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Egg incubation temperature influences the growth and foraging behaviour of juvenile lizards

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ABSTRACT

After laying their eggs, oviparous reptiles are reliant on the external environment to provide the required incubation conditions for successful embryonic development. Egg incubation temperature can impact the behaviour of various species of reptiles, but previous experiments have focused on the impact of incubation environment on hatchlings, with only a limited number of studies focussing on the longer-term behavioural consequences of incubation environment. This study investigated the effects of developmental environment on bearded dragon lizards (*Pogona vitticeps*) that were incubated at different temperatures within the natural range; half of them were incubated at a 'hot' temperature (30 ± 3 °C) and half at a 'cold' temperature (27 ± 3 °C). The growth and foraging behaviour of the lizards was then compared over 18 weeks of development. Although the lizards incubated at a cool temperatures grew more quickly, those incubated at the hotter temperature completed the foraging task more often and had significantly faster running speeds. These results show that egg incubation temperature impacts the foraging behaviour of juvenile lizards and suggest a potential trade-off between growth and foraging speed, which could influence an animal's life history trajectory.

1. Introduction

Sensitivity to environmental factors, such as egg incubation temperature, allows for the development of a variety of different phenotypes in oviparous reptiles (Deeming, 2004; Noble et al., 2018; Mitchell et al., 2018). Temperature-dependent sex determination is a well-documented example of this (Valenzuela, 2004) but incubation environment can also impact: hatching success, hatchling growth, physiology, morphology, locomotion, behaviour and cognition (Elphick and Shine, 1998; Flatt, 2001; Booth, 2004; Deeming, 2004; Burgess et al., 2006; Amiel and Shine, 2012; Amiel et al., 2014; Clark et al., 2014; Li et al., 2016; Siviter et al., 2017b,a). Despite this, there is a need for studies that investigate the longer term impact of egg incubation temperature on embryonic phenotypic plasticity beyond hatchlings (Mitchell et al., 2018). While evidence exists on the long-term impact of incubation environment on reptile morphology, size and survival (Mitchell et al., 2018), there are fewer studies that have investigated the potential impact on reptile behaviour (Elphick and Shine, 1998; Downes and Shine, 1999; Li et al., 2016; Siviter et al., 2017a,b; Noble et al., 2018).

The ability to forage effectively is crucial for survival. Lizards expend a large amount of energy foraging, making missed foraging opportunities extremely costly (Bennett and Gleeson, 1979). In certain cases, lizards can spend approximately 71% of energy expenditure on foraging, limiting the amount of time available for other activities such as finding mates and defending territories (Bennett and Gleeson, 1979). More importantly, if an animal cannot forage effectively it is more likely to grow at a slower rate, will take longer to reach sexual maturity, and is also more likely to die earlier (Dunham, 1978). Post hatchling growth is likely to be vital for reptile survival. In lizards, there are a variety of advantages to being bigger than a conspecific (Ferguson and Fox, 1984; Van Damme et al., 1992; Braña and Ji, 2000). Larger animals are more likely to retain body heat for longer, meaning that they can remain active for longer, (Avery et al., 1982) and are more likely to survive in times of hardship, such as during temperature drops (Ferguson and Fox, 1984). Further, social dominance in male lizards is strongly correlated with size (Ferguson and Fox, 1984; Tokarz, 1985) allowing dominant lizards to have control over resources, such as basking spots, food, territory and reproductive activity (Trivers, 1976; Stamps, 1977, 1984) while larger females produce larger clutches (Brandt and Navas, 2011).

The majority of studies assessing the impact of egg incubation temperature on behaviour have focused on hatchlings (for review see Mitchell et al., 2018). For instance, cold-incubated three-lined skinks

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(*Bassiana duperreyi*) exhibited more anti-predator behaviours than hot-incubated hatchlings despite comparable running speeds (Flatt, 2001). Pine snake (*Pituophis melanoleucus*) hatchlings incubated at cooler temperatures exhibited fewer anti-predator responses, were less effective at foraging, and were less likely to find shade during a thermoregulation test when compared with snakes incubated at hotter temperatures (Burger, 1991a,b, 1998). In one of the few studies to investigate the importance of incubation environment on reptile behaviour beyond hatchlings, Downes and Shine (1999) showed that incubation temperature can impact phenotypic traits, such as running speeds and the chemosensory response to a snake scent, for up to 42 days post-hatching in three species of Australian lizards. Similarly, Elphick and Shine (1998) showed that juvenile three-lined skinks incubated at a hotter incubation temperature were faster than those incubated at cooler temperatures. More recently, egg incubation temperature has been shown to have long lasting effects on cognition, with adult bearded dragon lizards (*Pogona vitticeps*) incubated at cool temperatures (average 27 °C) appearing to be quicker learners than those incubated at hotter temperatures (average 30 °C) (Siviter et al., 2017a). Despite this, we still have large gaps in our understanding of the longer-term effects of varying egg incubation temperature on the behavioural plasticity of oviparous reptiles.

In light of these issues we have examined the growth and foraging behaviour of bearded dragons incubated at two different temperatures. Bearded dragons typically live in deserts and woodland in central Australia where food is often scarce and males will fight for territories and reproductive opportunities (Brattstrom, 1971). Being able to forage effectively will give a lizard a direct advantage over competitors, as their longevity could increase. When bearded dragons are incubated within their optimal range (between 27 °C and 30 °C) the sex of the lizards is determined by genotypic sex determination (Ezaz et al., 2005, 2009; Holleley et al., 2015) making them an ideal species for this type of experiment. As we will show, differences in growth between lizards incubated at different temperatures were observed and as a result the ‘cold group’ was tested at the same age and the same mass as the animals incubated at the hotter temperature (‘hot group’). This allowed us to investigate the effects of egg incubation temperature on behavior when groups were matched for both age and size. We predicted that egg incubation temperature would influence bearded dragon foraging behavior, and that lizards incubated at hotter incubation temperatures would be more successful and quicker foragers (Burger, 1991a,b,1998).

2. Methodology

2.1. Animals

14 eggs from the same clutch were split into two groups of seven eggs at random and were incubated in multiple plastic boxes with vermiculite (Booth, 2004). The ‘hot group’, was incubated in a heat-controlled room maintained at an average temperature of 30 °C (± 3 °C) whilst the ‘cold group’ of eggs were incubated in a second heat-controlled room at an average temperature of 27 °C (± 3 °C). Animals in the ‘hot group’ hatched between 58 and 60 days (mean = 58.6 ± 0.3 days) after being laid, while the ‘cold group’ hatched between 83 and 91 (average 88.9 ± 1.0) days after being laid ($t = 28.76$ $p = 0.001$). See Siviter et al., 2017a for full details.

After hatching, the environmental conditions for rearing the lizards were kept the same for all animals: room temperature was maintained at 29 °C (± 3 °C) and the same food was provided for all animals. Initially the lizards were socially housed within the two treatment groups in two small glass vivariums (30 × 20 × 20 cm) and were later moved into bigger vivariums (145 × 48 ×60 cm) as they grew. All lizards had access to UV light, basking lamps and appropriate enrichment. The animals were not food deprived but were fed after their experiments were finished for the day. The lizards were sexed by vent inspection of the hemipenal bulges at 15 weeks of age and both groups contained 4 males and 3 females.

2.2. Experimental set-up and apparatus

An arena measuring 128 x 32.5 cm with 19 cm opaque high walls, was used for the foraging experiment. The wooden floor of the arena was marked at 25 cm intervals from the starting position up to the test distance of 1.0 m; these distances were used to calculate the speed of the lizards. A digital video camera (Sony HDR-CX22OE) was placed above the arena on a tripod and all trials were recorded. The testing room was maintained at 28.5 °C (± 1 °C).

2.3. Procedure: mass and size

The lizards were weighed (in grams) using an electronic scale (fx-3000i) every week from two weeks after hatching and were also measured (cm) throughout the testing period (from week 2 after hatching to 18 weeks post hatching). Body length was recorded with a tape measure from the snout to the vent. Tail length was recorded from the tip of the tail to the vent. These recordings were combined to give the lizard’s total length.

2.4. Procedure: foraging behaviour

The ‘hot group’ was tested 18 weeks after hatching, whilst for the ‘cold group’ was tested at 15 weeks post hatching as this was when the lizards were matched for mass (see results – Fig. 1). The ‘cold group,’ were then retested again at 18 weeks when they were the same age as the hot group.

All animals were habituated to the arena. During habituation trials, the lizards were individually placed at one end of the testing arena and a favoured food item was put at the opposite end. If the subject moved towards and ate the food on three consecutive trials, each of which was a maximum of 3 min long, it was considered habituated (Kis et al., 2015). This continued until all animals were habituated, which took 2 days.

At the start of each experimental trial the lizard was placed in the starting position, which was behind the zero-position line for speed calculation. A transparent plastic container (15.2 × 8 × 7.4 cm) containing a cricket was then placed in the arena 1.0 m from the lizard. The lizard had 3 min to approach the cricket. Once the lizard was within approximately 5 cm of the box, a second cricket was dropped in front of the lizard as a reward and the stimulus cricket was removed. The size of the cricket (1.4 cm in length) was kept constant for all trials. If the lizard did not approach the cricket within the 3-minute trial time then the stimulus was removed and the lizard was deemed to have been unsuccessful in that trial. To ensure that the lack of approach was not due to motivation, a second cricket was still presented. If the lizard did not eat the second cricket then the trial was excluded from the analysis.

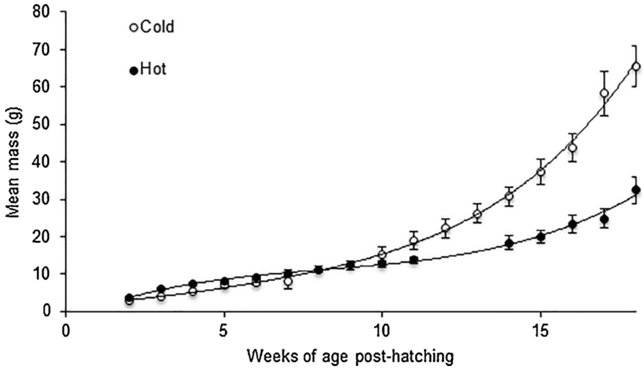

Fig. 1. Average mass (± SE) of bearded dragons incubated at 27 °C (‘cold group’) and 30 °C (‘hot group’) from 2 to 18 weeks from hatching.

Each lizard received 4 trials, regardless of success. This resulted in the ‘hot group’ having 26 completed trials, the ‘cold group’ at the same mass had 24 completed trials, and the ‘cold group’ at the same age had 28 completed trials. The order in which the lizards were tested was randomly assigned daily. Lizards from all treatments were tested between the hours of 9.00-16.00.

The video for each trial was analysed using Avidemux 2.6 software. The time taken for each lizard to move across each 25 cm segment of the arena was recorded and converted to speeds (metres per second). All videos were coded by HS. Ten percent of the videos were coded by a second coder who was blind to the experimental and incubation conditions. A Spearman’s rank correlation revealed an extremely strong correlation ($rho_8 = 0.97$, $p < 0.001$) between observers.

2.5. Data analysis

Our analysis used an information theoretic approach, whereby the initial model set included a full model containing all relevant factors. The full model was compared to other models containing all the subsets of the full model as well as a null model which just included the intercept and random factors. We selected models based on Akaike weights derived from AICc values, and in cases when models could not be rejected with a 95% certainty model averaging was used. The only exception to this approach was when analysis the foraging success (completed or not) data where our analysis did not allow this approach.

A linear mixed effects regression (lmer) model was used to assess the differences in the mass, tail length, body length and total length between incubation groups, with incubation temperature, sex, and week from hatching included in the full model and individual included as a random factor. Average foraging success (successful or unsuccessful) was calculated for each animal by assigning each trial a pass of fail mark (0 or 1) and the effect of incubation temperature and time was tested with a Kruskal Wallis test. Pairwise Wilcoxon tests were used to test differences in the successful trial completion data from the different test conditions ((i) hotter incubation group (ii) cooler incubation group same mass (iii) cooler incubation group same age). The foraging speed was analysed using a linear model with test condition and sex included as fixed factors and total body length of the lizards included as a covariate. We also included distance that speed was recorded (0.25, 0.50, 0.75, & 1 m) as a fixed factor, as lizards got progressively slower as they approached the cricket and thus it seemed to be an important variable to consider. Individual and trial were included as random factors (for full models and outputs see Tables S1 & S2). Analysis was conducted in R studio (version 1.0.136; R Core Development Team 2012)) and we used the packages *lme4* (Bates et al. 2015) & *MuMin* (Bartoń 2018).

3. Results

3.1. Impact of temperature on mass and size

Our results showed that by 10 weeks-of-age lizards in the ‘cold group,’ were heavier than those incubated at hotter temperatures, a trend that continued as both groups got older (Fig. 1; lmer: temperature, Z = 4.99, $p < 0.001$; temperature: week, Z = 17.50, $p < 0.001$). Lizards incubated at the cooler incubation temperature also had significantly larger tails, body lengths, and were therefore also larger in terms of total lizard length (see supplementary materials). We found no detectable impact of sex on any of the recorded measurements (for full list of results see table S1 & S2).

3.2. Impact of temperature on foraging behaviour

The lizards in the ‘hot-group’ completed the foraging task in every trial (27/27 motivated trials, i.e trials in which lizards ate provided crickets and were motivated to forage). By comparison, the ‘cold-group’ of bearded dragons failed to complete 9 trials out of 24 trials (38%) when they were matched for mass and failed to complete 11 trials out of 28 trials (39%) when matched for age (Fig. 2). An analysis of the mean foraging success showed a significant difference between the lizards from the three different treatment groups (Kruskal-Wallis test: $\chi^2 = 13.75$, $df = 2$, $p = 0.001$). Pairwise Wilcoxon tests revealed that the hot-incubated group was significantly more successful than the cold-incubated animals at both the same mass (w = 38.5, $p = 0.037$) and age (w = 38.5, $p = 0.034$). No differences were observed between the cold incubated lizards when tested at different times (w = 38.5, p = 0.941)

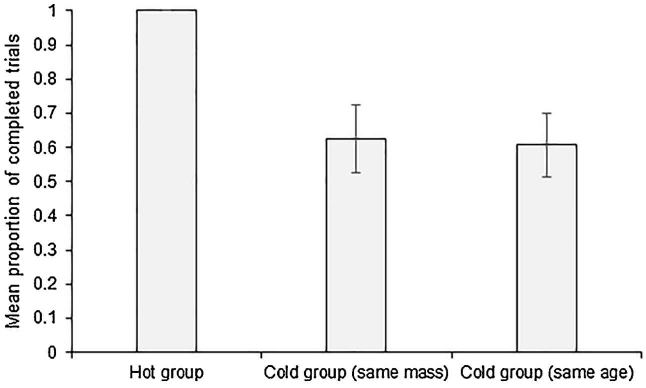

Fig. 2. Mean proportion (± SE) of trials that lizards from different test conditions completed.

Interestingly, the results showed no significant difference in the running speed of the two groups of lizards when matched for mass (Fig. 3; lmer: test condition - hot group & cold group same mass, Z = 0.92, p = 0.35). Lizards incubated at the hotter incubation temperature did however approach the crickets at significantly faster running speeds than lizards from the cold group when tested at the same age (Fig. 3; lmer: test condition - hot group & cold group same age, Z = 3.97, $p < 0.001$). *Post hoc* Tukey tests showed significant differences between the cold group tested at different times (Fig. 3; Tukey test: test condition – cold group same age & cold group same mass, Z = -3.76, $p < 0.001$) confirming that the lizard from the cooler incubation group were getting slower with increased mass.

4. Discussion

This experiment shows that egg incubation temperature impacts the post-hatching phenotypes of bearded dragons. Lizards incubated at a cooler temperature were significantly heavier than those incubated at the hotter temperature from 10 weeks of age adding to the evidence

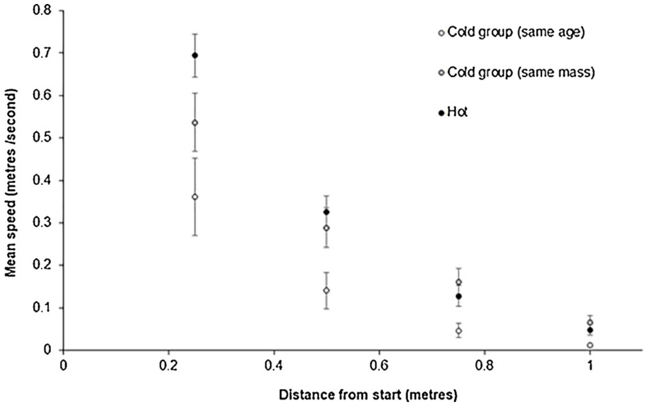

Fig. 3. Mean (± SE) running speeds for bearded dragons in the different test conditions measured at each 0.25 m intervals over the course of a 1 m track.

that egg incubation temperature influences lizard growth rates. This same trend was observed for multiple body dimensions, with lizards incubated at cooler temperatures being larger in all cases. By contrast, our results showed that the foraging speeds of juvenile lizards were significantly influenced by egg incubation temperature, with the hotter incubation temperature producing bearded dragons that had faster running speeds. Our results also showed that as the lizards from the cooler incubation group got larger their running speeds got slower, suggesting a potential trade-off between foraging ability and size/mass. These results demonstrate further how subtle differences in incubation environment can influence the phenotypes of oviparous reptile.

Egg incubation temperature has been shown to impact the growth of various different species of reptiles (Deeming, 2004). Previous studies have revealed that egg incubation temperature impacts the mass and size of lizard hatchlings, affecting body plan, head size and tail length (Alberts et al., 1997; Deeming, 2004; Noble et al., 2018; Mitchell et al., 2018). It would be expected that cooler incubation temperatures would produce larger animals, because incubation takes longer, allowing more time for nutrients from the yolk sac to be absorbed (Andrews, 2004). Alberts et al. (1997) showed that there were no size differences in Cuban rock iguanas hatchlings (*Cyclura nubila*) incubated at different temperatures but lizards incubated at a hotter temperature (31 °C) had faster post-hatching growth rates during their first year with differences persisting for up to 14 months. Van Damme et al. (1992) showed the opposite effect in wall lizard hatchlings (*Podarcis muralis*), with lizards incubated at cooler temperatures (24 °C) having quicker growth post-hatching to 20 days of age compared with lizards incubated at hotter temperatures (28 °C). Our results showed that bearded dragons incubated at a cool temperature grew more quickly than lizards incubated at a hotter temperature. While our results are limited to one clutch of eggs, the lack of any obvious directional trend of the effect of incubation temperature and growth between our data and other similarly related species (Mitchell et al., 2018) suggests that, although incubation temperature is clearly an important factor in determining reptile mass and size (Noble et al., 2018), the direction of these impacts are likely to be species specific and potentially related to the environment in which they are emerging (Deeming and Ferguson, 1989; Siviter et al., 2017a; Noble et al., 2018; Mitchell et al., 2018).

Egg incubation temperature can influence a range of different behaviours in oviparous reptiles, with running speeds and anti-predator responses typically being explored (Downes and Shine, 1999; Warner and Andrews, 2002; Deeming, 2004). Our methodology used a novel approach, which allowed lizards to move freely within an arena for foraging purposes. The results showed that bearded dragons incubated at a hot temperature had faster running speeds when foraging than those incubated at a cooler temperature, showing a similar trend to that observed in pine snakes and three lined skinks (Burger, 1991b; Elphick and Shine, 1998). By contrast, in the veiled chameleon (*Chamaeleo calyptratus*), chameleons incubated at a cool incubation temperature were faster at catching live prey (crickets) than those incubated at a hotter temperature (Ballen et al., 2015). Although it seems increasingly likely that incubation environment has an impact on oviparous reptile behaviour (Burger, 1991b; Elphick and Shine, 1998; Ballen et al., 2015; Siviter et al., 2017a,b; Dayananda and Webb, 2017), as with reptile growth, the directional effect appears to be species specific (Deeming, 2004; Noble et al., 2018).

The mechanisms that control differences in individual phenotypes are not that well understood. It has been suggested that embryonic sensitivity to environmental conditions, such as temperature, is adaptive as each individual egg in a clutch will have individual phenotypic profile as a consequence of temperature variance (Deeming and Ferguson, 1989,1991). Embryos that develop under different incubation temperatures may produce hatchlings that are suited to a variety of different environments, which is likely to increase survival and future reproduction (Deeming and Ferguson, 1989). While increasing evidence shows that incubation temperature will influence reptile fitness (Dayananda and Webb, 2017; Noble et al., 2018) the underlying mechanisms that drive 'how' incubation temperature influences reptiles are still poorly understood. Importantly, our results here show that egg incubation temperature can influence the growth and foraging behaviour of lizards beyond the early life hatchling phase on development, with potentially important consequences on life history trajectories.

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Conflict of interest

The authors have no conflicts of interest to declare.

Ethical approval

This experiment had approval from the College of Science ethical committee at the University of Lincoln (COSREC-2014-05), and the work was carried out in accordance with the relevant guidelines and regulations of the UK.

Informed consent

The animals are kept at the University of Lincoln and consent was given for their use.

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