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Long-lasting effects of among- but not within-litter timing of birth in a viviparous lizard

Geoffrey M. While[1], Tobias Uller[2], Jo McEvoy[1]
and Erik Wapstra[1]

[1]*School of Zoology, University of Tasmania, Tasmania, Australia and*
[2]*Edward Grey Institute, Department of Zoology, University of Oxford, Oxford, UK*

ABSTRACT

Background: Early developmental conditions can influence within- and among-brood variation in the timing of hatching/birth, which has been shown to affect offspring survival, growth, and reproductive success across a range of species.

Problem: How does within- and among-litter variation in the timing of birth affect offspring growth and survival in *Egernia whitii*?

Organism: *Egernia whitii*, a long-lived social reptile that exhibits within-litter variation in its timing of birth (i.e. birthing asynchrony).

Methods: We measured offspring growth and survival in a natural population of *E. whitii* by following three cohorts of offspring from birth to their second year of life (the year before the onset of reproduction).

Conclusions: (1) Year of birth is the strongest predictor of offspring survival over the first 2 years of life. (2) The effects of year of birth on offspring survival over the second year of life are independent of its effects over the first. (3) Within-year date of birth is the strongest predictor of offspring growth over the first 2 years of life, with offspring born early in the year having greater growth over their first 2 years of life than offspring born later in the year. (4) Examining only growth over the second year of life (i.e. controlling for growth over the first year) removed the effect of date of birth on offspring growth. (5) There are no effects of within-litter timing of birth (i.e. birthing asynchrony) on offspring growth or survival.

Keywords: birth date, *Egernia whitii*, hatching asynchrony, maternal effects.

INTRODUCTION

Early environmental conditions can have both short- and long-term consequences for individual fitness. Such conditions frequently involve maternal effects (Mousseau and Fox, 1998; Uller, 2008). In ecological settings, this has been most extensively studied in birds, where both

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Correspondence: G.M. While, School of Zoology, University of Tasmania, Private Bag 05, Tasmania 7001, Australia. e-mail: gwhile@utas.edu.au

within- and among-brood variation in developmental conditions, in particular the timing of hatching, has been shown to affect offspring growth, survival, and reproductive success (summarized in Lindstrom, 1999). Generally, offspring from later broods frequently have lower survival than offspring from earlier broods and this effect may last past fledgling (Perrins, 1967; Sheldon *et al.*, 2003). Timing of hatching within broods (i.e. hatching asynchrony) can also have significant effects on offspring phenotype and fitness (for a comprehensive review, see Stoleson and Beissinger, 1995). In particular, the degree of hatch spread and an individual's hatching position can mediate 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 and Brenninkmeijer, 2006). However, while the short-term consequences of hatching spread and position are well documented and frequently strong, the long-term consequences have been less well studied, despite the fact that it may be important for understanding selection on hatching asynchrony (Mock and Forbes, 1994).

Short- and long-term effects of the timing of hatching or birth are not well studied in reptiles. However, recent research has identified consistent, and in some cases long-lasting, effects of between-litter variation in hatch/birth date across a range of squamate reptiles (Olsson and Shine, 1997; Madsen and Shine, 2000; Qualls and Shine, 2000; Wapstra, 2000; Warner and Shine, 2005, 2007). In contrast, differences in within-litter timing of hatching or birth are virtually absent, as individual females typically lay their eggs, or give birth, synchronously (Norris, 1997; but see Radder and Shine, 2007). The viviparous lizard genus *Egernia* diverges from this pattern. Although embryo development within litters is synchronous, birth is spread over several days [i.e. birthing asynchrony (While *et al.*, 2007)]. This within-litter variation in the timing of birth is analogous to hatching asynchrony in birds and results in the creation of sibling size hierarchies that influence offspring growth and survival (While and Wapstra, 2008, 2009). In birds, the order of hatching is the primary mechanism governing the development of sibling hierarchies, and thus offspring size and survival, with first hatched offspring gaining an advantage over later hatching offspring through increased opportunity for growth and increased competitive ability (e.g. Badyaev *et al.*, 2002; Johnson *et al.*, 2003; Stienen and Brenninkmeijer, 2006). In contrast, short-term studies have failed to identify any effect of birth order on offspring size (both relative and absolute) or survival within *Egernia* (While and Wapstra, 2008). However, the long-term effects of birthing asynchrony are yet to be examined in natural populations. As the consequences of birthing asynchrony in the wild may be reliant on parameters unable to be replicated within the laboratory (e.g. the opportunity to disperse, the use of parental home ranges, the level of conspecific competition), examining the long-term effects of birthing asynchrony within a natural setting may give us valuable insights into the factors responsible for the evolution and maintenance of birthing asynchrony within this genus.

The aim of this study was to examine how within- and between-litter variation in the timing of birth affects offspring growth and survival within *Egernia whitii*, by following three cohorts of offspring from birth to their second year of life – that is, the year before the onset of reproduction (Chapple, 2005).

MATERIALS AND METHODS

Study species

White's skink (*Egernia whitii*) is a medium-sized (up to 100 mm snout-to-vent length) viviparous lizard found throughout southeastern Australia. Our study population is located at Orford, on the East Coast of Tasmania, Australia (42°57′S, 147°88′E). Males and females are sexually monomorphic, become reproductively mature at approximately 3 years, and display an overall lifespan of 9–10 years (Chapple, 2003). Reproduction is annual, with mating typically occurring during the spring (September to October) and gestation spanning 3–4 months (While *et al.*, 2007, in press). Birthing asynchrony has previously been documented in this population, and was reported to occur in 100% of litters (While *et al.*, 2007). In the field, females give birth to offspring with an average of 2 days between births (range 1–10 days), which, under experimental conditions, results in formation of size hierarchies (While and Wapstra, 2008, 2009). However, spread of births varies between litters within years and in the mean spread between years (While *et al.*, 2007).

Field and laboratory data collection

We conducted the field study during the lizards' activity season (August to April) over three consecutive years (2005 to 2007), with the methodology identical for all three field years (for detailed description of the field site and field and laboratory methodology, see While *et al.*, 2007, 2009a, in press). At the beginning of each season, all individuals in the population were (re)captured, measured for weight (±0.1 mg) and length (snout-to-vent and total length ±0.5 mm), and had their sex determined via eversion of the hemipenes. At the end of gestation (mid-January), all gravid females were caught and returned to the University of Tasmania, Hobart, Australia, to give birth. Females were housed individually in rectangular plastic terraria (300 × 600 × 400 mm), in temperature- and light-controlled rooms with lights set to ambient day lengths (Hobart, Tasmania, Australia). Housing terraria contained a basking rock and basking light at one end and a shelter at the opposite end. This provided a thermal gradient of 40°C to 17°C in the terraria, allowing females to actively thermoregulate. Food (*Tenebrio* larvae, crushed fruit) and water were available *ad libitum*. Basking lights were set on a timer to come on 1 h after the room lights were turned on and to turn off 1 h before the room lights went off. During the period of offspring birth, cages were checked twice daily for offspring. At birth, offspring were temporarily removed from their mother to be marked, weighed (±1 mg), and measured for snout-to-vent length and total length (±1 mm). Offspring condition was then calculated by regressing offspring mass over its snout-to-vent length. We were unable to identify sex of offspring as juvenile female *Egernia* retain their hemipenes (Chapple, 2003). In addition to offspring morphometrics, birthing asynchrony characteristics, including birth order and spread between births within a litter, were also recorded. Within 3 days of the birth of the final offspring, offspring were released, with their mother, at their mother's site of capture.

During each subsequent field year, we recaptured all surviving offspring at the study site and recorded date of recapture and morphometric traits (weight, ±1 mg; snout-to-vent and total length, ±1 mm), which allowed us to estimate offspring growth and survival (total observations per year = 1866 ± 126). As the study site is flanked on all sides by physical barriers (e.g. roads and unsuitable habitat), emigration into the site by unmarked individuals is limited, and capture of marked animals outside the study area is low (< 10 observations per year), estimates of offspring survival are highly unlikely to be compromised by dispersal of offspring out of the study site. Furthermore, only two offspring were recaptured following their second year that had not been recaptured during their first, suggesting our recapture methods are highly accurate.

Statistical analysis

Differences in female reproductive characteristics (clutch size and birth date) and offspring morphometrics (condition and snout-to-vent length) at birth as a function of year of birth and birth date were analysed using general linear mixed models (PROC MIXED in SAS STAT v.9.2). For all models, year of birth was entered as a fixed factor, date of birth (calculated as the number of days from 1 January each year) as a covariate, and female id as a random factor. The effect of among- and within-litter timing of birth on offspring growth and survival over their first 2 years of growth was analysed using general linear and generalized linear models (PROC GLM and PROC GENMOD respectively). For both sets of models, offspring growth (calculated as snout-to-vent at capture minus snout-to-vent at birth) or survival were entered as the dependent variable, season and birth order (1, 2 or 3) were entered as fixed factors, and date of birth, date of recapture (both calculated as the number of days from 1 January each year), and snout-to-vent length were entered as covariates. For the logistic survival models, date of recapture was not included in the model, as only surviving offspring had a date of recapture. We did not include litter identity as a random factor within the growth and survival models because the majority of litters (72%) only had one offspring surviving into subsequent years and thus we had relatively low statistical power to control for litter identification. For linear models, *post hoc* tests were carried out using a Ryan-Elliot-Garbriel-Walsh multiple range test. All models started with the full model including all interaction terms and we subsequently eliminated non-significant interaction terms backward, starting with higher-order interaction terms, at P-values > 0.25 (Quinn and Keogh, 2002). We report here results for models containing all main effects following backward elimination. Where mixed models were used, the significance of fixed effects was tested using F-tests, with the degrees of freedom calculated using Satterthwaite's approximation (Littell *et al.*, 1996). All data were checked for violations of assumptions, including homogeneity of slopes, where covariates were used. Means ±1 standard error (S.E.) are reported throughout.

RESULTS

Ninety-one females were brought into the laboratory to give birth over the 3-year field study. These females gave birth to a total of 182 offspring, with an average litter size of 2.03 ± 0.07. Date of birth differed between years, with females in 2006 giving birth later in the year than females in 2005 or 2007 ($F_{2,162} = 6.87$, $P < 0.01$) (Fig. 1). There were no differences in female litter sizes between years ($F_{2,59.41} = 0.84$, $P = 0.44$), and offspring size (snout-to-vent length) did not differ between ($F_{2,178} = 1.44$, $P = 0.24$) or within years ($F_{1,178} = 0.73$, $P = 0.39$). However, within years, there was a weak relationship between birth date and offspring condition ($F_{1,118} = 3.95$, $r^2 = 0.03$, $P = 0.05$), with offspring born later in the year in poorer condition at birth than offspring born earlier in the year.

Offspring exhibited relatively high survival over their first year, with 70 of the 182 offspring released with their mothers surviving, representing a survival rate of 38%. Of these offspring, 39 also survived over their second year, representing a survival rate of 54% between their first and second years and a total survival rate of 21% over both years. The most significant predictor of an offspring's survival was its year of birth, with offspring born in 2006 having lower survival, across both years of growth, than offspring born in 2005 or 2007 (Table 1; Fig. 2), although this effect failed to reach statistical significance over the

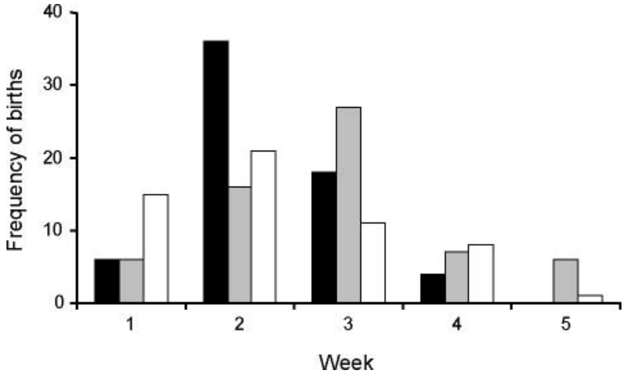

Fig. 1. Frequency of births for female *Egernia whitii* held under natural conditions in 2005 (■, $n = 64$ births), 2006 (▨, $n = 62$ births), and 2007 (□, $n = 56$ births). Week 1 begins 15 January each year and Week 5 begins 12 February.

Table 1. Factors contributing to variation in offspring survival over their first and first 2 years within a natural population of *Egernia whitii*

Years	Predictor variables	Offspring survival	
0–1 year	Year of birth	$\chi^2 = 5.40$	$P = 0.06$
	Birth order	$\chi^2 = 2.56$	$P = 0.27$
	Birth date	$\chi^2 = 0.04$	$P = 0.83$
	Snout-to-vent length at birth	$\chi^2 = 0.84$	$P = 0.36$
0–2 years	**Year of birth**	$\boldsymbol{\chi^2 = 12.84}$	$\boldsymbol{P < 0.01}$
	Birth order	$\chi^2 = 5.05$	$P = 0.08$
	Year × birth order	$\chi^2 = 8.56$	$P = 0.07$
	Birth date	$\chi^2 = 0.06$	$P = 0.81$
	Snout-to-vent length at birth	$\chi^2 = 0.72$	$P = 0.40$

Note: Interaction terms that did not alter the results of the main effects (i.e. *P*-values greater than 0.25) are not shown; values in **bold** face represent statistically significant effects.

first year of growth (Table 1). Importantly, the effects of year of birth on offspring survival across the second year of growth were independent of survival across the first. This was evident when we analysed offspring survival across only the second year (i.e. including only offspring that survived their first year) and year of birth remained significant ($\chi^2 = 8.37$, $P = 0.01$). These results suggest long-lasting year-of-birth effects on offspring survival. Offspring date of birth, birth order position, and offspring size did not predict survival across either the first or second year (Table 1).

We were able to calculate growth across these time periods for the 72 offspring that survived over their first winter and the 39 offspring that survived over both winters. As with survival, we found that there were strong year-of-birth effects on offspring growth across an individual's first 2 years (Table 2), with offspring born in 2006 having significantly lower growth than offspring born in either 2005 or 2007 (Fig. 3). We also found significant

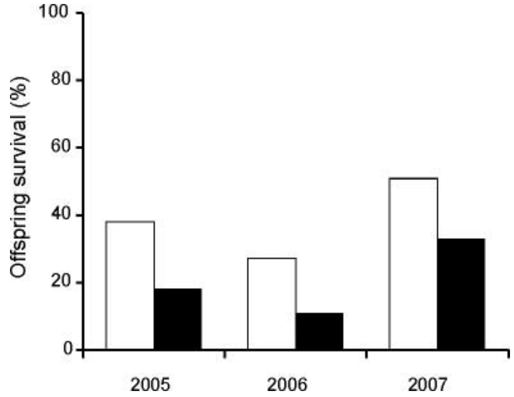

Fig. 2. Percentage of *Egernia whitii* offspring born in 2005, 2006, and 2007 surviving across their first year (□) and first 2 years (■).

Table 2. Factors contributing to variation in offspring growth over their first and first 2 years within a natural population of *Egernia whitii*

Years	Predictor variables	Offspring growth (mm)	
0–1 year	**Year of birth**	$\mathbf{F_{2,58} = 7.29}$	$\mathbf{P < 0.01}$
	Birth order	$F_{2,58} = 8.12$	$P = 0.37$
	Year × birth order	$F_{4,58} = 1.52$	$P = 0.21$
	Birth date	$\mathbf{F_{1,58} = 35.45}$	$\mathbf{P < 0.0001}$
	Snout-to-vent length at birth	$F_{1,58} = 0.02$	$P = 0.80$
	Date of recapture	$\mathbf{F_{1,58} = 48.39}$	$\mathbf{P < 0.0001}$
0–2 years	**Year of birth**	$\mathbf{F_{2,36} = 11.54}$	$\mathbf{P < 0.01}$
	Birth order	$F_{2,36} = 1.71$	$P = 0.20$
	Birth date	$\mathbf{F_{1,36} = 14.31}$	$\mathbf{P < 0.01}$
	Snout-to-vent length at birth	$F_{1,36} = 0.48$	$P = 0.49$
	Date of recapture	$\mathbf{F_{1,36} = 21.96}$	$\mathbf{P < 0.0001}$

Note: Interaction terms that did not alter the results of the main effects (i.e. *P*-values greater than 0.25) are not shown; values in **bold** face represent statistically significant effects.

within-year timing-of-birth effects, with a strong relationship between offspring date of birth and offspring growth (Table 2, Fig. 4a). Specifically, offspring born early in the year had greater growth than offspring born late in the year. These effects held when we re-ran models while controlling for differences in offspring condition at birth, suggesting that the effects of birth date on offspring growth were not influenced by the poorer condition of offspring born later in the season. These effects of birth date on offspring growth lasted into an offspring's second year of growth, although they became substantially weaker (Table 2, Fig. 4b). However, examining growth between the first and second years independently (i.e. controlling for snout-to-vent length growth over the first year) removed the significance of both between- and within-year effects on offspring growth (year of birth: $F_{2,29} = 2.36$, $P = 0.12$; date of birth: $F_{1,29} = 3.29$, $P = 0.08$). Thus, the effects of year of birth and birth date into the second year of growth were driven by their effects on offspring growth over the

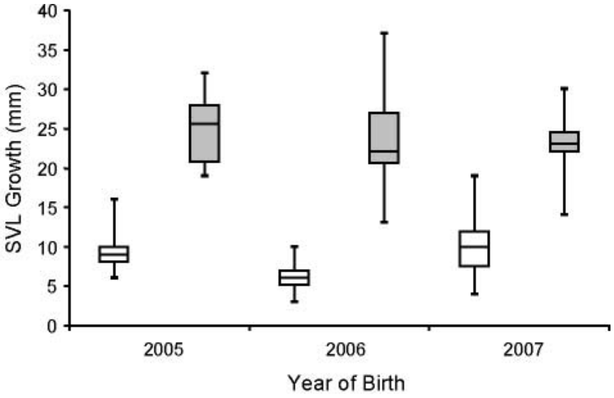

Fig. 3. Differences in snout-to-vent length (SVL) growth over the first year (☐) and first 2 years (■) of life between *Egernia whitii* offspring born in 2005, 2006, and 2007. The figure shows median growth (line), the 25% and 75% quartiles (boxes), and the ranges (whiskers).

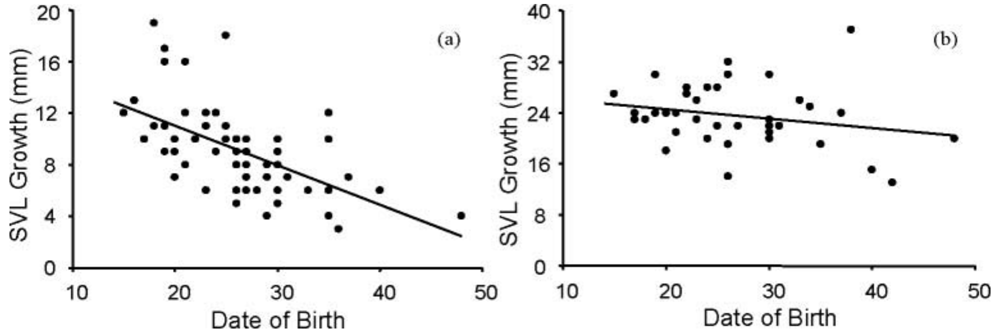

Fig. 4. The relationship between snout-to-vent length growth and date of birth (days from 1 January) for *Egernia whitii* offspring after 1 year of growth (a) and 2 years of growth (b).

first year, in contrast to the effects of birth date on survival. There were no differences in growth between offspring born at different birth-order positions over the first 2 years of growth, and growth was not influenced by an individual's size at birth (Table 2).

DISCUSSION

Our data demonstrate strong and long-lasting effects of between-litter variation in the timing of birth on fitness-related traits in a long-lived social reptile. Specifically, we show that between-litter timing of birth, both within and between years, is the key predictor of offspring growth and survival. As these effects were both strong and persistent, and may exert a significant influence on key life-history traits such as age at maturation (e.g. Warner and Shine, 2007, 2008), they suggest strong selection on embryonic development and, as a consequence, female basking behaviour. Conversely, we found no effect of within-litter timing of birth (i.e. birth order) on offspring growth and survival. Thus, the consequences of birthing asynchrony within *Egernia* may be different from those found in some birds, where later hatched offspring typically have reduced growth and survival.

Between-season effects

Variation in offspring growth and survival across years is expected due to annual variation in climate, demography, and resource abundance. Despite this, surprisingly little information exists on inter-annual variation among cohorts in lizards (Olsson and Shine, 1997). Here we show that offspring born in 2006 displayed lower rates of growth as well as lower survival across their first 2 years of growth than offspring born in the preceding or subsequent years. Importantly, offspring born in 2006 also had reduced survival across their second season of growth independent of survival across their first, suggesting long-lasting year-of-birth effects. Interestingly, the lower survival of offspring born in 2006 over their second year of growth coincided with relatively high survival rates exhibited by offspring born in 2007, who were concurrently experiencing their first year of growth.

These results suggest that conditions early in development, either before or after gestation, may result in intrinsic differences in offspring quality that can exert strong influences on an individual's fitness at later life-history stages. Such between-year 'silverspoon' effects have been described in other vertebrates (Madsen and Shine, 2000; Van de Pol *et al.*, 2006; Descamps *et al.*, 2008), but their ecological and physiological causes remain unknown. In the long term, between-generation variation in offspring quality, driven by maternal effects, could have important implications for population demography and both its causes and consequences deserve further study (Ginzburg and Colyvan, 2004; Inchausti and Ginzburg, 2009). One potential explanation for the long-term effects found in this study is that resource availability at birth may impair development or lead to lasting effects on physiological systems. For example, Madsen and Shine (2000) linked annual variation in cohort growth to variation in prey abundance in a population of water pythons, suggesting that early experience of resource availability can influence energy allocation strategies throughout life. Interestingly, within our population, females who gave birth in 2006 also did so, on average, later in the season than females in previous or subsequent years, suggesting relatively poor thermal conditions during gestation that may have had concomitant effects on offspring quality (Wapstra, 2000). Alternatively, social demographic factors may play a role. *Egernia* display relatively simple social systems typically consisting of stable adult pair-bonds and delayed offspring dispersal (for a review, see Chapple, 2003). However, there is considerable variation in the composition of social groups both within and between populations (Chapple, 2003; While *et al.*, in press). For example, we have recently demonstrated yearly variation in parental tolerance of offspring over the same time period, with 2006 having a higher proportion of sub-adults remaining within their parents' home range than 2005 and 2007 (While *et al.*, in press). Thus, competitive interactions between offspring born in that year and their older siblings could suppress growth and potentially increase mortality and/or dispersal out of the home range [resulting in reduced access to resources and protection from conspecific aggression (O'Connor and Shine, 2004; Sinn *et al.*, 2008)]. Long-lasting effects of sibling interactions have been shown in birds and mammals (Mock and Parker, 1997; see also Uller 2006), but the mechanisms are yet to be elucidated. Nevertheless, social conditions early in life have been shown to mediate hormone concentrations and responses to environmental conditions later in life (Clark and Galef, 1998; Oddie, 2000; Cushings and Kramer, 2005), both of which could have significant ramifications for growth and survival throughout life.

Within-season effects

In addition to strong effects of between-year timing of birth, we also showed that variation in within-year timing of birth has a strong influence on offspring growth. These results are consistent with recent research on lizards that have emphasized the importance of seasonal timing of birth for offspring growth and survival (e.g. Warner and Shine, 2005, 2007). This is in contrast to the general assumption that size, as opposed to birth date, is the key predictor of offspring growth and survival (Forsman 1993; Sorci and Clobert, 1999; Janzen *et al.*, 2000). Indeed, we found that while within-year timing of birth significantly influenced offspring growth, offspring size at birth had no effect. These effects of birth date on offspring growth are most parsimoniously explained by the shorter growth period before the onset of hibernation for offspring born later in the year (Uller *et al.*, 2007; Warner and Shine, 2007), but could also be driven by variation in maternal/offspring quality or maternal effects linked to birth date (Wapstra, 2000; Uller *et al.*, 2007). For example, mothers whose parturition of offspring is delayed may also invest relatively less into current reproduction or choose relatively cooler basking conditions that have a combined effect on date of parturition and offspring quality (e.g. Wapstra, 2000). We found a significant negative relationship between date of birth and offspring condition at birth across all years, thus offspring growth rate in relation to birth date may be driven by poorer condition at birth rather than their increased opportunity to grow. However, the strong effect of offspring birth date on growth remained when we controlled for offspring condition at birth. Consequently, maternal selection on the timing of birth (i.e. increased basking) may be stronger than resource allocation *per se*. This is perhaps unsurprising, as altering female basking frequency and thus parturition date, which can result in a 5-mm gain in offspring growth over their first year compared with offspring born later in the season (see Fig. 4a), may be relatively less expensive compared with increasing maternal investment itself.

Within-litter effects

The main goal of this study was to document the consequences of birthing asynchrony, a phenomenon that seems to be unique to *Egernia* but closely resembles hatching asynchrony in birds (While *et al.*, 2007). However, in contrast to the strong between-litter effects, within-litter variation in the timing of birth did not influence either offspring growth or survival. These results are in line with previous experimental work that failed to identify strong birth-order effects under controlled conditions on either of these traits or on an individual's competitive ability early in life (While and Wapstra, 2008). As birthing asynchrony is not a result of physiological constraints on the synchronous development of offspring (While *et al.*, 2007), the lack of a birth-order effect on growth and survival is surprising and raises questions regarding the adaptive basis of asynchronous birthing within this genus. Birthing asynchrony in *Egernia* is thought to be an adaptation to a highly competitive social environment (While *et al.*, 2007; While and Wapstra, 2008), where the establishment of a size hierarchy promotes dispersal of subordinate offspring and philopatry of dominant offspring, the latter gaining access to resources and protection from infanticide (see Bull and Baghurst, 1998; O'Connor and Shine, 2004; Sinn *et al.*, 2008; While *et al.*, 2009b). However, without birth order being a key predictor of the competitive asymmetries between siblings, it is difficult to understand why competitive hierarchies establish within asynchronous but not synchronous litters (e.g. While and Wapstra, 2008). We suggest that while giving birth asynchronously does not change the competitive ability of offspring *per se*, it does change the level of competition within the litter, allowing for other traits, such as size, sex, paternity or behavioural phenotype, to determine the outcome of such competition. For example, it has been suggested that an individual's relative size early in development, rather than its birth order, is most indicative of its position within the litter size hierarchy created by asynchronous birth and thus survival and growth (While and Wapstra, 2008). Considering the relatively modest sample size (despite high survival rates) and the potential multitude of causal factors on survival and growth, such effects will be difficult to detect without experimental work. In line with this, future work should experimentally manipulate offspring size itself, utilizing allometric engineering techniques (e.g. Sinervo and Huey, 1990; Olsson *et al.*, 2002), and compare its effects on size hierarchy establishment within both asynchronous and synchronous litters [using manipulation of synchrony (e.g. While and Wapstra, 2008)]. This would allow us to tease apart the role of asynchrony as a direct cause or a facilitator of sibling size hierarchies and thus the mechanism by which birthing asynchrony influences sibling competition.

In summary, survival and growth to maturity in *E. whitii* show inter- and intra-annual variation, the latter largely driven by variation in birth date. Importantly, an individual's survival rate over its second year of growth was largely independent of survival over its first year, suggesting long-lasting effects of changes or perturbations in environmental or social conditions on the demography of populations. In contrast to many birds, birth order did not significantly impact on survival or growth, suggesting that the evolution of birthing asynchrony in this genus should be understood from a perspective of costs and benefits of the creation of sibling hierarchies *per se* rather than any direct effects of within-litter position on offspring fitness.

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