Hotter nests produce smarter young lizards

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1. INTRODUCTION

An animal's developmental environment helps shape its phenotypic traits [1]. Thus, an adult's phenotype reflects not only its genetic constitution, but also the impacts of influences encountered earlier in life [2]. Indeed, the earliest developmental stages often are the most sensitive to external conditions [3]. Especially in oviparous species, where offspring develop outside the mother's body, incubation environments can have long-lasting effects [4,5]. Thermal, hydric and gas-exchange conditions all vary within [6] as well as among nests [7], generating variation among hatchlings in phenotypic traits such as sex, body size, shape and locomotor ability [5,8].

Most researchers have focused their attention on hatching traits that are easy to measure, and that are plausibly relevant to individual fitness. As a result, we have considerable data on developmental plasticity in traits such as morphology and locomotor ability, but a very limited understanding of how incubation environments affect behavioural traits such as learning ability (but see Burger [9]). Nonetheless, learning ability is important: a growing literature suggests that the resultant hatchling's learning performance. Hence, factors such as maternal nest-site selection and climate change affect not only the size, shape and athletic abilities of hatching reptiles, but also their ability to learn novel tasks.

Keywords: incubation; temperature; learning; climate change

2. MATERIAL AND METHODS

(a) Egg collection and incubation

We collected gravid three-lined skinks (Bassiana duperreyi) from the Brindabella Range, 40 km west of Canberra in the Australian Capital Territory, at elevations ranging from 1050 to 1700 m. Female lizards were transported to the University of Sydney, where they were kept in cages (22 × 13 × 7 cm) containing a substrate of moist vermiculite (water potential = −200 kPa) to lay their eggs. Newly laid eggs were weighed and transferred to individual 64 ml glass jars filled with the same vermiculite mixture (−200 kPa) and sealed with plastic cling wrap to prevent moisture loss during incubation. We tested hatchlings from 12 clutches between one and four months of age (six male and six female hot-incubated skinks and six male and six female cold-incubated lizards).

(b) Learning task

Reptiles are more likely to display significant learning if they are tested in a familiar environment [12]. Hence, we trained hatchlings with the same opaque plastic containers in which they were housed. The containers (64 × 41 × 21 cm) had a sand substrate, and two potential hides (inverted plastic flower-pot trays) positioned 60 cm apart. The hides were identical except that one had a Plexiglas cover over the opening, preventing ingress by the lizard. The position of the open and closed hides remained constant throughout the experiment, enabling lizards to learn the location of the open hide. Prior to the first trial, hatchlings had 24 h to acclimate to their surroundings. Water and crickets were provided ad libitum after daily testing. Room temperature was maintained at 24 °C, close to the mean body temperature recorded for this species in the field [14].

(c) Analyses

To compare learning ability among hatching lizards, we created an index of standardized learning scores (total number of successful ‘escapes’ in the last eight trials minus the total number of successful ‘escapes’ in the first eight trials). A positive score shows that a lizard located the retreat site more often in later trials, indicating learning.

We scored errors based on the first hide that the lizard attempted to enter. Statistical analyses were carried out using SPSS (v. 19.0.0) at a significance level of α = 0.05. We used ANOVAs to assess differences in learning scores among hot-versus cold-incubated hatchlings and male versus female hatchlings. We used correlation analysis to examine relationships between learning scores, body size and locomotor speed. ANCOVA with incubation treatment as the factor, SVL and speed as the covariates, and learning score as the dependent variable were used to explore the possibility that the effects of incubation treatment were secondary consequences of incubation-induced differences in size or speed.

3. RESULTS

Overall, hot-incubated lizards achieved higher learning scores than did cold-incubated lizards (mean learning score = 1.38, s.e. = 0.61, versus −1.11, 0.61; F1,19 = 9.36, p < 0.006; effect size r = 0.57; figure 1) and the number of errors they made decreased more from the first to the second half of the trials than was the case for cold-incubated lizards (F1,19 = 4.26, p = 0.05). Female lizards had non-significantly lower
ANCOVA (score remained significant even when lizard SVL and
\( p = 0.409 \)). The incubation-treatment effect on learning
ability in the honeybee, Apis mellifera [19]. Learning
responds plastically to prenatal and postnatal develop-
mental factors in humans [20] and rats [21]. Developmental stressors (e.g. drugs and alcohol)
applied during incubation cause learning deficits in
chickens [22]; however, the virtual absence of studies
on other oviparous taxa precludes any statements about the generality of incubation effects on learning.

The effects of incubation temperature on learning
ability may also have consequences for population-
level responses. For example, anthropogenically
induced shifts in air temperatures can influence nest
temperatures of ectotherms—and indeed, have already
affected nest thermal regimes in our study species,
B. duperreyi [23]. Thus, climate change may simul-
taneously generate novel challenges for post-hatching
organisms [24], while also modifying their ability to
respond flexibly to such challenges. In B. duperreyi,
hotter natural nests over recent decades (due to cli-
mate change: [23]) probably have produced hatchling
lizards with enhanced learning abilities. For other
species, however, the evoked plasticity may render
them less rather than more capable of dealing with a
changing environment. For example, some lizard taxa
sympatric with B. duperreyi benefit from cooler rather
than warmer incubation [25]. For such taxa, increas-
ingly warm nests may generate hatchlings that are
unlikely to possess the kind of behavioural flexibility
needed to confront novel challenges.

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4. DISCUSSION

The thermal regimes that lizards experienced during
incubation affected their learning ability after hatching.
This difference in learning ability does not appear to be
an indirect consequence of incubation-induced
shifts in other traits, because an animal’s learning
score was not related to its locomotor speed, body
size or sex; and the incubation effect on learning
remained significant even after controlling for these
other effects. Thus, our study adds learning ability to
a growing list of phenotypically plastic traits that incu-
bation temperature can modify during early squamate
development [5,8]. Our study was short-term, so it
remains possible that such effects are transitory; that is,
cold-incubated lizards eventually compensate through later development of learning abilities, or by
modifying other aspects of their behaviour. For example, an intrinsically poor learner might compen-
sate for that deficit by maintaining relatively high
temperatures, thus facilitating predator escape through
greater awareness and locomotor speed rather than
relying on cognitive faculties, such as spatial memory.
Future work could test that possibility.

What proximate mechanisms render learning sensi-
tive to incubation temperature? Endocrine pathways
can affect performance in learning tasks [15],
suggesting that incubation induced modifications
either to hormone levels or receptors may play some
role. Especially in reptile species with temperature-
dependent sex determination (TSD), such as B. dup-
perreyi, thermal regimes in the nest may affect the

hormones responsible for gonadal differentiation
[16,17]. These same hormones may influence brain
development [17]. Thus, thermal effects on hormone
levels during incubation may induce structural vari-
ation in parts of the brain that control behaviours such as learning [18].

Greater learning ability may facilitate an individual’s
responses to diverse environmental challenges, thus
increasing its chances for survival and reproduction.
Whether the effects of incubation temperature on
learning ability ultimately impact individual fitness
remains a challenge for future research. Our study is
just a beginning. We need studies on a broad range of
other taxa to determine whether it is commonly
true that an individual’s learning ability is modified
by the incubation regimes under which it develops.
We doubt that B. duperreyi is unique in this respect;
for example, incubation temperatures affect learning
ability in chickens [22]; however, the virtual absence of studies
on other oviparous taxa precludes any statements about the generality of incubation effects on learning.

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