

Effect of caudal autotomy on locomotor performance in a viviparous skink, *Niveoscincus metallicus*

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Summary

1. Tail loss has repeatedly been associated with the impairment of locomotor performance in lizards. However, although the immediate impact of tail loss may be severe, most previous studies have failed to establish how long such locomotory costs persist.
2. We investigated both the short-term (24–36 h) and long-term (4 and 12 weeks) consequences of tail loss on locomotor performance in a viviparous ground-dwelling skink, *Niveoscincus metallicus* (O'Shaughnessy 1874). Sprint speed, climbing ability and stamina were measured as performance variables. The locomotor performance of both adult males and pregnant females were tested during the study.
3. Male and female lizards responded differently to tail loss, although the immediate impact of autotomy on performance was generally minor. In males caudal autotomy imposed a significant immediate impact on sprint speed, while in females stamina was reduced immediately after autotomy.
4. Females regenerated their tails significantly faster than males. Recovery of locomotor performance over the 3-month duration of the study was observed in females (for endurance capacity) but not males (for sprint speed).
5. Overall, the impact of tail loss on locomotor performance was generally limited or short-lived in *N. metallicus*.

Key-words: Cost of reproduction, Scincidae, tail loss, tail regeneration

Functional Ecology (2002) **16**, 817–825

Introduction

Defensive tactics involving autotomy of body parts have evolved in both invertebrates (e.g. crustaceans, cnidarians, molluscs, spiders, insects; Stasek 1967; Robinson, Abele & Robinson 1970; Edmunds 1974; Roth & Roth 1984; Klawinski & Formanowicz 1994) and vertebrates (e.g. lizards, snakes, salamanders; Wake & Dresner 1967; Willis, Threkeld & Carpenter 1982; Arnold 1988) to facilitate escape from predators. The shed body portion often distracts the predator while the injured animal escapes (Arnold 1988). However, despite the immediate survival benefit of autotomy, the ensuing costs may seriously affect the individual's subsequent fitness. Reduced growth rates (Figiel & Miller 1995; Smith 1996; Stoks 2001), decreased reproductive investment or output (Smyth 1974; Dial & Fitzpatrick 1981; Wilson & Booth 1998; Bingham, Burr & Head 2000; Pomory & Lares 2000), modified activity levels (Formanowicz, Brodie &

Bradley 1990; Martin & Salvador 1992; Stoks 1999a), and diminished defensive and escape capabilities (Congdon, Vitt & King 1974; Bildstein, McDowell & Brisbin 1989; Robinson, Hayworth & Harvey 1991; Smith 1995) may all be consequences of autotomy, at least until the body part can be replaced.

The loss of body parts may influence locomotor performance (Semlitsch 1990; Robinson *et al.* 1991; Stoks 1999b; Amaya, Klawinski & Formanowicz 2001). Many lizards employ tail autotomy as a defensive tactic after other strategies such as crypsis and flight have failed (see review by Arnold 1988). However, the restriction of locomotor performance and mobility is probably the most documented effect of tail loss in lizards, potentially affecting terrestrial (Ballinger, Nietfeldt & Krupa 1979; Punzo 1982; Formanowicz *et al.* 1990; Martin & Avery 1998; Downes & Shine 2001), arboreal (Brown, Taylor & Gist 1995) and aquatic (Daniels 1985) forms of locomotion. Impairment of locomotor performance may contribute to the increased vulnerability of tailless lizards to predation that has been observed during staged encounters in the laboratory or outdoor enclosures (Congdon *et al.* 1974; Dial & Fitzpatrick 1984; Daniels, Flatherty & Simbotwe 1986; Downes & Shine 2001) or inferred from mortality rates in natural populations (Wilson

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1992; Althoff & Thompson 1994; Niewiarowski *et al.* 1997; Fox & McCoy 2000). Modification of activity levels, antipredator behaviour and habitat use (Dial & Fitzpatrick 1984; Formanowicz *et al.* 1990; Martin & Salvador 1992, 1995, 1997; Downes & Shine 2001) may represent compensation for the absence of the tail and reduced mobility. However, these behavioural shifts may in turn reduce social status and mating opportunities (e.g. Fox & Rostker 1982; Fox, Heger & Delay 1990; Martin & Salvador 1993a; Kaiser & Mushinsky 1994; Salvador, Martin & Lopez 1995).

In general, tail regeneration is the most effective way to counteract the costs of tail loss in lizards. However, our knowledge of the persistence of any initial costs stemming from autotomy is limited, making it difficult to assess the overall costs of autotomy. Only one study appears to have investigated the persistence of locomotory inhibition during tail regeneration. Downes & Shine (2001) demonstrated that female Garden Skinks, *Lampropholis guichenoti*, regained their sprint performance within 6 weeks of autotomy, by which time they had replaced around half of the tail. This result suggests that adverse impacts of caudal autotomy on locomotor performance may be temporary. However, more information is necessary to determine whether this is true for other species of lizards.

In this study we investigated the impact of complete tail loss on the locomotor performance of a viviparous skink, *Niveoscincus metallicus* (O'Shaughnessy 1874). Our study differed from most previous research in that it was performed over a period of 3 months. We measured a range of performance traits (sprint speed, climbing ability and endurance) that are all relevant to the lifestyle of *N. metallicus*. This species is a ground-dwelling active forager, associated primarily with vegetation and litter, but it regularly climbs onto rocks, fallen logs and branches to bask (Melville & Swain 1999, 2000). It relies heavily on running to escape predators, but readily employs autotomy as a 'last ditch' defensive tactic against predators, and a high proportion of individuals in natural populations exhibit signs of previous tail loss (60–80%; D. Chapple unpublished data). Prolonged consequences of tail loss could be particularly important for adult female lizards since they spend much of their active season pregnant. Since pregnancy involves carrying an increased mass (~23% body mass; Swain & Jones 2000), any addition to the locomotory 'cost of pregnancy' (e.g. Shine 1980) could be very significant. Our study addresses four specific questions:

1. Does tail loss influence locomotor performance in adult lizards?
2. If so, how are different performance traits affected by tail loss?
3. Does tail re-growth induce recovery of locomotor performance?
4. Are locomotory responses to tail loss consistent between the sexes in adult lizards?

Materials and methods

STUDY ANIMALS

Niveoscincus metallicus is a small viviparous skink (45–65 mm snout–vent length, SVL) that is abundant over a broad altitudinal range (sea level to 1400 m) in Tasmania and south-eastern Victoria, Australia (Melville & Swain 1999). Sixty (30 males and 30 females) *N. metallicus* with complete tails (original or regenerated) were collected from around Clarence Lagoon (970 m a.s.l.; 42°04' S 146°19' E) on the Central Plateau of Tasmania in late September–early October 1999 (i.e. spring). Animals were caught by noosing and transported back to the laboratory where measurements were taken of SVL and tail length (± 0.1 mm). Sexual dimorphism in tail length is not evident in *N. metallicus* (Chapple & Swain 2002). All were sexually mature adults (>45 mm SVL; Swain & Jones 1994; Jones & Swain 1996). Within each sex individuals were randomly allocated to two groups of 15 animals to obtain four treatment groups: (1) Control Males; (2) Experimental Males; (3) Control Females; and (4) Experimental Females. However, one female assigned to the control group died in captivity shortly after the commencement of the study. Lizards were uniquely marked with a small numbered piece of adhesive cloth tape that was replaced after each moult.

The lizards were maintained in an air-conditioned room (12–14 °C) under bright fluorescent tube lighting (~20 000 lux) and UV lighting (14L : 10D). They were housed in groups of five in plastic terraria (20 × 30 × 10 cm) with an absorbent substrate. Extensive research with this species has revealed no agonistic interactions between individuals. Basking surfaces were provided in the form of upturned terracotta pots, which also provided cover. The basking site was positioned under a 25-W basking light connected to an automatic timer to provide 10 h of light per day. This created a thermal gradient of approximately 14–33 °C and allowed normal thermoregulation. Animals were fed two to three times weekly on a diet of mealworms (*Tenebrio* larvae), commercial cat food and mashed banana. Water was available *ad libitum*.

EXPERIMENTAL DESIGN

The locomotor performance (sprint speed, climbing ability, stamina) of all 60 lizards was assessed shortly after arrival in the laboratory. Tail condition (original or regenerated) did not affect pretreatment performance. After a baseline measurement of locomotor performance for each trait was obtained for each individual, complete tail autotomy was induced in those males and females assigned to experimental groups. To achieve tail autotomy, experimental animals had their tail broken through a basal fracture plane using forceps. 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). The resulting tail stump was approximately 10 mm in length. 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 with the formation of a characteristic scab and concealment of the wound by a layer of skin (Bellairs & Bryant 1985). Visible tail regeneration was evident following a 'latent' period (e.g. Bellairs & Bryant 1985) of about 2 weeks. Control animals were cooled and handled in an identical manner to the experimental lizards except that caudal autotomy was not induced.

Locomotor performance of all lizards was re-tested within 36 h of caudal autotomy. The testing regime involved all three performance criteria to be completed over a 2-day period. Sprinting and climbing were tested on day 1, with a gap of at least 3 h between each performance criteria; stamina trials were conducted the following morning (day 2). Following the assessment of the initial consequences of autotomy, the locomotor performance of each animal was re-tested after 4 and 12 weeks. Animals were maintained in common laboratory conditions throughout the duration of the study. Tail length (± 0.1 mm) was measured at each testing period to assess the rate of tail regeneration. As recent food intake may inhibit locomotor performance (e.g. Huey *et al.* 1984), animals were not fed in the 24 h prior to each testing occasion. At the commencement of the study all females were in mid-pregnancy and had reached late pregnancy by testing in week 4. By the final tests they were all *postpartum*.

Locomotor performance exhibits a considerable degree of thermal sensitivity (e.g. Hertz, Huey & Nevo 1983); therefore, prior to each test individuals were warmed to their optimal performance temperature of 26 °C (McCoull 2001). Warming was carried out in a metal box immersed in a water bath, thermostatically controlled to ± 1 °C for at least 30 min prior to each trial.

SPRINT SPEED

Estimates of sprint speed were obtained by running lizards down a heated (26 ± 1 °C) 'racetrack' 2 m in length. Lizards were sprinted twice per testing occasion, with a minimum rest of at least 30 min and re-warming between trials. They were encouraged to run by tapping their tails lightly with a small paintbrush. Three photodiodes, at 50 cm intervals along the track, linked to a computer were used to record sprint speed. Each run generated two times, and the fastest of the four times obtained was taken as the maximum sprint speed (m s^{-1}). Trials in which animals refused to run, stopped, or turned and ran the wrong way were excluded from the analysis.

CLIMBING ABILITY

Climbing ability was assessed by inducing lizards to climb along a wooden rod (40 cm in length, 2.5 cm diameter) positioned at a 45° angle with gentle taps on the tail with a small paintbrush. The surface of the rod was roughened with sandpaper to improve traction. The time taken for the lizard to climb the rod was recorded with a handheld stopwatch. Lizards were tested twice on each test occasion; they were re-warmed and allowed a minimum rest of 30 min between trials. The faster of the two times was used to calculate climbing speed for the individual (cm s^{-1}). Trials in which individuals refused to climb or fell off before reaching the end were excluded from the analysis.

ENDURANCE CAPACITY

Stamina was measured using a treadmill (50 cm long \times 20 cm wide) set at a constant speed of 10 cm s^{-1} . Lizards were tapped on the tail with a small paintbrush to run at a constant speed on the treadmill. Individuals appeared to run at a comfortable speed on the treadmill that they were able to maintain (~5–13 min). The neoprene belt on the treadmill provided traction. The trial ended when the individual refused to continue running and lagged to the rear of the treadmill. The elapsed time recorded for each trial was recorded as the endurance capacity. To avoid stress and excessive fatigue, only a single trial was conducted for each lizard on each testing occasion.

STATISTICAL ANALYSIS

There was no relationship between body size (SVL) and locomotor performance (linear regression; $P > 0.1$ for both sexes); therefore analyses excluded SVL as a factor. Sexual differences in the rate of tail regeneration (amount of tail re-grown over the 12-week duration of the study) were investigated using analysis of variance (ANOVA).

A repeated measures ANOVA (with sex and tail status as factors and time [locomotor performance] as the repeated measure) was completed for each performance attribute to determine if there were significant sexual differences in locomotor performance. There were no sexual differences in climbing ability; however, males and females showed clear differences for stamina ($F_{1,41} = 9.76$; $P = 0.003$), and approached significance for sprint speed ($F_{1,37} = 3.72$; $P = 0.062$). Accordingly males and females were analysed separately. For consistency we also analysed climbing responses separately. Tail status was significant for the sprint speed data ($F_{1,37} = 4.17$; $P = 0.048$). There were no interaction effects for any of the performance attributes. The separate treatment of the sexes was further necessitated by the fact that females were pregnant for the majority of the study.

Table 1. Percentage (\pm SE) of original tail length at each testing period for male ($n = 15$) and female ($n = 15$) *Niveoscincus metallicus* assigned to the experimental group

Testing period	Males	Females
24–36 h postautotomy	19.2 \pm 1.05	19.9 \pm 1.55
4 weeks' recovery	23.2 \pm 1.66	31.2 \pm 2.94
12 weeks' recovery	46.5 \pm 2.01	73.1 \pm 4.48

The effect of tail autotomy on each performance trait was then analysed for each sex using repeated measures ANOVA (with Tail condition as the factor and Time as the repeated measure). If there was a significant interaction the data were then split into two sets, enabling examination of the immediate effect of tail loss (initial, 24–36 h) and recovery during tail regeneration (24–36 h, 4 weeks, 12 weeks). Data were also split if there was a strong tendency for a decrease in locomotor performance as a result of tail loss (i.e. $P < 0.1$). Significant interactions between Tail condition and Time indicated that there was either an immediate impact of autotomy (initial effect) or that recovery of locomotor performance occurred during tail regeneration (recovery effect). For females, repeated measures ANOVA (with Tail condition as the factor and Time as the repeated measure) was conducted to determine whether parturition coincided with a change in locomotor performance (4 week, 12 week).

Results

REGENERATION CHARACTERISTICS

Following autotomy, both males and females had tail stumps that were around 20% of their original lengths

Table 2. Repeated measures analysis of variance table for the effect of tail autotomy on locomotor performance over the entire study in male and female *Niveoscincus metallicus*

Trait	Sex	Group			Time			Interaction		
		df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Sprint speed	Male	1, 21	3.76	0.066	3, 63	18.05	<0.001	3, 63	4.34	0.008
	Female	1, 16	0.97	0.340	3, 48	11.36	<0.001	3, 48	2.97	0.041
Climbing	Male	1, 25	5.52	0.027	3, 75	4.79	0.004	3, 75	0.93	0.430
	Female	1, 20	0.37	0.551	3, 60	11.63	<0.001	3, 60	2.20	0.098
Stamina	Male	1, 22	0.30	0.589	3, 66	5.97	0.001	3, 66	1.85	0.147
	Female	1, 19	2.05	0.169	3, 57	18.04	<0.001	3, 57	3.26	0.028

Table 3. Repeated measures analysis of variance table for the initial impact (initial vs 24–36 h-testing periods) of tail autotomy on locomotor performance in male and female *Niveoscincus metallicus*

Trait	Sex	Group			Time			Interaction		
		df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Sprint speed	Male	1, 21	2.27	0.147	1, 21	15.89	<0.001	1, 21	20.23	<0.001
	Female	1, 16	2.21	0.156	1, 16	6.32	0.023	1, 16	3.08	0.099
Climbing	Female	1, 20	0.03	0.873	1, 20	11.10	0.003	1, 20	4.18	0.054
Stamina	Female	1, 19	1.19	0.288	1, 19	45.85	<0.001	1, 19	12.24	0.002

(Table 1). Visible tail regeneration commenced after a short 'latent period' of about 2 weeks. Females (1.8 ± 0.03 mm week⁻¹; mean \pm SE) regenerated their tails significantly faster than males (1.2 ± 0.07 mm week⁻¹) over the 12 weeks of the study (ANOVA: $F_{1,29} = 59.52$, $P < 0.001$). After 4 weeks males had limited tail regeneration, but had replaced almost half of their original tail length by 12 weeks (Table 1). In contrast, females had tails one-third of their original length after 4 weeks, and after 12 weeks they had regenerated three-quarters of their tail (Table 1).

LOCOMOTOR PERFORMANCE

Sprint speed

Tail autotomy influenced the sprint speed of male *N. metallicus* (Tail condition \times Time: $P = 0.008$; Table 2, Fig. 1). The loss of the tail immediately impacted upon running performance in males (Tail condition \times Time: $P < 0.001$; Table 3, Fig. 1) and this inhibitory effect was maintained over the entire 12-week duration of the study (i.e. no interaction to indicate recovery; Tail condition \times Time: $P = 0.481$; Table 4, Fig. 1). However, sprint speed of both groups of lizards decreased over the course of the study (Table 2, Fig. 1), possibly due to prolonged captivity or reduced motivation.

Tail loss resulted in a slight decrease in sprint performance in females (Tail condition \times Time: $P = 0.041$; Table 2, Fig. 2) and although there was a strong tendency for autotomy to reduce sprint speed immediately following tail loss (Tail condition \times Time: $P = 0.099$; Table 3, Fig. 2) this was not statistically significant. The significant interaction effect during recovery (Tail condition \times Time: $P = 0.009$; Table 4;

Table 4. Repeated measures analysis of variance table for the recovery of locomotor performance following tail autotomy (24–36 h, 4 weeks and 12 weeks testing periods) in male and female *Niveoscincus metallicus*

Trait	Sex	Group			Time			Interaction		
		df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Sprint speed	Male	1, 21	5.98	0.023	2, 42	16.34	<0.001	2, 42	0.75	0.481
	Female	1, 16	0.98	0.337	2, 32	10.06	<0.001	2, 32	5.41	0.009
Climbing	Female	1, 20	1.32	0.264	2, 40	7.94	0.001	2, 40	0.39	0.678
Stamina	Female	1, 19	1.45	0.243	2, 38	16.36	<0.001	2, 38	4.68	0.015

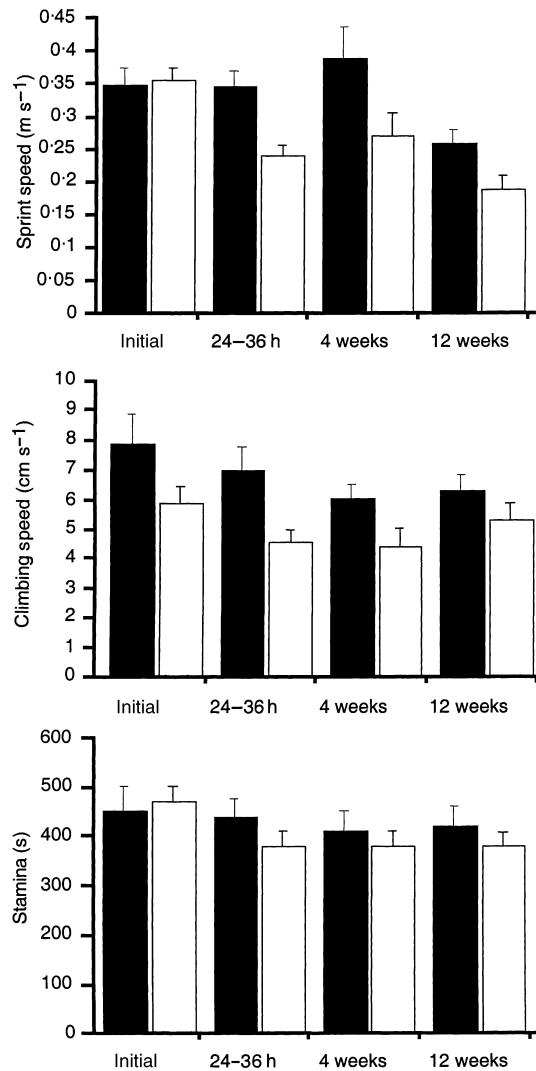
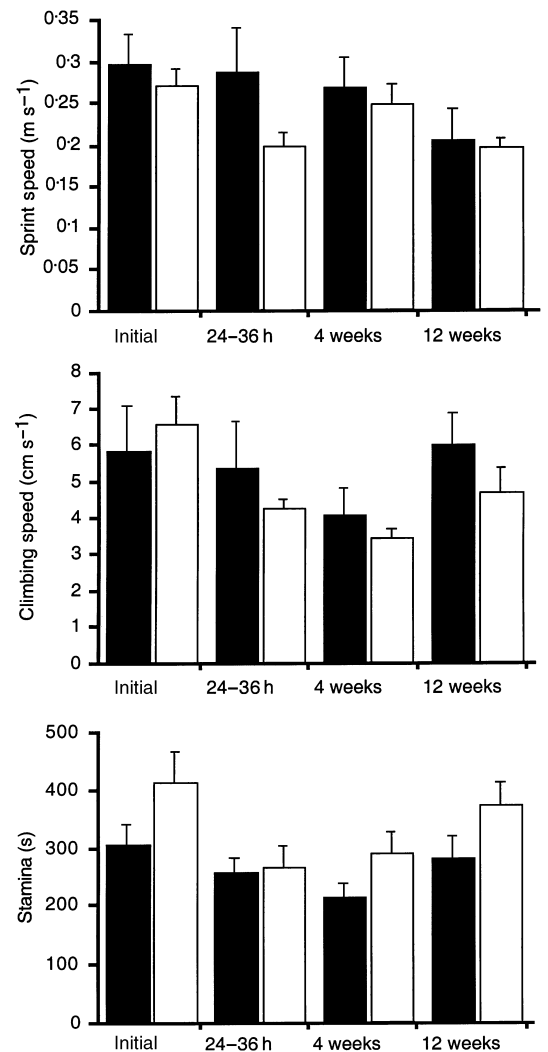
**Fig. 1.** Locomotor performance of control (tailed; black bars) and experimental (tailless; white bars) male *Niveoscincus metallicus* immediately before autotomy, 24–36 h postautotomy and after 4 and 12 weeks' recovery. Sprint speed ($\text{m s}^{-1} \pm \text{SE}$; $n = 14$ and 9, respectively, for control and experimental animals), climbing ability ($\text{cm s}^{-1} \pm \text{SE}$; $n = 14$, 13) and endurance capacity ($\text{s} \pm \text{SE}$; $n = 14$, 10) for both groups are indicated for each testing period.**Fig. 2.** Locomotor performance of control (tailed; black bars) and experimental (tailless; white bars) female *Niveoscincus metallicus* immediately before autotomy, 24–36 h postautotomy and after 4 and 12 weeks' recovery. Sprint speed ($\text{m s}^{-1} \pm \text{SE}$; $n = 8$ and 10, respectively, for control and experimental animals), climbing ability ($\text{cm s}^{-1} \pm \text{SE}$; $n = 10$, 12) and endurance capacity ($\text{s} \pm \text{SE}$; $n = 11$, 10) for both groups are indicated for each testing period. Parturition occurred between the 4 and 12-week recovery testing periods in both groups.

Fig. 2) indicates that females fully regained their sprinting abilities during tail regeneration. Following parturition, sprint speed decreased significantly in both tailed and tailless females (Group: $F_{1,16} = 0.14$, $P = 0.706$; Time: $F_{1,16} = 22.13$, $P < 0.001$; Fig. 2).

Climbing ability

Male climbing performance was not inhibited by caudal autotomy at any stage after tail loss (Tail condition \times Time: $P = 0.430$; Table 2, Fig. 1). Although there was a significant difference in the climbing ability

between treatment groups (Group: $P = 0.027$; Table 2, Fig. 1), this pattern reflects the initial difference in climbing performance of lizards assigned to each group.

There was a strong trend for females to decrease their climbing ability as a result of tail loss (Tail condition \times Time: $P = 0.098$; Table 2, Fig. 2), although the immediate impact of tail autotomy was not statistically significant (Tail condition \times Time: $P = 0.054$; Table 3, Fig. 2). No significant interaction was evident during tail re-growth (Tail condition \times Time: $P = 0.687$; Table 4, Fig. 2), indicating that females did not recover from the slight impact of tail loss during the study. However, parturition in both treatment groups coincided with a significant increase in climbing ability (Group: $F_{1,20} = 1.48$, $P = 0.238$; Time: $F_{1,20} = 15.90$, $P < 0.001$).

Endurance capacity

Stamina in male *N. metallicus* was not affected by tail autotomy at any stage during the study (Tail condition \times Time: $P = 0.147$; Table 2, Fig. 1). However, in females tail loss resulted in a significant decrease in endurance capacity (Tail condition \times Time: $P = 0.028$; Table 2, Fig. 2). There was an immediate impact of autotomy on stamina (Tail condition \times Time: $P = 0.002$; Table 3, Fig. 2); however, during tail re-growth females regained their endurance capabilities (Tail condition \times Time: $P = 0.015$; Table 4, Fig. 2). Recovery appeared to occur within 1 month of autotomy (Fig. 2). In both tailed and tailless females parturition coincided with a significant increase in stamina (Group: $F_{1,19} = 2.82$, $P = 0.11$; Time: $F_{1,19} = 21.89$, $P < 0.001$; Fig. 2).

Discussion

The locomotor performance of lizards may play a vital role in prey capture, escape from predators and the initiation of social interactions, and is therefore considered to represent an 'ecologically relevant' function (Arnold 1983; Avery 1993; Garland & Losos 1994; Avery & Tosini 1995; Van Damme, Aerts & Vanhooydonck 1998; Robson & Miles 2000). Most of the well-documented effects of caudal autotomy such as reduced activity and smaller home range size (e.g. Formanowicz *et al.* 1990; Martin & Salvador 1992), modified foraging behaviour (e.g. Martin & Salvador 1993b; Martin & Avery 1997), diminished mating opportunities (e.g. Salvador *et al.* 1995) and increased susceptibility to predation (Dial & Fitzpatrick 1984; Daniels *et al.* 1986; Downes & Shine 2001) are believed to result, at least in part, from a reduction in locomotory capacity. Accordingly, limiting either the severity or duration of such a potentially deleterious impact through rapid tail regeneration or locomotory compensation may be selectively advantageous.

The sprint speed of male *N. metallicus* decreased by 33% immediately following tail loss. This reduction is

consistent with the results from previous studies, e.g. *Cnemidophorus sexlineatus* (36%; Ballinger *et al.* 1979), *Cophosaurus texanus* (32%; Punzo 1982), *Uma notata* (42%; Punzo 1982), *Scincella lateralis* (35%; Formanowicz *et al.* 1990) and *Psammotromus algerius* (40%; Martin & Avery 1998). However, although caudal autotomy resulted in a slight decrease in sprint speed in female *N. metallicus*, it did not significantly influence the sprint performance of tailless lizards immediately following tail loss. Most of the previous studies in this area have not considered the sexes separately when investigating the effect of tail loss on locomotor performance. This study provides evidence that such effects may be gender specific. Reproductive status (i.e. pregnancy) may have influenced the locomotory cost of autotomy. Indeed, pregnancy (or gravidity) has been widely associated with inhibition of locomotor performance in lizards (e.g. Shine 1980; Cooper *et al.* 1990) including other species of *Niveoscincus* (Olsson, Shine & Bak-Olsson 2000; Wapstra & O'Reilly 2001). Thus, pregnancy may have confounded any effect of tail loss on locomotor performance in female *N. metallicus*.

Laboratory studies of endurance capacity may provide vital information on the likely locomotor behaviour in the field (Garland 1999). Tail loss was found to substantially reduce (~36%) the endurance capacity of female *N. metallicus*. Studies on lizard biomechanics have shown that there is an intimate relationship between stride length and stride frequency (Hamley 1990; Martin & Avery 1998). One major effect of tail loss on lizard locomotion is the reduction of stride length (Hamley 1990; Martin & Avery 1998). If stride length is decreased, stride frequency has to be increased to maintain the same velocity. Thus, tailless animals have to 'work harder' to sustain the equivalent speed of tailed lizards and therefore stamina may be affected. However, there has only been one previous report of autotomy influencing the endurance capacity of a lizard. Daniels (1985) showed that tail loss reduced the swimming stamina of the Water Skink *Eulamprus quoyii*. Since tail loss in *N. metallicus* reduced stamina in females only, this may have been a consequence of the added burden of pregnancy. Thus, adverse consequences of tail loss in females may be indirect. However, since adult females of this species are almost invariably pregnant during the activity period (Jones & Swain 1996), tail loss will result in different locomotory costs in males and females.

Climbing ability in *N. metallicus* was not affected by tail loss, although there was a slight tendency (but non-significant) for females to decrease climbing speed. This may be because this species is not predominantly arboreal, or perhaps because the tail is less functional while climbing. When climbing, the feet are always firmly attached to the substrate and therefore uncontrolled lateral oscillation of the hindquarters is not a problem. This was suggested by Arnold (1984) to account for the observation that the frequency of tail loss in a wide range of lizards is greater among climbing species than

among ground-dwellers. However, in *Podarcis muralis*, a lacertid that climbs extensively, tail loss is associated with decreased climbing ability (Brown *et al.* 1995). Whatever the reason, the absence of any effect of autotomy on the climbing ability of *N. metallicus* does highlight the fact that the impact of tail loss can vary markedly between performance traits. Unfortunately, with few exceptions (e.g. Daniels 1985; Brown *et al.* 1995) most investigations of the locomotor costs of autotomy have focused solely on one aspect of performance, generally sprint speed. In species such as *N. metallicus* that use several forms of locomotion to move through their environment, caudal autotomy may influence certain locomotory characteristics, such as sprint speed or stamina that are particularly relevant to escape behaviours, more than others, such as climbing ability, that are utilized more in basking and foraging behaviour.

Caudal autotomy has been reported to have no influence on locomotor performance in some species of lizard (e.g. Hamley 1990; Huey *et al.* 1990). Hamley (1990) suggested that some of the immediate impacts of autotomy that have been reported may be a consequence of investigators damaging locomotor muscles rather than a genuine effect of tail loss. He found that animals allowed to recover and begin tail regeneration before they were tested exhibited no ill-effects of autotomy. Indeed, the positioning, morphology and evolution of a major locomotory muscle (m. caudifemoralis longus) is believed to have coevolved with caudal autotomy (Russell & Bauer 1992). However, the presence of non-autotomous caudal vertebrae in the basal region of the tail acts to limit damage to locomotor muscles (Bellairs & Bryant 1985) and autotomy does not necessarily result in this muscle being surrendered (Russell, Bergmann & Barbadillo 2001). In the present study we induced autotomy within an autotomous caudal vertebrae, leaving a reasonably sized tail stump (~10 mm). Consequently, it is unlikely that damage to major locomotor muscles is responsible for the locomotor costs observed in this study.

Lizards that have completely regenerated their tails exhibit few detrimental effects from tail loss (Downes & Shine 2001). Presumably the rate of tail regeneration determines the duration of any cost experienced by an individual since there must be a point at which costs, at least those associated with locomotion, become negligible. Such a relationship has been investigated and demonstrated only once previously, in female Garden Skinks, *Lampropholis guichenoti* (Downes & Shine 2001). The absence of data on the temporal effect of tail autotomy is surprising given that both the severity and the duration of locomotory inhibition involve fitness consequences. Tailless lizards have been demonstrated to compensate for the reduction in locomotor abilities by reducing their level of activity (Formanowicz *et al.* 1990; Martin & Salvador 1995), decreasing their home range (Salvador *et al.* 1995) and modifying their foraging behaviour (Martin & Salvador 1993b;

Martin & Avery 1997). Prolonged behavioural compensation may affect their access to females and mating opportunities (e.g. Salvador *et al.* 1995), nutritional condition (e.g. Martin & Salvador 1993b) and probability of survival (e.g. Wilson 1992; Niewiarowski *et al.* 1997; Fox & McCoy 2000). In some cases, alteration of escape tactics may actually increase predation risk when faced with certain types of predators (Downes & Shine 2001). Hence, selective pressures may act upon lizards to either adapt to locomotion without a tail or rapidly regenerate the tail. *Niveoscincus metallicus* appears able to maintain mobility without a tail while also exhibiting signs of swift recovery following autotomy.

Caudal autotomy produced only two major locomotory impacts in *N. metallicus*: reduction in endurance in females and sprint speed in males. Females regained their endurance capacity within the duration of the study. The majority of these animals had tails that were between 50 and 70% of their original tail length, with both the time taken to recover and the tail length at recovery similar to that previously observed for sprint speed in female *Lampropholis guichenoti* (Downes & Shine 2001). However, male *N. metallicus* failed to recover their sprinting ability within the 12 weeks, even though their tails were about 45–50% of their original tail length. Clearly, male *N. metallicus* endure the locomotory costs of tail loss for substantially longer than females.

In conclusion, with the exception of sprint speed in males, the locomotory costs of caudal autotomy on *N. metallicus* appear to be limited and transient. Tail loss in this species may thus represent little more than a temporary 'inconvenience', especially since the entire tail is lost only rarely, with little impact on important caudal fat reserves (Chapple & Swain 2002). *Niveoscincus metallicus* exhibits high frequencies of tail loss in natural populations (60–80%; D. Chapple unpublished data) suggesting that autotomy is an effective, low-cost antipredator tactic in this species.

Acknowledgements

Colin McCoull provided valuable field and laboratory assistance throughout this project. We thank Leon Barmuta for his statistical advice and Sharon Downes for advice and constructive criticism on earlier drafts of this manuscript. Experimental work was carried out with the approval of the University of Tasmania Animal Ethics Committee (Permit No. A0005657).

References

- Althoff, M.M. & Thompson, J.N. (1994) The effects of tail autotomy on survivorship and body growth of *Uta stansburiana* under conditions of high mortality. *Oecologia* **100**, 250–255.
- Amaya, C.C., Klawinski, P.D. & Formanowicz, D.R. (2001) The effects of leg autotomy on running speed and foraging ability in two species of wolf spider (Lycosidae). *American Midland Naturalist* **145**, 201–205.

- Arnold, S.J. (1983) Morphology, performance and fitness. *American Zoologist* **23**, 347–361.
- Arnold, E.N. (1984) Evolutionary aspects of tail shedding in lizards and their relatives. *Journal of Natural History* **18**, 127–169.
- Arnold, E.N. (1988) Caudal autotomy as a defense. *Biology of the Reptilia*, Vol. 16 (eds C. Gans & R.B. Huey), pp. 236–273. Alan Liss, New York.
- Avery, R.A. (1993) Experimental analysis of lizard pause-travel movement: pauses increase probability of prey capture. *Amphibia-Reptilia* **14**, 423–427.
- Avery, R.A. & Tosini, G. (1995) Dynamics of predation in Lacertidae: the relationship between locomotor pattern and prey-capture probability in three contrasted species. *Amphibia-Reptilia* **16**, 1–10.
- Ballinger, R.E., Nietfeldt, J.W. & Krupa, J.J. (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. & Bryant, S.V. (1985) Autotomy and regeneration in reptiles. *Biology of the Reptilia*, Vol. 15 (eds C. Gans & F. Billet), pp. 301–410. John Wiley and Sons, New York.
- Bildstein, K.L., McDowell, S.G. & Brisbin, L.L. (1989) Consequences of sexual dimorphism in sand fiddler crabs, *Uca pugilator*: differential predation to avian predation. *Animal Behaviour* **37**, 133–139.
- Bingham, B.L., Burr, J. & Head, H.W. (2000) Causes and consequences of arm damage in the sea star *Leptasterias hexactis*. *Canadian Journal of Zoology* **78**, 596–605.
- Brown, R.M., Taylor, D.H. & Gist, D.H. (1995) Effect of caudal autotomy on locomotor performance of wall lizards (*Podarcis muralis*). *Journal of Herpetology* **29**, 98–105.
- Bustard, H.R. (1968) Temperature dependent tail autotomy mechanism in gekkonid lizards. *Herpetologica* **24**, 127–130.
- Chapple, D.G. & Swain, R. (2002) Distribution of energy reserves in a viviparous skink: Does tail autotomy involve the loss of lipid stores? *Austral Ecology* **27**, 565–572.
- Congdon, J.D., Vitt, L.J. & King, W.W. (1974) Geckos: adaptive significance and energetics of tail autotomy. *Science* **184**, 1379–1380.
- Cooper, W.E., Vitt, L.J., Hedges, R. & Huey, R.B. (1990) Locomotor impairment and defense in gravid lizards (*Eumeces laticeps*): behavioural shift in activity may offset costs of reproduction in an active forager. *Behavioural Ecology and Sociobiology* **27**, 153–157.
- Daniels, C.B. (1985) The effect of tail autotomy on the exercise capacity of the water skink, *Sphenomorphus quoyii*. *Copeia* **1985**, 1074–1077.
- Daniels, C.B., Flatherty, S.P. & Simbotwe, M.P. (1986) Tail size and effectiveness of autotomy in a lizard. *Journal of Herpetology* **20**, 93–96.
- Dial, B.E. & Fitzpatrick, L.C. (1981) The energetic costs of tail autotomy to reproduction in the lizard *Coleonyx brevis* (Sauria: Gekkonidae). *Oecologia* **51**, 310–317.
- Dial, B.E. & Fitzpatrick, L.C. (1984) Predator escape success in tailed versus tailless *Scincella lateralis* (Sauria: Scincidae). *Animal Behaviour* **32**, 301–302.
- Downes, S. & Shine, R. (2001) Why does tail loss increase a lizard's later changes of being consumed by snake predators? *Ecology* **82**, 1293–1303.
- Edmunds, M. (1974) *Defense in Animals: A Survey of Anti-predator Defenses*. Longman, New York.
- Figli, C.R. & Miller, G.L. (1995) The frequency of chela autotomy and its influence on the growth and survival of the crayfish *Procambrus clarkii* (Girard, 1852) (Decapoda, Cambaridae). *Crustaceana* **68**, 472–483.
- Formanowicz, D.R., Brodie, E.D. & Bradley, P.J. (1990) Behavioural compensation for tail loss in the ground skink, *Scincella lateralis*. *Animal Behaviour* **40**, 782–784.
- Fox, S.F. & McCoy, K.J. (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. & Rostker, M.A. (1982) Social cost of tail loss in *Uta stansburiana*. *Science* **218**, 692–693.
- Fox, S.F., Heger, N.A. & Delay, L.S. (1990) Social cost of tail loss in *Uta stansburiana*: lizard tails as a status-signalling badges. *Animal Behaviour* **39**, 549–554.
- Garland, T. (1999) Laboratory endurance capacity predicts variation in field locomotor behaviour among lizard species. *Animal Behaviour* **58**, 77–83.
- Garland, T. & Losos, J.B. (1994) Ecological morphology of locomotor performance in squamate reptiles. *Ecological Morphology: Integrative Organismal Biology* (eds P.C. Wainwright & S.M. Reilly), pp. 240–302. University of Chicago Press, Chicago, IL.
- Hamley, T. (1990) Functions of the tail in bipedal locomotion of lizards, dinosaurs and pterosaurs. *Memoirs of the Queensland Museum* **28**, 153–158.
- Hertz, P.E., Huey, R.B. & Nevo, E. (1983) Homage to Santa Anita: thermal sensitivity of sprint speed in agamid lizards. *Evolution* **37**, 1075–1084.
- Huey, R.B., Bennett, A.F., John-Alder, H. & Nagy, K. (1984) Locomotor capacity and foraging behaviour of Kalahari lacertid lizards. *Animal Behaviour* **32**, 41–50.
- Huey, R.B., Dunham, A.E., Overall, K.L. & Newman, R.A. (1990) Variation in locomotor performance in demographically known populations of the lizard *Sceloporus merriami*. *Physiological Zoology* **63**, 845–872.
- Jones, S.M. & Swain, R. (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.
- Kaiser, B.W. & Mushinsky, H.R. (1994) Tail loss and dominance in captive adult male *Anolis sagrei*. *Journal of Herpetology* **28**, 342–346.
- Klawinski, P.D. & Formanowicz, D.R. (1994) Ontogenetic change in survival value of leg autotomy in a wolf spider, *Gladicosa pulchra* (Keyserling) (Araneae: Lycosidae), during scorpion attacks. *Canadian Journal of Zoology* **72**, 2133–2135.
- Martin, J. & Avery, R.A. (1997) Tail loss affects prey capture 'decisions' in the lizard *Psammodromus algirus*. *Journal of Herpetology* **31**, 292–295.
- Martin, J. & Avery, R.A. (1998) Effects of tail loss on the movement patterns of the lizard, *Psammodromus algirus*. *Functional Ecology* **12**, 794–802.
- Martin, J. & Salvador, A. (1992) Tail loss consequences on habitat use by the Iberian rock lizard, *Lacerta monticola*. *Oikos* **65**, 328–333.
- Martin, J. & Salvador, A. (1993a) Tail loss reduces mating success in the Iberian rock-lizard. *Behavioral Ecology and Sociobiology* **32**, 185–189.
- Martin, J. & Salvador, A. (1993b) Tail loss and foraging tactics of the Iberian rock-lizard, *Lacerta monticola*. *Oikos* **66**, 318–324.
- Martin, J. & Salvador, A. (1995) Effects of tail loss on activity patterns of rock-lizards, *Lacerta monticola*. *Copeia* **1995**, 984–988.
- Martin, J. & Salvador, A. (1997) The effects of tail loss on the time-budgets, movements and spacing patterns of Iberian rock lizards, *Lacerta monticola*. *Herpetologica* **53**, 117–125.
- McCoull, C.J. (2001) *Geographic variation and adaptation in the Metallic Skink Niveoscincus metallicus*. PhD Thesis, University of Tasmania, Australia.
- Melville, J. & Swain, R. (1999) Habitat associations and natural history of the Tasmanian 'snow skink' (*Niveoscincus* spp.). *Papers and Proceedings of the Royal Society of Tasmania* **133**, 57–64.
- Melville, J. & Swain, R. (2000) Evolutionary relationships between morphology, performance and habitat openness

- in the lizard genus *Niveoscincus* (Scincidae: Lygosominae). *Biological Journal of the Linnean Society* **70**, 667–683.
- Niewiarowski, P.H., Congdon, J.D., Dunham, A.E., Vitt, L.J. & Tinkle, D.W. (1997) Tales of lizard tails: effects of tail autotomy on subsequent survival and growth rates of free-ranging hatchling *Uta stansburiana*. *Canadian Journal of Zoology* **75**, 542–548.
- Olsson, M., Shine, R. & Bak-Olsson, E. (2000) Locomotor impairment of gravid lizards: is the burden physical or physiological? *Journal of Evolutionary Biology* **13**, 263–268.
- Pomory, C.M. & Lares, M.T. (2000) Rate of regeneration of two arms in the field and its effect of body components in *Luidia clathrata* (Echinodermata: Asteroidea). *Journal of Experimental Marine Biology and Ecology* **254**, 211–220.
- Punzo, F. (1982) Tail autotomy and running speed in the lizards *Cophosaurus texanus* and *Uma notata*. *Journal of Herpetology* **16**, 329–331.
- Robinson, J.V., Hayworth, D.A. & Harvey, M.B. (1991) The effect of caudal lamellae loss on swimming speed of the damselfly *Argia moesta* (Hagen) (Odonata: Coenagrionidae). *American Midland Naturalist* **125**, 240–244.
- Robinson, M.H., Abele, L.G. & Robinson, B. (1970) Attack autotomy: a defense against predators. *Science* **169**, 301–302.
- Robson, M.A. & Miles, D.B. (2000) Locomotor performance and dominance in male Tree Lizards, *Urosaurus ornatus*. *Functional Ecology* **14**, 338–344.
- Roth, V.D. & Roth, B.M. (1984) A review of appendectomy in spiders and other arachnids. *Bulletin of the British Arachnological Society* **6**, 137–146.
- Russell, A.P. & Bauer, A.M. (1992) The *m. caudifemoralis longus* and its relationship to caudal autotomy and locomotion in lizards (Reptilia: Sauria). *Journal of Zoology* **227**, 127–143.
- Russell, A.P., Bergman, P.J. & Barbadillo, A.J. (2001) Maximal caudal autotomy in *Podarcis hispanica* (Lacertidae): the caudofemoralis is not surrendered. *Copeia* **2001**, 154–163.
- Salvador, A., Martin, J. & Lopez, P. (1995) Tail loss reduces home range size and access to females in male lizards, *Psammotromus algirus*. *Behavioural Ecology* **6**, 382–387.
- Semlitsch, R.D. (1990) Effects of body size, sibship, and tail injury on the susceptibility of tadpoles to dragonfly predation. *Canadian Journal of Zoology* **68**, 1027–1030.
- Shine, R. (1980) 'Costs' of reproduction in reptiles. *Oecologia* **46**, 92–100.
- Smith, G.R. (1996) Tail loss in the striped plateau lizard, *Sceloporus virgatus*. *Journal of Herpetology* **30**, 552–555.
- Smith, L.D. (1995) Effects of limb autotomy and tethering on juvenile blue crab survival from cannibalism. *Marine Ecology Progress Series* **116**, 65–74.
- Smyth, M. (1974) Changes in the fat stores of the skinks *Morethia boulengeri* and *Hemiergis peronii* (Lacertilia). *Australian Journal of Zoology* **22**, 135–145.
- Stasek, R. (1967) Autotomy in the mollusca. *Occasional Papers of the Californian Academy of Sciences* **61**, 1–44.
- Stoks, R. (1999a) Autotomy shapes the trade-off between seeking cover and foraging in larval damselflies. *Behavioral Ecology and Sociobiology* **47**, 70–75.
- Stoks, R. (1999b) The effect of lamellae autotomy and sexual size dimorphism on startle-response performance in larvae of a lested damselfly (Odonata). *Journal of Zoology* **247**, 269–273.
- Stoks, R. (2001) Food stress and predator-induced stress shape developmental performance in a damselfly. *Oecologia* **127**, 222–229.
- Swain, R. & Jones, S.M. (1994) Annual cycle of plasma testosterone and other reproductive parameters in the Tasmanian skink, *Niveoscincus metallicus*. *Herpetologica* **50**, 502–509.
- Swain, R. & Jones, S.M. (2000) Maternal effects associated with gestation conditions in a viviparous lizard, *Niveoscincus metallicus*. *Herpetological Monographs* **14**, 432–440.
- Van Damme, R., Aerts, P. & Vanhooydonck, B. (1998) Variation in morphology, gait characteristics and speed of locomotion in two populations of lizards. *Biological Journal of the Linnean Society* **63**, 409–427.
- Wake, D.B. & Dresner, I.G. (1967) Functional morphology and evolution of tail autotomy in salamanders. *Journal of Morphology* **122**, 265–306.
- Wapstra, E. & O'Reilly, J.M. (2001) Potential 'costs of reproduction' in a skink: inter- and intrapopulation variation. *Austral Ecology* **26**, 179–186.
- Willis, L., Threkeld, S.T. & Carpenter, C.C. (1982) Tail loss patterns *Thamnophis* (Reptilia: Colubridae) and the probable fate of injured individuals. *Copeia* **1982**, 98–101.
- Wilson, B.S. (1992) Tail injuries increase the risk of mortality in free-living lizards (*Uta stansburiana*). *Oecologia* **92**, 145–152.
- Wilson, R.S. & Booth, D.T. (1998) Effect of tail loss on reproductive output and its ecological significance in the skink *Eulamprus quoyii*. *Journal of Herpetology* **32**, 128–131.

Received 26 September 2001; revised 3 May 2002; accepted 22 May 2002