MULTIENNIAL REPRODUCTION IN FEMALES OF A VIVIPAROUS, TEMPERATE-ZONE SKINK, TILIQUA NIGROLUTEA

Ashley Edwards[1] and Susan M. Jones

School of Zoology, University of Tasmania, GPO Box 252-05, Hobart, Tasmania, 7001, Australia
[1]PRESENT ADDRESS: Department of Biological Sciences, Macquarie University, Sydney, NSW, 2109, Australia

Abstract: Reproductive frequency in captive and wild-caught female Tiliqua nigrolutea was examined over five consecutive reproductive seasons. Reproductive frequency (0.38 ± 0.035) was clearly different from an annual pattern of 1.0 (i.e. all females reproducing every year). Individual females did not reproduce every year, but "skipped" seasons were staggered such that a proportion of the population produced a clutch each season. Skipped reproductive opportunities are attributed to a combination of a long gestation, high relative clutch mass (0.43 ± 0.034), parturition late in the active season, a cessation of feeding in the latter stages of gestation and low autumn temperatures limiting post-partum feeding opportunities.

Keywords: Lizard; Multiennial cycle; Relative clutch mass; Reproductive frequency; Skink; Temperate-zone; Tiliqua nigrolutea, Viviparous

INTRODUCTION

Cool- and cold-temperate zone squamates are constrained by the need to reproduce during the warmer months of the year (Saint Girons, 1985; Shine, 1985) and parturition usually occurs at the time of year that provides optimal conditions for growth and survival of neonates (Abts, 1988; Callard et al., 1972; Goldberg, 1971; Olsson and Shine, 1997; 1998; Vitt and Lacher, 1981). In temperate regions, this is generally summer or early autumn (James and Shine, 1985; Jones and Swain, 1996; Jones et al., 1997; Naulleau and Fleury, 1990; Van Wyk, 1994; Whittier et al., 1987).

The timing of ovulation and the length of gestation are key variables determining when parturition occurs in viviparous squamates (Heatwole and Taylor, 1987; Wapstra et al., 1999), and are themselves determined, at least in part, by the length of the activity season. In most viviparous squamates, females are able to reproduce annually (Gavaud, 1983; Shine, 1985; Yokoyama and Yoshida, 1994), but if the active season is short, there may be insufficient time to complete vitellogenesis, ovulation, gestation and parturition in a single season (Olsson and Shine, 1999; 1998; Cree and Guillette, 1995; Saint Girons 1985). In such cases, females are unable to reproduce annually, and bi-, tri- or multiennial cycles are observed (Luiselli et al., 1996; Naulleau and Fleury, 1990; Olsson and Shine, 1999; Van Wyk, 1991).

Multiennial patterns of reproduction may be achieved in one of two ways: the reproductive cycle may be extended to span more than one active season, or a reproductive opportunity may be “skipped” in the year(s) following a reproductive effort. Lengthening of the reproductive cycle so that it extends over more than 12 months may be achieved in different ways. Extending vitellogenesis may prolong the ovarian cycle, as occurs in the viviparous biennially breeding lizards Barisia monticola (Vial and Stewart, 1985) and Hoplodactylus maculatus (Cree and Guillette, 1995), in which ovarian activity is effectively continuous. Gestation may be greatly extended by holding embryos over winter, as in *Niveoscincus microlepidotus* and *Niveoscincus greeni* (Hutchinson et al., 1989; Olsson and Shine, 1998). The lengthening of the cycle in either of these ways usually occurs in species living in cool- or cold-temperate regions (Cree and Guillette, 1995; Hutchinson et al., 1989).

Another strategy for achieving a multiennial cycle is exemplified by the viviparous lizard *Liolaemus pictus*. This species responds to short, cold activity seasons by assigning vitellogenesis and gestation to separate activity seasons with a period of gonadal latency during the intervening winter (Ibargüengoytia and Cussac, 1996). Several other viviparous squamate species, including the snakes *Vipera berus* (Prestt, 1971) and *Vipera aspis* (Naulleau and Fleury, 1990), and the lizards *Anguis fragilis* (Patterson, 1983) and *Xantusia riversiana* (Goldberg and Bezy, 1974), are reported to display multiennial reproductive cycles, but the mechanisms by which these are achieved is uncertain.

Alternatively, a reproductive effort may be completed within one active season, but the female may then “skip” one or more years before reproducing again. Such multiennial cycles occur in females of some temperate-zone reptile species that produce clutches of moderate to large size (Whittier and Crews, 1987), particularly in females of large, long-lived species (Bull and Shine, 1979; Whittier and Crews, 1987) and those which are viviparous (e.g. *Cordylus giganteus* (Van Wyk, 1991)) or egg-brooding (e.g. *Eumeces okadae* (Hasegawa, 1984)) (Bull and Shine, 1979). It has been suggested that females of some species exhibit greater lifetime reproductive success by “skipping” reproductive opportunities than by reproducing annually (Whittier and Crews, 1987; Whittier et al., 1987), because a greater proportion of their reserves can be devoted to growth in those seasons in which they do not produce a clutch (Schwarzkopf, 1993) and SVL is often positively correlated with clutch size (Shine, 1980). However, it is difficult to measure lifetime reproductive success in long-lived species, particularly in the wild (Madsen and Shine, 1996), and there is a distinct lack of such linear studies, particularly in species that do not reproduce annually. We have studied a captive population of wild-caught blotched blue-tongued skinks, Tiliqua nigrolutea, over five consecutive reproductive seasons in Tasmania, Australia, at the cold extreme of it's range. During this time we also gathered information on wild individuals.

Tiliqua nigrolutea is a large, viviparous skink with a cool-temperate zone distribution in south eastern Australia (Rawlinson, 1974). Males display a clear annual pattern of spermatogenesis, mating and quiescence (Edwards and Jones, in press a), but females display several life history characteristics suggestive of a multiennial pattern of reproduction. They exhibit a reproductive cycle that is completed within a single active season (Edwards, 1999), despite their cool-temperate zone distribution in Tasmania, Australia and the associated limited active season (late September – April). Gestation of the single clutch is long (approximately 4 – 4.5 months (Edwards and Jones, in press b; Shea, 1992)) by comparison with 3.5 - 4 months for sympatric viviparous species (Jones and Swain, 1996; Jones et al., 1997; Wapstra et al., 1999). Parturition in T. nigrolutea usually occurs late in the active season (Austral autumn: March - April). Females feed little, or not at all, during the final weeks of gestation, and cease feeding altogether in late autumn (late April - May), ahead of the start of the hibernation period (late May) (Edwards and Jones, in press b). A previous study, based solely on museum specimens of T. nigrolutea from throughout their range (Tasmania and south-eastern mainland Australia), suggested that females did not reproduce annually (Shea, 1992). Of 50 adult-sized specimens examined, only 24 showed vitellogenic or ovulated follicles during the time when gravid females were present in the population (Shea, 1992). The present study aims to confirm the existence of a non-annual reproductive cycle in female T. nigrolutea in Tasmania using captive-, wild-mated and autopsied road-killed specimens, and to characterize the mechanism by which such a cycle is achieved.

MATERIALS AND METHODS

Female lizards were captured opportunistically by hand or collected as fresh road-killed specimens around Hobart (42°53’S, 147°19’E), Tasmania, Australia, during their active season. Captive animals were housed in roofed enclosures 1.9 x 3.4 x 2.1 m, which were wire-fronted allowing access to UV light and a natural photoperiod. Direct sunlight and a 120-W globe as an additional heat source suspended 30 cm above the floor at the front of each cage provided a thermal gradient across which the lizards could thermoregulate. Bark and leaf litter, in which the animals could hide, were also provided. Mixed-sex groups of approximately five animals were maintained in each cage, so that females could mate. Lizards were fed three times weekly during the active season (September – April). Their diet consisted of tinned catfood (meat varieties), snails when available, and a selection of fresh fruits, including apple and banana. Water was available ad libitum. Wild-mated individuals were held under the same conditions, but for much shorter periods of time, as these were caught after the mating period (November) in any given year. A colony of approximately 25 females and 15 males was maintained for the duration of the study, although individuals were held for a varying number of seasons determined by the requirements of a larger study into the reproductive physiology of the species (Edwards, 1999).

Female snout-vent length (SVL) (cm ± 0.1) and mass (g ± 0.01) at capture and/or regularly throughout gestation, female post-parturient mass, clutch mass and clutch number were all recorded. From intact road-killed individuals and several animals killed for parallel physiological experiments, total body and total gonadal mass were recorded and a gonadosomatic index (GSI) was calculated.

In a subset of captive females (N = 8) held for at least one quiescent season before a reproductive effort, SVL was recorded at the start (September) and finish (April) of both the quiescent and subsequent reproductive season, to compare female growth differences between reproductive conditions. Growth was recorded as:

(SVL (end of season) - SVL (start of season) / SVL (start of season)) * 100.

Reproductive frequency (RF) was examined over five consecutive reproductive seasons (1995/1996 – 1999/2000), both within each season in sub-samples of the wild population around Hobart, Tasmania, and over time in captive individuals . Females that had vitellogenic or ovulated follicles at autopsy or on palpation, or were observed to produce a clutch in autumn (March-April) were considered to be reproductively active in that year. The presence of corpora lutea (CLs) or corpora atretica (CAs) at autopsy were assumed to infer a recent reproductive effort. Non reproductive females were those in which ovaries were completely quiescent, containing only small (< 5mm), non-vitellogenic follicles, or those which did not produce a clutch. Reproductive frequency within each season was assessed in each of the five reproductive seasons of this study in a total of 112 individual adult females, by comparing the ratio of reproductively active and quiescent females. Reproductive frequency over time was calculated for each captive individual as:

Total number of clutches produced / Number of seasons in captivity.

Many females in the captive population (N = 30) were held for two or more consecutive reproductive seasons, so RF could be determined for these females individually. The population RF was assessed in each season for captive- and wild-mated individuals separately.

Relative clutch mass (RCM) was examined as a measure of female reproductive effort and was calculated for each parturition event as:

Total neonate (live and stillborn) mass (g) / Maternal post-partum mass (g)

This avoids the maternal mass occurring in both the numerator and the denominator (Shine, 1980). Females occasionally expelled a yolky, unfertilized egg during parturition; the mass of such eggs was not included in the calculation of clutch number or RCM. This calculation also excluded the mass of the amniotic fluid expelled at birth, and therefore represents a conservative estimate of female reproductive effort. At parturition a small amount of yolk remained in the embryonic yolk sac. This was immediately consumed by the neonate, and as it represents a maternal contribution towards her clutch and so a reproductive cost, the mass of this residual yolk was included in the total neonate mass used to calculate RCM.

All statistical analyses were performed using SYSTAT 7.0 for the PC (Wilkinson et al., 1998). A significance level of $\alpha = 0.05$ was used throughout. All data satisfied the assumptions of normality and homogeneity of variance. Chi squared analysis was used to assess whether the frequency of reproduction varied significantly from an annual pattern (i.e. all females reproduce every year) in captive- and in wild-mated females. Regression analysis was used to examine the relationship between female body size and both clutch number and RF over time. Analysis of variance (ANOVA) was used to examine the variation in both RCM and clutch number between seasons. Unpaired Student's *t* tests examined the differences in RCM and clutch number between captive- versus wild-mated individuals over all seasons combined and a paired Student's *t* test was used to examine differences in growth between seasons. All values presented are means ± one standard error (1 SE).

RESULTS

Yolked follicles were observed at autopsy only in spring, but not in all animals examined. In reproductively active females, vitellogenesis commenced at spring emergence (late September) and was completed relatively rapidly by late spring (mid-November). There was no indication of any yolk deposition in follicles during the post-partum period (April). The timing of the ovarian cycle is reflected by changes in the GSI (Fig. 1).

Adult female T. nigrolutea ranged from 26 - 31.5 cm SVL and weighed between 270 - 500 g, increasing to as much as 700-800 g during late gestation. A subset of females (n = 8) held for a quiescent followed by a reproductively active season demonstrated a greater mean percentage increase in SVL in the quiescent season (1.6 ± 0.58 %) than in the season in which a clutch was produced (0.6 ± 0.30 %), although this was not a significant difference (t = 1.848, df = 7, P = 0.107).

Mean RCM and mean clutch number in both captive- and in wild-mated females did not vary significantly between years for the five consecutive reproductive seasons of this study (1995/1996 - 1999/2000). Relative clutch mass also did not differ between mating states (captive versus wild) when data were combined across seasons. There was no significant difference in SVL or clutch number between captive- and wild-mated females over the five consecutive seasons of this study. Therefore, data were pooled to give a mean RCM for T. nigrolutea of 0.43 ± 0.034 (n

= 24). Mean clutch number was 8.3 ± 0.68 (range 2-15) and it was significantly correlated with maternal snout-vent length (SVL) ($y = 1.17x - 26.08$, $\underline{r}^2 = 0.346$, $\underline{P} = 0.003$) (Fig. 2).

When captive- and wild-mated individuals were considered separately by season, RF differed significantly from an annual pattern in several seasons in the captive (1996/1997, $\chi^2 = 13.00$, df = 1, $\underline{P} < 0.005$) and wild (1995/1996, $\chi^2 = 8.47$, df = 21, $\underline{P} < 0.005$; 1999/2000: $\chi^2 = 8.64$, df = 1, $\underline{P} < 0.005$) populations (Table 1). However, in seasons which did not differ significantly from an annual pattern, not all females were reproductively active. There were no differences in clutch number, RCM or female SVL between captive- and wild-mated individuals within each season, so a combined data set is also included (Table 1). From the combined data, in three of the five seasons considered, RF differed significantly from an annual pattern of reproduction (1995/1996, $\chi^2 = 12.89$, df = 1, $\underline{P} < 0.002$; 1996/1997, $\chi^2 = 15.04$, df = 1, $\underline{P} < 0.0005$; 1999/2000, $\chi^2 = 10.71$, df = 1, $\underline{P} < 0.0005$).

Mean RF over time (n = 30) was 0.38 ± 0.035, which is clearly different from the frequency of 1.0 expected for an annual pattern of reproduction. Within this data set, some (n = 11) animals reproduced after one quiescent season, some (n = 15) after more than one skipped opportunity and some (n = 4) did not reproduce during the study (Table 2). In five successive seasons, only two individuals produced clutches in successive seasons. Regression analysis showed that RF over time was not related to female SVL ($y = 0.01x + 0.14$, $\underline{r}^2 = 0.014$, $\underline{P} = 0.666$).

DISCUSSION

Females of the blue-tongued skink, Tiliqua nigrolutea display a multiennial reproductive cycle in Tasmania, Australia. Females of this species are not strictly bior triennial reproducers, but exhibit plasticity in RF, both between seasons and between individuals. This reproductive pattern is achieved by completing all phases of the reproductive cycle within a single active season, then skipping one or more reproductive opportunities in subsequent seasons.

This infrequent and irregular reproduction by females is unlikely to be a reflection of eggs or embryos being resorbed, either spontaneously in the wild or as a consequence of capture. There is, indeed, little evidence for embryo resorption in squamate reptiles (Blackburn, 1998). Captive female T. nigrolutea in this study were observed, on several (N = 4) occasions, to pass and consume large yolky masses (unfertilised ova) during parturition, implying that such masses are not resorbed during gestation. This phenomenon has been previously reported for Tiliqua scincoides (LeBreton, 1990), and we have observed unfertilised ova in the oviducts in pregnant female T. nigrolutea (N=3) at autopsy.

Vitellogenesis is initiated and completed over a relatively short time in the active season in T. nigrolutea (Fig. 1), as in the snake species Naja naja (Lance and Lofts, 1978), Nerodia sipedon (Aldridge, 1982), Tropidoclonion lineatum (Krohmer and Aldridge, 1985) and Trimeresurus flavoviridis (Yokoyama and Yoshida, 1994). This is in contrast to the strategy of commencing vitellogenesis in the post-partum period and completing it the following spring, utilised by several other viviparous squamates which are able to reproduce annually, such as Crotalus viridus (Aldridge, 1979), Pseudocordylus m. melanotus (Flemming, 1993). Similarly, two viviparous lizard species sympatric with T. nigrolutea, Niveoscincus metallicus (Jones and Swain, 1996) and Niveoscincus ocellatus (Wapstra et al., 1999; Jones et al., 1997), mate in autumn during mid-vitellogenesis and store sperm until spring ovulation (Jones et al., 1997; Swain and Jones, 1994; Wapstra et al., 1999). This allows ovulation to occur earlier (September) than in T. nigrolutea (November), and gestation is slightly shorter, so that parturition occurs in mid-summer (January) (Jones et al., 1997; Swain and Jones, 1994).

In some species, late parturition and low autumn temperatures do not allow females time to store sufficient reserves both to endure winter hibernation and to become vitellogenic in the following spring (Saint Girons, 1985). Female T. nigrolutea noticeably reduced feeding during the latter stages of gestation. Although this phenomenon has not been quantified, it is likely to amplify the effects of a long gestation, high relative clutch mass, parturition late in the active season and low autumn temperatures limiting post-partum feeding on the ability to store fat reserves for future reproductive efforts. Some or all of these factors may regularly result in missed opportunities for reproduction (Saint Girons, 1985) as is reported, for example, in the lizards Eulamprus tympanum (Schwarzkopf, 1996), C. giganteus (Van Wyk, 1991) and A. fragilis (Patterson, 1983). A similar reduction in feeding during the latter stages of gestation has been demonstrated in several snake (Gregory et al., 1999; Macartney and Gregory, 1988) and lizard (Schwarzkopf, 1996) species, and may be due to limited space in the body cavity due to the presence of eggs or embryos (Schwarzkopf, 1996).

In some viviparous squamates, females display a plastic reproductive cycle in that they have the ability to breed annually if conditions (with respect to stored energy or warm thermal conditions) are good. In the snakes V. aspis, (Zuffi et al., 1999), E. longissima (Bonnet and Naulleau, 1994) and Thamnophis sirtalis parietalis (Whittier and Crews, 1990) and the lizard E. tympanum (Rohr, 1997), stored energy is the limiting factor in the regulation of reproduction; females do not become vitellogenic in a given year if their stored fat reserves are below a threshold level.

Reproductive frequency in captive- and wild-mated female T. nigrolutea in each season varied from 20.8 - 67.9%, suggesting an element of plasticity to their cycle, which would allow them to cope with the somewhat unpredictable climate of Tasmania. Given the variation in reproductive frequencies between individual females and the observation of two females reproducing in consecutive seasons, it seems possible that female T. nigrolutea could utilize this type of plasticity as a strategy for coping with the unpredictable climate in Tasmania, where the length and thermal quality of the active season are variable. In those years that the active season is relatively cool or short and post-partum feeding opportunities are limited, females are able to devote the following season to growth and storing reserves for future reproductive efforts, rather than production of a smaller clutch. Such a strategy has been reported in the lizard E. tympanum (Schwarzkopf, 1996; 1993) and the snake N. sipedon (Brown and Weatherhead, 1997). The data presented here do not strongly support the existence of this strategy in female T. nigrolutea, but sample size was small and several individuals had already attained near maximal recorded body size. While SVL in ectotherms does continue to increase throughout life, growth rate declines with age (Castanet et al., 1988; Chinsamy et al., 1995; Montori, 1990). This may explain the lack of a significant difference between growth in quiescent and reproductive seasons in this study.

Reproductive frequency in captive-mated female T. nigrolutea in each season varied significantly from an annual pattern in only a single season. This is likely to be an artifact, as other aspects of a physiological study on the captive population resulted in post-partum females being released to maximize space for potentially reproductively active females in an attempt to characterize cycles of steroid hormones throughout reproduction (Edwards and Jones, in press b). However, the linear study clearly demonstrates that individuals generally do not reproduce every year, and there may be one, two or even three seasons between reproductive efforts, as has been reported for the viviparous snakes V. berus (Prestt, 1971), V. aspis and Elaphe longissima (Bonnet and Naulleau, 1994) and the lizards E. tympanum (Schwarzkopf, 1993) and C. giganteus (Van Wyk, 1991).

A mean RCM of 0.43 ± 0.034 for female T. nigrolutea over the five seasons of this study suggests that the effort of reproduction is high. This mean RCM is comparable with those of other viviparous squamates that are regarded as having a high RCM (0.52 in Lerista bougainvillii (Qualls and Shine, 1995) and 0.482 in Aspidelaps scutatus (Shine et al., 1996)). It is also well above the RCM of two sympatric, annually reproducing viviparous skinks, N. metallicus (0.307) (C. McCoull, personal communication) and N. ocellatus (0.230 (in 1995/1996) and 0.290 (in 1996/1997)) (Wapstra and Swain, in press). The mean RCM for T. nigrolutea reported in this study is also very similar to the RCM of 0.4 reported for Tiliqua rugosa, (Fergusson and Algar, 1986), although these authors did not provide details of the calculation used. Thus, although T. nigrolutea does not reproduce annually, once the commitment to produce a clutch is made, a large reproductive effort is allocated, perhaps offsetting the cost to life-time fecundity of not producing a clutch each year.

Tasmania represents the southernmost part of the range of T. nigrolutea, in which any effects of the cool environment and limited active season are likely to be amplified, although a study using museum specimens indicated that female T. nigrolutea on the Australian mainland are also likely to be non-annual breeders (Shea, 1992). However, no measures of RF or RCM have been reported for any mainland populations of this species. Other members of the genus with more northerly ranges usually reproduce annually (Shea, 1992). It is likely that the multiennial cycle of female T. nigrolutea reflects a combination of high RCM and limited thermal opportunities (short active season).

Acknowledgements.— This work was conducted under University of Tasmania Animal Ethics Approval numbers 95046 and 98015. We thank the School of Zoology, University of Tasmania, for financial and infrastructure support. We also thank Erik Wapstra for valuable comments on the manuscript.

LITERATURE CITED

ABTS, M. L. 1988. Reproduction in the saxicolous desert lizard, Sauromalus obesus: the female reproductive cycle. Copeia 1988:382-393.

ALDRIDGE, R. D. 1982. The ovarian cycle of the watersnake Nerodia sipedon, and effects of hypophesectomy and gonadotropin administration. Herpetologica 38:72-79.

ALDRIDGE, R. D. 1979. Female reproductive cycles of the snakes Arizona elegans and Crotalus viridis. Herpetologica 35:256-261.

BLACKBURN, D. G. 1998. Resorption of oviductal eggs and embryos in squamate reptiles. Herpetological Journal 8:65-71.

BONNET, X., AND G. NAULLEAU. 1994. A body condition index (BCI) in snakes to study reproduction. Comptes Rendus de l' Academie des Sciences Serie III-Sciences de la Vie-Life Sciences. 317:34-41.

BROWN, G. P., AND P. J. WEATHERHEAD. 1997. Effects of reproduction on survival and growth of female northern water snakes, Nerodia sipedon. Canadian Journal of Zoology 75:424-432.

BULL, J. J., AND R. SHINE. 1979. Iteroparous animals that skip opportunities for reproduction. American Naturalist 114:296-303.

CREE, A., AND L. J. GUILLETTE, Jr. 1995. Biennial reproduction with a fourteen-month pregnancy in the gecko Hoplodactylus maculatus from southern New Zealand. Journal of Herpetology 29:163-173.

CALLARD, I. P., C. G. BAYNE, AND W. F. MCCONNELL. 1972. Hormones and reproduction in the female lizard Sceloporus cyanogenys. General and Comparative Endocrinology 18:175-194.

CASTANET, J., D. G. NEWMAN, AND H. SAINT GIRONS. 1988. Skeletochronological data on the growth, age, and population structure of the Tuatara, Sphenodon punctatus, on Stephens and Lady Alice islands, New Zealand. Herpetologica 44:25-37.

CHINSAMY, A., S. A. HANRAHAN, R. M. NETO, AND M. SEELY. 1995. Skeletochronological assessment of age in Angolosaurus skoogi, a cordylid lizard living in an aseasonal environment. Journal of Herpetology 29:457-460.

EDWARDS, A. 1999. Steroids and Reproduction in Tiliqua nigrolutea. Unpublished Ph.D. Thesis, University of Tasmania, Tasmania, Australia.

EDWARDS, A., AND S. M. JONES. Changes in plasma testosterone, estrogen and progesterone concentrations throughout the annual reproductive cycle in Male viviparous blue-tongued skinks, Tiliqua nigrolutea, (Scincidae), in Tasmania. Journal of Herpetology (in press a).

EDWARDS, A., AND S. M. JONES. Changes in plasma progesterone, estrogen and testosterone concentrations throughout the reproductive cycle in female viviparous blue-tongued skinks, Tiliqua nigrolutea, (Scincidae), in Tasmania. General and Comparative Endocrinology (in press b).

FERGUSSON, B., AND D. ALGAR. 1986. Home range and activity patterns of pregnant female skinks, Tiliqua rugosa. Australian Wildlife Research 13:287-294.

FLEMMING, A. F. 1993. The female reproductive cycle of the lizard Pseudocordylus m. melanotus (Sauria: Cordylidae). Journal of Herpetology 27:103-107.

GAVAUD, J. 1983. Obligatory hibernation for completion of vitellogenesis in the lizard Lacerta vivipara J. Journal of Experimental Zoology 225:397-405.

GOLDBERG, S. R. 1971. Reproductive cycles of the ovoviviparous iguanid lizard Sceloporus jarrovi Cope. Herpetologica 27:123-131.

GOLDBERG, S. R., AND R. L. BEZY. 1974. Reproduction in the island night lizard, Xantusia riversiana. Herpetologica 30:350-360.

GREGORY, P. T., L. H. CRAMPTON, AND K. M. SKEBO. 1999. Conflicts and interactions among reproduction, thermoregulation and feeding in viviparous reptiles: are gravid snakes anorexic? Journal of Zoology, London 248:231-241

HASEGAWA, M. 1984. Biennial reproduction in the lizard Eumeces okadae on Miyake-jima, Japan. Herpetologica 40:194-199.

HEATWOLE, H., AND J. TAYLOR. 1987. Reproductive Ecology, p. 147-166. In Ecology of Reptiles. H. Heatwole (ed.). Surrey Beatty and Sons Pty Ltd, N.S.W., Australia.

HUTCHINSON, M. N., P. ROBERTSON, AND P. A. RAWLINSON. 1989. Redescription and ecology of the endemic Tasmanian scincid lizards Leiolopisma microlepidotum and L. pretiosum. Papers and Proceedings of the Royal Society, Tasmania 123:257-274.

IBARGÜENGOYTÍA, N. R., AND V. E. CUSSAC. 1996. Reproductive biology of the viviparous lizard, Liolaemus pictus (Tropiduridae) - biennial female reproductive cycle. Herpetological Journal 6:137-143.

JAMES, C., AND SHINE R. 1985. The seasonal timing of reproduction: a tropical – temperate comparison in Australian lizards. Oecologia 67:464-474.

JONES, S. M., AND R. SWAIN. 1996. Annual reproductive cycle and annual cycles of reproductive hormones in plasma of female Niveoscincus metallicus (Scincidae) from Tasmania. Journal of Herpetology 30:140-146.

JONES, S. M., E. WAPSTRA, AND R. SWAIN. 1997. Asynchronous male and female gonadal cycles and plasma steroid concentrations in a viviparous lizard, Niveoscincus ocellatus (Scincidae) from Tasmania. General and Comparative Endocrinology 108:271-281.

KROHMER, R.W., AND R. D. ALDRIDGE. 1985. Male reproductive cycle of the lined snake (Tropidoclonion lineatum). Herpetologica 41:33-38.

LANCE ,V., AND B. LOFTS. 1978. Studies on the annual reproductive cycle of the female cobra, Naja naja. IV. Ovarian histology. Journal of Morphology 157:161-180.

LEBRETON, M. 1990. Reproductive notes on the eastern blue-tongue lizard Tiliqua scincoides (White 1790). Herpetofauna 20:30-32.

LUISELLI, L., M. CAPULA, AND R. SHINE. 1996. Reproductive output, costs of reproduction, and ecology of the smooth snake, Coronella austriaca, in the eastern Italian alps. Oecologica 106:100-110.

MACARTNEY, J. M., AND P. T. GREGORY. 1988. Reproductive biology of female rattlesnakes (Crotalus viridis) in British Columbia. Copeia 1988:47-57.

MADSEN, T., AND R. SHINE. 1996. Determinants of reproductive output in female water pythons (Liasis fuscus: pythonidae). Herpetologica 52:146-159.

MONTORI, A. 1990. Skeletochronological results in the pyrenean newt Euproctus asper (Dugës,1852) from one prepyrenean population. Annales des Sciences Naturelles, Zoologie, Paris, Sèrie 13^{e}, 11:209-211.

NAULLEAU, G., AND F. FLEURY. 1990. Changes in plasma progesterone in female Vipera aspis L. (Reptilia, Viperidae) during the sexual cycle in pregnant and nonpregnant females. General and Comparative Endocrinology 78:433-443.

OLSSON, M., AND R. SHINE 1997. The seasonal timing of oviposition in sand lizards (Lacerta agilis) - why early clutches are better. Journal of Evolutionary Biology 10:369-381.

OLSSON, M., AND R. SHINE 1998. Timing of parturition as a maternal care tactic in an alpine lizard species. Evolution 52:1861-1864.

OLSSON, M., AND R. SHINE 1999. Plasticity in frequency of reproduction in an alpine lizard, Niveoscincus microlepidotus. Copeia 1999:794-796.

PATTERSON, J. W. 1983. Frequency of reproduction, clutch size and clutch energy in the lizard Anguis fragilis. Amphibia-Reptilia 4:195-203.

PRESTT, I. 1971. An ecological study of the viper Vipera berus in southern Britain. Journal of Zoology, London 164:373-418.

QUALLS, C. P., AND R. SHINE. 1995. Maternal body-volume as a constraint on reproductive output in lizards - evidence from the evolution of viviparity. Oecologica 103:73-78.

RAWLINSON, P. A. 1974. Biogeography and ecology of the reptiles of Tasmania and the Bass Strait area. Pp. 230-269. In W. D. Williams (Ed.), Biogeography and Ecology in Tasmania. W. Junk, The Hague, Netherlands.

ROHR, D. H. 1997. Demographic and life-history variation in two proximate populations of a viviparous skink separated by a steep altitudinal gradiant. Journal of Animal Ecology 66:567-578.

SAINT GIRONS, H. 1985. Comparative data on lepidosaurian reproduction and some time tables, p. 35-58. In C. Gans and F. Billet (Eds.), Biology of the Reptilia, Development B, Vol 15. Wiley, New York.

SCHWARZKOPF, L. 1996. Decreased food intake in reproducing lizards: a fecundity-dependent cost of reproduction? Australian Journal of Ecology 21:355-362.

SCHWARZKOPF, L. 1993 Costs of reproduction in water skinks. Ecology 74:1970-1981.

SHEA, G. M. 1992. The systematics and reproduction of blue-tongued lizards of the genus Tiliqua (Squamata: Scincidae). Ph.D. Thesis, University of Sydney, NSW, Australia.

SHINE, R. 1985. The reproductive biology of Australian reptiles: a search for general patterns, p. 297-303. In G. Grigg, R. Shine and H. Ehmann (Eds.), Biology of Australasian Frogs and Reptiles. Surrey Beatty and Sons Pty, Ltd, Australia.

SHINE, R. 1980. “Costs” of reproduction in reptiles. Oecologica 46:92-100.

SHINE, R., G. V. HAAGNER, W. R. BRANCH, P. S. HARLOW, AND J. K. WEBB. 1996. Natural history of the African shieldnose snake Aspidelaps scutatus (Serpentes, Elapidae). Journal of Herpetology 30:361-366.

SWAIN, R., AND S. M. JONES. 1994. Annual cycle of plasma testosterone and other reproductive parameters in the Tasmanian skink, Niveoscincus metallicus. Herpetologica 54:502-509.

VAN WYK, J. H. 1991. Biennial reproduction in the female viviparous lizard Cordylus giganteus. Amphibia-Reptilia 12:329-342.

VAN WYK, J. H. 1994. Physiological changes during the female reproductive cycle of the viviparous lizard Cordylus giganteus (Sauria: Cordylidae). Herpetologica. 50:480-493.

VIAL, J. L., AND J. R. STEWART. 1985. The reproductive cycle of Barisia monticola: a unique variation among viviparous lizards. Herpetologica 41:51-57.

VITT, L. J., AND T. E. LACHER, Jr. 1981. Behavior, habitat, diet, and reproduction of the iguanid lizard Polychrus acutirostris in the Caatinga of northeastern Brazil. Herpetologica 37:53-63.

WAPSTRA, E., R. SWAIN, S. M. JONES, AND J. O'REILLY. 1999. Geographic and annual variation in reproductive cycles in the Tasmanian spotted snow skink, Niveoscincus ocellatus (Squamata: Scincidae). Australian Journal of Zoology 47:539-550.

WAPSTRA, E., AND R. SWAIN. Geographic and annual variation in life history traits in a temperate zone Australian skink. Journal of Herpetology (in press).

WHITTIER, J. M., AND D. CREWS. 1990. Body mass and reproduction in female red-sided garter snakes (Thamnophis sirtalis parietalis). Herpetologica 46:219-226.

WHITTIER, J. M., AND D. CREWS. 1987. Seasonal reproduction: patterns and control, p385-409. In Hormones and Reproduction in Fishes, Amphibians and Reptiles. D. O. Norris and R. E. Jones (eds.). Plenum Press, New York.

WHITTIER, J. M., R. T. MASON, AND D. CREWS. 1987. Plasma steroid hormone levels of female red-sided garter snakes, Thamnophis sirtalis parietalis: relationship to mating and gestation. General and Comparative Endocrinology 67:33-43.

WILKINSON, L., H. A. HILL, S. MIALLA, AND E. VANG. 1998. SYSTAT for the Macintosh, Version 7.0, Evanston, Illinois.

YOKOYAMA, F., AND H. YOSHIDA. 1994. The reproductive cycle of the female habu, Trimeresurus flavoviridis. Journal of Herpetology 28:54-59.

ZUFFI, M. A. L., F. GIUDICI., AND P. IOALÈ. 1999. Frequency and effort of reproduction in female Vipera aspis from a sourthern population. ACTA Oecologia 20:633-638.

Table 1 Reproductive frequency of captive- and wild-mated female *Tiliqua nigrolutea* in each of five reproductive seasons from 1995 – 2000, NS = not significantly different from an annual pattern of reproduction.

Where mated	**1995/1996**	**1996/1997**	**1997/1998**	**1998/1999**	**1999/2000**
Captivity (n)	11	13	19	9	7
(% Reproductive)	57.1	0	57.9	55.5	28.6
	NS	$P < 0.0005$	NS	NS	NS
Wild (n)	17	11	9	6	14
(% Reproductive)	71.4	45.5	88.9	50.0	21.4
	$P < 0.0005$	NS	NS	NS	$P < 0.005$
Combined (N)	28	24	28	15	21
(% Reproductive)	37.5	20.8	67.9	53.3	23.8
	$P < 0.002$	$P < 0.0005$	NS	NS	$P < 0.0005$

Table 2 Reproductive frequency, number of seasons in captivity and number of clutches produced by captive individuals (n = 30) held for two or more consecutive seasons between 1995 and 2000.

Reproductive frequency	**Captive seasons**	**Reproductive events**	**n**
0.67	3	2	3
0.5	2	1	11
0.4	5	2	2
0.34	3	1	6
0.25	4	1	3
0.2	5	1	1
0	2-5	0	4

FIGURE LEGENDS

Figure 1 Gonadosomatic index for female Tiliqua nigrolutea showing the vitellogenic period confined to spring. Hibernation (n = 2), Early vitellogenesis (n = 3), Late vitellogenesis (n = 4), Gestation (n = 3), Post-parturition (n = 4). Values are means and standard errors are not included due to small sample sizes.

Figure 2 Relationship between female snout-vent length and number of offspring (n = 24). The equation for the linear regression is: $y = 1.17x - 26.09$, $r^2 = 0.346$, $P = 0.003$.

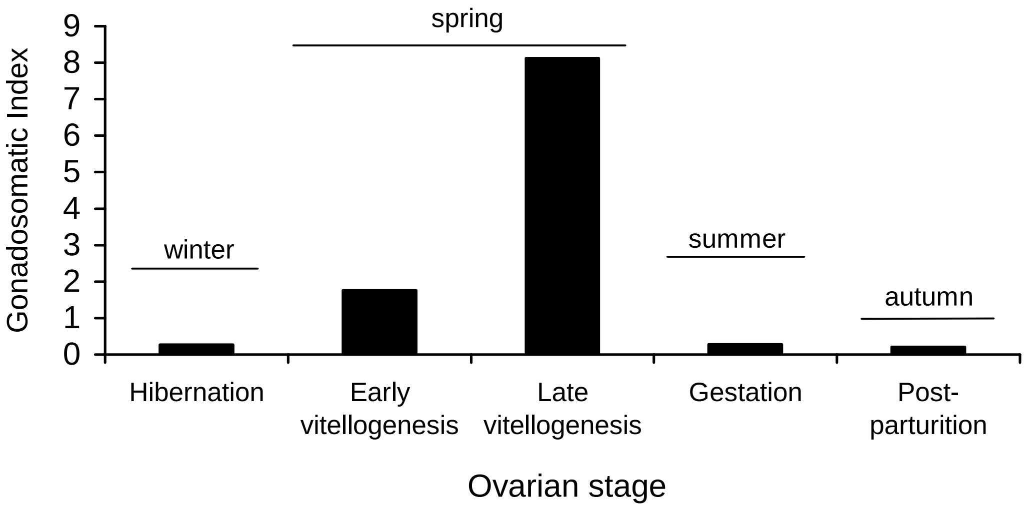
Gonadosomatic Index
0
1
2
3
4
5
6
7
8
9
winter
spring
summer
autumn
Hibernation
Early vitellogenesis
Late vitellogenesis
Gestation
Post-parturition
Ovarian stage

Figure 1

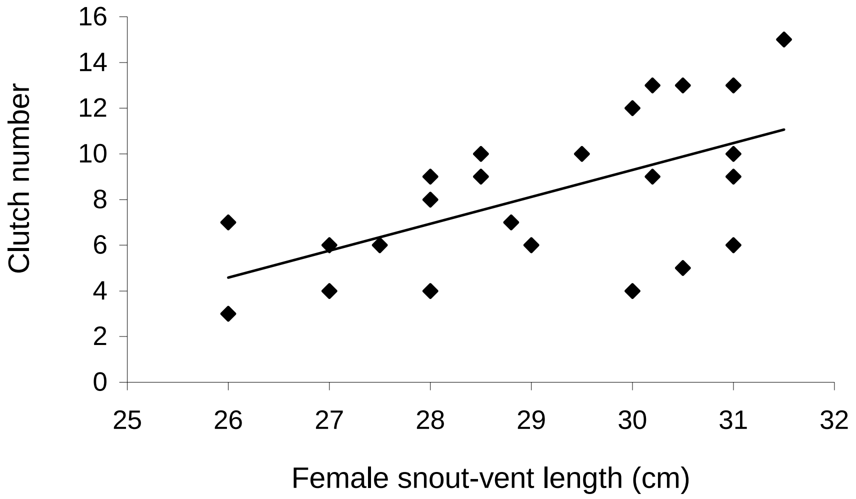
Clutch number
0
2
4
6
8
10
12
14
16
25
26
27
28
29
30
31
32
Female snout-vent length (cm)

Figure 2