

Effect of Tail Loss on Sprint Speed and Growth in Newborn Skinks, *Niveoscincus metallicus*

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ABSTRACT.—Most studies that examined effects of caudal autotomy on lizards focused on adults and largely neglected the potential for contrasting effects in newborns and juveniles. We examined the impact of tail autotomy on locomotor performance and growth in newborn Metallic Skinks, *Niveoscincus metallicus*. Two siblings were randomly selected from each of 12 litters, with one assigned to a control group (tail intact) and the other to an experimental group (tail removed). Removal of the tail at the base 24 h after birth resulted in a significant decrease in sprint speed 72 h after birth (approximately 50% reduction compared to speed within 24 h of birth). This impairment is substantially greater than that observed previously in adults of this species (35%). However, caudal autotomy at birth did not inhibit growth, measured as the increase in snout–vent length, during the first eight weeks of life. Despite maintaining growth rate, newborns were still able to regenerate at least one-third of their tail over the eight weeks of the study. We discuss how the absence of the tail, the presumed energetic cost of tail replacement, and the lack of caudal fat stores, may influence the ability of newborn *N. metallicus* to survive their first winter.

Many species of lizard employ the strategy of tail autotomy as a means to escape from predators (Arnold, 1984, 1988). Although there is an immediate survival benefit from tail loss, tailless individuals may incur a range of subsequent costs (reviewed in Arnold, 1988; McConnachie and Whiting, 2003). Inhibited locomotor performance (Formanowicz et al., 1990; Brown et al., 1995; Downes and Shine, 2001) and reduced growth (Ballinger and Tinkle, 1979; Smith 1996) are two of the most recognized costs of tail loss. Reduced growth may result directly from the loss of caudal energy reserves, or indirectly as a result of modified foraging behavior or habitat use (e.g., Martin and Salvador, 1993; Downes and Shine, 2001), which decreases food intake or exposes the individual to alternate thermal microclimates. In addition, tail regeneration may be energetically expensive (e.g., Bellairs and Bryant, 1985) and may, therefore, require the diversion of energetic resources from reproduction or growth (Congdon et al., 1974; Vitt et al., 1977; Dial and Fitzpatrick, 1981), although some energetic resources may also be obtained from increased food intake (Dial and Fitzpatrick, 1981). Even when autotomy rarely results in the loss of significant caudal fat reserves (Chapple and Swain, 2002b; Doughty et al., 2003), reproductive output may be decreased, presumably because abdominal reserves are diverted to facilitate tail regeneration (Chapple et al., 2002). However, tail loss does not always have adverse effects on lizards. For example,

lower mobility and growth are not invariably consequences of tail autotomy (e.g., Althoff and Thompson, 1994; Niewiarowski et al., 1997; Van Sluys, 1998; Fox and McCoy, 2000; Chapple and Swain, 2002a; McConnachie and Whiting, 2003).

Most studies of the consequences of autotomy have focused on adults and the conclusions from this work may not be applicable to juveniles that are free of reproductive constraints. Indeed, because mortality is often highest in the first year of a lizard's life, growing and attaining a large body size may be the priority of juveniles. Larger juveniles can experience improved survival under suboptimal thermal environments, limited food resources and high levels of predation (Ferguson and Fox, 1984; Sinervo, 1990). Although there may be numerous benefits of rapid growth and an associated earlier onset of sexual maturity, such benefits may come at the expense of reduced longevity (e.g., Olsson and Shine, 2002).

We examined the effect of tail loss at birth on sprint speed and growth in the Metallic Skink, *Niveoscincus metallicus*. Tail loss is extremely common in wild populations of newborn and juvenile *N. metallicus* (~50%; DGC and RS, unpubl. data), indicating that many individuals experience tail loss soon after birth. In this species, early growth rate may be important because newborns encounter their first hibernation period 8–12 weeks after birth. Caudal fat reserves represent 55–78% of the total fat stores in adult *N. metallicus* (Chapple and Swain, 2002b) and such energy stores may be used during hibernation (e.g., Avery, 1970; Derickson, 1976). Although increased foraging during this short prehibernation period may aid to make up this nutritional shortfall, restricted mobility (e.g., Chapple and Swain, 2002a), energetic constraints associated with tail regeneration, and a reduced capacity to store fat in the tail following autotomy may decrease the probability of surviving overwinter. For example, in the European Common Lizard (*Lacerta*

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vivipara) juveniles with partially regenerated tails, and presumably reduced fat deposits, have been shown to be less likely to survive overwinter than juveniles with intact for fully regenerated tails (Bauwens, 1981).

MATERIALS AND METHODS

Study Species.—The Metallic Skink (*N. metallicus*) is a small viviparous lizard (45–65 mm adult snout–vent length, SVL; 2–5 g, mean 3.51 g) that has a widespread distribution across a range of habitats from sea level to subalpine environments (altitude 1400 m) in Tasmania and southeastern Victoria, Australia (Melville and Swain, 1999). It is a relatively cryptic ground-dwelling species that occupies shaded microhabitats with medium to dense vegetation cover and thick litter (Melville and Swain, 1999). Females reproduce annually with vitellogenesis beginning in March. Most matings occur in autumn (April) with sperm stored over winter by females until ovulation and fertilization in spring (September to October) following emergence (Jones and Swain, 1996; McCoull, 2001). At our population, females give birth to 2–7 young (mean 3.4) in late summer (late February) prior to entering winter hibernation approximately 8–12 weeks later (late April to early May; Jones and Swain, 1996; McCoull, 2001). Neonatal SVL of animals born to females at our study site is 22.1 ± 1.07 mm, mass is 218.5 ± 28.5 mg, and tail length is 26.3 ± 1.54 mm (McCoull, 2001).

Field and Laboratory Methods.—During January 2000 we used noosing to collect 12 adult females in an advanced state of pregnancy from around a small glacial lake on the central plateau of Tasmania, Australia (Clarence Lagoon, $42^{\circ}04'S$, $146^{\circ}19'E$; altitude ~ 970 m). Measurements of SVL and tail length (± 0.1 mm) were taken of each female. All lizards collected had original or completely regrown tails to avoid potential confounding effects of maternal tail loss on juvenile morphology and growth (Chapple et al., 2002). We have previously shown that there are no differences in growth or sprint speed among juveniles from mothers with original and completely regenerated tails (Chapple et al., 2002). Females were transported back to the laboratory, where they were housed individually in terraria ($20 \times 30 \times 10$ cm) lined with absorbent bedding. We provided upturned terracotta pots as cover and basking surfaces. These pots were placed beneath 25-W lights that provided 10 h of basking per day, and a temperature gradient of 12–35°C within each container; this encompassed the species' normal thermal range (Melville and Swain, 1997; McCoull, 2001). Fluorescent room lighting provided 14 h of light each day, which mimicked the levels in the surrounding environment. 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.

Females were housed in the laboratory until parturition commenced in early February 2000. Terraria were checked twice daily for newborns. When births occurred, the mothers were gently palpated to ensure that parturition was complete. Two newborns were randomly selected from each litter, with one being assigned to an experimental group and the other to a control group. Each newborn was weighed immediately (± 0.1 mg) and measurements were taken of SVL and tail length (± 0.1 mm). It was then given a unique

toe-clip for identification. Sexing of newborn *N. metallicus* by hemipenis eversion is difficult and often leads to tail loss (McCoull, 2001), so newborns were not sexed. However, no sexual dimorphism exists in newborn *N. metallicus*, although it is present in adults (McCoull, 2001). We measured the sprint speed of each newborn within 24 h of birth. Neonates were warmed to 26°C (optimal performance temperature: McCoull, 2001) and acclimated to this temperature for at least 30 min before being sprinted along a track maintained at $26^{\circ}\text{C} \pm 1^{\circ}\text{C}$ as described in Chapple and Swain (2002a). Trials in which animals refused to run, stopped, turned or appeared to run suboptimally were excluded (see Losos et al., 2002) and the newborn resprinted after being reacclimated to the test temperature for 30 min. For each testing occasion, one successful trial was conducted for each newborn. 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 maximal sprint speed (m sec^{-1}).

After these initial measurements were completed forceps were used to induce tail autotomy in the newborns assigned to the experimental group. The point of autotomy was standardized across individuals and was induced through the most basal caudal fracture plane. Animals were not anaesthetized prior to tail autotomy as this process is neurologically controlled and shown only by live conscious animals. However, the lizards were cooled prior to inducement of autotomy to increase the ease of tail removal (e.g., Bustard, 1968). Stress and blood loss during the procedure were minimal and no animals exhibited any ill-effects from our procedures. Wound healing commenced within a few days (e.g., Bellairs and Bryant, 1985) and visible tail regeneration was apparent within two weeks. Control animals were cooled and handled in an identical manner to the experimental lizards except that caudal autotomy was not induced. All newborns were remeasured and an estimate of sprint speed recorded within 48 h of the procedure to determine the effect of tail loss on locomotor performance. No visible signs of stress were evident during the sprint trials and we conclude that our results reflect the effects of tail loss. Newborns were housed under standard laboratory conditions for eight weeks to assess growth in tailed and tailless individuals. All animals were fed mashed banana and commercial cat food ad libitum, and daily observations indicated that each individual appeared to use the food and basking resources during the eight-week period. All juveniles were measured (SVL, tail length; ± 0.1 mm) at eight weeks of age. After several weeks in captivity, we were unable to obtain reliable and repeatable measures of what we considered optimal sprint performance for the newborns (see Losos et al., 2002); therefore we were unable to determine the long-term effects of autotomy on locomotor performance. All mothers and offspring were released at the site of maternal capture at the completion of the study.

Data Analysis.—Maternal effects are common in reptiles and may confound the comparison of newborn or juvenile lizards exposed to different treatments. Consequently, we controlled for potential maternal effects by using a Randomized Complete Block (RCB) ANOVA to determine the effect of autotomy on growth and sprint speed in newborn *N. metallicus*. Maternal SVL (litter effect) was treated as the block, with the

treatment (tail loss) allocated to lizards within a block (i.e., autotomy induced in one of the two newborns from each litter). Performance was measured as the difference in sprint speed between the initial trial and the postexperimental procedure trial. We used change in SVL as our measure of growth, since mass may reflect recent nutritional history rather than a change in body size, especially in small lizards (Dunham, 1978). Thus, growth was assessed as the increase in SVL over the first eight weeks of life in newborns.

RESULTS

The relative tail lengths (tail length/SVL) of newborns assigned to each of the experimental groups did not significantly differ (mean \pm SE; control: 1.18 ± 0.01 , experimental: 1.18 ± 0.02 , $N = 12$; ANOVA: $F_{1,23} = 0.15$, $P = 0.70$); nor did their initial sprint speed ($\text{m sec}^{-1} \pm$ SE, $N = 12$; control: 0.295 ± 0.014 , experimental: 0.306 ± 0.01 ; ANOVA: $F_{1,23} = 0.98$, $P = 0.33$).

Newborns subjected to tail loss within 48 h of birth experienced a significant decrease in sprint speed during trials 72 h after birth ($\text{m sec}^{-1} \pm$ SE, $N = 12$; control: 0.330 ± 0.017 ; experimental: 0.163 ± 0.011 ; RCB ANOVA: $F_{1,23} = 72.96$, $P < 0.001$). This reduction in sprint speed was not affected by maternal effects ($F_{11,23} = 0.60$, $P = 0.796$).

Growth over the eight-week duration of the study did not differ between control and tailless newborns (control: 1.48 ± 0.13 mm, experimental: 1.52 ± 0.13 mm, $N = 12$; $F_{1,23} = 0.03$, $P = 0.860$). However, maternal SVL appeared to have a significant influence on the early growth rate of newborns ($F_{11,23} = 4.85$, $P = 0.007$), with offspring from larger mothers having faster rates of growth. Despite the absence of any significant inhibition of growth as a result of autotomy, tailless newborns were able to replace approximately one-third to half of their tail within the eight weeks of the study (tail regeneration: 0.61 ± 0.10 mm/week).

DISCUSSION

Tail autotomy within a few days of birth in newborn *N. metallicus* substantially reduced locomotor performance but failed to influence growth during the eight-week prehibernatory period. Newborn *N. metallicus* experienced a substantial reduction (~50%) in sprint speed following autotomy, indicating that tail loss inhibits locomotor performance of juveniles more than that of adults (~35% reduction in sprint speed using the same methods outlined herein; Chapple and Swain, 2002a) and other lizard species (e.g., 35% in *Scincella lateralis*, Formanowicz et al., 1990; 40% in *Psammodromus algirus*, Martin and Avery, 1998). However, although the initial impact of tail loss on mobility may have been severe, we were unable to determine whether rapid recovery of locomotor performance occurred as in adults (Chapple and Swain, 2002a), because of an inability to obtain reliable and repeatable measures of maximal sprint performance after two weeks in captivity.

Tailless newborn *N. metallicus* failed to experience decreased growth rates over the eight-week duration of the study. This contrasts with previous studies on juveniles (Ballinger and Tinkle, 1979) and adults (Smith, 1996) of other species where tail loss was found to significantly decrease the rate of growth. This may be an artificial consequence of the ample laboratory food supply enabling animals to increase their food intake to

compensate for the energetic costs of replacing the tail. Although the decreased sprint speed of tailless individuals may have had the potential to decrease their foraging success in the wild (e.g., Martin and Salvador, 1993), the abundance of small invertebrate prey (e.g., arthropods and terrestrial amphipods) at Clarence Lagoon (our observations) indicates that food availability is unlikely to be limited even for newborns with restricted mobility. Regardless, our finding is in agreement with several other studies that have demonstrated that autotomy has no significant impact of growth rate in both adults (Althoff and Thompson, 1994; Van Sluys, 1998; Fox and McCoy, 2000) and juveniles (Vitt and Cooper, 1986; Althoff and Thompson, 1994). Although there is evidence of stored fat in the tails of newborns (our observations), there has been no quantitative analysis of the amount of caudal lipid reserves in newborns with complete or regenerating tails. Consequently, it is possible that the newborns in our study were growing at the expense of tail regeneration or storing fat in the tail. Indeed, Vitt et al. (1977) found that in three species of lizard (a gecko, *Coleonyx variegates*, and two skinks, *Eumeces skiltonianus* and *Eumeces gilberti*) juveniles invested relatively more energy into body growth than tail regeneration compared to adults.

The ability to maintain normal growth rates while regenerating the tail may be important for survival through the critical 8–12-week period before the neonates experience their first winter. The high frequency of tail loss in juvenile *N. metallicus* (~50%, DGC and RS, unpubl. data) suggests that predation on juveniles may be intense. Predation is frequently size-related (e.g., Blomberg and Shine, 2000) and newborn *N. metallicus* are vulnerable to a range of invertebrate predators, especially spiders and scorpions, which are of little concern to larger animals. Consequently, juveniles that progress rapidly through these vulnerable size classes should be advantaged.

Extensive tail loss involves loss of caudal fat stores that are vital for winter survival (e.g., Avery, 1970). Thus, together with the presumed energetic cost of tail regeneration (Bellairs and Bryant, 1985), newborn *N. metallicus* without tails might be expected to have poorer winter survival than their tailed counterparts (see Bauwens, 1981). However, newborn *N. metallicus* were able to regenerate at least one-third of their tail in the prehibernatory period. This approaches the threshold (half original tail length) where *N. metallicus* (Chapple and Swain, 2002a) and other skinks (e.g., Downes and Shine, 2001) regain full locomotor performance following autotomy. More important, since the majority of the caudal fat reserves are stored in the proximal third of the tail (e.g., Chapple and Swain, 2002b; Doughty et al., 2003), *N. metallicus* that lose their tails early in life are likely to be able to store sufficient fat in their shortened tail to survive overwinter (e.g., Avery, 1970).

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