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Thermal parental effects on offspring behaviour and their fitness consequences

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Environmental and developmental conditions can drive substantial variation in offspring behaviour and developmental trajectory. While incubation temperature is well known to influence development in oviparous animals, little is known of the role of parental temperature on offspring phenotype (i.e. thermal parental effects). Following exposure of male and gravid female jacky dragons, *Amphibolurus muricatus*, to one of two thermal treatments (short-bask versus long-bask) and incubation of their eggs at a constant temperature, we examined whether the preovipositional parental treatment influenced offspring performance-related behaviours. We detected main and interactive effects of parental treatment on offspring behaviours including feeding, exploration and antipredator. Sex-specific effects of parental treatment included long-bask sons being more likely to feed and being bolder following predatory attack than short-bask sons, while the differences between treatments for daughters were smaller. Behaviours were not consistent between 1 week and 1 month of age and showed little correlation across behavioural contexts. Some behaviours emerged as promising mechanisms of documented parental effects on offspring growth and survival in these individuals. In particular, boldness among long-bask sons in an antipredator context may be linked to their greater rates of growth posthatching. Overall, our findings suggest that thermal parental effects influence variation in animal behaviours relevant for subsequent fitness outcomes.

Parental effects occur when the parental environment impacts aspects of offspring phenotype in ways unrelated to the offspring's genotype (Bernardo, 1996). Maternal and paternal environment can affect the behaviour (e.g. Amiel & Shine, 2012), condition and morphology (e.g. Cadby, Jones, & Wapstra, 2014) and viability (e.g. Bonduriansky & Head, 2007) of offspring. The pervasiveness and evolutionary significance of such effects are now widely appreciated (Bernardo, 1996). Whether parental effects hold adaptive significance, however, remains an ongoing debate (Marshall & Uller, 2007; Mousseau, Uller, Wapstra, & Badyaev, 2009). Parental effects may be adaptive if the offspring environment is correlated with the parental environment (Reddon, 2012), and the altered offspring phenotype provides advantages in the anticipated environment. Such effects are termed ‘anticipatory parental effects’ (Marshall & Uller, 2007). Alternatively, parental effects can be detrimental for offspring if they act as a conduit for the transfer of negative environmental influences that decrease offspring fitness (Burgess & Marshall, 2011), or they may hold no adaptive value and be physiological side-effects (Marshall & Uller, 2007). Parental effects on offspring behaviour may be particularly important for fitness, since behavioural traits expressed early in life may influence the developmental trajectory of individuals via the differential fitness costs of a given predator avoidance or feeding strategy, mating tactic, cognitive ability or locomotor performance (Noble, Carazo, & Whiting, 2012; Stamps & Groothuis, 2010; Warner, Lovern, & Shine, 2008).

An important environmental aspect in driving the phenotypic plasticity of offspring is their developmental temperature, most notably in temperature-sensitive ectothermic species (Deeming, 2004). Because externally deposited eggs are particularly vulnerable to environmental conditions (Lorioux, DeNardo, Gorelick, & Lourdais, 2012), the emphasis for thermal parental effects in oviparous species has largely been on indirect, postoviposition environmental effects such as alterations in nest site selection and incubation temperature (e.g. Refsnider & Janzen, 2010; Schwanz & Janzen, 2008).

When parents carry eggs or embryos, temperature of the parental environment may also directly influence offspring

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developmental temperature (Lorioux et al., 2012). For viviparous (live-bearing) species in particular, the thermal environment experienced by developing embryos is a direct consequence of the maternal thermal environment (Shine & Harlow, 1993) and leads to phenotypic effects in offspring (Shine, 2006; Wapstra et al., 2009). Evidence for equivalent effects of parental thermal environment on offspring phenotype in oviparous (egg-laying) species, however, remains scarce, possibly as a result of the reduction or absence of embryo retention.

Nevertheless, there is growing evidence to suggest thermal parental effects preoviposition are possible. First, many mechanisms of parental effects are established prior to oviposition (e.g. Cohen & Wade, 2010), including epigenetics, egg size and variable deposition of egg yolk constituents (e.g. Cohen & Wade, 2010; Shama, Strobel, Mark, & Wegner, 2014; Warner et al., 2008). In some taxa, early embryonic development takes place within the mother prior to oviposition (Lorioux et al., 2012); in lizards, females retain developing embryos in utero for at least one-quarter of the total developmental period, during a time of altered thermoregulation (Lorioux et al., 2012; Shine, 2006). Second, studies emerging across a diversity of animal taxa demonstrate that parental temperature can impact offspring growth, survival and performance (e.g. Burgess & Marshall, 2011; Gilchrist & Huey, 2001; Salinas & Munch, 2012; Schwanz, 2016; Shine, 2006). Clearly, the temperature of oviparous parents has potential to exert profound influences on their offspring preoviposition.

Key behavioural traits related to feeding, predation, locomotor performance, exploration, cognition, aggression and boldness have been shown to be influenced by yolk hormones or incubation temperature (Stamps & Groothuis, 2010; Warner et al., 2008). Thus, there remains great unexplored potential for thermal parental effects to influence offspring behaviour preoviposition in ways related to their subsequent fitness. In reptile taxa, few studies have explored parental effects on offspring traits beyond those that are easy to measure, such as morphology and sex (Reddon, 2012). This has meant that the fields of parental effects and reptile behaviour have largely progressed independently of one another (Reddon, 2012), generating a limited understanding of how they may be linked and of subsequent ecological and evolutionary consequences.

Recent findings from a study on jacky dragons, *Amphibolurus muricatus* (Schwanz, 2016) showed that parental basking opportunity during preovipositional stages influenced the growth and survival of subsequent offspring. Offspring from parents subjected to a short-bask treatment had enhanced growth and survival throughout their first growing season compared to offspring from parents in a long-bask treatment. Effects on growth were sex specific, with long-bask sons and short-bask daughters growing faster than their same-sex counterparts. Here, we were interested in whether relevant and common offspring behaviours could explain the observed general advantage in 'short-bask' offspring and the sex-specific effects of parental treatment. Specifically, we examined offspring performance in feeding, exploratory and antipredator behaviours to (1) examine whether biologically realistic thermal variation in the parental environment during preovipositional stages can drive variation in offspring behaviour and (2) evaluate the association of such variation in offspring behaviour with patterns in growth and survival.

METHODS

Study Species

The jacky dragon is a medium-sized agamid lizard that occupies southeastern Australia (Cogger, 2000). Females produce on average two to three clutches of three to nine eggs per year. Offspring phenotypes exhibit strong sensitivity to temperature (e.g. via temperature-dependent sex determination), and significant parental effects on morphology, growth, survival and sex have been demonstrated (e.g. due to diet, Warner & Shine, 2005; Warner, Uller, & Shine, 2013; Radder, Warner, & Shine, 2007). Despite being influenced by multiple environmental factors, the outcomes and fitness consequences of this plasticity in jacky dragons is still poorly understood (Warner, 2014), making this species a promising model system for addressing thermal parental effects on offspring behaviour.

Study Design

All animals were housed indoors at the University of New South Wales as part of a large, continuing breeding colony. Breeding adults used in this experiment were either wild-caught in the 2012/2013 or 2013/2014 summers, or were laboratory-born offspring of wild-caught individuals. They had spent at least one hibernation cycle in the laboratory prior to this experiment in spring 2014. Because wild jacky dragons have a long flight distance, wild-caught animals were collected from the wild via the standard procedure of noosing. This required extending a fishing rod towards the animal and slipping a thin nylon line over their head to prevent them from running away. The animal was then captured by hand and the noose removed from their neck within 30 s. They were transported to the captive facility in an opaque bag in an air-conditioned vehicle to prevent visual or thermal distress (transport time <2 h).

As part of a larger experiment on thermal effects on reproduction (Schwanz, 2016), basking conditions of breeding adults were experimentally manipulated prior to and during egg formation to assess effects on offspring. Upon emergence from hibernation (August 2014), parents were randomly assigned between two treatment groups: animals in the 'short-bask' (SB; $N = 21$ females, 7 males) treatment were given 7 h of opportunity to bask under a 40 W incandescent bulb (from 09:00 to 16:00 hours), while those in the 'long-bask' (LB; $N = 21$ females, 7 males) treatment were allowed 11 h of basking (from 07:00 to 18:00). These basking durations were chosen based on a lower bound that is sufficient to allow reproduction (>5 h) and an upper bound estimating the maximum access to basking opportunities by wild jacky dragons (11–14 h; Schwanz, 2016). Under similar basking treatments, jacky dragons have been shown to bask as long as the opportunity is available, acquiring higher mean daily temperatures and staying closer to their preferred body temperature when basking opportunities are extended compared to when they are restricted (Halstead & Schwanz, 2015). Thus, extended basking treatments lead to greater total heat acquisition and greater matching to presumed physiological optima compared to restricted treatments.

Lizards were housed in cages of three females and one male to allow for mating and fertilization. Individuals were uniquely identified by toe clipping, performed upon capture from the wild or at 1 week of age for laboratory-born animals (see Ethical Note). Each animal received four to six crickets three times per week, ad libitum water and UV light (natural daylength adjusted every 2 weeks). Females were weighed weekly, and inspected daily for signs of gravidity and egg laying. Cages were searched daily for new eggs. Gravidity is accompanied by weight gain and typically involves obvious visual signs of eggs bulging under the wall of the abdomen. Egg laying can be detected by obvious deflation of the abdomen and loose folds of skin along a female's side, followed by confirmation of sudden weight loss. Maternal ID was assigned by the co-occurrence of new eggs in the cage and