistakes was held constant, the warm-incubated hatchlings completed the task faster than the hot-incubated hatchlings ($F_{1,\ 46} = 12.45$, $p = 0.001$).

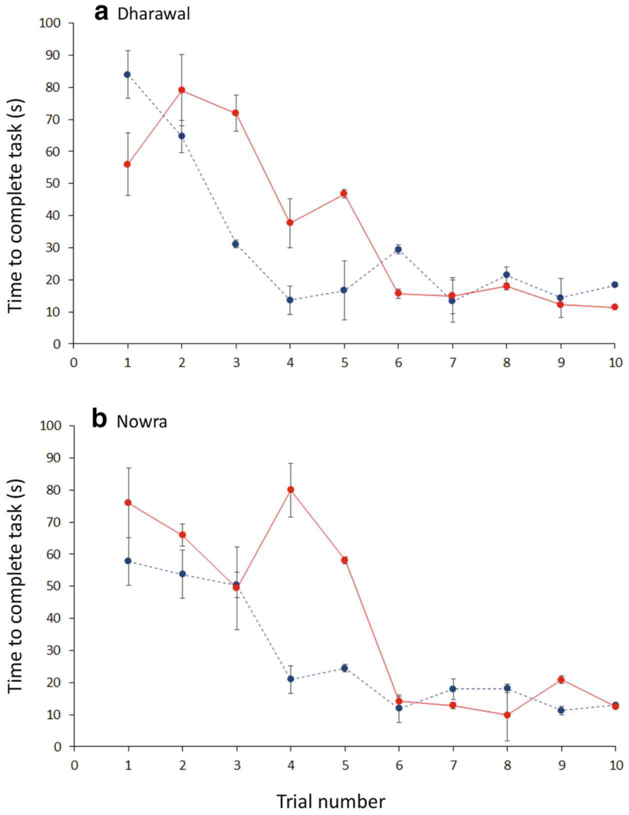

Fig. 3 Time taken by hatchling velvet geckos to complete the learning task versus trial number for hot-incubated (red solid line) and warm-incubated lizards (blue dotted line) from **a** Dharawal, **b** Nowra. Graphs show means ± standard errors (color figure online)

Effects of local cues

The number of mistakes made by geckos were similar among the four groups in which local cues varied (means ± SD: group 1 = 14.3 ± 6.93, group 2 = 13.14 ± 6.94, group 3 = 15.73 ± 6.51, group 4 = 16.40 ± 5.42). The results of a repeated measures ANOVA showed a significant effect of trial number ($F_{4.1,\ 169.2} = 32.65$, $p = 0.0001$), a significant interaction between trial number and incubation treatment ($F_{4.1,\ 169.2} = 3.38$, $p = 0.01$), but no significant interaction between trial number and group ($F_{4.1,\ 169.2} = 0.88$, $p = 0.58$), or between trial number, incubation treatment and group ($F_{4.1,\ 169.2} = 0.89$ $p = 0.56$). The main effects (between-subject effects) were not significant for incubation treatment ($F_{1,\ 41} = 0.65$, $p = 0.43$), group ($F_{1,\ 41} = 0.17$, $p = 0.68$), or the interaction between incubation and group ($F_{1,\ 41} = 1.14$, $p = 0.35$).

Discussion

Heatwaves are a common occurrence in Australia, but their intensity and duration is predicted to increase in coming decades (Anderson et al. 2018; Cowan et al. 2014; Kang and Eltahir 2018) which could elevate nest temperatures of many lizards, including our study species (Dayananda and Webb 2017). To understand how increases in incubation temperature may affect the cognitive abilities of hatchling velvet geckos we measured their ability to locate a safe refuge in a Y-maze. Warm-incubated hatchlings learned to locate an open refuge in the Y-maze faster than did hot-incubated hatchlings (Fig. 3). Although incubation treatment did not affect the total number of mistakes made by geckos across the 10 trials, the trajectories and slopes of learning curves differed between incubation treatments and populations, indicating that there were subtle differences in learning abilities (Fig. 2). Overall, our results confirm that higher incubation temperatures produce slower geckos (Dayananda et al. 2017), that took longer to complete the learning task (Dayananda and Webb 2017). Importantly, our results extend on previous work (Dayananda and Webb 2017) by showing that this pattern was consistent for two populations: one from the southern edge of the species' geographic range (Nowra), and another approximately 100 km north (Dharawal).

Incubation temperatures can affect other traits that may affect fitness, such as egg hatching success and hatchling body size (Noble et al. 2018). In this study, egg hatching success was higher in our warm-incubation treatment (40%) than in the hot treatment (22%), while hot-incubated hatchlings were also smaller than warm-incubated hatchlings (mean snout-vent lengths of 21.4 versus 25.4 mm Abayarathna et al. 2019,). Collectively, the results presented here, in conjunction with published data for our study species, provide strong evidence that above-average incubation temperatures produce smaller hatchlings with poorer cognitive abilities (Dayananda and Webb 2017). Both of these traits could potentially influence fitness in wild populations (Morand-Ferron et al. 2016).

Currently, inconsistent terminology as to what constitutes 'hot' hampers our understanding of the effects of incubation temperatures on lizard cognitive abilities. For example, research on three-lined skinks found that lizards from hot-temperature incubation were better learners (Amiel et al. 2014; Amiel and Shine 2012; Clark et al. 2014). However, closer examination of the 'hot' temperatures used in those experiments (22 ± 7.5 °C and 24 ± 5 °C) reveals that they were similar to the temperatures of our warm treatment (24.3 °C, range 18.4–31.1 °C). Thus, the 'hot' temperatures of the three lined skink studies were within the natural range of nest temperatures, and are unlikely to be thermally stressful to embryos. It may be that reaction norms for cognitive functions are not linear, but rather, may show inverse U-shaped curves with temperature (Noble et al. 2018). To clarify the generality of our findings, additional studies on lizards, using higher than normal (and stressful) incubation temperatures, are necessary.

What mechanisms might explain the differences in learning ability in hatchlings from our two incubation treatments? In vertebrates, a large proportion of brain development occurs during embryogenesis, making it highly susceptible to changes in the incubation environment (Purves and Lichtman 1985). In reptiles, incubation temperature may affect several biochemical pathways that influence brain development. In leopard geckos, a species with temperature dependent sex determination (TSD), incubation temperatures directly affected the volumes of the preoptic area and ventromedial nucleus of the hypothalamus, while an individual's sex influenced their metabolic capacity (Coomber et al. 1997; Crews et al. 1997; Sakata et al. 2000). Follow up work on this species showed that incubation temperatures induced differential expression of several genes involved in neural and gonadal differentiation (Pallotta et al. 2017). In three-lined skinks (*B. duperreyi*) lizards from an 18 ± 5 °C incubation treatment had larger telencephalons than lizards from a 24 ± 5 °C treatment irrespective to the body size, while incubation temperature also produced stark differences in neuronal density in the medial cortices (Amiel et al. 2017). While the molecular pathways responsible for these incubation-induced changes in brain structure in lizards have not been elucidated, it is clear that incubation temperatures can influence the structure and activity of parts of the brain involved in learning and social behaviours (Sakata and Crews 2004; Sakata et al. 2005).

Although our primary goal was to investigate how incubation temperature affected the learning ability of hatchlings, we also explored, to some degree, whether local cues influenced learning. We provided hatchlings with salient local cues consisting of a colour cue and a contrast cue, using blue colours that geckos can see, whilst keeping positional cues constant, and vice versa. Had geckos used positional cues (i.e. remember left, or right), then we would have expected to see differences across the four groups. However, no such effects were evident, but it could be that geckos used distal cues to navigate (since these were constant), or a combination of positional, local, and distal cues. Future studies, using a more elegant design, such as a Morris Water Maze, could help to answer the question of how lizards navigate (LaDage et al. 2012).

In conclusion, our results show that higher incubation temperatures that are likely to occur inside natural nests during prolonged summer heatwaves in future (Dayananda et al. 2016), produced poorer learners. While we do not know whether this incubation-induced effect is long-lasting, a previous mark-recapture study at one of our sites (Dharawal) showed that learning scores of hatchlings obtained in the laboratory were correlated with their subsequent survival in the field during their first year of life (Dayananda and Webb 2017). However, learning scores encapsulate several skills associated with spatial learning (speed, accuracy, memory), which makes it difficult to determine which aspects of cognition are subject to natural selection (Rowe and Healy 2014). Although current research on this question has focused mostly on birds and mammals (Morand-Ferron et al. 2016), many lizard species have high recapture rates (While et al. 2018), making them excellent model organisms for clarifying how developmental plasticity shapes cognitive traits, and whether those traits are subject to natural selection in the wild.

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Compliance with ethical standards

Conflict of interest Theja Abayarathna and Jonathan Webb declare that they have no conflict of interest.

Ethical approval All applicable international, national, and institutional guidelines for the care and use of animals were followed. The procedures described herein were approved by the UTS Animal Care and Ethics Committee (protocol #2012000256 to JKW). The collection of geckos from the study sites was approved by the NSW National Parks and Wildlife Service (scientific licence SL101013 to JKW).

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