

Caudal autotomy does not influence thermoregulatory characteristics in the metallic skink, *Niveoscincus metallicus*

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Many species of lizard implement the strategy of tail autotomy as a means to escape from predators (Arnold, 1984, 1988). However, although caudal autotomy may facilitate escape from a potential predator, it may result in longer-term costs (Arnold, 1984, 1988). Following tail autotomy lizards may exhibit reduced levels of reproductive investment (Smyth, 1974; Dial and Fitzpatrick, 1981; Wilson and Booth, 1998), inhibited locomotor performance (Martin and Avery, 1998; Downes and Shine, 2001), restricted growth rates (Smith, 1996), diminished escape capabilities (Congdon et al., 1974; Downes and Shine, 2001), modified habitat use (Martin and Salvador, 1992, 1995), lowered social status (Fox and Rostker, 1982), and reduced survival in natural populations (Wilson, 1992; Fox and McCoy, 2000). However, tail autotomy does not invariably result in adverse consequences being inflicted upon the lizard. Several studies have reported tail loss to have no impact upon survival (Althoff and Thompson, 1994; Niewiarowski et al., 1997 [in some seasons]) or growth (Althoff and Thompson, 1994; Van Sluys, 1998; Fox and McCoy, 2000).

However, the impact of tail autotomy on the thermoregulatory characteristics or behaviour in lizards is poorly understood (Martin and Salvador, 1993; Wilson, 1994). The absence of the tail itself has the potential to modify the heat balance of the lizard through the alteration of its shape and surface area to volume ratio. More importantly, the reduction in activity levels (Formanowicz et al., 1990) and shifts in habitat use (Martin and Salvador, 1992, 1995, 1997; Downes and Shine, 2001) exhibited by several species following tail loss may reduce their basking opportunities or expose them to suboptimal basking environments. Consequently, tail loss has the potential to influence or inhibit thermoregulation in lizards. Such alteration in thermoregulatory characteristics or behaviour as a consequence of tail autotomy may also influence the speed with which an individual can re-grow its tail since the process of tail regeneration is sensitive to both temperature and photoperiod (Turner and Tipton, 1972; Bellairs and Bryant, 1985; Ndukuba and Ramachandran, 1988). Higher body temperatures are generally more conducive to faster rates of tail regeneration (Bellairs and Bryant, 1985). Increasing the mean body temperature, spending less time at cooler temperatures, or elevating the thermal setpoints are all ways to maintain high body temperature and therefore represent potential mechanisms through which tailless lizards

might enhance the rate of tail regeneration. However, simply maintaining normal thermal preferences during tail regeneration, whilst activity and habitat use is restricted (e.g. Formanowicz et al., 1990; Martin and Salvador, 1992, 1995, 1997), may also facilitate rapid tail replacement.

We investigated the effect of tail loss on the thermoregulatory characteristics of the metallic skink, *Niveoscincus metallicus*. Most natural populations of *N. metallicus* exhibit high frequencies of tail loss (60-80%; our unpublished data) and tail autotomy in this species has been demonstrated to impose energetic, reproductive and locomotor performance costs (Chapple and Swain 2002a, b; Chapple et al., 2002). Locomotor performance costs, at least, appear to be temporary and related to tail length in *N. metallicus* (Chapple and Swain, 2002b), therefore providing a meaningful opportunity to examine the effect of tail loss on thermoregulation. The potential alteration of thermoregulatory characteristics following tail loss (i.e. selecting different temperatures, altering thermal setpoints) was examined. Since almost all adult females of this species breed each year and are pregnant for most of the activity season at our study site (4 out of 6 months), we limited our study to male *N. metallicus* to avoid any confounding effects associated with pregnancy.

Study species and collection of animals. *Niveoscincus metallicus* is a small skink (45-65 mm adult snout-vent length; SVL) that is widely distributed over a range of habitats from sea level to sub alpine regions (1400 m) in Tasmania and southeast Victoria, Australia (Melville and Swain, 1999). It is a relatively cryptic species that occupies shaded microhabitats with medium to dense vegetation cover and thick litter (Melville and Swain, 1999). Predominantly a shuttling heliotherm with an active diurnal pattern, *N. metallicus* utilizes both rocks and logs close to the ground to behaviourally thermoregulate (Melville and Swain, 1997).

We collected 14 adult male lizards (i.e. SVL > 45 mm SVL; Swain and Jones, 1994) from around Clarence Lagoon (1000 m a.s.l.; 42°04'S 146°19'E), a small glacial lake on the Central Plateau of Tasmania, Australia, during late September and early October 1999. Lizards were captured by hand or noose and transported back to the laboratory where measurements (± 0.1 mm) were taken of SVL and tail length. All animals had original or completely regenerated tails. Animals were randomly assigned to one of two groups: control ($n = 6$) and experimental ($n = 8$). Initial body size (SVL $\pm s_{\bar{x}}$; mm) did not differ between lizards assigned to each tail loss treatment (Control Males: 54.0 ± 0.77 ; Experimental Males: 54.4 ± 0.80).

Housing conditions. Lizards were housed in an air-conditioned room maintained at 12-14°C under bright fluorescent tube lighting ($\sim 20\,000$ lux) and UV lighting (14L:10D). They were housed in plastic terraria (20 × 30 × 10 cm) lined with an absorbent substrate. 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 that provided 10 h of heat/light per day. A thermal gradient from 33°C at the basking site to ~ 14 °C in the remainder of each terrarium allowed the lizards to thermoregulate while the basking light was activated. Animals were fed 2-3 times weekly on a diet of mealworms (*Tenebrio* larvae), commercial catfood and mashed banana. Water was available ad libitum.

Experimental design. The thermoregulatory characteristics of each lizard were assessed upon arrival in the laboratory. Caudal autotomy was induced in the experimental animals within five days of the initial test and all lizards were re-tested within one week of this manipulation. The thermoregulatory characteristics of every individual were subsequently re-tested after four and twelve weeks. The length of tail regrowth (± 0.1 mm) for each experimental lizard was measured, using callipers, at each testing period. Consequently, the thermal preferences of lizards were assessed for the first three months of tail regeneration.

Tail autotomy was induced as described in Chapple and Swain (2002b). Visible tail regeneration was evident following a 'latent period' (e.g. Bellairs and Bryant, 1985) of 2-3 weeks. Control animals were handled in an identical manner to the experimental animals except that caudal autotomy was not induced.

A large wooden, open-topped terrarium ($1.2 \times 1.2 \times 0.3$ m) located in an air-conditioned room (ambient temperature $12\text{--}14^\circ\text{C}$) was used as the test arena during the study. The test arena was subdivided into eight separate sections (0.55×0.3 m) by wooden partitions, allowing up to eight lizards to be tested simultaneously each day. However, only one lizard was placed into each of the eight sections to avoid any possibility of social interactions influencing the thermoregulatory characteristics. A 3 cm layer of sand acted as the substrate. Basking sites (ceramic tiles) positioned on wooden blocks positioned under a heat source (25 W light bulb) were set-up in each of the eight sections. The set-up provided a temperature gradient of 15 to 38°C within each section allowing behavioural thermoregulation to occur. This temperature gradient encompassed the normal body temperature range of *N. metallicus* in the field (Melville and Swain, 1997; McCoull, 2001). The body temperature of lizards was recorded throughout the daily activity period (9am–5pm). Small temperature probes (0.5 mm diameter) were inserted into the cloaca and securely held in position with a strip of adhesive cloth tape around the tail. Each probe was connected to a data logger by a 1.5 m lead that allowed uninhibited movement around the arena, permitting shuttling heliothermy. The data logger was linked to a Macintosh computer that was programmed to record the body temperature of up to eight lizards simultaneously at five-minute intervals over the activity period (~ 100 data points per animal). Although up to eight lizards were tested on a given day, each lizard was tested individually in one of the eight partitioned sections of the test arena. Animals were familiarized with the testing arena with cloacal probes in place approximately half an hour prior to the commencement of each trial. Due to the potential effect of recent food intake on body temperature (e.g. Witten and Heatwole, 1978), animals were not fed during the 24 h prior to their trial. However, water was available ad libitum at all times.

For each animal the overall mean body temperature (average of the ~ 100 T_b measurements over the entire activity period), mean upper and lower basking setpoints (average T_b at which each basking event was initiated and ceased; see Tosini and Avery, 1993), and proportion of time (~ 100 T_b measurements) spent at low ($< 25^\circ\text{C}$) temperatures was recorded. Repeated measures ANOVA was used to determine the effect of tail autotomy on each thermoregulatory characteristic of *N. metallicus* (tail condition as the factor and time as the repeated measure). The pre-autotomy testing period and the three post-autotomy testing periods were included in each analysis to determine whether the thermoregulatory characteristics of experimental (tailless) lizards differed significantly through time, as a result of autotomy and/or tail regeneration, compared to the control group.

Caudal autotomy did not significantly affect any of the thermoregulatory characteristics that were tested in male *Niveoscincus metallicus* (table 1), although experimental animals did appear to have re-grown substantial portions of their tail during the 12-week study, most having tails approximately half their original length at the completion of the study ($48.1 \pm 1.81\%$). Both mean body temperature and the lower setpoint varied significantly between testing periods, possibly due to seasonal fluctuations in thermoregulatory characteristics and behaviour previously demonstrated in this species (McCoull, 2001). However, these two thermoregulatory traits fluctuated in a similar manner in both control and tailless lizards (table 1). Tailless lizards maintained similar thermal setpoints to tailed individuals over the entire 12 weeks of the study (table 1). Following autotomy, *N. metallicus* did not modify the time spent at low body temperatures (table 1). Tail loss therefore does not appear to influence the thermoregulatory characteristics of *N. metallicus*.

Niveoscincus metallicus was not observed to alter any of the measured thermoregulatory characteristics as a result of tail autotomy. However, more importantly, lizards did not lower their thermal preferences following tail autotomy, which would have been detrimental to their rate of tail regeneration. Although our sample size is relatively small, our data clearly indicate that tailless *N. metallicus* maintain similar thermoregulatory characteristics to that of tailed individuals immediately following tail autotomy and throughout the first three months of tail regeneration (table 1). Despite our sample size, we found

Table 1. Thermoregulatory characteristics of control and experimental (tailless) male *Niveoscincus metallicus* during the 12 weeks of the study. Thermal characteristics prior to tail loss (initial) and during tail regeneration (1, 4, 12 weeks) are indicated. Mean thermal setpoints (SP; upper and lower) and mean body temperature (T_b) are presented as $^{\circ}\text{C} \pm s_{\bar{x}}$. The percentage of time ($\%$ $\pm s_{\bar{x}}$) spent at low ($<25^{\circ}\text{C}$) temperatures is also indicated. The results of the Repeated Measures ANOVA are presented. Asterisks indicate significance at ** $P < 0.01$, *** $P < 0.001$.

Trait	Treatment	Testing Occasion				ANOVA		
		Initial	1 week	4 weeks	12 weeks	Tail Loss	Time	Interaction
Upper SP	Control ($n = 6$)	34.7 \pm 0.7	35.2 \pm 0.4	35.3 \pm 0.9	35.7 \pm 0.3	$F_{1,12} = 0.54$	$F_{3,36} = 1.08$	$F_{3,36} = 0.54$
	Tailless ($n = 8$)	34.4 \pm 0.5	35.1 \pm 0.5	34.9 \pm 0.7	34.7 \pm 0.3			
Lower SP	Control ($n = 6$)	22.8 \pm 0.5	25.1 \pm 0.8	25.6 \pm 0.2	28.1 \pm 0.4	$F_{1,12} = 0.13$	$F_{3,36} = 32.92^{***}$	$F_{3,36} = 1.01$
	Tailless ($n = 8$)	23.7 \pm 0.7	24.6 \pm 0.3	24.9 \pm 0.5	27.8 \pm 0.2			
Mean T_b	Control ($n = 6$)	30.1 \pm 1.2	30.3 \pm 0.7	30.7 \pm 0.7	31.9 \pm 0.4	$F_{1,12} = 0.50$	$F_{3,36} = 4.64^{**}$	$F_{3,36} = 0.58$
	Tailless ($n = 8$)	29.3 \pm 0.7	30.6 \pm 0.5	29.9 \pm 0.7	31.2 \pm 0.2			
<25°C	Control ($n = 6$)	15.3 \pm 8.0	12.7 \pm 4.4	11.2 \pm 3.0	5.7 \pm 1.4	$F_{1,12} = 0.16$	$F_{3,36} = 2.80$	$F_{3,36} = 0.34$
	Tailless ($n = 8$)	19.5 \pm 4.7	10.0 \pm 1.7	11.7 \pm 2.5	8.3 \pm 1.1			

mean body temperature and lower thermal setpoints to fluctuate in a similar manner in both the control and experimental between testing periods. Such temporal fluctuation may have been the result of lizards changing their thermal preferences as a result of prolonged captivity or simply seasonal variation in thermoregulatory characteristics, as has previously been demonstrated for this species (McCoull, 2001). However, this temporal fluctuation highlights the need to compare changes in thermoregulatory preferences in tailless *N. metallicus* to that in the control group in order to fully gauge the impact of caudal autotomy on thermoregulatory characteristics.

Although thermoregulatory behaviour was not directly measured in our study, the thermoregulatory characteristics of tailed and tailless lizards enable some inference to be made concerning the thermoregulatory behaviour of lizards following autotomy. Previous studies that have examined the effect of caudal autotomy on thermoregulatory behaviour of lizards have produced some conflicting results; however, each has shown that tailed and tailless lizards are able to maintain similar body temperatures. Wilson (1994) found that the water skink (*Eulamprus quoyii*) did not alter its preferred body temperature or thermoregulatory precision following tail loss or during tail regeneration. Furthermore, both preferred body temperature and thermoregulatory precision were similar in tailed and tailless lizards. In contrast, Martin and Salvador (1993) reported that the Iberian rock lizard (*Lacerta monticola*) did modify aspects of its thermoregulatory behaviour following tail loss. Tailless *L. monticola* were found to increase the maximal duration of basking events, maintain lower body temperatures in the morning, and select rockier basking sites that were closer to a refuge. Increasing the maximal duration of basking events and the maintenance of lower morning body temperatures appears to have allowed tailless *L. monticola* to achieve the same thermoregulatory precision, albeit through subtle modification of thermal preferences, as tailed lizards (Martin and Salvador, 1993). This presumably enabled tailless *L. monticola* to maintain body temperatures conducive to tail regeneration despite their reduced locomotor performance and modified habitat use (Martin and Salvador, 1992, 1993, 1995, 1997). Consequently, this study and the other studies to date on the influence of caudal autotomy on thermoregulation have indicated that tailless lizards maintain similar thermoregulatory precision to that of tailed lizards. However, what consequences are the thermal preferences of tailless *N. metallicus* likely to have on the rate of tail regeneration and duration of costs experienced in this species?

Once a lizard has shed its tail it is unable to employ the strategy of caudal autotomy again until it has sufficiently re-grown its tail (Arnold, 1984, 1988). This is because both the length and movement of the shed tail determine the effectiveness of caudal autotomy as an escape strategy (Congdon et al., 1974; Dial and Fitzpatrick, 1983, 1984; Daniels et al., 1986; Downes and Shine, 2001). The extremely high incidence of tail autotomy in most natural populations of *N. metallicus* (60-80%; our unpublished data), suggests that tail loss is an extremely effective defensive strategy for this species. Given that many (but not all) lizard species experience restricted growth rates (Ballinger and Tinkle, 1979; Smith, 1996) and reduced survival (Wilson, 1992; Fox and McCoy, 2000) following caudal

autotomy, tailless lizards are exposed to many dangers until they are able to replace the tail. Indeed, tail loss in *N. metallicus* may reduce energetic reserves (Chapple and Swain, 2002a), decrease reproductive output (lower litter size; Chapple et al., 2002) and reduce locomotor performance (Chapple and Swain, 2002b), and consequently has the potential to significantly decrease fitness. Thus, rapid regeneration of the tail may be vitally important in *N. metallicus*.

Recent evidence indicates that the costs of caudal autotomy are only incurred until a certain proportion of the tail (~half) has been regenerated. Downes and Shine (2001) demonstrated that garden skinks (*Lampropholis guichenoti*) that experienced an initial reduction in sprint speed following autotomy regained their normal sprint performance once they had regenerated about half of their tail (~6 weeks). Similarly, tailless *N. metallicus* regain their locomotor performance once they have replaced about half of their tail, which takes approximately 6-12 weeks (Chapple and Swain, 2002b). *Niveoscincus metallicus* is capable of completely regenerating the tail within 3-5 months, whilst maintaining the thermal preferences presented in this study (Chapple and Swain, 2002b; our unpublished data). It is unknown whether increasing any aspect of thermoregulatory behaviour would significantly increase the rate of tail regeneration in *N. metallicus*. However, given that a large proportion of *N. metallicus* in natural populations have tails that have been substantially regenerated following previous tail loss events (Chapple et al., 2002a), it appears that this species is capable of enduring the short-term costs of autotomy until it is able to sufficiently replace its tail without the need to alter its thermoregulatory characteristics to assist the regeneration of the tail.

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Communal nesting of *Psammodromus algirus* (Linnaeus, 1758), under extreme environmental conditions

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On 9 July 2000, among the rear dunes of Lariño beach (Muros, A Coruña province, N Spain; 9°8'W-42°47'N, 5 m asl), a lizard nest containing 32 eggs was found. The nest, hidden beneath a stone, 60 × 45 cm in size, in loose siliceous sand with very little organic matter, averaged 4 cm in depth. All eggs were together but formed two sets of different size. The smaller eggs measured (mean ± one standard deviation): 12.9 mm ± 0.5 mm long (range 11.9-13.8 mm; $n = 18$) and 7.9 ± 0.3 mm wide (range 7.5-8.6 mm; $n = 18$). The larger eggs measured 13.8 ± 0.3 mm in length (range 13.6-14.0 mm; $n = 14$) and 10.6 ± 0.4 mm in width (range 10.0-11.5 mm; $n = 14$). The two sets attained significantly different sizes (unpaired t -test, $t = 5.20$ for the length of the eggs, $t = 17.28$ for the width of the eggs; $df = 30$ and $p < 0.001$ in both comparisons). These results suggest two sets to correspond to two different incubation stages (therefore to different laying dates), the smaller ones apparently corresponding to more recent clutches, and the larger ones apparently corresponding at a more advanced incubation stage (especially because of their larger width). The eggs were removed from the wild and young of *Psammodromus algirus* hatched under laboratory conditions, after 31-33 days for the larger eggs, and 52-59 days for the smaller ones. Newborns were released in the wild close to the nest.

On 16 July 2002, on the southern slope of Sierra Elvira (Atarfe, Granada province, S Spain, 3°42'W-37°14'N, 650 m a.s.l.), a lizard nest containing 42 eggs was found buried in