Life history and reproductive ecology of White's skink, *Egernia whitii*

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Abstract.   The life history and reproductive ecology of White's skink, *Egernia whitii*, was examined in a population in the Australian Capital Territory using both field and genetic studies. Colour pattern polymorphism was evident within the population, with both patterned and plain-back morphs present. Lizards typically took 3 years to reach sexual maturity, with the size at maturity being ~75 mm snout–vent length (SVL) in both sexes. There was an even overall adult sex ratio, although a slight female-bias was evident in plain-back individuals. Sexual dimorphism was evident, with males having longer and wider heads, and females having larger body size. Females generally bred annually, with mating occurring in September–October and parturition in late January–February, although the litter was produced over several days (2–10 days, mean 4 days). Litter size ranged from one to four (mean of 2.5). There was a significant relationship between maternal SVL and both litter size and relative clutch mass, but these trends were not consistent between colour morphs. An inverse relationship between litter size and offspring size (SVL and mass) was found. Comparison of the results with previous investigations of *E. whitii* indicates substantial geographic variation in life-history traits that is presumably associated with latitudinal variation in climatic conditions.

Introduction

Skinks (Family Scincidae) represent the largest lizard family, with ~1400 species and 120 genera (Greer 1989; Pianka and Vitt 2003). Australia is a major centre of skink diversity with over 370 species in 33 genera (Wilson and Swan 2003). Although skinks are one of the most morphologically, ecologically and behaviourally diverse lizard groups, surprisingly little is known about the biology of many species (Greer 1989, 2004). For instance, even though it contains some of Australia's most ubiquitous and easily identifiable lizards, accurate and detailed life-history information is available for only seven of the 32 species of *Egernia* (Chapple 2003). However, species of *Egernia* appear to exhibit considerable inter- and intraspecific variation in reproductive ecology and several life-history traits (Greer 1989, 2004; Chapple 2003).

Little is known about the geographic variation in life-history traits in widespread *Egernia* species whose distribution spans numerous habitats and climatic regions (Chapple 2003). Cunningham's skinks (*Egernia cunninghami*), which occur commonly throughout south-eastern Australia (Wilson and Swan 2003), appear to exhibit considerable geographic variation in life-history traits (Barwick 1965; Van Weenan 1995; Chapple 2003). Most *Egernia* species live in stable social aggregations, and several life-history traits (e.g. litter size, age at maturity, life span) are believed to shape both the composition and size of social groups in many species (Chapple 2003; Chapple and Keogh, in press). Consequently, examination of the factors respon-

sible for geographic variation in life history within *Egernia* species is not only vital for better understanding the process of life-history evolution, but will also provide a framework in which to examine the evolution of social systems within this lizard lineage.

The present study examines aspects of reproductive ecology and life history in a population of White's skink (*Egernia whitii*) in the Australian Capital Territory (ACT). Recent studies on this population have demonstrated that *E. whitii* lives in small but stable social groups (Chapple and Keogh, in press) and has a mating system that is characterised by both polygyny and within-season monogamy (Chapple and Keogh 2005). Previous work on *E. whitii* has suggested that it exhibits variation in life history across its range (Hickman 1960; Milton 1987; Donnellan *et al.* 2002). The location of the present study (ACT) is intermediate in latitude to the locations of two previous life-history studies that have been conducted in south-east Queensland (Qld) (Milton 1987) and Tasmania (Tas.) (Hickman 1960), enabling geographic variation in reproductive ecology and life history in *E. whitii* to be examined. *E. whitii* exhibits colour pattern polymorphism and therefore the presence of variation in reproductive ecology and life history between colour morphs was also considered.

Materials and Methods

Study species

Egernia whitii is a medium-sized viviparous skink (up to 100 mm snout–vent length; SVL) that occurs across a broad altitudinal range from sea-level to 1600 m above sea level and inhabits a diverse range of

habitats in south-eastern Australia, including coastal heaths, grasslands, woodlands and dry sclerophyll forests (Chapple 2003; Wilson and Swan 2003). It is typically found in close association with rocky outcrops, where it uses crevices and exfoliating rock slabs as retreat sites, although throughout much of its range it also excavates deep and complex burrow systems under or at the base of rocks and shrub vegetation (Chapple 2003; Wilson and Swan 2003). These lizards concentrate most of their basking and foraging activities close to a permanent shelter site (i.e. rock crevice or burrow: Greer 1989; Chapple 2003). *E. whitii* is an opportunistic forager that is primarily insectivorous (Hickman 1960).

Three distinct colour-pattern morphs are present in *E. whitii*: patterned, plain-back (lacking dorsal patterning), and patternless (lacking dorsal or lateral patterning) (Donnellan *et al*. 2002). Apart from differences in colour pattern, *E. whitii* morphs appear to be morphologically indistinguishable (Milton *et al*. 1983; Milton 1990). There is considerable geographic variation in the relative frequency of *E. whitii* colour morphs (Milton 1990; D. Chapple, unpublished data). The patternless morph appears to be extremely uncommon, occurring in low frequencies in a small number of distinct regions (Donnellan *et al*. 2002; D. Chapple, unpublished data). The patterned and plain-back colour morphs occur in varying relative frequencies across the distributional range of *E. whitii*, although the patterned morph is generally the most abundant, and is the only form present in Tasmania (Milton 1990; D. Chapple, unpublished data).

Study site and field methods

Aspects of life history and reproductive ecology in *E. whitii* were examined at a study site (150 m × 150 m) located adjacent to Westermans Hut (35°53′S, 148°58′E) near Grassy Creek in Namadgi National Park in the Australian Capital Territory. This research formed part of a larger capture–mark–recapture and genetic study (DNA microsatellites) that investigated the social behaviour (Chapple and Keogh, in press) and mating system (Chapple and Keogh 2005) of *E. whitii* at the site. The study area is located 1250 m above sea level and consists predominately of open grassland interspersed with small patches of remnant semi-alpine woodland. *E. whitii* is abundant at the site, with both the patterned and plain-back colour morphs present within the population. Small granite outcrops are widely distributed across the study site, creating ample retreat sites for *E. whitii*. Lizards at the site excavated complex burrow systems at the base of, or beneath, rocks. Burrows were used as daily retreat sites and during winter hibernation. *E. whitii* at the site appeared to favour rocky microhabitats in open grassland that provided plentiful basking opportunities, and were located close to low shrub vegetation that offered shade and cover.

The study was conducted at the site over two field seasons (2001–2002 and 2002–2003) during the active period for *E. whitii* (October–March). Lizards at the site were caught by noosing, by hand, or by 'mealworming'. Mealworming involves tying a mealworm to a piece of string and placing it in front of the lizard. When the lizard grabs the mealworm it is lifted into the air and placed into a collection bucket. Upon initial capture, measurements (±0.01 mm) were taken of SVL, tail length (TL; vent to the tip of the tail), head width (HW; horizontal line joining the anterior edge of each ear aperture) and head length (HL; measured from tip of snout to the anterior edge of the tympanic opening). Each lizard was weighed (±0.1 g) using digital field scales. Lizards were marked and identified using a unique toe-clip. The tip of the tail (~1 cm) was removed and stored in 70% ethanol for genetic analysis (see Chapple and Keogh 2005). The sex of each individual was determined via eversion of hemipenes in males, and female reproductive status was assessed by abdominal palpation. The colour pattern (patterned or plain-back) of each lizard also was recorded. Individuals caught during the first season were recaught and remeasured during the second season. However, some lizards (mostly juveniles and subadults)

from the first season were not present within the study site during the second season and were assumed to have either died or dispersed out of the study area.

Pregnant females at the site in late January of each season were caught and brought into the laboratory to give birth. While in the laboratory, females were housed individually in plastic containers 350 mm (L) × 250 mm (W) × 140 mm (H) in a room maintained at 18–20°C. Retreat sites were provided and heat tape (set at 35°C) positioned under one-half of the container enabled lizards to maintain their preferred temperatures for 14 h each day. Lizards were provided food (mealworms, crickets) and water *ad libitum*. Containers were checked twice daily for births, with parturition commencing within 2 weeks of being brought into the laboratory. Upon birth, each newborn was weighed (±0.001 g) and measurements (±0.01 mm) taken of SVL and TL. The colour morph of each neonate was recorded and its tail tip (~1 cm) removed for genetic analysis. Although older juveniles in the field could easily be sexed, the sex of offspring born in the laboratory could not be determined owing to the presence of evertible 'hemipenes' in both sexes. Females were palpated when births were detected to ensure that parturition was complete, with the *post partum* mass of each mother being recorded. Females and their neonates were returned to the site of maternal capture once parturition was complete. Two females in January 2002 and seven females in January 2003 could not be caught while pregnant to give birth in the laboratory.

All individuals at the study site, including all offspring born in the laboratory, were genotyped for four tetranucleotide microsatellite loci (EST1, EST2, EST4, EST12: Gardner *et al*. 1999), as described in Chapple and Keogh (2005). CERVUS 2.0 (Marshall *et al*. 1998) was used to assign paternity to all laboratory-born offspring, as outlined in Chapple and Keogh (2005), enabling the size of males at sexual maturity and the inheritance of colour pattern to be assessed.

Statistical analyses

All statistical analyses were conducted using SPSS version 11.0. Since only two previously unmarked adult lizards (one adult male, one adult female) were caught in the second field season, analyses of morphology and sexual dimorphism are limited to those lizards caught in the 2001–2002 season. Chi-square tests were conducted to determine whether biased sex-ratios were evident in patterned and plain-back lizards at the site. Differences in morphology between the sexes and colour morphs were examined using analysis of variance (ANOVA). Heterogeneity of slopes tests and analysis of covariance (ANCOVA) were used to assess sexual dimorphism in head and tail morphology. Linear regression analyses were conducted to examine relationships between morphological variables, while univariate General Linear Models (GLM) were used to examine whether these relationships differed between the sexes or colour morphs.

The relative clutch mass (RCM) was calculated for all pregnant females (total litter mass divided by *post partum* maternal mass). Relationships between various reproductive life-history traits were examined using linear regression. General Linear Models were used to examine the consistency of these relationships between seasons and colour morphs. Variation in litter size and RCM between seasons and colour morphs was investigated using ANOVA.

Results

Life history, morphology and sexual dimorphism

A total of 115 *E. whitii* were caught at the study site during the 2001–2002 season (Table 1). The smallest pregnant female was 77.4 mm SVL before parturition in late January to early February, but would have been ~75 mm SVL during the mating season in October. Paternity analysis revealed

Table 1.   Sex and colour morph of *Egernia whitii* caught at the Grassy Creek field site in the 2001–2002 season

	Patterned			Plain-back			Overall		
	Male	Female	Total	Male	Female	Total	Male	Female	Total
Adults	36	32	68	3	7	10	39	39	78
Juveniles	18	12	30	1	6	7	19	18	37
All lizards	54	44	98	4	13	17	58	57	115

that the smallest male that fathered offspring from laboratory-born litters was 80.0 mm SVL; however, several smaller (75–80 mm SVL) males at the site appeared to be sexually mature but failed to achieve paternity. Consequently, male and female *E. whitii* over 75 mm SVL were considered to be sexually mature adults.

The patterned colour morph was the most abundant at the field site (85.2%), a trend that was consistent in both adults (87.2%) and juveniles (81.1%) (Table 1). Overall, there was an even sex ratio in adults, juveniles and for all lizards (Table 1), although a sex bias was evident in plain-backed lizards. Plain-backed lizards exhibited a significant female-bias ($\chi^2 = 4.77$, d.f. = 1, $P = 0.029$), possibly an artefact of the low incidence of plain-back lizards at the site, while no bias was evident in patterned lizards ($\chi^2 = 1.02$, d.f. = 1, $P = 0.312$) (Table 1).

The snout–vent length histogram for individuals at the site, in combination with capture–mark–recapture data, indicates that *E. whitii* at the Grassy Creek site reaches sexual maturity (i.e. 75 mm SVL) during its third season (Fig. 1). The histogram shown in Fig. 1 is based on animals caught during the 2001–2002 season between December and February. *E. whitii* is ~40 mm SVL at birth in late January–February (see below), reaching 55–67 mm SVL during the following season, 68–75 mm SVL during its second season, and adult body size (i.e. >75 mm SVL) during its third season (Fig. 1). The body size differences between first-year (55–67 mm SVL) and second-year (68–75 mm SVL) juveniles indicates that body size represents a reliable method of assigning juveniles to particular cohorts (Fig. 1).

The mean body size (SVL) of adult females at the site was significantly larger than that of adult males ($F_{1,74} = 9.12$, $P = 0.003$) (Table 2). Body size did not differ between the patterned and plain-back morphs ($F_{1,74} = 0.40$, $P = 0.527$), with no association evident between morph and sex ($F_{1,74} = 1.97$, $P = 0.165$) (Table 2). Owing to the smaller sample size of the plain-back adult males at the site (Table 1), the remaining sexual dimorphism analyses did not consider morph-specific variation. ANCOVA was used to examine sexual dimorphism in adult head and tail morphology (Table 3). Adult males had significantly longer and broader heads than did adult females, but no dimorphism was evident in relative tail length (Table 3). Heterogeneity of slopes for both HL ($F_{1,110} = 51.86$, $P < 0.001$) and HW ($F_{1,110} = 18.73$,

$P < 0.001$) precluded detailed examination of whether sexual dimorphism exists in these traits in both juveniles and adults (Fig. 2). However, it is clear from Fig. 2 that sexual dimorphism in HL and HW is more pronounced in adults than in juveniles.

Reproductive life history

Most adult females at the Grassy Creek study area were pregnant in each season. During the 2001–2002 season 33 of the 39 (84.6%) adult females at the site were pregnant. The 2002–2003 season was considerably drier than the first season (Bureau of Meteorology Data), and although 40 adult females were present at the site during second season, only 22 of the 31 (71.0%) adult females caught during January 2003 were pregnant. In the first season females gave birth between 29 January 2002 and 28 February 2002, while births occurred between 21 January 2003 and 17 February 2003 during the second season. Except for litters that comprised a single neonate, *E. whitii* was never observed to complete parturition within a single day, with most females producing their litter over several days (up to 10 days: Table 4).

Egernia whitii produced litters comprising one to four offspring (mean 2.5), with a RCM of 0.24 (Table 5). Although litter size was consistent between years ($F_{1,50} = 0.18$, $P = 0.673$), plain-back females produced significantly
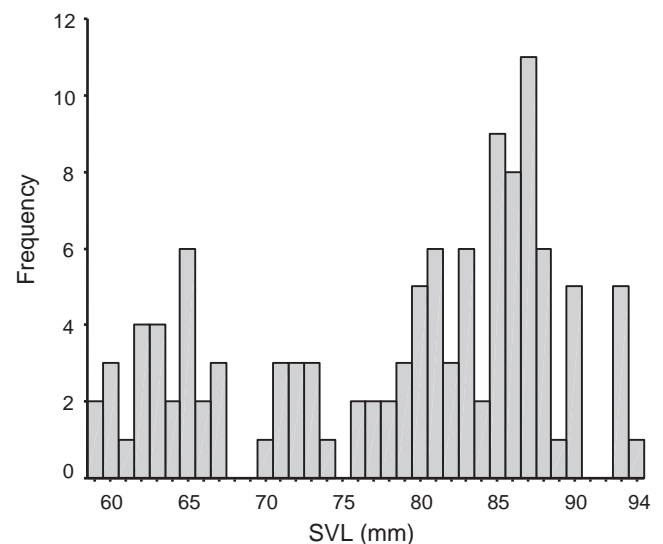
Fig. 1.   Snout–vent length (SVL) frequency histogram for *Egernia whitii* at the Grassy Creek site during 2001–2002.

Table 2. Mean snout–vent lengths (SVL; mm) of *Egernia whitii* at the Grassy Creek field site in the 2001–2002 season

Sex		Patterned			Plain-back			Overall	
	n	Mean ± s.e.	Range	n	Mean ± s.e.	Range	n	Mean ± s.e.	Range
Male	36	83.7 ± 0.55	75.0–88.3	3	82.6 ± 3.09	77.7–88.3	39	83.6 ± 0.55	75.0–88.3
Female	32	86.2 ± 0.86	76.0–93.9	7	89.3 ± 1.44	83.2–94.3	39	86.7 ± 0.77	76.0–94.3
Overall	68	84.9 ± 0.52	75.0–93.9	10	87.3 ± 1.63	77.7–94.3	78	85.2 ± 0.50	75.0–94.3

larger litters than did patterned females ($F_{1,50} = 10.91$, $P = 0.002$) (Table 5). Similarly, RCM was constant between seasons ($F_{1,48} = 0.01$, $P = 0.922$), but significantly greater in plain-back females ($F_{1,48} = 5.61$, $P = 0.022$) (Table 5). Although this disparity might stem from the trend for larger body size (SVL) in plain-back females (Table 2), differences between colour morphs in litter size (ANCOVA: $F_{1,51} = 6.90$, $P = 0.011$), but not RCM (ANCOVA: $F_{1,49} = 3.85$, $P = 0.055$), remained after accounting for maternal SVL.

General linear models analyses indicated that the relationship between female SVL and litter size was consistent between seasons ($F_{1,49} = 0.02$, $P = 0.904$), but differed significantly between colour morphs ($F_{1,49} = 4.86$, $P = 0.032$). Although the relationship between SVL and litter size was significant for patterned females ($R^2 = 0.34$, $F_{1,40} = 20.32$, $P < 0.001$; $y = 0.10x – 6.24$) and overall ($R^2 = 0.36$, $F_{1,52} = 29.44$, $P < 0.001$; $y = 0.11x – 6.85$), a strong relationship between female body size and fecundity was not evident in plain-back females ($R^2 = 0.14$, $F_{1,10} = 1.62$, $P = 0.232$; $y = 0.06x – 1.88$). The relationship between female SVL and RCM was consistent between seasons (GLM: $F_{1,47} = 0.10$, $P = 0.753$) and colour morphs (GLM: $F_{1,47} = 2.72$, $P = 0.106$). Overall, female SVL had a weak but significant influence on RCM ($R^2 = 0.09$, $F_{1,50} = 5.04$, $P = 0.029$; $y = 0.004x – 0.143$), with larger females producing heavier litters relative to their *post partum* mass. Litter size was strongly related to RCM ($R^2 = 0.72$, $F_{1,50} = 128.95$, $P < 0.001$; $y = 0.07x + 0.06$), with larger litters comprising heavier relative litter masses. This relationship was consistent between seasons (GLM: $F_{1,47} = 0.37$, $P = 0.544$) and colour morphs (GLM: $F_{1,47} = 0.53$, $P = 0.470$).

The mean newborn characteristics (SVL, mass, tail length, relative tail length, body condition) are shown in Table 6. These characteristics were consistent between the two seasons and both colour morphs ($P > 0.05$ in all
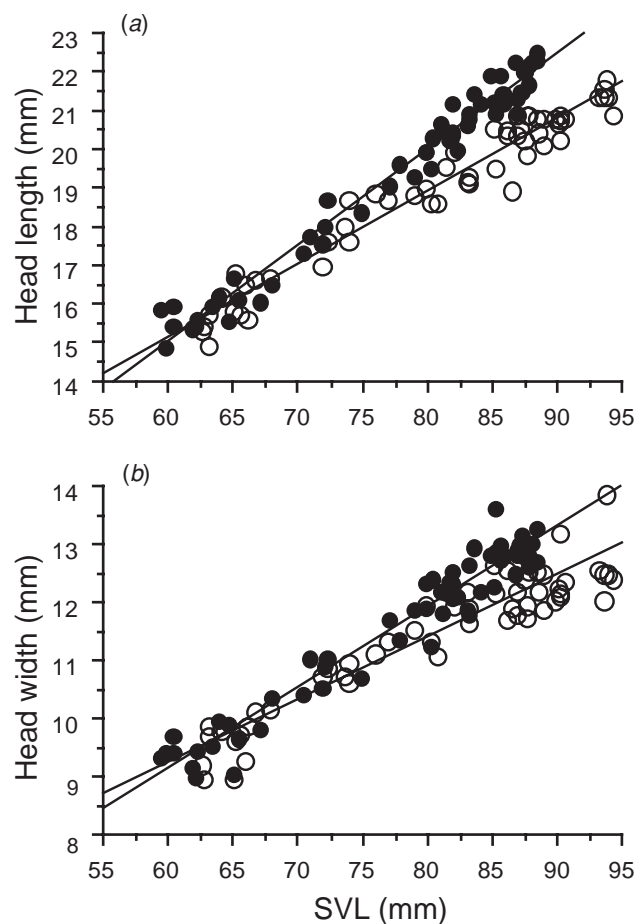
Fig. 2. Sexual dimorphism in head morphology in *Egernia whitii*. At the same snout–vent length (SVL) males have both (*a*) longer and (*b*) broader heads than females, although differences are more pronounced in adults.

Table 3. Sexual dimorphism in head width, head length and relative tail length (RTL) in adult *Egernia whitii* from the Grassy Creek field site

Measurements are in millimetres, except for RTL, which represents tail length/snout–vent length (SVL). For head width and length, the last three columns present the results of ANCOVA for the sex effect, with SVL as the covariate. ANOVA results are presented for RTL

Trait		Adult male			Adult female			ANCOVA/ANOVA	
	n	Mean ± s.e.	Range	n	Mean ± s.e.	Range	d.f.	F	P
Head width	39	12.44 ± 0.10	10.72–13.62	39	12.16 ± 0.09	11.10–13.87	1,75	282.15	<0.0001
Head length	39	20.93 ± 0.16	18.38–22.48	39	20.20 ± 0.15	18.61–21.81	1,75	79.63	<0.0001
RTL	39	1.36 ± 0.05	0.50–1.82	39	1.39 ± 0.04	0.52–1.73	1,76	0.08	0.783

Table 4. Time taken (days) for female *Egernia whitii* to complete parturition
No litter sizes of four were produced in the 2002–2003 season

| | 2001–2002 | | | 2002–2003 | | | Overall, both seasons | | |
	n	Mean ± s.e.	Range	*n*	Mean ± s.e.	Range	*n*	Mean ± s.e.	Range
Litter size of 2	8	4.5 ± 0.96	2–10	9	2.9 ± 0.26	2–4	17	3.6 ± 0.50	2–10
Litter size of 3	14	4.6 ± 0.58	2–9	12	3.8 ± 0.41	2–6	26	4.3 ± 0.37	2–9
Litter size of 4	4	4.0 ± 0.41	3–5	–	–	–	4	4.0 ± 0.41	3–5
Overall	26	4.5 ± 0.42	2–10	21	3.4 ± 0.27	2–6	47	4.0 ± 0.27	2–10

instances). On the basis of litter averages, there was a significant relationship between litter size and offspring SVL ($R^2 = 0.21$, $F_{1,52} = 13.97$, $P < 0.001$; $y = -0.61x + 42.01$), with mean body size decreasing in larger litters. Likewise, offspring in larger litters were significantly lighter than those in smaller litters ($R^2 = 0.28$, $F_{1,52} = 20.52$, $P < 0.001$; $y = -0.12x + 1.90$). Maternal SVL was inversely related to juvenile mass ($R^2 = 0.08$, $F_{1,52} = 4.61$, $P = 0.036$; $y = -0.01x + 2.53$), but maternal body size was not significantly related to offspring SVL ($R^2 = 0.02$, $F_{1,52} = 0.90$, $P = 0.348$; $y = -0.03x + 43.06$).

Inheritance of colour pattern polymorphism

Paternity assignment in CERVUS revealed that mating between individuals with different colour patterns was relatively frequent (Table 7). Paternity could not be assigned to four entire litters; for the rest, patterned offspring were always produced when patterned females mated with patterned males. Matings between individuals with different colour patterns resulted in litters comprising both patterned and plain-back offspring (1.3 : 1 patterned : plain-back ratio). Matings between two plain-back individuals resulted in predominately plain-back offspring (0.3 : 1 patterned : plain-back ratio).

Discussion

Geographic variation in life-history traits

The results of the present study, when combined with those of two previous studies (Hickman 1960; Milton 1987), indicate that there is substantial geographic variation in both life history and reproductive ecology between populations of *E. whitii* (Table 8). Although recent phylogenetic studies

have indicated that the Tasmanian population of *E. whitii* might be part of a different subspecies or species to populations in Queensland, NSW and the ACT (Chapple and Keogh 2004; Chapple *et al.* 2005), they are considered conspecific here because of their close evolutionary relationships and similarities in morphology, ecology and behaviour. Litter size (mean and range) and offspring size did not appear to differ substantially between the three populations, although latitudinal clines are evident in adult body size (mean and maximum SVL), age and size at maturity and the timing of reproductive activities (i.e. mating and parturition: Table 8). Adult body size and size at maturity decreases with increasing latitude, while age at maturity increases at higher latitudes (Table 8). Climatic conditions associated with latitude are presumably responsible for the later periods of mating and parturition in *E. whitii* populations at higher latitudes (Table 8). *E. whitii* in the present study displayed life-history traits that were intermediate between those reported previously for populations in Queensland and Tasmania (Table 8). Intriguingly, a concordant cline in relative morph frequency was evident (Table 8), suggesting that the factors driving geographic variation in life-history traits might also play an important role in maintaining colour pattern polymorphism in *E. whitii*.

Geographic variation in life-history traits also has been documented in *E. cunninghami* (Barwick 1965; Van Weenan 1995; reviewed in Chapple 2003) and several other lizard species (Forsman and Shine 1995; Rohr 1997; Wapstra and Swain 2001). Given that lizards are ectothermic, it is not surprising that such variability in life-history traits has been demonstrated to be intimately related to altitudinal or latitudinal variation in climatic conditions (Forsman and Shine

Table 5. Litter size and relative clutch mass (RCM) of *Egernia whitii* at the Grassy Creek study site
Sample sizes for RCM are lower in some instances due a stillborn in one litter and one newborn losing its tail before being weighed and measured

| Trait | Year | Patterned | | | Plain-back | | | Overall | | |
		n	Mean ± s.e.	Range	*n*	Mean ± s.e.	Range	*n*	Mean ± s.e.	Range
Litter size	2001–2002	25	2.28 ± 0.18	1–4	7	3.29 ± 0.29	2–4	32	2.50 ± 0.17	1–4
	2002–2003	17	2.35 ± 0.15	1–3	5	3.00 ± 0.00	3	22	2.50 ± 0.13	1–3
	Both years	42	2.31 ± 0.12	1–4	12	3.17 ± 0.17	2–4	54	2.50 ± 0.11	1–4
RCM	2001–2002	23	0.22 ± 0.018	0.08–0.42	7	0.29 ± 0.019	0.20–0.35	30	0.24 ± 0.015	0.08–0.42
	2002–2003	17	0.24 ± 0.013	0.15–0.35	5	0.28 ± 0.007	0.25–0.29	22	0.25 ± 0.010	0.15–0.35
	Both years	40	0.23 ± 0.011	0.08–0.42	12	0.28 ± 0.011	0.20–0.35	52	0.24 ± 0.010	0.08–0.42

Table 6. Mean *Egernia whitii* newborn characteristics
Relative tail length (RTL) is the tail length/snout–vent length (SVL). Body condition represents the mass in mg/SVL in mm

| Trait | Year | Patterned | | | | Plain-back | | | | Overall | |
		n	Mean ± s.e.	Range	*n*	Mean ± s.e.	Range	*n*	Mean ± s.e.	Range
SVL (mm)	2001–2002	64	40.3 ± 0.16	36.2–42.9	14	40.1 ± 0.25	38.2–41.3	78	40.2 ± 0.14	36.2–42.9
	2002–2003	45	40.5 ± 0.17	38.4–43.4	10	40.2 ± 0.33	37.9–41.1	55	40.4 ± 0.15	37.9–43.4
	Both years	109	40.4 ± 0.12	36.2–43.4	24	40.1 ± 0.20	37.9–41.3	133	40.3 ± 0.10	36.2–43.4
Mass (g)	2001–2002	64	1.57 ± 0.03	1.09–2.12	14	1.54 ± 0.04	1.31–1.80	78	1.56 ± 0.02	1.09–2.12
	2002–2003	45	1.60 ± 0.03	1.18–2.19	10	1.56 ± 0.06	1.30–1.94	55	1.59 ± 0.03	1.18–2.19
	Both years	109	1.58 ± 0.02	1.09–2.19	24	1.55 ± 0.03	1.30–1.94	133	1.58 ± 0.02	1.09–2.19
Tail length (mm)	2001–2002	62	55.9 ± 0.37	45.7–63.9	14	55.7 ± 0.62	52.0–60.7	76	55.9 ± 0.32	45.7–63.9
	2002–2003	45	56.3 ± 0.46	50.0–63.9	10	57.7 ± 1.05	52.4–63.9	55	56.6 ± 0.42	50.0–63.9
	Both years	107	56.1 ± 0.29	45.7–63.9	24	56.5 ± 0.59	52.0–63.9	131	56.2 ± 0.26	45.7–63.9
RTL	2001–2002	62	1.39 ± 0.007	1.26–1.54	14	1.39 ± 0.013	1.34–1.48	76	1.39 ± 0.006	1.26–1.54
	2002–2003	45	1.39 ± 0.008	1.29–1.53	10	1.44 ± 0.020	1.34–1.56	55	1.40 ± 0.008	1.29–1.56
	Both years	107	1.39 ± 0.005	1.26–1.54	24	1.41 ± 0.012	1.34–1.56	131	1.39 ± 0.005	1.26–1.56
Body condition	2001–2002	64	39.0 ± 0.53	30.0–49.5	14	38.5 ± 0.79	32.6–43.8	78	38.9 ± 0.46	30.0–49.5
	2002–2003	45	39.4 ± 0.57	30.8–51.1	10	38.7 ± 1.33	34.2–47.4	55	39.3 ± 0.52	30.8–51.1
	Both years	109	39.1 ± 0.39	30.0–51.1	24	38.6 ± 0.71	32.6–47.4	133	39.0 ± 0.35	30.0–51.1

1995; Rohr 1997; Wapstra and Swain 2001). The geographic variation in life history evident in *E. whitii* is consistent with latitudinal variation in climatic conditions (Table 8).

Egernia whitii at the Grassy Creek site exhibited sexual dimorphism, with males having longer and broader heads and females having larger body size. Sexual dimorphism in head size has been documented in many lizard species (e.g. Brana 1996), including other *Egernia* species (Arena and Wooller 2003; Clemann *et al*. 2004). Male lizards with larger heads appear to have an advantage in male–male competition and fights, and consequently head size could be subject to sexual selection (e.g. Vitt and Cooper 1985). Indeed, the fact that *E. whitii* is an extremely aggressive species, with fights potentially resulting in serious injury or death (Chapple 2003), is consistent with this idea. In contrast, disparity in body size typically has been explained by the fecundity advantages conferred from large female size (reviewed in Cox *et al*. 2003). The positive relationship between female size and litter size found in the present study is supportive of the fecundity advantage hypothesis (see Cox *et al*. 2003).

In the present study litter size, rather than maternal SVL, appeared to be the primary determinant of offspring size (both SVL and mass). A similar inverse relationship

between litter size and offspring size has been reported in the congener *E. stokesii* (Duffield and Bull 1996). The trade-off between litter and offspring size is well recognised in squamates and believed to result from differential maternal allocation of finite resources (Olsson and Shine 1997; Olsson *et al*. 2002). Most adult female *E. whitii* at the study site were found to reproduce annually (71–85%). Those that failed to reproduce in a particular season were typically smaller females (i.e. 75–85 mm SVL). Although it is believed that most *Egernia* species reproduce annually (Chapple 2003), the only comparable data indicate that ~75% of adult female *E. stokesii* are pregnant in any season (Duffield and Bull 1996). An intriguing aspect of the reproductive ecology of *E. whitii* is the length of time taken to complete parturition. In the present study *E. whitii* was never observed to complete parturition within a single day, taking up to 10 days to produce a litter. Such a phenomenon appears widespread in *Egernia*, having also been reported in *E. stokesii* (1–12 days, mean 2.8 days, mean litter size 5.1: Duffield and Bull 1996), *E. striolata* (1–7 days, mean litter size 3.3: Bull and Bonnett 2004) and *E. coventryi* (2–3 days, mean litter size 2.55: Manning 2002). However, the significance of such prolonged litter production remains elusive (Chapple 2003).

Table 7. Inheritance of colour pattern polymorphism in *Egernia whitii*
Paternity was assigned using CERVUS for litters born in the laboratory

| Pairing | No. litters | Offspring colour pattern | | |
		Patterned	Plain	Ratio (Patterned : Plain)
Patterned female and patterned male	37	80	0	1 : 0
Patterned and plain-back	10	17	13	1.3 : 1
Patterned female and plain-back male (*n* = 2)		4	2	2 : 1
Plain-back female and patterned male (*n* = 8)		13	11	1.2 : 1
Plain-back female and plain-back male	3	2	7	0.3 : 1

Table 8.   Comparison of the main findings of the present study with those reported in previous studies of the life history of *Egernia whitii* conducted in Queensland (Qld) and Tasmania (Tas.)

	Milton (1987)	Present study	Hickman (1960)
Study location	Amiens, Qld (28°35′S, 151°49′E)	Namadgi NP, ACT (35°53′S, 148°58′E)	Queen's Domain, Tas. (42°51′S, 147°19′E)
Altitude (m)	~800	1250	30
Mean daily maximum temperature (°C)[A]	21.6	17.4	17.0
Mean daily minimum temperature (°C)[A]	8.8	2.9	7.8
Mean annual rainfall (mm)[A]	769.6	768.9	569.3
Patterned morphs (%)	73	85	100
Mean adult SVL (mm)	~90	85.2 ± 0.5 ($n = 78$)	~85
Male		83.6 ± 0.5 ($n = 39$)	
Female		86.7 ± 0.8 ($n = 39$)	
Maximum SVL (mm)	~100	94.3	90
Size at maturity (mm)	85	75–80	78
Age at maturity (years)	2	3	4
Litter size (range)			
Patterned	1–5	1–4	1–5
Plain-back	1–4	2–4	–
Litter size (mean ± s.e.)			
Patterned	2.9 ± 0.4 ($n = 52$)	2.3 ± 0.1 ($n = 42$)	2.8 ($n = 27$)[B]
Plain-back	2.6 ± 0.8 ($n = 18$)	3.2 ± 0.2 ($n = 12$)	–
Newborn SVL (mm)			
Patterned	41.2 ± 0.6 ($n = 34$)	40.4 ± 0.1 ($n = 109$)	35–39
Plain-back	38.9 ± 1.1 ($n = 17$)	40.1 ± 0.2 ($n = 24$)	–
Sex ratio (overall)	Female-bias	Even	–
Patterned	Female-bias	Even	–
Plain-back	Even	Female-bias	–
Timing of parturition	January–early February	Late January–February	February
Mating period	September–October	September–October?	October

[A]Climate data were obtained from the Australian Bureau of Meteorology (http://www.bom.gov.au). The weather stations closest to each study site are: Stanthorpe Leslie Parade (Queensland population), Gudgenby (ACT population), and Hobart Botanical Gardens (Tasmanian population).
[B]Additional data for Tasmanian *E. whitii* from Rawlinson (1974).

Life-history variation between colour morphs and mode of colour morph inheritance

The relatively low incidence of the plain-back morph at the study site impeded any substantial examination of life-history variation between *E. whitii* colour morphs. However, slight differences in several life-history traits were documented in the present study. Plain-back females were found to have significantly larger litters and RCMs for their SVL than patterned females. The strength of the relationship between SVL and litter size also differed between colour morphs. Such results could simply be an artefact of the smaller sample size for plain-back females combined with the overall larger body size of these individuals (Table 2). Indeed, this contrasts with Milton (1987), who failed to identify differences between *E. whitii* colour morphs in any aspect of life history or reproductive ecology. Milton (1987) also reported a female-biased sex ratio in patterned *E. whitii* that contradicts the slight female bias found in plain-back morphs in the present study. Consequently, the potential exists for life-history variation in *E. whitii*, but the current evidence remains largely anecdotal until more detailed studies can be conducted on populations with sufficient abundance of both colour morphs.

The limited number of pairings between two plain-back individuals restricts the ability to comment extensively on the inheritance of colour pattern morphs in *E. whitii*. However, the breeding-pair data indicate that colour pattern is under genetic control. The presence of colour morphs in both sexes, with an even sex ratio at birth in both sexes (Milton 1987), suggests autosomal inheritance. The mode of inheritance is largely consistent with simple Mendelian inheritance as in other reptile species (e.g. Johnston 1996), with the patterned allele being dominant over the plain-back allele. However, the presence of patterned offspring from matings involving two plain-back individuals is not consistent with this mode of inheritance. The exact mechanism of morph inheritance therefore remains unclear.

Acknowledgments

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