Effects of basking opportunity on birthing asynchrony in a viviparous lizard

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The optimal degree of hatching asynchrony may depend on environmental conditions, with synchrony favoured in some environments and asynchrony in others. Therefore, in such a context there should be strong selection on the ability of females to adjust their degree of asynchrony facultatively to match local conditions. While this scenario has traditionally only been of interest to avian biologists, hatching asynchrony, and processes analogous to hatching asynchrony (i.e. birthing asynchrony), have now been identified in a number of nonavian taxa. For example, in an Australian lizard genus, *Egernia*, birth of offspring within a litter occurs asynchronously, with females having considerable control over the degree of asynchrony. As with birds, if the advantages of birthing asynchrony depend on the environment, females should facultatively adjust the degree of birthing asynchrony based on the prevailing conditions. We examined the birthing asynchrony patterns of female White’s skink, *Egernia whitii*, placed under different thermal environments (basking conditions) during gestation. We found that the birthing conditions females experienced during gestation influenced offspring phenotype, both directly, by affecting offspring size, and indirectly, by affecting birthing asynchrony patterns. Specifically, we showed that females held under reduced basking conditions increased the spread over which they gave birth compared to females held under extended basking conditions. As birth spread can influence both offspring growth and survival, our results suggest strong selection on female behaviour (e.g. basking and birthing) in order to maximize offspring and/or parental fitness.

Maternal effects arise when the phenotype of a female affects the phenotype of her offspring, over and above that of her direct genetic effects (Rossiter 1996; Mousseau & Fox 1998; Ransanen & Kruuk 2007; Uller 2008) providing a bridge between maternal and offspring environments (Duckworth, 2009; Mousseau et al. 2009). One specific way in which this can occur is through alteration of the social environment during pre- or postnatal development (e.g. sex ratio adjustment, Oddie 2000; Uller et al. 2004; clutch size/number adjustment, Messina 1998; Plaistow et al. 2007). Perhaps the best example comes from avian systems and is achieved through maternal adjustment of hatching asynchrony (Wiebe 1995).

Hatching asynchrony, in particular the degree of spread and an individual’s hatching position, can have significant effects on offspring competitive ability and competition levels within the brood, which themselves influence offspring growth and survival (e.g. Badyaev et al. 2002; Johnson et al. 2003; Stienen & Brenninkmeijer 2006). Given the links between offspring survival and hatching asynchrony associated with increased competition levels, theory predicts that where the benefits of competition are context dependent (i.e. driven by environmental conditions), and those conditions are not predictable, selection should favour plasticity in asynchrony (Pijanowski 1992; Wiebe 1995). For example, high levels of within-brood competition are suggested to be beneficial when conditions are poor, as they allow for simple brood reduction, alleviating pressure on parents when resources are limiting (Lack 1954; Pijanowski 1992; Wiebe 1995). Therefore, under suboptimal conditions, females are predicted to increase the level of asynchrony within their broods facultatively (Wiebe 1995). In contrast, under good conditions, a decreased hatch spread is predicted to be favoured, as it reduces sibling competition and the associated decrease in offspring survival, allowing the maximum number of offspring to fledge (Wiebe 1995). However, despite the fact that examining shifts in the degree of asynchrony according to environmental factors could provide valuable insights into the adaptive significance of hatching asynchrony (Wiebe et al. 1998; Vinuela 2000; Valkama et al. 2002), there have been few experimental or correlational studies that have examined plasticity in hatching asynchrony.

While the above scenarios have traditionally only been of interest to avian biologists, the extent to which the environment affects female asynchrony decisions may also be of importance to other taxa (e.g. Smiseth et al. 2006, 2008; While et al. 2007; Smiseth & Morgan 2009). In the majority of reptiles, females typically
lay their eggs synchronously, or, in the case of viviparous species, give birth to their entire litter synchronously (Norris 1997; but see Radder & Shine 2007). However, the viviparous Australian lizard genus Egernia differs from this pattern. Within many species of Egernia, birth within litters occurs asynchronously (up to 9-day intervals between first- and last-born offspring; Duffield & Bull 1996; Chapple 2005; While et al. 2007), with considerable variation between females in the degree of spread between births within years and in the average spread between years (While et al. 2007). Unlike birds, birthing asynchrony is not a result of developmental asynchrony but rather females delay the birth of fully developed offspring (While et al. 2007). Furthermore, the extent to which females give birth asynchronously has significant effects on offspring fitness through differences in growth rate, performance and survival (While & Wapstra 2008; While et al., in press a). Importantly, female control over parturition, variation in birth spread and effects on offspring fitness are the key traits on which selection for facultative manipulation of birth spread could act (Wiebe 1995). Therefore Egernia represents an ideal organism with which to examine the causes and consequences of facultative hatching/birthing asynchrony.

In avian systems, facultative hatching asynchrony has been primarily associated with variation in food availability as this is the key trait influencing offspring growth and survival (e.g. Wiebe et al. 1998; Vinuela 2000; Valkama et al. 2002). In contrast, the key environmental factor for many biological processes in reptiles is temperature. Not only does temperature dictate activity patterns and resource availability, but it can also be important during development, shaping offspring morphology (including sex), physiology and behaviour (e.g. Rhen & Lang 1995; Shine & Harlow 1996; Wapstra 2000; Wapstra et al. 2004). Furthermore, an individual's growth rate and adult body size are highly dependent on its ability to thermoregulate (Adolph & Porter 1993; Sinervo & Adolph 1994). Even in areas of high food availability, if thermal resources are limiting, metabolism and, therefore, growth rate are constrained by the thermal environment (Sinervo & Adolph 1989; Carlsbeek & Sinervo 2002). Therefore, temperature can exert a strong influence on fitness-related traits within both the pre- and postnatal environments, and acts as a strong selective force on female incubation and basking behaviour in both oviparous and viviparous species (e.g. Bernardo 1996; Doody et al. 2004; Wapstra et al. 2004).

Specifically, temperature is likely to have a significant impact on a number of factors that influence the costs/benefits of birthing asynchrony in Egernia. Egernia typically live in small family groups characterized by intense competition for resources, high levels of conspecific aggression and high levels of juvenile mortality (Chapple 2003; Sinn et al. 2008). Birthing asynchrony is thought to be an adaptation to this highly competitive social environment (While & Wapstra 2008; While et al., in press a), with the establishment of a size hierarchy promoting dispersal of subordinate offspring and philopatry of dominant offspring, the latter gaining access to resources (including basking sites) and protection from conspecific aggression (see Bull & Baghurst 1998; O’Connor & Shine 2004; Sinn et al. 2008). Importantly, the costs and benefits of parental tolerance and consequently offspring dispersal are likely to be governed by resource availability within the parental home range (Komdeur 1992; Baglione et al. 2005; Covas & Griesser 2007). For example, in Egernia, there is yearly variation in the number of offspring tolerated within the parents’ home range, which may be linked to resource availability (While et al., in press b). As the key resource for reptiles is an ability to thermoregulate, temperature represents an ideal starting point from which to examine the effects of environmental conditions on female birthing asynchrony behaviour. Crucially, we can make similar predictions to those made in avian systems. Under good thermal conditions, where resources within the parental home range can support multiple offspring, females should facultatively reduce their birth spread to decrease sibling competition and reduce offspring dispersal. Alternatively, under poor thermal conditions, females should increase birth spread to increase sibling competition and facilitate dispersal of subordinate offspring.

To address these predictions, the primary aim of this study was to examine experimentally how thermal environment/basking availability influence female birthing asynchrony patterns and the consequences for offspring phenotype and the level of within-litter sibling competition in White’s skink, Egernia whitii.

METHODS

Study Species

White’s skink is a medium-sized (up to 100 mm snout–vent length) viviparous lizard found throughout a broad range in southeastern Australia. Egernia display relatively complex sociality, with considerable variation in social organization both between and within species (reviewed in Chapple 2003). We used skinks from a population on the east coast of Tasmania, Australia (42° 57’S, 147° 58’E). In Tasmania, E. whitii live in small family groups based on a monogamous male/female pair bond (While et al., in press b), similar to that found in mainland populations (Chapple & Keogh 2006). Birthing asynchrony, hereafter defined as a spread in birth separated by a minimum of 12 h (i.e. not within the same day), has previously been documented in this species, occurring in 100% of litters (While et al. 2007). In the field, females give birth to offspring with an average of approximately 2 days between births (range 1–9); however, the spread of births varies between litters within years and in the mean spread between years (While et al. 2007).

Field and Laboratory Procedures

We caught 44 female Egernia, using mealworm fishing or noosing techniques, at the onset of gestation in spring (October). Given our aim was to examine the effect of maternal basking behaviour on aspects of birthing asynchrony, we palpated females in the field and retained only those assigned to have more than one follicle/developing embryo. Egernia whitii litter sizes vary from one to four in this population (see While et al. 2007). Palpation of embryos involves gently rolling the fingers along the abdomen and confirming the presence (and number) of recently ovulated eggs/follicles. Palpations are completed in less than 5 s and have no adverse effects on the embryo. There are no differences in offspring size, weight or embryonic development between offspring used in this experiment and those from our natural population studies in which palpation is not required (e.g. While et al. 2007). Once, caught, female lizards were taken to the laboratory in cloth bags filled with vegetation and cooled with water to minimize stress, specifically heat stress. Travel time from the field site to the laboratory was less than 1 h. Once in the laboratory, females were weighed (±0.1 mg), measured for length (snout–vent and total length ± 0.5 mm), and housed individually in plastic terraria (30 × 60 cm and 40 cm high) in a room maintained at an ambient temperature of 14 °C throughout the day and 10 °C at night. Each terrarium was supplied with a 40 W spotlight suspended 15 cm above a basking rock, food (Tenebrionid larvae, crushed fruit) and water. Females were randomly assigned to two treatment groups representing different thermal regimes (each creating a temperature gradient from ca. 35 °C at the basking surface and ca. 14 °C at the shelter; Wapstra 2000). Each regime allowed females to bask to their preferred body temperature of 34 °C (Bennett & John-Adler 1986) for a different length of time per day, with 22 females kept in...
a short basking treatment (4 h access to the heat lamp per day) and 22 females in a long basking treatment (10 h access to the heat lamp per day). These conditions represent the variation in temperature typically encountered during gestation by skinks at this site (Wapstra et al. 1999; Wapstra 2000) and result in birth dates that typically fall either side of the birth dates of a typical year (Wapstra et al. 2009). Bright overhead lights provided identical daylengths for both treatments. These were set to come on at 0600 hours and were turned off at 1800 hours, resulting in a 12:12 h light:dark photoperiod for all females in both treatments. All individuals were maintained under these conditions until offspring were born. Each terrarium was positioned randomly with regard to the experimental treatment, with terraria repositioned between shelves fortnightly throughout the experimental period to minimize positional effects.

At the end of gestation (late January) until the completion of the experiment (April), terraria were checked hourly for birth of offspring. At birth, birth date, offspring weight (±1 mg), snout–vent length and total length (±1 mm) were recorded. In addition to offspring morphometrics, birthing asynchrony characteristics, including birth order and spread between births within a litter (total and average spread between births in hours), were also recorded. Offspring were then returned to their mother’s terraria. Offspring from 13 randomly chosen litters from each treatment were then held, with their mother and siblings, for a 3-week period following birth under identical conditions to those experienced during gestation. During this time they were supplied with food and water ad libitum so that neither resource was limiting. As asynchronous hatching/birth normally results in a size hierarchy being established within a litter (e.g. Vinuela 1996), including in our species (While & Wapstra 2008), we calculated the difference in size between siblings within a litter, as a proportion of the average offspring mass, at both birth and 3 weeks using the formula [(mass of the largest in a litter – mass of the smallest in a litter)/average mass of the litter] × 100 (e.g. Vinuela 1996; While & Wapstra 2008). After the experiment, all females and their offspring were returned to their exact site of capture.

**Statistical Analysis**

Differences in female characteristics (morphometric and reproductive), birthing asynchrony characteristics and offspring clutch characteristics were all analysed using general linear models (GLM; PROC GLM). For all models treatment was entered as a fixed factor. As spread of births between offspring may depend on clutch size, for examination of birthing asynchrony characteristics clutch size was included as a covariate. Individual offspring characteristics were analysed using a general linear mixed model (GLMM; PROC MIXED). Female identity nested within treatment was included as a random factor and treatment as a fixed factor. To determine whether the between-treatment results were driven by the effect of treatment on date of birth (see Results), we also examined within-treatment effects of date of birth on offspring characteristics using a general linear mixed model (GLMM; PROC MIXED). In this model, offspring birth order position was included to examine whether females were differentially allocating resources based on offspring birth order. Thus, we included female identity as a random factor, birth order position as a fixed factor, and date of birth as a covariate. We were unable to achieve this by adding date of birth to the original model (testing differences between treatments) because of the strong difference in date of birth between treatments (see Results; Quinn & Keogh 2002).

For all mixed models, significance of fixed effects was tested using F tests, with the degrees of freedom calculated using the Satterthwaite’s approximation (Littell et al. 1996). All models started with the full model including all interaction terms and we subsequently eliminated nonsignificant interaction terms backwards, starting with higher order interaction terms, at P values >0.25 (Quinn & Keogh 2002). We report here results for models containing all main effects following backward elimination. All data were checked for violations of assumptions, including homogeneity of slopes where covariates were used. For all analyses we log transformed average spread between births as inspection of the data showed it was right skewed. Means ± SEs are reported throughout. Owing to mortality of offspring throughout the experiment, sample sizes differed between analyses. All analyses were carried out in SAS STAT version 9.2 (SAS Institute Inc., Cary, NC, U.S.A.).

**Ethical Note**

Collection of lizards and experimental methods were approved by the University of Tasmania’s Animal Ethics Committee and the Tasmanian Department of Primary Industries and Water.

**RESULTS**

Of the 44 females brought into the laboratory to give birth, 38 did so resulting in 80 offspring; the remaining six females either failed to give birth (N = 4), or gave birth to stillborn offspring (N = 2). Twenty-one females in the long basking treatment gave birth to 46 offspring (average litter size: 2.25 ± 0.10) and 17 females in the short basking treatment gave birth to 34 offspring (average litter size: 2.08 ± 0.08; Table 1). Of these 38 females, five (four in the short basking treatment and one in the long treatment) gave birth to only one offspring, reducing the number of litters to 20 and 13 in the long and the short basking treatment, respectively.

There were no differences between basking treatments in female snout–vent length, body mass at the beginning of gestation or litter size (Table 1). This result remained when litters in which females had single offspring were added to the data set (χ² = 1.83, P = 0.18). Relative clutch mass (sensu Shine 1980) did differ between treatments, with females giving birth to relatively heavier litters in the long basking treatment than in the short basking treatment (Table 1). Date of offspring birth, and therefore gestation length, also differed significantly between treatments, with females in the long basking treatment giving birth earlier than females in the short basking treatment (F₁,₁₂ = 125.40, P < 0.01; Fig. 1).

Basking treatment had a significant effect on the degree of birthing asynchrony within a litter, with the log transformed average spread between birth of each offspring greater for females from the long basking treatment than for those in the short basking treatment (Table 1, Fig. 2). There was no effect of treatment on the size of the litter mass hierarchy created at birth; however, at 3 weeks litters from females kept in the long basking treatment, and therefore with the longer spread between births, had a greater litter mass hierarchy than those in the shorter basking treatment (Table 1). Basking treatment did not have a significant effect on offspring survival to 3 weeks (χ² = 0.02, P = 0.90).

Basking treatment, and its concomitant effect on gestation length/birth date, also had effects on offspring mass at birth, with offspring born to females under the long basking treatment larger than those born to females under the short basking treatment (Table 2). This difference was not mirrored when we examined offspring snout–vent length at birth (Table 2), suggesting an associated decrease in offspring condition between the two conditions (we could not assess offspring condition itself because of the lack of a relationship between mass and snout–vent length). Mass at birth did not differ between offspring born in different birth order positions in either basking treatment (long: F₂,₂₅₁ = 1.52, P = 0.24; short: F₁,₁₁₅ = 1.91, P = 0.19).
TABLE 1

Characteristics of female *Egernia whitii* held under long and short basking treatments

<table>
<thead>
<tr>
<th>Female trait</th>
<th>10 h basking</th>
<th>4 h basking</th>
<th>N</th>
<th>Statistic</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Snout–vent length at birth (mm)</td>
<td>30.90±0.74</td>
<td>29.79±0.65</td>
<td>13</td>
<td>F1,32=0.32</td>
<td>0.56</td>
</tr>
<tr>
<td>Initial mass</td>
<td>13.00±0.37</td>
<td>13.00±0.33</td>
<td>13</td>
<td>F1,32=0.01</td>
<td>0.91</td>
</tr>
<tr>
<td>Litter size</td>
<td>2.25±0.10</td>
<td>2.08±0.08</td>
<td>13</td>
<td>F1,32=16.77</td>
<td>0.04</td>
</tr>
<tr>
<td>Relative clutch mass</td>
<td>0.23±0.01</td>
<td>0.18±0.01</td>
<td>13</td>
<td>F1,32=15.65</td>
<td>0.01</td>
</tr>
<tr>
<td>Spread of birth (h)</td>
<td>33.85±5.71</td>
<td>18.07±3.20</td>
<td>13</td>
<td>F1,32=6.76</td>
<td>0.01</td>
</tr>
<tr>
<td>Litter mass hierarchy (birth; %)</td>
<td>7.43±1.42</td>
<td>7.24±1.60</td>
<td>11</td>
<td>F1,32=0.91</td>
<td>0.37</td>
</tr>
<tr>
<td>Litter mass hierarchy (3 weeks; %)</td>
<td>27.53±7.49</td>
<td>9.60±2.64</td>
<td>9</td>
<td>F1,32=5.61</td>
<td>0.03</td>
</tr>
</tbody>
</table>

Means are shown ±1 SE. Significant P values are given in bold.

DISCUSSION

Our results show that the thermal regime to which a female lizard is exposed during gestation can have significant effects on offspring traits. These maternal effects were primarily indirect and mediated by the influence of basking opportunity on gestation length/date of birth and on female birthing asynchrony patterns. This resulted in significant differences between treatments in offspring mass at birth and the establishment of sibling size hierarchies. As both date of birth and spread between births can have further effects on offspring growth and survival (e.g. Olsson & Shine 1997; Wapstra 2000; Atkins et al. 2007; Warner & Shine 2007; While & Wapstra 2008), our results suggest there is strong selection on female behaviour (e.g. basking and birthing) in order to maximize offspring and/or parental fitness.

In contrast to the patterns predicted by theory (Wiebe 1995), females with extended basking opportunities had a greater spread between births than those with reduced basking opportunities. These results are likely to have significant effects on offspring phenotype and fitness as shifts in the extent of birthing asynchrony in *Egernia* can result in the establishment of a litter size hierarchy, which itself exerts a strong influence on offspring growth and survival (While & Wapstra 2008). While we did not examine the long-term consequences of birth spread on offspring growth and survival in this study, we did examine the establishment of the litter size hierarchy. In line with the above prediction, we found that although there were no differences in the sibling size hierarchy produced between the two treatments at birth, after 3 weeks litters in the extended basking treatment, and therefore with the larger spread between births, had a significantly greater size hierarchy than litters in the reduced basking treatment. Thus, the prolonged spread between births of females with extended opportunity to bask appears to result in increased competitive asymmetries between siblings. Similar effects have been observed in avian systems where hatch spread has been shown to influence within-brood competition levels (Mock & Ploger 1987; Vinuela 1996; Hillstrom et al. 2000), as well as offspring growth (Vinuela 1996, 2000; Wiehn et al. 2000) survival (Hillstrom et al. 2000; Vinuela 2000; Wiehn et al. 2000) and parental care load (Hussell 1972; Slagsvold et al. 1994). However, as all offspring were kept under identical postnatal conditions to those of their mothers during gestation we cannot determine whether these results were driven by the differences in birth spread between the two treatments or were a result of postnatal basking conditions on offspring growth.

The above results raise an obvious question: are these maternal effects, specifically the shift in birth spread in relation to thermal regime (and the potential effects on the litter mass hierarchy and offspring phenotype), adaptive or a direct physiological/transmissive response to temperature (e.g. Marshall & Uller 2007)? While this remains to be explicitly tested, our results suggest the former. First, we have shown previously that birthing asynchrony in this species is not a result of physiological constraints on asynchronous embryo development but rather females delay giving birth to all offspring synchronously despite their being fully developed (While et al. 2007). This suggests that the timing of birth for each individual offspring is under female control (While et al. 2007; While & Wapstra 2008) allowing for facultative manipulation of birth spread. Second, if shifts in birth spread were driven by a direct physiological response to basking treatment, potentially related to temperature-dependent embryo development (e.g. Shine & Harlow 1996), we would expect females to have a reduced birth spread in the longer basking treatment where development would be most rapid. We observed the opposite, suggesting differences in birth spread between the two treatments were not driven by differences in offspring development but rather by female control of parturition, resulting in facultative shifts in birthing asynchrony patterns.

Figure 1. Frequency of births for female *Egernia whitii* held under both long (●; N = 46 births) and short (○; N = 34 births) basking conditions during gestation. Week 1 begins 15 January 2007 and week 14 thus begins 16 April 2007.

Figure 2. The difference in spread of births (h) between females held under long (N = 20) and short basking treatments (N = 13).
If the patterns observed in this study are the result of adaptive evolution, then we need to consider how an increased birth spread, and the associated establishment of a size hierarchy, is beneficial under good conditions? These patterns are opposite to theoretical predictions, which suggest that increased hatch/birth spread should be favoured in suboptimal conditions (Lack 1954; Pijanowski 1992; Stoleson & Beissinger 1995; Wiehn et al. 2000; Forbes et al. 2001; Smiseth et al. 2008). We suggest that the principal explanation for the contrast between our system and avian systems is the effect of environmental conditions (thermal regime) on other fundamental offspring traits, such as birth date, within reptile systems. For example, selection against birthing asynchrony (or hatching asynchrony) in suboptimal conditions may occur if the associated later birth date reduces the benefits of the sibling hierarchies. This could occur if (1) prolonged gestation reduces the opportunity to establish sibling hierarchies prior to hibernation, or (2) offspring natal dispersal, which may be driven by the creation of sibling hierarchies (Wapstra & Wapstra 2008; see also Duckworth, 2009), is more costly late in the season. As Egernia are reliant on constructed crevice sites for their basking and foraging activity as well as for shelter (Chapple 2003), this latter scenario may occur if late-born dispersing offspring are unable to establish their own crevice sites (away from their parents’ home range) before the onset of winter. Alternatively, these results may be explained as a mechanism by which females reduce the costs of delayed parturition itself. For example, the poor thermal conditions during gestation had negative effects on offspring phenotype (mass at birth), potentially related to the increase in gestation length (Wapstra 2000). This is consistent with research into other reptile systems in which delayed parturition has been shown to have significant consequences for offspring size, growth, and survival across a range of taxa (e.g. Olsson & Shine 1997: Wapstra 2000; Warner & Shine 2005, 2007; Atkins et al. 2007). Therefore, it may be a reduction in the spread of birth itself, rather than in the hierarchy produced, that drives female manipulation of birthing asynchrony patterns in this system.

The results from this study have demonstrated the strong effect of thermal environment/basking opportunities on maternal birthing asynchrony behaviour. However, the degree of variation in birth spread between females within both treatments, despite mean level shifts, suggests that we do not yet fully understand the extent to which birth spread is individually optimized within Egernia. While females may be constrained in their birthing asynchrony decisions under suboptimal basking conditions, we believe that individual optimization of birth spread, for females in both treatments, is likely to be governed by additional factors (environmental and social). For example, although indirect, the level of parental care in Egernia potentially imposes significant short- and long-term costs on females through increased energy expenditure, competition for resources, infanticide and predation risk (O’Connor & Shine 2004; Sinn et al. 2008; see also While et al. 2009). Thus, the optimal level of birth spread, and sibling competition, may be governed by additional (social) factors that also influence the costs of parental care, such as territory size/quality, level of competition/social density or female age (see also Planka & Parker 1975; Baglione et al. 2006; Plaistow et al. 2007). While this remains to be tested in the wild, it allows predictions regarding where differences in the extent of birthing asynchrony may be found within natural populations. Testing these predictions will allow us to examine links with common factors driving hatching asynchrony patterns within other taxa.

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