CHAPTER 3

**Growth and reproduction in *Egernia whitii*
in South Australian off-shore islands**

ABSTRACT

Growth and reproduction in *Egernia whitii* are subject to environmental influences. Here litter size, size/age to sexual maturity, reproduction, longevity, and growth and survival rates are investigated as a prerequisite to understanding the social environment of *E. whitii* at a mid-latitude location in its distribution. Morphological and reproductive data derived from preserved specimens on the SA mainland and off-shore islands are analysed and presented in conjunction with data from field populations on Wedge Island showing juvenile survival rates and morphological plasticity.

Using frequency histograms two juvenile size classes can be identified before sexual maturity at > 70 mm SVL, and skeletochronology suggests that these skinks reach ≥ 13 years old. Average litter size is 2.2 and considerable morphological plasticity can be demonstrated in altered feeding regimes. Growth is accelerated with decrease in latitude and increase in temperature. Juvenile survival rates, which are low in the field, do not appear to be connected to predation pressure. Tail loss constitutes a substantial source of morbidity which may be exacerbated by the need to use tail tips for social signalling.

A modified form of parental care whereby juveniles remain within family groups for a period of time until new young are born may form the basis of social development for this aggressive lizard species. The link between these characteristics requires further testing.

INTRODUCTION

Sociality and life history

Survival in a changing environment is dependent on sufficient genetic variation to facilitate maximisation of some components of fitness (Roff 1992). Differences in body dimensions and sexually dimorphic traits can be demonstrated amongst different populations of the social species *Egernia whitii* within South Australia

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(SA), the western limit of the species' range (Chapter two). Growth and reproductive patterns are also subject to environmental influences. The dynamics involved in group living depend upon the features that characterise the species and where life history components vary, activity and motivation may also be affected.

Essential life history information on *E. whitii* in South Australia is presented here so that new scientific evidence concerning the behavioural adaptations of scat piling and chemosensory communication may be placed in the context of the species' physical and biological constraints. This paper investigates aspects of maternal investment, size and age to sexual maturity, reproductively active periods during the year, litter size, longevity, and growth and survival rates as a prerequisite to understanding the social environment of *E. whitii* at a mid-latitude location in its distribution. Morphological and reproductive data derived from preserved specimens at the South Australian Museum, Adelaide (SAMA) and originating on the SA mainland and on Kangaroo and other off-shore islands, are analysed and presented in conjunction with data from active populations on Wedge Island (in the Spencer Gulf of SA) showing juvenile survival rates and morphological plasticity.

Growth and longevity

The occurrence of *E. whitii* in Australia over a geographically and climatically extensive area, from sub-tropical in Queensland to cool temperate in Tasmania (Rawlinson 1974, Chapple 2003), allows a comparison of data from a range of latitudes. Research undertaken on Wedge Island is compared with information on variations in birth size, growth patterns, size at reproduction and maximum size attained which has been gleaned from previous historical and scientific publications at different locations. A table integrating these studies and observations has been placed in the Discussion section to separate the records generated by other researchers (Hickman 1960, Milton 1986, Milton 1987, Donnellan *et al.* 2002, Chapple 2005) from information generated in this study.

A number of studies have shown the reliability of assessing longevity in reptiles and amphibians by skeletochronology (Castanet 1975, Castanet 1978, Hemelaar & Van Gelder 1980, Hudson 1988, Schulz 1990, Driscoll 1999, Sinsch *et al.* 2002). Some studies (Castanet 1978, Hudson 1988) have focused on comparing the number of lines of arrested growth (LAG) that occur during the hibernation period in phalanges

and femoral bones. By demonstrating that the LAG concur in individuals, they have established precedents for using toe sections from live animals to be used to study populations and longevity, rather than sacrificing whole animals.

Skeletochronology studies have been missing from the available research to date and are needed to establish a minimum lifespan for those skinks that survive to adulthood. *E. whitii* mature over several years, and produce no more than one litter of well formed offspring per year (Chapple 2003). Previously they have been estimated to live between three (Milton 1987), and ≥ 8.5 (Hickman 1960), years, but their longevity is not well understood. Juvenile survival numbers are also unknown for this species, and as longevity in this context is likely to play a vital role in species social status, a study of age and size was undertaken.

Juvenile survival

There is a shortage of general research on juvenile survival in most lizard taxa, and in *Egernia* species in particular (Chapple 2003). The cause of this may be that studies on dispersal patterns in social skinks and multiple threats to immature reptile survival are difficult and complex areas of research. However there is general agreement that tail loss leads to an increased risk of death in other juvenile lizard species (Civantos & Forsman 2000, Fox & McCoy 2000, Blomberg & Shine 2001). The relationship between caudal autotomy and juvenile survival in *E. whitii* are explored using available data from field trips and laboratory births.

Viviparity and foetal nourishment in *E. whitii*

Traditionally the evolution of viviparity has been attributed to the need to incubate embryos within the body of the mother in colder regions rather than relying on variable climate or the occurrence of suitable egg nest sites (Rawlinson 1974). However *E. whitii,* like others of its genus, is viviparous throughout its range (Hickman 1960, Milton 1987, Greer 1989).

Females nourish developing embryos directly via a yolk-sac, and indirectly via the close apposition of maternal and embryonic vascular systems distinctive of type 1 allantoplacentation (Weekes 1935, Stewart & Thompson 2000). Immediately before the birth of a foetus, the yolk-sac and accompanying vitelline vessels are drawn out

of the encircling allantoic folds and into the gut of the embryo, the yolk-stalk is torn away from the body, and the allantoic folds meet and grow together (Weekes 1935). Post-natally newborns have been observed eating the placenta and membranes shortly after birth (unpublished data). These birth strategies deliver nutrients immediately before and after the birth process to relatively helpless newborn juveniles. They entail passive maternal care and in this way provide an important advantage to the newborn, which is especially evident when placed in the context of small litters of well-formed young entering a social environment.

MATERIALS AND METHODS

Wherever possible live captures were used to gain life history information or supplement SAMA data. No live animals were sacrificed for the study.

The research site was Wedge Island in the Spencer Gulf of South Australia (35°09'S, 136°27'E). A total 365 lizards were captured during a three year study between March 2001 and March 2004. In March 2001, 24 *E. whitii* individuals from Wedge Island were toe clipped for skeletochronology and retained as a laboratory colony for communication experiments, and in April 2002, 26 individuals in three separate groups were captured and retained for group communication experiments.

During early December in 2002 and 2004, 23 gravid females were captured and retained for sibling relationship observations. During a capture/mark/recapture trial in December 2003 and a home range study in March 2004 a total of 110 lizards were processed and released, and during north-south transects at 200 metre intervals across the island between March 2001 and April 2003, 182 lizards were processed and released.

Records of location and social proximity of wild caught specimens were used to establish familiar groups in the laboratory. Morphometric data on weight, snout to vent length (SVL), tail length, tail regeneration, hind leg and foot length, head length, head width and head depth were analysed for each skink and results are presented in this chapter. For both live and preserved specimens SVL and tail length were measured from snout tip to vent and vent to tail tip respectively, by stretching the skink along a metal ruler. A dial calliper was used to record head dimensions. Head length was measured from the lower ear opening to the snout tip, head width

was measured transversely in line with the anterior interparietal scale, and head depth was measured centrally from the interparietal scale to a point on the neck directly in line below.

Measurement data from captured individuals was used to trace growth and development to reproductive maturity. Measurement and experimental data obtained from a cohort of 23 juveniles born in 2004 in the laboratory was used in a comparison of growth rates with field data, and statistics from laboratory births were used in combination with South Australian Museum, Adelaide (SAMA) data to confirm number and size of offspring. A more detailed description of the island can be found in Chapter Two. Twenty-four *E. whitii* individuals were toe clipped for skeletochronology.

South Australian Museum specimens

An examination and analysis of the preserved specimens in the South Australian Museum, Adelaide (SAMA) for information on age to maturity, gonad activity, and size and number of offspring gained from the island specimens was used as a guide for the study population on Wedge Island. In all, 208 *E. whitii* specimens collected over a 90 year span were used. Of these 95 were from the mainland (Figure 2: Clades 2 & 3), and 113 were from island populations, primarily Kangaroo Island (N= 93) but including Thistle Island located 7.4 km east of the southern tip of Eyre Peninsula (N = 2), Wedge Island (N= 10), and West Island located in Encounter Bay, Fleurieu Peninsula (N = 8). Island specimens were measured internally in addition to external examination, for reproductive information.

The identification number, date of capture when available, location, weight, snout to vent length (SVL), tail length, tail regeneration, head length, head width, head depth and combined hind leg and foot measurement for each specimen was recorded. Each intact offshore island specimen which had a recorded month of capture (N = 97: female = 48, male = 49), was examined internally for signs of reproductive activity.

Gonad number, size and condition were measured in both sexes. As found by Weekes (1935) pregnant females retained follicles in two sizes – both small and considerably enlarged. Embryo development and follicle measurements and were used in this study to investigate fecundity.

Specimens were drained and blotted with absorbent paper immediately prior to weighing, and re-sprayed before and during examination to prevent drying. Some of them were very fragile and the preserving process had caused some dehydration. Where any dimensions were clearly distorted as a result of age, compression, or condition, missing values were recorded for analyses.

Skeletochronology

Toes from individuals were removed according to a standard numbering system on a rotating basis to ensure the majority of the group had only one toe removed, with a maximum of two per animal. The longest toe (4th) was left intact. Prior to commencing the procedure the toe and precision nail clippers were cleaned with an ethanol 70% solution, the complete toe was removed with one cut, and at completion of the procedure the stump was dipped in Betadine® antiseptic solution and allowed to dry before release, to avoid contamination or infection.

The group of 20 specimens selected for processing included three juveniles from the South Australian Museum, Adelaide (SAMA), two adult-juvenile pairs, and four field observation specimens, comprising a total of six juveniles, 14 Wedge Island adults across a range from 72 to 86 mm SVL (Table 1). A female that died post-capture carrying three fertilised embryos was included.

Table 1: Size classes of animals toe-clipped for skeletochronology.

Number	Snout to vent length (mm)	Size classes: 39–56, 57–69, 70–92	Predicted number of seasons	Origin and comments
1	40	1	0	SAMA, Kangaroo Island
2	53	1	0	Wedge Island
3	54	1	0	SAMA, Kangaroo Island
4	61	2	1	SAMA, Kangaroo Island
5	69	2	1	Wedge Island (paired)
6	69	2	1	Wedge Island (paired)
7	72	3	2	Wedge Island
8	73	3	2	Wedge Island
9	74	3	2	Wedge Island
10	75	3	2	Wedge Island
11	75	3	2	Wedge Island
12	75	3	2	Wedge Island
13	77	3	2	Wedge Island
14	78	3	2	Wedge Island (paired)
15	78	3	2	Wedge Island (paired)
16	78	3	2	Wedge Island
17	83	3	2	Wedge Island
18	83	3	2	Wedge Island, 3x embryos
19	86	4	3	Wedge Island
20	89	4	3	Wedge Island

Specimens were initially fixed and stored in 70% ethanol. Processing was completed in the Department of Anatomy and Histology, School of Medicine, Flinders University by Ms Michelle Lewis. Preparation of material consisted of decalcification in Decal® solution for 24 hours, dehydration in ethanol, replacing lost water with the solvent chloroform, and then infiltrating the tissue with molten wax. Finally the specimens were embedded in fresh molten paraffin at 62°C and set to a solid block on a refrigerated plate. Seven micron sections were cut and mounted on gelatine coated slides using a rotary microtome and sections were dried in a 37°C oven for 24 hours. Slides were then stained with Haematoxylin and Eosin using a standard method.

The mid-shaft section of toe bones was selected for sampling as indicated by Driscoll (1999) and three sections were taken from each specimen, each on a separate slide with identity concealed to avoid bias during interpretation. The remaining 17 specimens (51 slides) were independently assessed in random order by myself and two other researchers, and the results were compared. Unanimous results were

automatically accepted, and the remainder of slides were reassessed until consensus was achieved.

RESULTS

Reproduction

SAMA preserved specimens were used to obtain information about gonad activity in South Australian off-shore island populations. In 113 off-shore island specimens, 97 (female = 48, male = 49) had a recorded month of capture. There were no data available for the months of April, July or August. A frequency histogram of SVL is provided separately for specimens captured between September and January (Figure 1) and February and June (Figure 4).

Specimens were divided into two time periods to reflect gonad size during the post hibernation period which begins in August and continues until the birth of young in early February on Wedge Island, and the post-natal period which begins in February and continues through to hibernation which lasts for only a few of the colder months in May, June, and July. On Wedge Island some animals are sometimes active during May and August. Figure 4 indicates a greater proportion of juveniles. No full term pregnant females were represented in the available specimens, so consequently gonads of both sexes had reduced in size by this time.

Mean female follicle size ($\pm$ 1 SE) as a function of SVL for specimens captured between September and January is shown in Figure 2. During this time female follicle size increased through vitellogenesis and fertilisation to full term pregnancy. Young are usually born in early February, after which there is a return to quiescent gonad size (Figures 2 & 5). Males experience a shorter period of reproductive activity, with gonads showing steady growth with increasing size (Figures 3 & 6).

It was not straightforward establishing an exact size for sexual maturity for females using available measurement data. Although follicle enlargement was apparent in one Kangaroo Island specimen (Fig. 2) at 73 mm SVL, indicating the minimum size in the sample group at which females might successfully mate to reproduce by the end of the season, there is no surety that this individual did reproduce. A SVL of 76–77 mm was a more common size for follicle enlargement.

Four mature females of sizes 82, 85, 87 and 90 mm SVL respectively, captured in the months of May and June had follicles of between 3.7 mm and 6.6 mm in size. Only females with follicles larger than this were likely to be undergoing vitellogenesis leading to fertilisation later in the same year. Two females captured during late November and late December with follicle sizes of 2.2 mm and 3.8mm respectively, were therefore thought unlikely to produce young that season even though they were 76 and 75 mm SVL at the time of death. The difficulty of nominating a size at sexual maturity for *E. whitii* is compounded by complicated research findings both in this thesis and other studies. Missing data recorded for the months of April, July and August make the trend of vitellogenic activity for autumn unclear.

Male testis size showed a linear increase with SVL over the February to June period. No off-shore island specimens were available for July, August or September and consequently it was not possible to trace the seasonal increase in testis size. However testis size showed a substantial increase during October, November and December compared to the cooler months. All males developed larger testes once they had reached 76 mm SVL, which may indicate male sexual maturity for the Wedge Island population.
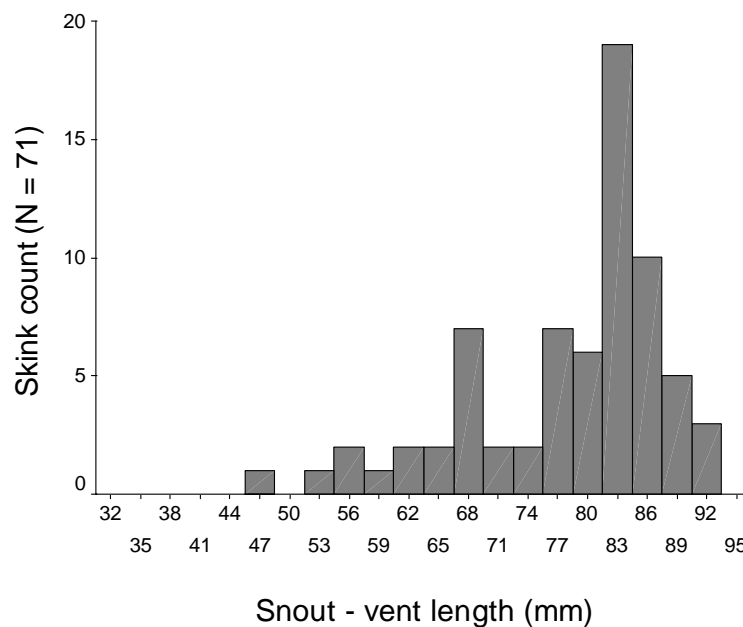

Figure 1: A frequency histogram of SVL for SAMA male and female offshore island specimens captured between September and January (N = 71).
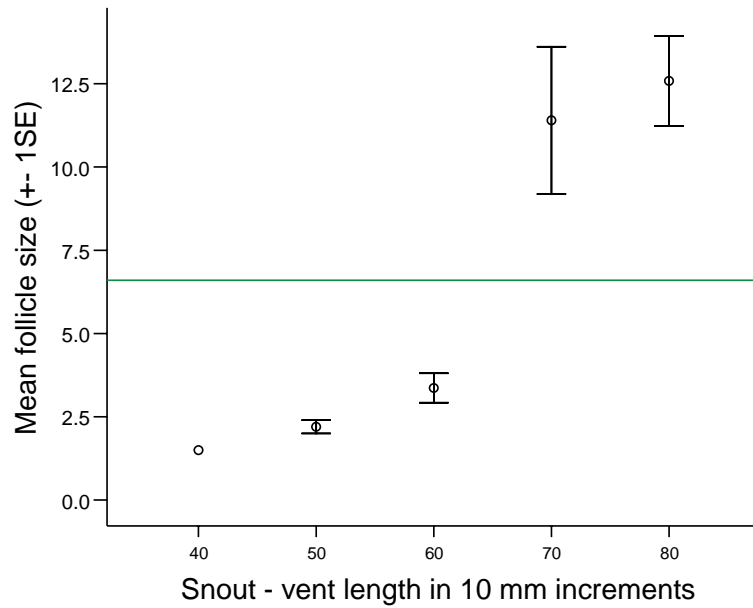
Figure 2: SAMA offshore island specimens showing mean follicle size in mm (± 1 SE) for females grouped in 10 mm SVL increments from September to January. Green reference line at 6.6 mm separates the largest gonad size in the sample during the non-reproductive period, from follicles undergoing vitellogenesis and fertilisation.
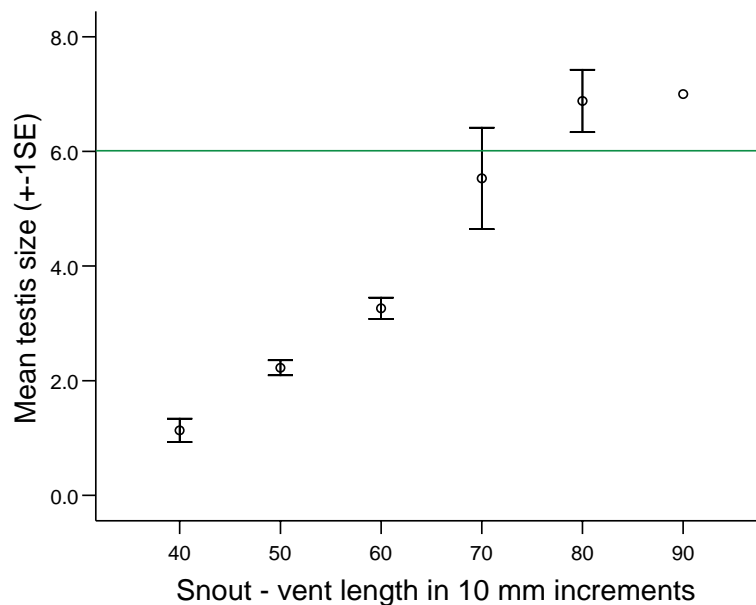

Figure 3: SAMA offshore island specimens showing mean testis size in mm (± 1 SE) for males grouped in 10 mm SVL increments from October to January. Green reference line at 6 mm separates the largest gonad size in the male sample during the non reproductive period, from the testis peak during the reproductive season.
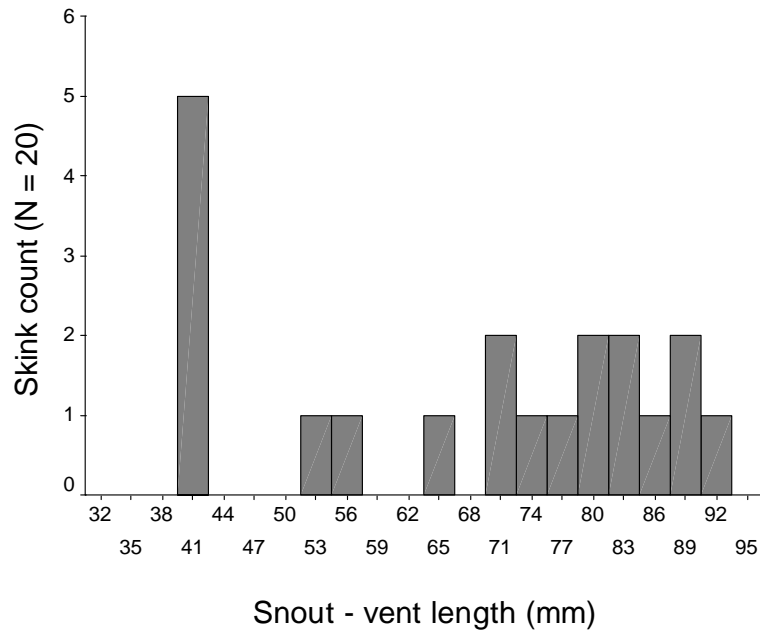
Figure 4: A frequency histogram of SAMA male and female offshore island specimens captured between February and June (N = 20).
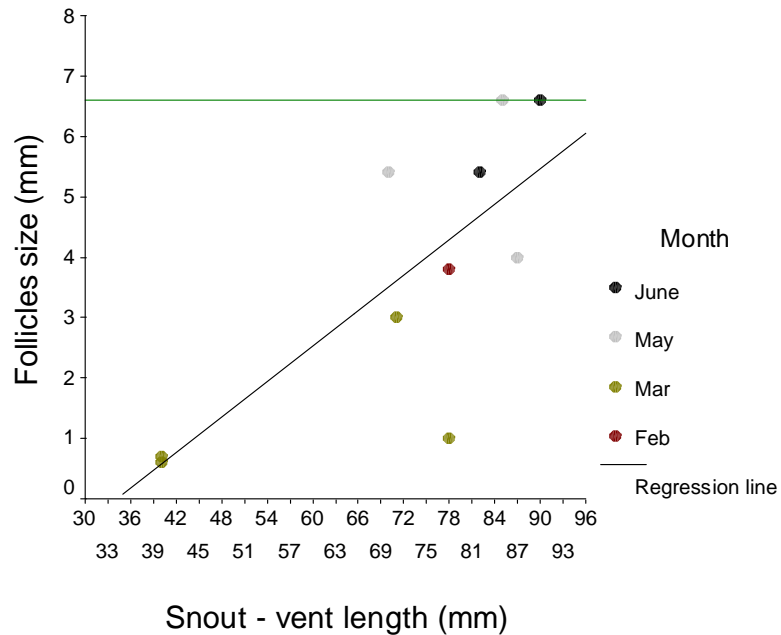

Figure 5: SAMA female follicle size from February to June, as a function of SVL. Green reference line at 6.6 mm follicle size indicates the maximum follicle size in the sample. A linear regression line has been fitted.
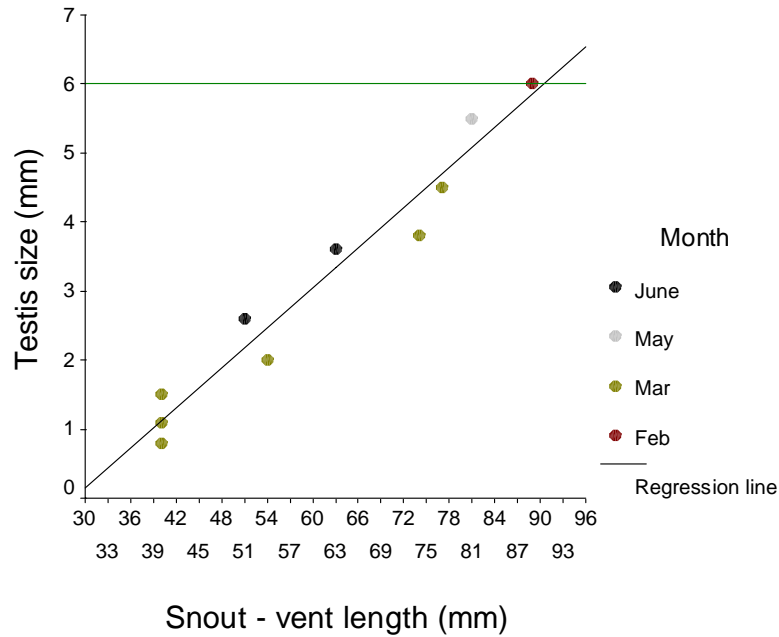
Figure 6: SAMA male testis size as a function of SVL based on specimens collected from February to June. Green reference line at 6 mm indicates maximum testis size in the sample. A linear regression line has been fitted.

Number and size of offspring

SAMA specimens are not included for comparison in this analysis because the sample size was too small for meaningful analysis. I considered all the Wedge Island juveniles in the smallest size class separately (N = 61), and they appear in the main graphs where appropriate. The juveniles were allocated to three different categories:

1) Newborn laboratory juveniles from females captured on Wedge Island in early December, and born in the laboratory the following February (neonates, N = 23).

2) Wedge Island pre-hibernation captures (March/April, N = 27).

3) Post hibernation captures from Wedge Island (August/December, up to 56 mm SVL, N = 32).

Juveniles born in the laboratory to different mothers arrived within six days of each other with parturition taking between one and four days to complete. All juveniles were weighed and measured within five days of birth. In total 15 pregnant mothers delivered 33 young in litters of between one and four (average litter size = 2.2).

The only female to deliver four newborn young had inadvertently bred in captivity in early 2003 within her social group, and two of her progeny were stillborn. The two

live births from her litter and six other juveniles born in the laboratory the same year to four Wedge Island females, were video taped at intervals, for up to 24 hour periods, to observe their social interactions.   To preserve the integrity of their instinctive behaviour these individuals experienced minimal human contact and thus were not weighed and measured until several months old.

In 2004 a cohort of 23 juveniles born in the laboratory were observed and handled from birth. Table 2 summarises some morphological parameters within the first five days of birth. Two newborn (8.69%) had already experienced autotomy when first handled at two and four days old respectively. Six juveniles failed to survive the neonatal period, leaving a cohort of 17 to reach 70 mm SVL (adult size).

Table 2: Wedge Island laboratory born neonatal measurements, N = 23.

Morphological measurements	Number	Minimum	Maximum	Mean	Standard error
Mass	23	1.1	1.8	1.46	0.42
SVL	23	36	42	39.3	0.29
Tail length	23	33	63	56	1.35
Tail regrowth	23	0	1	0.09	0.06
Hind leg & foot	23	15	18	16.52	0.16
Head length	23	9.9	10.9	10.38	0.06
Head width	23	6.8	7.9	7.26	0.05
Head depth	23	5.5	6.9	6.27	0.06

The March and April Wedge Island field juveniles (N = 27) were captured after the neonatal period (first four weeks of life) but before hibernation (May, June and July). Table 3 describes their morphology.   Four of these juveniles (14.8%) had experienced autotomy prior to capture.

Table 3: Wedge Island pre-hibernation (March and April) capture measurements of juveniles less than 57 mm SVL (N = 27).

Morphological measurements	Number	Minimum	Maximum	Mean	Standard error
Mass	27	1.4	2.5	0.74	0.05
SVL	27	39	45	42.15	0.32
Tail length	27	26	75	61.70	2.35
Tail regrowth	27	0	24	2.67	1.28
Hind leg & foot	27	16	20	18.07	0.22
Head length	27	10.1	11.9	10.94	0.10
Head width	27	7.1	8.2	7.58	0.05
Head depth	27	5.8	7.4	6.53	0.08

The August to December Wedge Island field juveniles (N = 32) were captured after hibernation but before the annual reproductive period. Table 4 summarises some of their morphological parameters. Fourteen juveniles (43.8%) had experienced autotomy prior to capture. If these numbers are representative of the field population, approximately 24% (20 from a population of 82) of juveniles in their first year of life experience autotomy of $\geq$ 64% of their SVL and survive (Chapter 2).

Table 4: Wedge Island post-hibernation (August to December) capture measurements of juveniles less than 57 mm SVL (N = 32).

	Number	Minimum	Maximum	Mean	Standard error
Mass	32	2.0	4.0	2.72	0.09
SVL	32	44	56	49.25	0.57
Tail length	32	19	90	63.66	3.49
Tail regrowth	32	0	50	7.78	2.24
Hind leg & foot	32	15	29	18.88	0.49
Head length	32	10.2	13.1	11.83	0.12
Head width	32	6.8	9.4	8.08	0.10
Head depth	32	6.1	8.5	7.16	0.10

Table 5 records tail length as a percent of snout to vent length from all of the capture dates, and includes laboratory born individuals.

Table 5: Intact tail length as a percent of snout to vent length

Source	Number	Minimum	Maximum	Tail as % of SVL
Wedge Island: field captures	16	136.4	172.1	157.9
Wedge Island: laboratory born neonates	21	137.5	161.5	147.2

The March and April field captures differed significantly in head depth (independent-samples t-tests $t_{(20)}$ = -2.33, P = 0.031), but no other measurement variables were significant (P = > 0.05 for all comparisons). Consequently March and April captures were combined and GML Multivariate (SPSS 11.5) analyses of mass, SVL, hind leg and foot length, tail length, head length, head width and head depth were conducted on the remaining three groups. As expected, all measurements recorded significant size differences in all other variables between groups, with values of P = <0.001. Over the first 10 months of life growth rate appears to accelerate (Figure 7).

Hickman (1960) records growth in the first year as sometimes exceeding twice the length of that obtained in second and third years in a Tasmanian population.
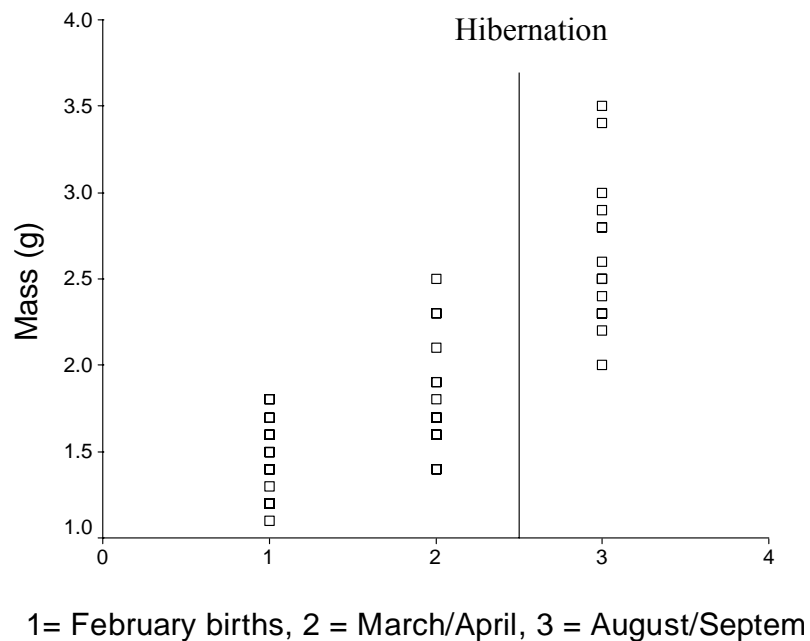

1= February births, 2 = March/April, 3 = August/Septem

Figure 7: Scattergram of juvenile mass in first year of growth with reference line indicating hibernation period.

Growth to sexual maturity

Figures 8, 9 and 10 plot the snout to vent length of captures over three different capture periods. March and April (N = 152), August and September (N = 95), and November and December (N = 117) comprising a total sample of 364 individuals. The histograms point to patterns seen in long-lived species with initial low survival but followed by high survival in adulthood.

The results suggest that the neonatal size class, first seen in the field at 39mm SVL, has reached a maximum of 56 mm SVL by the following year, 69 mm SVL in the second year of growth, and $\geq$ 70 mm SVL in the third year of growth.   The histograms indicate that many new juveniles survive hibernation but their number decline rapidly by November/December. As predations pressure is low on Wedge Island other causes of this failure to survive need to be posited.

Table 6 presents a composite result of SVL measurements for Wedge Island field captures (N = 364) during 2001, 2002, and 2003. It indicates a trend for three size classes based on frequency histograms (Figures 8, 9 & 10), with maturity occurring some time after 70 mm SVL.

Table 6: Projected annual growth of field captures Wedge Island from 2001 to 2003.

Size class (mm)	Annual growth	Reproductive activity
39 - 56	1st year of growth	No reproductive activity
57 - 69	2nd year of growth	No reproductive activity
70 - 92	3rd year or more of growth	Early vitellogenesis at 73 mm SVL. Fertilization at approximately 77 mm SVL. Gravid females common at 80 mm SVL.

Figures 8, 9 & 10 are presented consecutively for comparison.
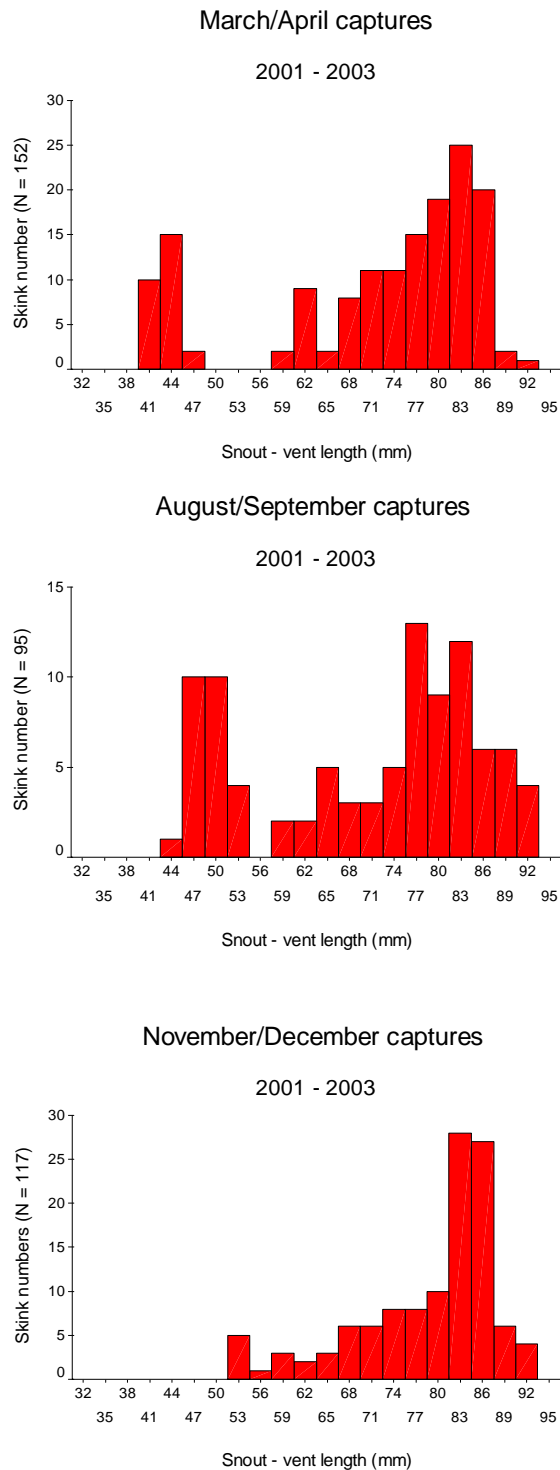
Figures 8, 9 & 10: Frequency histograms of SVL for field captures plotted season by season.

In the third size class the females that became gravid were those that were larger at the beginning of the mating season in October and November. Growth continues after the attainment of this size. The relatively long period of sexual immaturity (2-3 years) in medium-sized species usually co-exists with a life-span of up to 10 years (Chapple 2003). All adults that attain ≥ 80mm SVL appear to be reproductively mature, with females producing one litter each year.

Lifespan derived from skeletochronology

Three of the 20 specimens selected for skeletochronology were not suitable for inclusion because the toe sections for these skinks were located near the joint and it was not possible to reliably identify concentric lines of arrested growth (LAG) radiating from the marrow. Results of the remaining 17 specimens (51 slides) are presented in Table 7. The live lizards continued to grow in SVL over the next three years in the laboratory environment where they were provided with food and protection from environmental mishap. SVL's in 2004 are recorded in Table 8 for live captured animals.

Table 7: Skeletochronology results for individual skinks showing LAG, size when toe clipped, and size three years later.

Number	Identification	LAG	Snout - vent length (mm) 2001	SVL (mm) of live captures in 2004
1	SAMA 20594	0	40	Preserved
2	F7000	0	53	Field release
3	SAMA 1355F	2	54	Preserved
5	100	2-3	69	92
6	400	3	69	90
7	20	3	72	85
8	1	4	73	87
9	2000	8	74	85
10	2	5	75	92
11	10	4	75	87
12	107	3	75	Died
13	6	7	77	89
14	70	5	78	91
17	F1000	5	83	Field release
18	F700	6	83	Field release
19	3	4	86	93
20	9	8	89	90

Figures 11 & 12: Cross-section overview of foetal (skink 1) and mature (skink 20) bone structure (Table 7). Arrows indicate the cartilage and bone structure for these specimens.
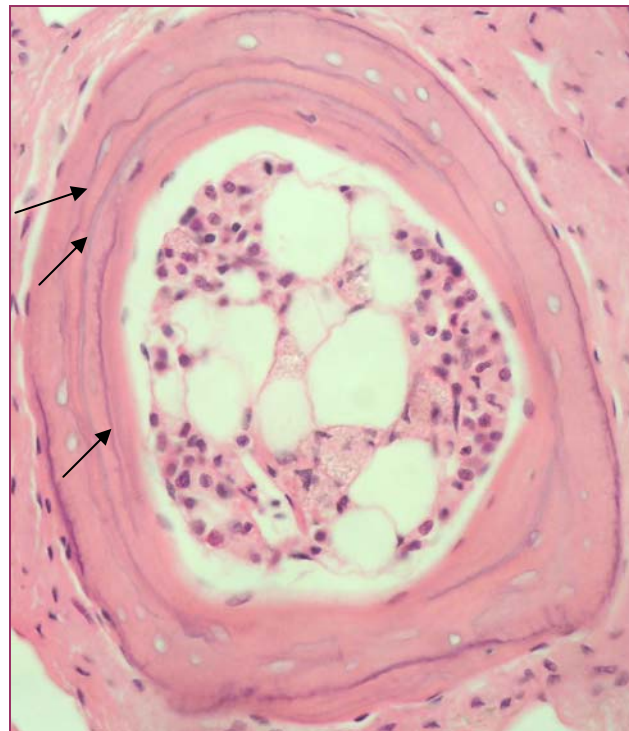

Figure 13: Three visible rings in the bone structure of skink 6 are indicated by arrows (Table 7).
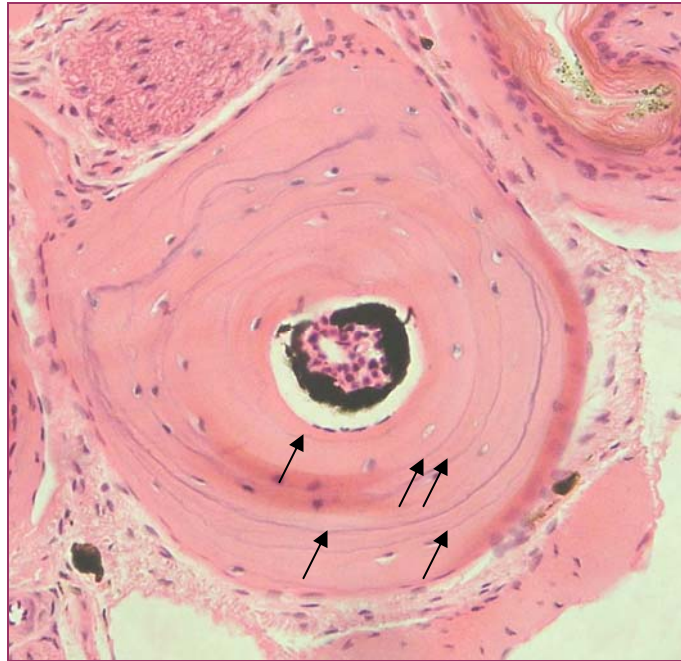
Figure 14: Five visible rings in the bone structure of skink 10 are indicated by arrows (Table 7).
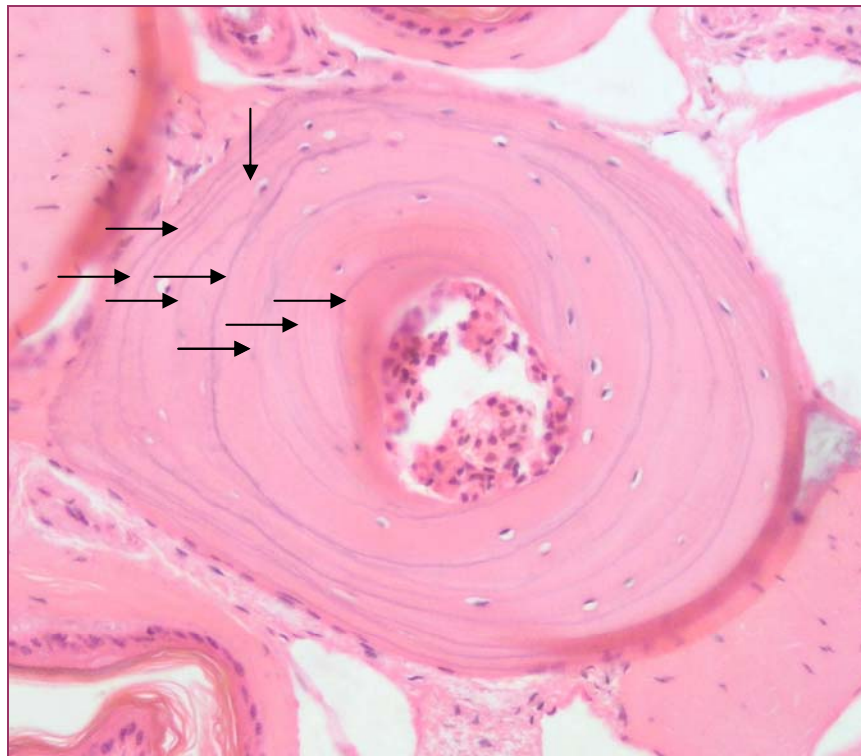

Figure 15: Eight visible rings in the bone structure of skink 9 are indicated by arrows (Table 7). The scalloped inner area shows where reabsorbtion has taken place.

The relationship between snout to vent length and the number of extant LAG were studied using a scatter plot (Figure 16). Consensus between two researchers across three bone sections for each specimen is indicated by filled triangles. Consensus in two out of the three ring counts for each individual, with disparity in one bone section, is indicated by a hollow circle.
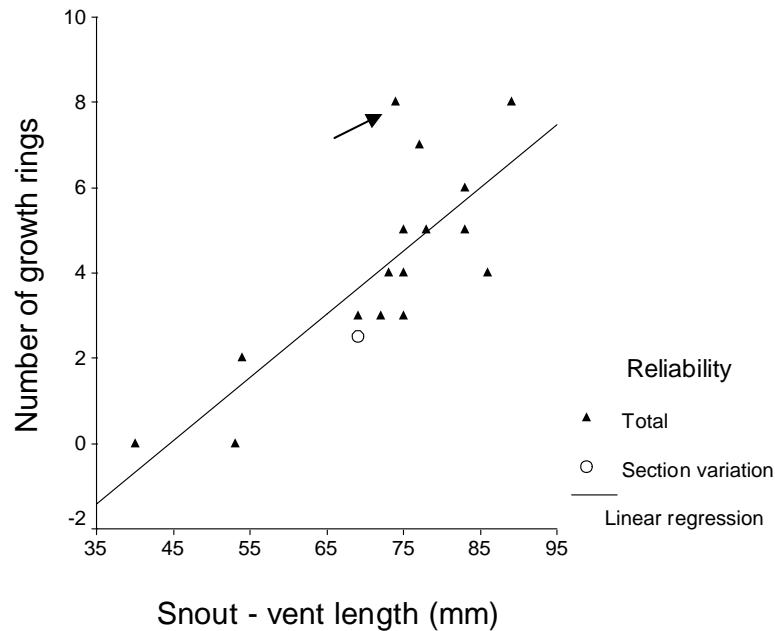

Figure 16: Relationship between snout to vent length and age (LAG) in years with a liner regression line fitted. Filled triangles indicate researcher consensus and identical ring count for each slide. Hollow circles indicate researcher consensus with ring count disparity between bone sections in individual specimens. The arrow points to an adult of 74 mm SVL with 8 LAG.

This (Figure 16) indicated that while growth rates exhibited marked variation, skinks 69mm SVL or less had between zero and three LAG, and skinks 70mm SVL or greater varied between 3 and 8 LAG. The precise age of the lizards was not known, but the distribution with LAG's is positively associated with SVL. The slow growth of skink nine, which although only 74mm SVL was in the oldest age category, was an interesting development (arrow in figure 16 indicates this individual).

Figure 17 shows the distribution of skink sizes (snout-vent length) with actual age as determined by skeletochronology. The mix of ages and sizes after the skinks reach

73 mm SVL indicates that some have grown very quickly in length and others much more slowly. This may reflect habitat quality.
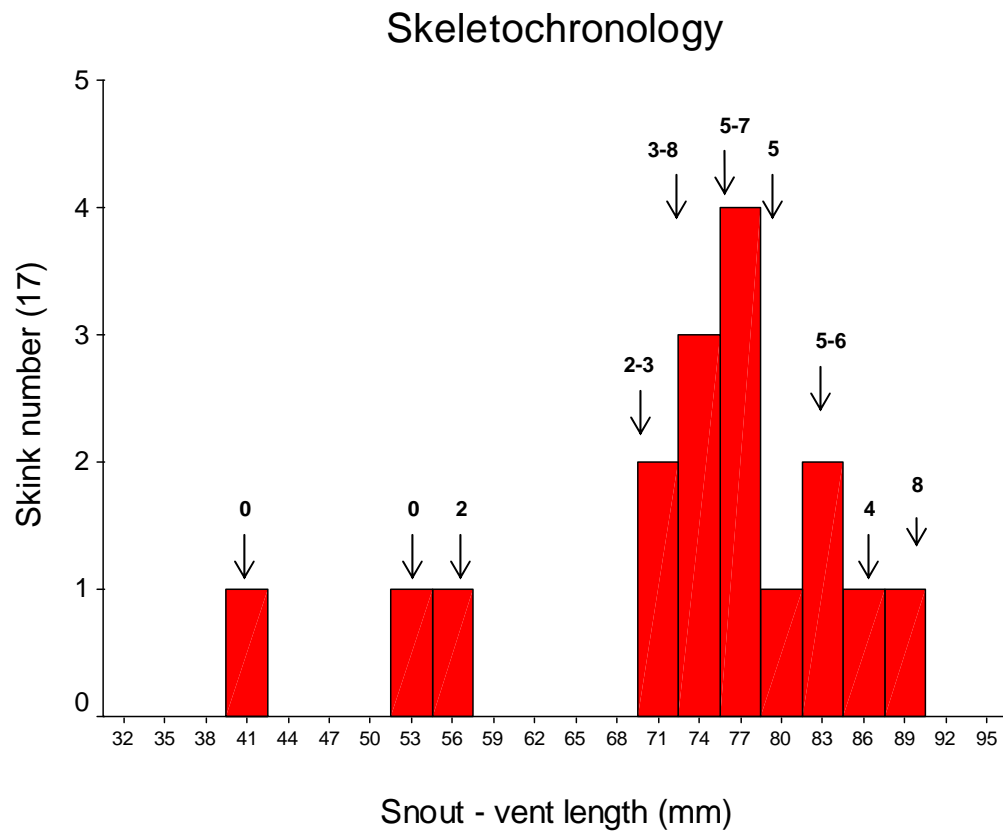
Skeletochronology

Figure 17: Distribution of individual skink sizes (snout-vent length), with age in years based on skeletochronology indicated by numbers above arrows.

Accelerated laboratory growth rates

Juvenile growth in the laboratory population was plotted for the first nine months of life.   Plentiful food, protection from predators and aggressive adults, and manipulation of temperature to prevent hibernation, led to highly accelerated growth rates (Figure 18) when compared to field populations. In contrast to field juveniles, laboratory reared young reached an adult size class within their first 10 months of life (compare with figures 8, 9 & 10).
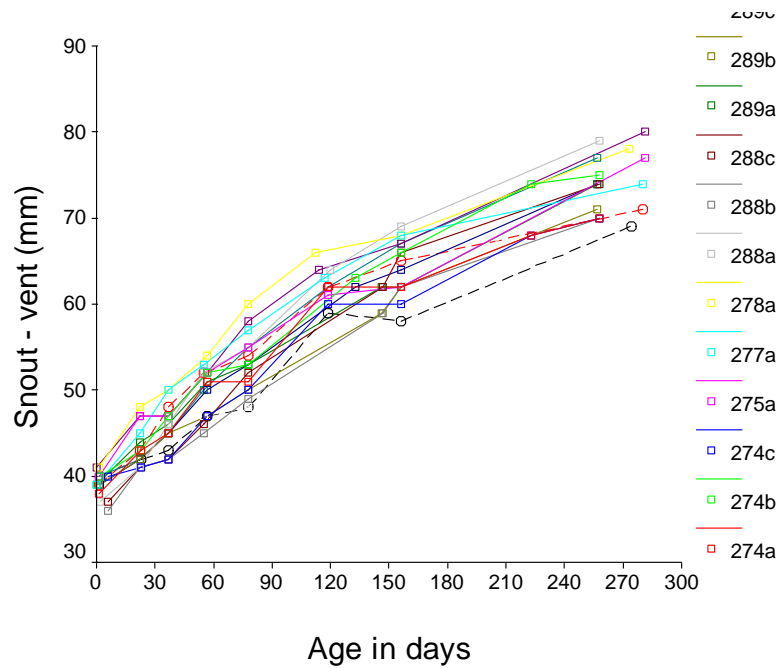
Figure 18: Growth, in days from birth, for laboratory born juveniles in the 2004 cohort that survived to ten months (N = 17).

Six of 23 juveniles born in the 2004 cohort failed to survive their first 30 days. The remainder from the 2003 and 2004 cohorts are presented in Table 8. Six individuals that died were from litters of two or three. Only one litter of three recorded deaths, but two of three neonates failed to survive. Juveniles in litters of two appeared to be most at risk, recording a higher death rate than the combined one and three litters groups. Total death rate for this sample was 20.7%, excluding stillborn young.

Table 8: Status of laboratory reared juveniles from 2003 and 2004.

Litter group size	Number of litters	Live births	Stillborn	Deaths
One	3	3	0	0
Two	7	14	0	4
Three	4	12	0	2
Four	1	2	2	0
Totals	**15**	**31**	**2**	**6**

Figure 12 shows tail length at birth, autotomies, regrowth and length at maturity of surviving laboratory reared juveniles from the 2004 cohort.
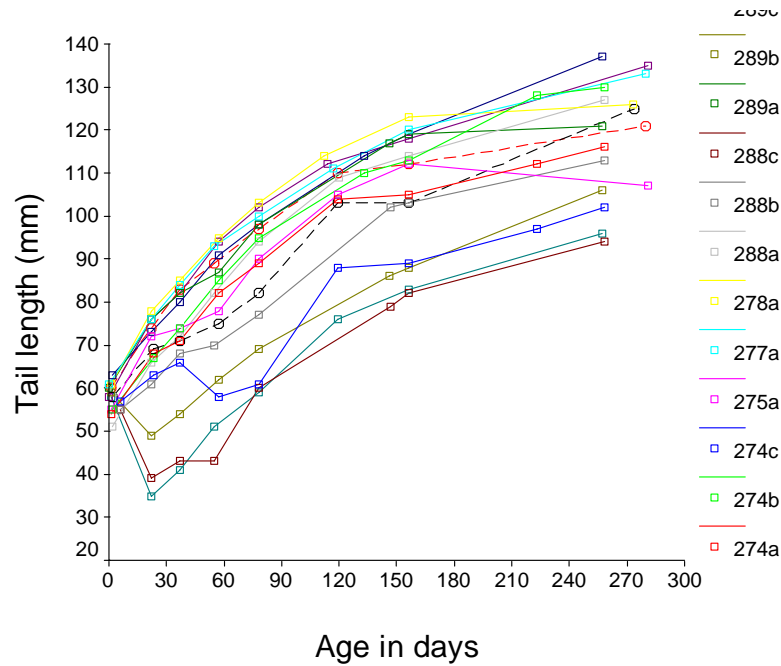
Figure 19: Tail growth in days, from birth to 10 months, in surviving laboratory born juveniles from the 2004 cohort (N = 17).

Three juveniles lost toes in their first five months in the laboratory (mean SVL ranged from 60 – 62 mm), and two juveniles suffered broken legs at about 4 weeks of age, which healed rapidly without treatment in a 2 week period.

Wedge Island tail data

A total of 365 *E. whitii* on Wedge Island were captured, ranging in body size from 39 - 92 mm SVL. Tail lengths recorded a minimum of 16 mm and a maximum of 155 mm. Regeneration lengths were between 1mm (recorded for nil regrowth) and 104 mm. Figure 20 records the tail length of all captures against SVL, and is placed consecutively with Figure 1 (intact tail length) for comparison.

Intact tails varied between 60 - 155 mm depending on the size of the skink, with variability in length for skinks of the same body length (Figure 21). The minimum was 125.3% of body length and the maximum was 189.4% of body length (Average 161.5%).
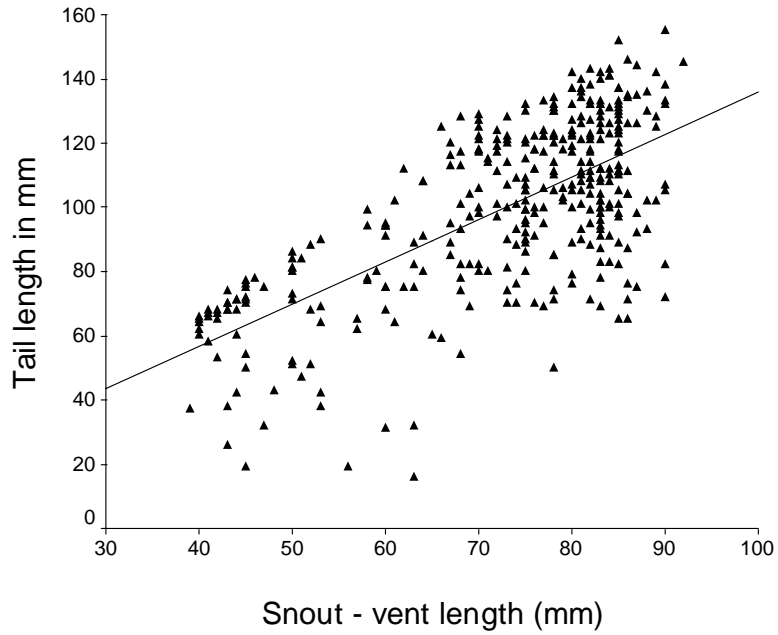
Figure 20: Tail length of *E. whitii* against relative body size, with a regression line fitted to the total field population.
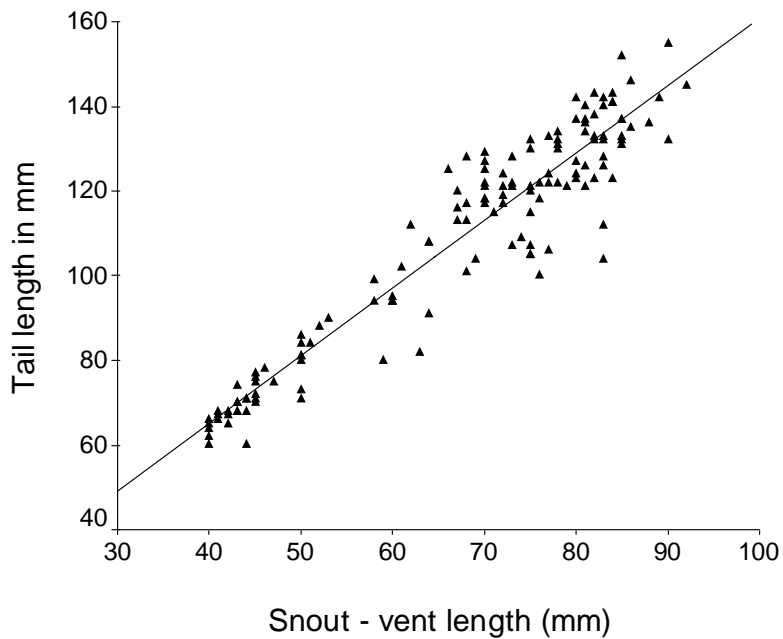

Figure 21: Intact tail length of *E. whitii* against relative body size, with a regression line fitted.

Table 9 records the status of skink tails in the total field population. The number, condition and percentage of the sample group reflect field conditions on Wedge

Island. Of 13 autotomies recorded, three occurred during capture, and the remaining ten were presumed to prior to capture - probably within a few days, as they displayed no regrowth.

Table 9: Tail status of _E. whitii_ on Wedge Island in the total field population.

Tail condition	% of population	Number of individuals
Intact tails	38.3%	140
Regenerating tails	58.1%	212
Recent autotomies	3.6%	13
Totals	**100%**	**365**

Juvenile _E. whitii_ on Wedge Island measure 39 - 69 mm SVL, and adults are ≥70mm (Chapter Three). A greater percentage of the juvenile population retain intact tails than the adult population $\chi^2 = 19.46$, p<0.001 (Table 10).

Table 10: Proportion of adults and juveniles with intact and regenerating tails.

Age	Intact tails	% of age group	Regenerating tails	% of age group
Juveniles	61	56	48	44
Adults	80	31.4%	175	68.6%

When tail length as a percentage of SVL was calculated for juvenile and adult skinks with intact tails and regenerated tails, no significant difference was recorded for those with intact tails, but there was a significant difference between age groups for skinks with regenerated tails (Table 11, Figure 22).

Table 11: Tail length in juvenile and adult groups

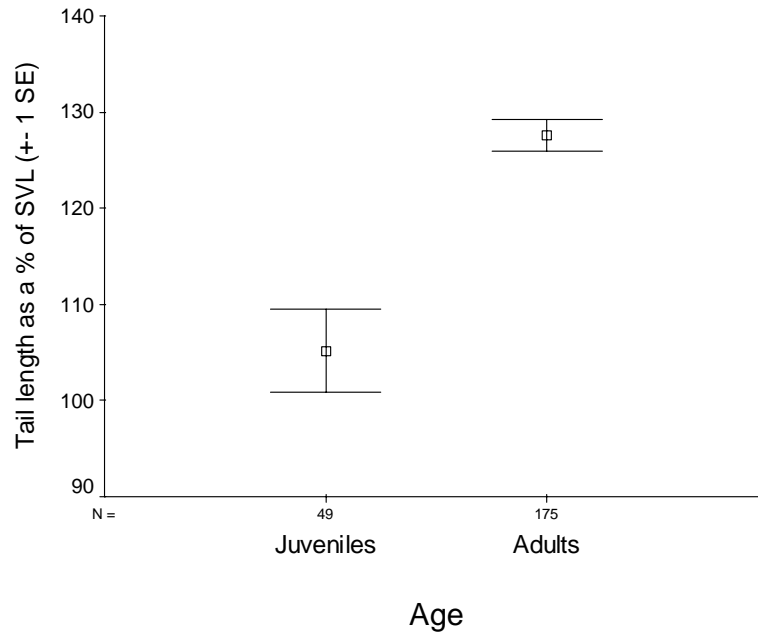| Tail status	Age	Independent samples T test	Min. length (mm)	Max. length (mm)	Tail length as % of SVL
Intact tails	Juvenile	P = 0.877	60	128	130.1 - 189.4
	Adult	Nil sig.	100	155	125.3 – 184.3
Regenerating tails	Juvenile	P <0.001	16	97	25.4 – 151.7
	Adult	Highly significant	50	144	64.1 – 166.7

Figure 22: Average percentage of regenerated tail length as a proportion of SVL for juveniles and adults.

DISCUSSION

In a comparison of the life history strategies between the tropics and the temperate zone in oviparous Australian lizards, James & Shine (1988) concluded that in congeneric lizards more rapid growth and earlier maturation in warmer climates may well be phenotypic responses to environmental conditions rather than genetically based life history adaptations.

Table 12 compares age to maturity, size classes, maximum body length, smallest pregnant female found and litter size in *E whitii* across a range of latitudes. Data from each different region are presented in a way that allows comparison across sites. The period between birth and 12 months is now designated 1st juvenile year, the following 12 months is 2nd juvenile year, the next two 12 month periods are 3rd years and 4th years respectively.

Table 12: Growth acceleration with decrease in latitude and increase in temperature. Pregnant females have been allocated minus ~ 2.5 mm for SVL at mating as an alternative prediction for size for maturity.

Location:	Age to maturity & size classes	Maximum body length	Smallest pregnant female (SVL)	Litter size range	Mean number
Queensland 28°35'S, 151°48'E (Milton 1987)	Birth size : ~ 40 I[st] year: 40-70 2nd year: 71- 86 3rd year: 87-97.1	97.1	≥85 mm (~ 82.5 at mating)	1-5	2.9 ± 0.4 (n=52)
A.C.T. 35°53'S, 148°58'E (Chapple 2005)	Birth size: ~ 40 I[st] year: 40-54 2nd year: 55-67 3rd year: 68-75 4th year: 76-100	94.3	77.4 mm (~ 75 when mating)	1-4	2.3.± 0.1 (n=42)
S.A. Wedge Island 35°09'S, 136°27'E (Bellamy 2006)	Birth size: 36-41 I[st] year: 35-56 2nd year: 57–69 3rd year: 70–92	92	78 mm (~ 75.5)	1-4	2.2 ± 0.2 (n=15)
Tasmania 43°14'S, 147°47'E (Hickman 1960)	Birth size: 35-39 I[st] year: 51-60 2nd year: 60-69 3rd year: 70-79 4th year: 80-90	90	78 mm (~ 75.5)	1-5	2.8 (n=27)

As the Queensland population (Milton 1987) reach sexual maturity at the end of their second year (presumably 24 months after birth the previous January/February) they are unable to produce offspring until the following year, or their third year. Skinks captured in the Australian Capital Territory (Chapple 2005) become reproductive at the end of their third year and therefore it takes a fourth year before they are able to reproduce. This study area was more southerly in latitude and was also 1250 m above sea level and therefore had a substantially colder climate than the Queensland study.

In the *Egernia* genus age to maturity, in those species that are known, takes more than one year, and some of the larger species have been known to live from 10 to 20 years in captivity (Greer 1989). On Wedge Island, where latitude is high but altitude is low (the landscape is < 200 m above sea level) skinks become reproductively active some time after reaching their third year. Those with larger body sizes at the beginning of the season (September/October) may reproduce in their third year, but it is more likely that another year of growth is necessary before they are reproductively

active. Only one modal group was clearly distinguishable and skeletochronology suggested that one skink of 74 mm SVL was at least 13 years old.

In Tasmania (Hickman 1960) skinks were not sexually mature until their 4th year. A pattern of delayed sexual maturation and smaller gravid size is apparent at higher latitudes and altitudes, or colder areas.

E. whitii resemble egg laying species studied by James & Shine (1988) in which clutches did not differ substantially between the tropics and temperate zone. Although litters of up to six in number are possible (SAMA specimen 23746 captured on Kangaroo Island in 1982), these are an anomaly. The majority of female *E. whitii* deliver between one and three offspring with the mean litter size between 2.2 ($\pm$ 0.2) and 2.9 ($\pm$ 0.4) across regions. Within the *Egernia* genus there is little available data on annual reproductive rates, but in *E. whitii* (Chapple 2005), and *E. stokesii* (Duffield & Bull 1996) the proportion of adult females that have been verified as pregnant during short studies were 71-85% and ~ 75% respectively. Two possible explanations are that reproduction is suppressed in social groups, or even that females breed biennially (Van Wyk 1991). More research is required to identify the cause of this reproductive pattern.

Parturition in the Wedge Island group (N = 15) took place over 1 – 4 days for each litter produced with a mean of 2.20 $\pm$ .22 days. Chapple (2005) reports parturition taking up to ten days, although in the present study the majority of births in each litter took place on consecutive days. There were 3 single births, seven litters of two juveniles, four litters of three, and one litter of four, which was inadvertently conceived in captivity, with two stillbirths preceding two live births.

Unlike some oviparous skinks (James & Shine 1988), body size in *E. whitii* increases with a decrease in latitude, and maximum body lengths of 90 mm SVL in Tasmania, 92 mm SVL in South Australia, 94.3 mm SVL in the A.C.T., and 97.1 mm SVL in Queensland show a gradient. Chapple (2005) recognises that females pregnant immediately prior to parturition may have grown by about ~ 2.5 mm in SVL since mating, and a slightly smaller size at maturity than that shown in Table 9 is likely.

The absence of large land masses, and in consequence, warmer land temperatures experienced in the Southern Hemisphere, has meant that in Australia reptiles have a

relatively short hibernation period of approximately three months. No more than 5-8 LAG are identifiable before the internal lines becomes ambiguous, which makes reliably identifying longer-lived species difficult. A maximum of eight LAG could be identified in *E. whitii* before they were reabsorbed and redeposited in the marrow cavity. However the individuals toe clipped for this exercise remained alive and well five years after toe-clipping, and a maximum life span of ≥ 13 years seems probable.

Size in the adult population was not indicative of age. Skeletochronology revealed an older mature individual (≥ 13) at the relatively small size of 74 mm SVL. Juveniles and some sub-adults reared in the laboratory grew quickly, reaching a maximum size of 96 mm SVL after 48 months. Diet is not controlled in the field or the laboratory, but food is more plentiful in the laboratory and as a consequence morphological plasticity becomes markedly evident when the growth rates of juveniles reared in the field and juveniles reared in the laboratory, and derived from the same population source, are compared. The extremely rapid growth rates of the laboratory juveniles serves as an unequivocal reminder that size does not necessarily predict age in mature individuals. Sinsch *et al.* (2002) concluded that most of the total size variance in their study remained unexplained by age.

However size largely determines outcome in agonistic interludes in both interspecific social dominance hierarchies (Melville 2002, Langkilde & Shine 2004) and intraspecific interactions between *E. whitii* individuals (Bruyn 1994), and thus is an essential element in determining survivorship. The relationship between competition for food, morphological plasticity and survival is especially relevant to a highly aggressive social species like *E. whitii* where sibling rivalry appears to determine juvenile survival (unpublished data).

Environmental factors such as food, temperature and shelter availability appear play a major role in shaping patterns of life history within species (Sorci *et al.* 1996, Civantos & Forsman 2000, Clobert 2000). In some lizard species rapid early growth has an effect of reducing survival in the field (Corci *et al.* 1996, Civantos & Forsman 2000), perhaps from greater activity and higher risks of predation. Individuals with low endurance at birth tend to have reduced activity, slower growth rate and higher parasite load, but lower tail loss (Clobert *et al.* 2000) and a lower mortality rate (

Sorci *et.al* 1996). However on Wedge Island *E. whitii* are subjected to very little predation pressure, but more intense social pressure than many other lizard species.

Autotomy and juvenile survival

Although intact juvenile *E. whitii* tail length as a percentage of SVL is not significantly different than intact adult tail length as a percentage of SVL, the mean proportion is 5% longer for juveniles across the size range. Post autotomy however, the disparity is reversed. Adult tail length is significantly greater than juvenile tail length after autotomy Table 11, Figure 22). While the shortest regenerated tail length in the adult population was 64.1% of SVL, the shortest regenerated tail length in the juvenile population was only 25.4% of SVL.

Caudal fat is disproportionately stored within the base, or proximal one-third of the tail (Chapple 2002, Doughty *et al.* 2003). It can comprise a considerable proportion of total energetic reserves in some species (Clark 1971, Dial & Fitzpatrick 1981, Vitt & Cooper 1986). A factor indicating that *E. whitii* may use their tails for vital lipid storage is the report by Clark (1971) of high rates of ingestion of autotomised tails in lizards which use the tail as a major fat-storage organ, compared to lizards in which fat reserves are not stored in the tail.

During my study two out of the three *E. whitii* that experienced voluntary autotomy during capture, ingested their tails soon afterwards while still captive – a process called 'autophagy'. Lucas & Frost (1894) also report this behaviour in *E. whitii* (op. cit. Hickman 1960), and Clemann (2001) reports a tail fragment in the stomach contents of a preserved *Egernia coventryi* (Swamp Skink) specimen but he attributes this to ingestion of another individual's tail.

Tail loss leads to an increased risk of death in other juvenile lizard species (Civantos & Forsman 2000, Fox & McCoy 2000, Blomberg & Shine 2001). Low survival rates for juvenile *E. whitii* in their first year of life are evident in capture graphs plotted season by season. The pattern of early mortality for young juveniles is evident in another *Egernia* species with similar social grouping. Duffield and Bull (2002) report juvenile survival rates of 60.8%, and then 33.3% of the remnant number, during the first and second seasons for *Egernia stokesii* juveniles, followed by high

subsequent survival. *Egernia stokesii* is a larger member of the *Egernia* genus which takes >6 years to reach maturity.

Autotomy is generally acknowledged as an adaptive mechanism evolved to reduce the risk of predation (Arnold 1988, Medel *et al*. 1988, Wilson 1992, Perez-Mellado *et al*. 1997, Fox *et al*. 1998, Clobert *et al*. 2000, Herczeg *et al*. 2004, Lin & Ji 2005, Langkilde *et al*. 2005). Tail loss is also widely acknowledged to incur costs (Fox *et al*. 1994, Martin & Avery 1998, Downes & shine 2001, McConnachie & Whiting 2002, Cooper 2003, Langkilde *et al*. 2005).

Table 11 indicates the difference between regenerating tail lengths in adults and juveniles. While some of the juveniles that experienced autotomy lost tail lengths of up to 74.6% of their SVL's, the greatest adult loss of tail was 35.9% of SVL. Tail length was calculated as a percentage of body length to standardise the measurement across size classes, and to minimise any effect of growth in the tail base during tail regeneration (Tinkle 1967, *op. cit*. Chapple 2002) which, presumably, grows proportionately as the lizard increases in body length.

Juveniles generally allocate proportionately less energetic reserves to tail regeneration and more to body growth than adults (Vitt *et al*. 1977). The small body size of *E. whitii* newborn and their late appearance in summer, given Australia's unpredictable weather, allows little time for them to build lipid reserves before food becomes scarce and hibernation is necessary. The loss of tail from the proximal section in juveniles, rather than the middle or distal end, as seen in mature survivors, suggests that proximal tail loss at an early stage of development imposes severe costs for juveniles.

Adding to this, some species have proven to be significantly less active during tail regeneration and this reduction in activity is likely to lead to a decrease in foraging (Maginnis 2006). When growth is retarded until immediate damage has been repaired via physiological processes, very small skinks are likely be more adversely affected than adults when deprived of opportunities to store energy in fat reserves. It is probable that juveniles with tail loss $\geq$ 64% of their SVL fail to thrive and are eliminated from the adult population.

Juveniles with toe loss are also less likely to survive (Chapter 6). Particularly adverse circumstances arising at an early stage of development such as excessively vigorous sibling rivalry, aggression from unfamiliar adults, scarce food resources, and predator attacks are all likely to reduce survivorship for juveniles. Their vulnerability because of unfavourable physical factors is compounded by the requirement to use tail tips for social responses.

In species that use tails for social signalling, animals with missing tails are at a disadvantage (Maginnis 2006). Rapid lateral twitching of the distal end of the tail is regarded as a submissive signal in *E. whitii* (Bellamy 2006). Juvenile *E. whitii* must be able to signal submission by vibrating their tail tips if they are to avoid potential aggression in family groups, and they must use speed to escape aggressive and persistent rival siblings (unpublished data). Further study on the use of tails for social purposes and the implications of loss need to be conducted more fully to examine juvenile *E. whitii* survival.

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