

## Changes in Reproductive Investment following Caudal Autotomy in Viviparous Skinks (*Niveoscincus metallicus*): Lipid Depletion or Energetic Diversion?

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**ABSTRACT.**—The effect of caudal autotomy on reproductive investment in females of a viviparous skink, *Niveoscincus metallicus*, was investigated to examine the relative importance of lipid depletion and energetic diversion to this activity. Although abdominal fat bodies are present, this species stores most of its energetic reserves in the tail. Since caudal fat is preferentially aggregated toward the base of the tail, autotomy and lipid depletion may be mutually exclusive events. Reproductive consequences following tail loss associated with significant loss of caudal fat were compared with those following autotomy involving no fat loss in two groups of females: females that had lost their tail during their most recent vitellogenic period; and females in which tail loss had occurred in a previous reproductive season. Caudal autotomy during vitellogenesis resulted in a significant reduction in litter size, irrespective of the position of tail loss, suggesting that smaller litters were a consequence of the diversion of energetic resources from reproduction to tail regeneration, rather than the loss of fat reserves per se. However, offspring from mothers that experienced tail loss during vitellogenesis without associated loss of fat reserves were significantly larger in size (snout-vent length and mass) and had longer tails than those from any other group. We suggest that this was probably achieved through facultative placental transfer during gestation, although the possibility that more yolk was allocated to each egg cannot be discounted. Sprint speed and the size of abdominal fat reserves at birth and postnatal growth were not correlated with either recency of autotomy or the location of the tail break.

Caudal autotomy in lizards is an effective means of escape from predators. However, although there is an immediate survival benefit from tail loss, tailless individuals may incur a range of subsequent costs (Arnold, 1988). Tail loss has been shown to inhibit locomotor performance (Ballinger et al., 1979; Formanowicz et al., 1990; Brown et al., 1995), decrease growth rate (Ballinger and Tinkle, 1979; Smith, 1996), reduce social status and mating opportunities (Fox and Rostker, 1982; Martin and Salvador, 1993a; Salvador et al., 1995), alter foraging behavior (Martin and Salvador, 1993b), and reduce the probability of future survival (Wilson, 1992; Fox and McCoy, 2000). In addition, the impact of autotomy on reproductive investment during vitellogenesis is generally severe, resulting in decreased clutch size or reduced yolk allocation to each egg, or both (e.g., Smyth, 1974; Dial and Fitzpatrick, 1981; Wilson and Booth, 1998).

Stored lipid reserves in lizards are a major source of energy for reproductive events such as vitellogenesis (Derickson, 1976; Doughy and

Shine, 1998). Many lizards have lipid energy reserves in both the abdomen and tail, and in some species caudal fat constitutes a substantial proportion of the total energetic reserves (Clark, 1971; Dial and Fitzpatrick, 1981; Vitt and Cooper, 1986). Consequently, caudal autotomy has the potential to reduce the amount of energy reserves available for reproductive investment. In addition, subsequent tail regeneration involves intensive cellular and physiological activity to replace the caudal structures (Bellairs and Bryant, 1985) and may itself be energetically expensive. Accordingly, autotomy may lead to the diversion of energetic resources from reproduction or growth (Congdon et al., 1974; Vitt et al., 1977; Dial and Fitzpatrick, 1981). Hence, energetic restrictions, which are believed to cause the reduced levels of reproductive investment following autotomy may result from either direct depletion of caudal lipids or diversion of energy allocated to reproduction, or both.

Previous studies of tail loss have been unable to decouple the effects of each of these energy depleting processes. This is in part caused by a common assumption that caudal fat is depleted as a result of tail loss. However, recent work on our test species, *Niveoscincus metallicus*, has shown that the majority of naturally occurring tail breaks do not result in the direct depletion of caudal fat since lipid is aggregated in the

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proximal regions of the tail (Chapple and Swain, 2002). Consequently *N. metallicus* offers the possibility of determining the relative costs of lipid depletion and energy diversion on reproductive investment by comparing the reproductive costs of tail breaks that result in lipid depletion and those that do not. In this paper, we examine the impact of naturally occurring tail breaks on litter size and offspring phenotype and evaluate relative importance of lipid depletion and energetic diversion as sources of reproductive costs.

#### MATERIALS AND METHODS

*Study Species.*—The metallic skink, *N. metallicus*, is a small viviparous skink (45–60 mm snout–vent length, SVL) that is widely distributed throughout Tasmania and the southeastern corner of the Australian mainland. Both abdominal and caudal fat stores are present in this species, although the majority (55–75%) of these reserves are located in the tail, mostly (~90%) within the proximal third of the tail (Chapple and Swain, 2002). Females reproduce annually with vitellogenesis beginning in late summer (March in our population), approximately one month after parturition. The first matings occur in autumn (April) with sperm stored overwinter by females until ovulation and fertilization in spring (September) following emergence (Jones and Swain, 1996). *Niveoscincus metallicus* remains primarily lecithotrophic (Jones et al., 1998; Thompson et al., 1999), although a degree of facultative placentotrophy has been demonstrated (Swain and Jones, 1997, 2000a,b).

*Collection of Animals and Laboratory Housing Conditions.*—We collected lizards from around Clarence Lagoon (146°19'E, 42°04'S), a small glacial lake located on the edge of the Central Plateau World Heritage area in central Tasmania (970 m). They were captured by hand or by noose and transported back to the laboratory, where they were housed in pairs in terraria (20 × 30 × 10 cm) lined with absorbent bedding. We provided upturned terracotta pots as cover and basking surfaces beneath 25-W lights that provided 10 h of basking per day, and a temperature gradient of 12–35°C within each container. Fluorescent lighting provided 14 h of light each day at natural levels. Ambient temperature was maintained around 12–14°C. We fed the lizards a diet of mealworms (*Tenebrio* larvae), commercial cat food and mashed banana. Water was available ad libitum.

*Determination of Tail Regeneration Rates.*—We estimated the rate of tail regeneration in the field from data obtained in the laboratory. Fifteen adult females, collected in September 1999, were held on ice until fully torpid, and complete tail autotomy induced through the basal frac-

ture, leaving a stump of ~10 mm. We maintained these animals under laboratory conditions for four months, taking monthly measurements of total tail length and regeneration length ( $\pm 0.1$  mm) to determine the rate of tail regeneration.

The rate of tail regeneration under laboratory conditions was  $1.78 \pm 0.03$  mm/week (mean  $\pm$  SE). However, since both photoperiod and temperature influence the rate at which tail regeneration occurs (e.g. Turner and Tipton, 1972; Ndukuba and Ramachandran, 1988; Ramachandran and Ndukuba, 1989), the estimated field regeneration rate was adjusted accordingly. We provided animals with 10 h of radiant heat each day. However, at Clarence Lagoon the average daily access to sunlight during the activity season is only 6.3 h (Bureau of Meteorology data). Assuming that there is a 10–15% loss of activity time resulting from constraints such as rain and cloud, the basking opportunities at Clarence Lagoon are approximately 50% of those in the laboratory. Consequently, we assumed that the rate of tail regeneration under field conditions is half that found in the laboratory (i.e., 0.89 mm/week).

*Formation of Experimental Groups.*—To calculate each female's original tail length, and hence estimate the point at which autotomy occurred, we regressed tail length (TL) against SVL in 10 pregnant females that lacked any evidence of caudal autotomy. For these females, there was a significant relationship between SVL and TL ( $TL = 1.16 \times SVL + 5.28$ ;  $R^2 = 0.73$ ;  $P = 0.0001$ ). The regression equation was used to estimate the original tail lengths (OTL) of the remaining animals that displayed signs of previous tail loss. By dividing the distance from the vent to tail break by the OTL, the relative position of the tail break along the length of the original tail was estimated.

We assumed that late stage females with regenerated portions of the tail between 16–30 mm in length had experienced tail autotomy during vitellogenesis for the current reproductive period (after allowing for the May to September/October hibernation period). All animals in the process of regenerating the tail were assumed to be incurring an energetic cost. Using both the position of tail loss and the length of the regenerated tail, we assigned animals to one of four groups using the following criteria.

Group 1: Animals with tail breaks within the proximal third of the tail and regeneration between 16 and 30 mm in length; that is, females that experienced significant loss of caudal fat (~90%) during vitellogenesis for their current pregnancy and were still undergoing regeneration. (Animals with less than 16 mm regenera-

TABLE 1. Estimated relative position of tail loss ( $\pm$  SE) and tail regeneration length (mm  $\pm$  SE) for *Niweoscincus metallicus* assigned to each group.

Group	N	Position of tail loss	Regeneration length (mm)
1	10	0.20 $\pm$ 0.03	22.64 $\pm$ 1.70
2	8	0.19 $\pm$ 0.03	34.58 $\pm$ 1.32
3	14	0.50 $\pm$ 0.03	21.35 $\pm$ 1.33

tion were deemed to have autotomized during gestation and were excluded from our study).

Group 2: Animals with tail breaks within the proximal third of the tail and regeneration of more than 35 mm in length; that is, females that experienced significant loss of caudal fat ( $\sim$  90%) during a previous breeding season and had completed regeneration (control for tail loss).

Group 3: Animals with tail breaks within the distal region of the tail and regeneration between 16 and 30 mm in length; that is, females that experienced minimal loss of tail fat ( $\leq$  10%) from autotomy during vitellogenesis for their current pregnancy but were still undergoing regeneration (control for fat loss).

Group 4: Animals exhibiting no signs of previous tail loss (control for both fat loss and tail loss).

*Experimental Procedure.*—We collected 42 pregnant females shortly before parturition in early February 2000. Dissection of animals collected at the same time for other purposes confirmed that embryos were fully developed and had reached stage 40 (staging according to Dufaure and Hubert, 1961). Upon return to the laboratory, we weighed each female ( $\pm$  0.1 mg) and took measurements of SVL, tail length, tail break length and tail regeneration length ( $\pm$  0.1 mm). From these measurements we assigned 10, 8, 14, and 10 females to groups 1, 2, 3 and 4, respectively. The mean regeneration length and estimated position of tail loss for each group is provided in Table 1. Since the tail base (i.e., break length) may grow during tail regeneration (Tinkle, 1967), the true position of tail loss was probably slightly more proximal. However, our groups were sufficiently distinct (Table 1) for this to have no bearing on our selection of groups.

Each female was given a unique toe-clip, and animals were randomly housed in pairs. All females gave birth within two and a half weeks of arrival in the laboratory. Terraria were checked twice daily for newborns, and these and their mothers were removed immediately. Females within each pair never overlapped in the timing of parturition, and in every instance the mother of the newborns was unambiguously

determined through abdominal palpation. We measured the sprint speed of each neonate within 24 h of birth. Neonates were warmed to 26°C (optimal performance temperature: McCoull, 2001) and sprinted along a track maintained at 26  $\pm$  1°C. Photodiodes linked to a computer generated two estimates (each of 50 cm) for each trial, the fastest of which was taken as the measure of sprint speed (m s<sup>-1</sup>).

We chose two juveniles at random from each litter and maintained them in the laboratory to assess growth rate. In the case of litter sizes of two, only the growth rate of one individual was measured. These juveniles were weighed ( $\pm$  0.1 mg) and measured (SVL, tail length;  $\pm$  0.1 mm) within 24 h of birth and every two weeks for eight weeks. Juveniles were fed mashed banana and cat food and housed in groups of 4–6. All juveniles appeared to gain equal access to food and basking surfaces. They were released at the site of maternal capture after the experiment. The remaining neonates, along with their mother, were killed by exposure to  $-20^\circ\text{C}$  (Cogger, 1992) and dissected for assessment of abdominal fat reserves. The number of corpora lutea was used to confirm litter size and the stomach was dissected to ensure that there were no consumed stillborns.

*Data Analysis.*—Discriminant function analysis was conducted using the DISCRIM routine of SYSTAT 5.2 for Macintosh (L. H. Wilkinson, H. A. Hill, S. Mialla, and E. Vang, Systat, Inc., Evanston, IL, 1992) to test the validity of our assignment of animals to groups. All maternal and offspring data were incorporated in the analysis except those for postnatal growth rate, where three datapoints were missing because of the death of juveniles. Litter averages were used wherever data were obtained from more than one animal in a litter. Juvenile growth rate was calculated using the increase in SVL over the eight-week period. Snout–vent length was chosen because mass, especially in small lizards, may reflect changes in recent nutritional history rather than change in body size (Dunham, 1978).

Differences between the four experimental groups in terms of maternal investment and offspring morphology were analyzed by MANCOVA using SYSTAT 5.2 with maternal SVL as the covariate. Significant response variables identified by this procedure were subsequently analyzed using a one-way ANCOVA design with maternal size (SVL) as the covariate. Assumptions of the analysis were checked by testing for homogeneity of variances and homogeneity of slopes using standard methods (Tabachnick and Fidell, 1989). If the covariate was not significant, the analysis became a one-way ANOVA. Posthoc HSD (when ANOVA) or LSD

TABLE 2. Litter size and relative clutch masses (RCM—combined clutch mass/postpartum maternal mass) for female *Niveoscincus metallicus* assigned to each of four groups according to the time and extent of tail loss. Asterisk indicates that the covariate, maternal SVL, was not significant; therefore, actual means are shown and the statistics are derived from an ANOVA. Means (and least-squares means) with the same superscript are not significantly different as determined by posthoc LSD or HSD tests.

Offspring trait	Group	Least-squares mean	SE	ANCOVA/ANOVA*		
				df	F	P
Litter size	1	2.88 <sup>a</sup>	0.19	3, 37	3.81	0.018
	2	3.48 <sup>b</sup>	0.22			
	3	2.82 <sup>a</sup>	0.16			
	4	3.49 <sup>b</sup>	0.19			
RCM*	1	0.25 <sup>a</sup>	0.02	3, 38	1.90	0.146
	2	0.29 <sup>a</sup>	0.02			
	3	0.23 <sup>a</sup>	0.15			
	4	0.26 <sup>a</sup>	0.02			

(when ANCOVA) tests were used to investigate differences between groups.

#### RESULTS

A single discriminant function was revealed, based upon a correlation between high values

for juvenile mass and SVL and low values for litter size and relative clutch mass. Thirty of the 42 individuals (71%) were reclassified correctly into the groups to which they were assigned. Group 1 was the least satisfactory, with two animals moved to Group 2 and three animals to Group 3. Three animals from Group 2 were placed in Group 4, one from Group 3 was assigned to Group 4, two from Group 3 moved to Group 1, and one animal from Group 4 was allocated to Group 3. Consequently, we considered our assignment of females to each of the four groups to be valid.

MANCOVA conducted on all response variables, using maternal SVL as covariate, was significant (by Pillai Trace,  $F_{24,87} = 1.661$ ;  $P = 0.046$ ), identifying litter size, juvenile mass, and neonatal SVL for further analysis.

Mean litter sizes were significantly larger in Groups 2 and 4 than in Groups 1 and 3 (Table 2). Relative clutch mass (RCM), measured as litter mass/postpartum maternal mass, did not differ significantly (Table 2).

Offspring mass differed significantly among groups with mothers from Groups 1 and 3 giving birth to heavier offspring (Table 3). Although neonatal SVL differed significantly, this was limited to Group 3 juveniles which were

TABLE 3. Morphological and performance characteristics of newborn *Niveoscincus metallicus* from mothers assigned to each of four groups according to the time and extent of tail loss. Means are calculated from litter averages for each mother. The covariate (maternal SVL) was nonsignificant for each analysis; therefore ANOVA was used. Means with the same superscript are not significantly different as determined by post hoc HSD tests.

Offspring trait	Group	Mean	SE	ANOVA		
				df	F	P
SVL (mm)	1	23.34 <sup>a,b</sup>	0.20	3,38	5.77	0.0024
	2	22.82 <sup>b</sup>	0.22			
	3	23.55 <sup>a</sup>	0.13			
	4	22.79 <sup>b</sup>	0.12			
Mass (mg)	1	241.81 <sup>a</sup>	7.03	3,38	3.70	0.0198
	2	219.93 <sup>b</sup>	5.76			
	3	241.98 <sup>a</sup>	5.44			
	4	222.94 <sup>b</sup>	5.73			
Tail length (mm)	1	26.19 <sup>a,b</sup>	0.33	3,38	3.26	0.0319
	2	26.47 <sup>a,b</sup>	0.78			
	3	27.38 <sup>a</sup>	0.33			
	4	25.71 <sup>b</sup>	0.25			
Fat stores (mg)	1	2.37 <sup>a</sup>	0.45	3,38	0.54	0.6584
	2	2.33 <sup>a</sup>	0.31			
	3	2.49 <sup>a</sup>	0.24			
	4	1.97 <sup>a</sup>	0.22			
Sprint speed (m s <sup>-1</sup> )	1	0.36 <sup>a</sup>	0.01	3,38	0.65	0.5889
	2	0.39 <sup>a</sup>	0.02			
	3	0.38 <sup>a</sup>	0.01			
	4	0.38 <sup>a</sup>	0.02			
Growth (mm)	1	1.38 <sup>a</sup>	0.13	3,35	1.84	0.1578
	2	1.81 <sup>a</sup>	0.21			
	3	1.31 <sup>a</sup>	0.14			
	4	1.49 <sup>a</sup>	0.11			

larger than those from Groups 2 and 4 (Table 3). Mean juvenile tail length also differed significantly, but the only significant difference was between juveniles born to Group 3 females and those born to Group 4 females (Table 3). There were no differences in the locomotor performance of neonates, abdominal fat stores at birth, or the rate of growth over the first eight weeks (Table 3).

#### DISCUSSION

Female *N. metallicus* that experience tail autotomy during vitellogenesis, regardless of the amount of tail lost (i.e., Groups 1 and 3), suffer substantial reductions in litter size (~ 17.5%) compared to females with no previous tail autotomy or those that experienced tail loss during a previous season. The magnitude of the response observed is similar to the figure of 14% reported for *Morethia boulengeri* (Smyth, 1974), an oviparous skink that also has both abdominal and caudal energy reserves. Our values are considerably less than those found in species that lack abdominal fat bodies. In such species, clutch/litter sizes are severely reduced following autotomy (55% in *Hemiergis peronii*: Smyth, 1974; 55–100% in *Ctenotus taeniolatus*: Taylor, 1984 cited in Wilson and Booth, 1998; and 75% in *Eulamprus quoyii*: Wilson and Booth 1998). Because skeletochronology data indicate that *N. metallicus* females at Clarence Lagoon have a reproductive life of 9–12 yr (McCoull, 2001), a 17.5% reduction in one breeding season is unlikely to have a substantial impact on lifetime fecundity.

Previous studies of the effect of caudal autotomy on reproductive investment have agreed that costs are incurred as a consequence of energetic restriction, but they have been unable to pinpoint the principal source of these costs (Smyth, 1974; Dial and Fitzpatrick, 1981; Wilson and Booth, 1998). *Niveoscincus metallicus* provides an opportunity to separate the direct costs associated with autotomy (loss of energy reserves) from the indirect costs (regeneration costs), because most caudal fat (~ 90%) is aggregated within the proximal third of the tail (Chapple and Swain, 2002). Because fewer than 30% of breaks occur in this region, most tail breaks in this species do not result in a significant loss of caudal fat (Chapple and Swain, 2002). Because our data indicate that reduction in clutch size following recent tail loss is independent of the direct loss of energy reserves, we conclude that, in *N. metallicus*, diversion of energy to fuel tail regeneration is the major cause of reproductive costs associated with autotomy. However, the reduction in reproductive investment following autotomy may also be caused by several possible behavioral modifications. Tail-

less lizards have been observed to modify their thermoregulatory behavior (Martin and Salvador, 1993c), alter their habitat use, and reduce activity (Formanowicz et al., 1990; Martin and Salvador, 1992; Downes and Shine, 2001), and experience decreased foraging efficiency (Martin and Salvador, 1993b). Such behavioral modifications have the potential to restrict reproductive investment through decreased nutritional condition and energy intake and conversion.

Although an effect of tail loss on clutch/litter size has been demonstrated on several occasions, we are not aware of any other study that has determined whether such reduction in reproductive investment affects juvenile phenotype. Our data provide indirect evidence that, although loss of any part of the tail during vitellogenesis results in smaller litters in *N. metallicus*, the substantial loss of fat involved in proximal breaks may have additional consequences for offspring phenotype. The offspring from mothers with regenerating distal breaks were significantly larger (SVL and mass), and had longer tails, than those from any other group. Thus, although the regeneration cost incurred by autotomy anywhere along the tail during vitellogenesis resulted in reduced litter size, females that retained their caudal fat stores were apparently able to increase the size of their remaining young, an option not available to females that suffered proximal tail breaks. Females that lose their entire tail will suffer a two-fold energetic cost: in addition to losing important energy stores, the cost of regeneration will itself be much greater than that required to regenerate only a section of the tail.

In *N. metallicus* postnatal growth rate is independent of size at birth, so there is no short-term capacity to compensate for small birth size (Swain and Jones, 2000a). Because larger offspring sometimes show improved survival under poor environmental conditions (Ferguson and Fox, 1984; Sinervo, 1990; Sinervo et al., 1992), size at birth may be a particularly important parameter in *N. metallicus*. Although larger females do not ovulate larger eggs in *N. metallicus*, they do produce larger young as a result of facultative placentotrophy (Swain and Jones, 2000a,b). It appears more probable that increased size at birth in young whose mothers experienced distal tail breaks is achieved through facultative placentotrophy during gestation rather than by increased vitellogenesis before ovulation.

*Acknowledgments.*—We thank L. Barmuta for his statistical advice. This work was completed under Animal Ethics Permit A0005657 from the University of Tasmania. G. Smith and two anon-

ymous reviewers provided helpful comments on an earlier version of this manuscript.

## LITERATURE CITED

- ARNOLD, E. N. 1988. Caudal autotomy as a defense. *In* *Biology of the Reptilia*. Vol. 16, pp. 236–273. C. Gans and R. B. Huey (eds.), Alan Liss, New York.
- BALLINGER, R. E., AND D. W. TINKLE. 1979. On the cost of tail regeneration to body growth in lizards. *Journal of Herpetology* 13:374–375.
- BALLINGER, R. E., J. W. NIETFELDT, AND J. J. KRUPA. 1979. An experimental analysis of the role of the tail in attaining high running speed in *Cnemidophorus sexlineatus* (Reptilia: Squamata: Lacerta). *Herpetologica* 35:114–116.
- BELLAIRS, A. D'A., AND S. V. BRYANT. 1985. Autotomy and regeneration in reptiles. *In* *Biology of the Reptilia*. Vol. 15, pp. 301–410. C. Gans and F. Billet (eds.), John Wiley and Sons, New York.
- BROWN, R. M., D. H. TAYLOR, AND D. H. GIST. 1995. Effect of caudal autotomy on locomotor performance in wall lizards. *Journal of Herpetology* 29: 98–105.
- CHAPPLE, D. G., AND R. W. SWAIN. 2002. Distribution of energy reserves in a viviparous skink: Does tail autotomy involve the loss of lipid stores? *Australian Ecology* 27(1):in press.
- CLARK, D. R. 1971. The strategy of tail autotomy in the ground skink, *Lygosoma laterale*. *Journal of Experimental Zoology* 176:295–302.
- COGGER, H. G. 1992. *Reptiles and Amphibians of Australia*. Reed Books, Sydney, New South Wales, Australia.
- CONGDON, J. D., L. J. VITT, AND W. W. KING. 1974. Geckos: adaptive significance and energetics of tail autotomy. *Science* 184:1379–1380.
- DERICKSON, W. K. 1976. Lipid storage and utilization in reptiles. *American Zoologist* 16:711–723.
- DIAL, B. E., AND L. C. FITZPATRICK. 1981. The energetic costs of tail autotomy to reproduction in the lizard *Coleonyx brevis* (Sauria: Gekkonidae). *Oecologia* 51:310–317.
- DOUGHTY, P., AND R. SHINE. 1998. Reproductive energy allocation and long-term energy stores in a viviparous lizard (*Eulamprus tympanum*). *Ecology* 79:1073–1083.
- DOWNES, S., AND R. SHINE. 2001. Why does tail loss increase a lizard's later vulnerability to snake predators? *Ecology* 82:1293–1303.
- DUFAURE, P. J., AND J. HUBERT. 1961. Table de développement du lézard vivipare: *Lacerta* (Zootoca) *vivipara* Jacquin. *Archives d'Anatomie Microscopique et de Morphologie Experimentale* 50:309–328.
- DUNHAM, A. E. 1978. Food availability as a proximate factor influencing growth rates in the iguanid lizard *Sceloporus merriami*. *Ecology* 59:770–778.
- FERGUSON, G. W., AND S. F. FOX. 1984. Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana*: its causes and evolutionary strategy. *Evolution* 38:342–349.
- FORMANOWICZ, D. R., E. D. BRODIE, AND P. J. BRADLEY. 1990. Behavioural compensation for tail loss in the ground skink, *Scincella lateralis*. *Animal Behaviour* 40:782–784.
- FOX, S. F., AND K. J. MCCOY. 2000. The effects of tail loss on survival, growth, reproduction, and sex ratio of offspring in the lizard *Uta stansburiana* in the field. *Oecologia* 122:327–334.
- FOX, S. F., AND M. A. ROSTKER. 1982. Social cost of tail loss in *Uta stansburiana*. *Science* 218:692–693.
- 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. J. BENNETT, AND K. M. SWADLING. 1998. Lipids in yolks and neonates of the viviparous lizard *Niveoscincus metallicus*. *Comparative Biochemistry and Physiology* 121B:465–470.
- MARTIN, J., AND A. SALVADOR. 1992. Tail loss consequences on habitat use by the Iberian rock lizard, *Lacerta monticola*. *Oikos* 65:328–333.
- . 1993a. Tail loss reduces mating success in the Iberian rock-lizard. *Behavioral Ecology and Sociobiology* 32:185–189.
- . 1993b. Tail loss and foraging tactics of the Iberian rock-lizard, *Lacerta monticola*. *Oikos* 66:318–324.
- . 1993c. Thermoregulatory behaviour of rock lizards in response to tail loss. *Behaviour* 124:123–136.
- MCCOULL, C. J. 2001. Geographic variation and adaptation in the Tasmanian metallic skink *Niveoscincus metallicus*. Unpubl. Ph.D. diss., University of Tasmania, Hobart, Tasmania, Australia.
- NDUKUBA, P. I., AND A. V. RAMACHANDRAN. 1988. Extraretinal photoreception in lacertilian tail regeneration: the lateral eyes are not involved in photoperiodic photoreception in the gekkonid lizard *Hemidactylus flaviviridis*. *Journal of Experimental Zoology* 248:73–80.
- RAMACHANDRAN, A. V., AND P. I. NDUKUBA. 1989. Parachlorophenylalanine retards tail regeneration in the gekkonid lizard *Hemidactylus flaviviridis* exposed to continuous light. *Journal of Experimental Biology* 143:235–243.
- SALVADOR, A., J. MARTIN, AND P. LOPEZ. 1995. Tail loss reduces home range size and access to females in male lizards, *Psammmodromus algirus*. *Behavioral Ecology*. 6:382–387.
- SINERVO, B. 1990. The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution* 44:279–294.
- SINERVO, B., P. DOUGHTY, R. B. HUEY, AND K. ZAMUDIO. 1992. Allometric engineering: a causal analysis of natural selection on offspring size. *Science* 258:1927–1930.
- SMITH, G. R. 1996. Tail loss in the striped plateau lizard, *Sceloporus virgatus*. *Journal of Herpetology* 30: 552–555.
- SMYTH, M. 1974. Changes in the fat stores of the skinks *Morethia boulengeri* and *Hemiergis peronii* (Lacertilia). *Australian Journal of Zoology* 22:135–145.
- SWAIN, R., AND S. M. JONES. 1997. Maternal-fetal transfer of <sup>3</sup>H-labelled leucine in the viviparous lizard *Niveoscincus metallicus* (Scincidae: Lygosominae). *Journal of Experimental Zoology* 277:139–145.
- . 2000a. Maternal effects associated with ges-

- tation conditions in a viviparous lizard. *Herpetological Monographs* 14:432–440.
- . 2000b. Facultative placentotrophy: half-way house or strategic solution. *Comparative Biochemistry and Physiology* 127:441–451.
- TABACHNICK, B. G., AND L. S. FIDELL. 1989. *Using Multivariate Statistics*. 2nd ed. Harper and Row, New York.
- THOMPSON, M. B., B. K. SPEAKE, J. R. STEWART, K. J. RUSSELL, R. J. MCCARTNEY, AND P. F. SURAI. 1999. Placental nutrition in the viviparous lizard *Niveoscincus metallicus*: the influence of placental type. *Journal of Experimental Biology* 202:2985–2992.
- TINKLE, D. W. 1967. The life and demography of the side-blotched lizard, *Uta stansburiana*. *Miscellaneous Publications of the Museum of Zoology University of Michigan* 132:1–182.
- TURNER, J. E., AND S. R. TIPTON. 1972. The effect of unnatural day lengths on tail regeneration in the lizard *Anolis carolinensis*. *Herpetologica* 28:47–50.
- VITT, L. J., AND W. E. COOPER. 1986. Tail loss, tail color, and predator escape in *Eumeces* (Lacertilia: Scincidae): age specific differences in costs and benefits. *Canadian Journal of Zoology* 64:583–592.
- VITT, L. J., J. D. CONGDON, AND N. A. DICKSON. 1977. Adaptive strategies and energetics of tail autotomy in lizards. *Ecology* 58:326–337.
- WILSON, B. S. 1992. Tail injuries increase the risk of mortality in free-living lizards (*Uta stansburiana*). *Oecologia* 92:145–152.
- WILSON, R. S., AND D. T. BOOTH. 1998. Effect of tail loss on reproductive output and its ecological significance in the skink *Eulamprus quoyii*. *Journal of Herpetology* 32:128–131.

Accepted 19 December 2001.