Tail loss reduces locomotor ability but not metabolic rate in a viviparous skink, *Sphenomorphus indicus*

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Abstract

Tail autotomy is an efficient predator escape form, but imposes locomotor costs in many lizard species. It has been hypothesized that locomotor impairment following tail autotomy results from the altered running dynamics or loss of energy available for locomotion, but there is a paucity of data available to demonstrate such effects. We evaluated the locomotor costs of tail loss in a viviparous skink, *Sphenomorphus indicus*, and examined whether locomotor costs were related to changes in gait characteristics and metabolic rate. Of 24 field-captured adult males with original intact tails, 12 individuals were used as experimental animals, and the remaining 12 as controls. Locomotor performance and CO_2 production were measured for the experimental skinks before and after tail removal; the same parameters were measured at the same time for the control skinks. Compared with tailed skinks, the mean locomotor speed and stamina of tailless skinks was reduced by approximately 26% and 17%, respectively. At any given speed, tailless skinks had a shorter stride length for hindlimbs (but not for forelimbs) and a greater stride frequency than did tailed skinks. In *S. indicus*, locomotor impairment may be a result of the reduced stride length, and energetic constraints on stride frequency. We found no significant change in standard metabolic rate after the skinks underwent tail removal, which may reflect a minor effect on energy expenditure for maintenance. Although the reduction in metabolically active tissue might cause a lower metabolic rate, tail regeneration counteracted such an effect because it was energetically expensive.

Keywords

Locomotor performance; metabolic rate; *Sphenomorphus indicus*; stride length; tail autotomy

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Introduction

Tail autotomy is used by a diverse range of lizards (Arnold, 1984) and salamanders (Wake & Dresner, 1967) to avoid potentially fatal attacks from predators. The autotomized tails often thrash vigorously for a prolonged period of time to distract a predator, thereby facilitating the animal's escape (Clause & Capaldi, 2006; Higham & Russell, 2012). While tail autotomy potentially increases an animal's survival probability, it entails several costs that may reduce the animal's subsequent fitness. Of the costs associated with tail autotomy, changes in locomotor performance have received the most attention. Tail autotomy in most species of lizards has been demonstrated to have negative impacts on several aspects of locomotor performance, such as speed, stamina, agility, climbing and jumping ability (e.g., Lin et al., 2006; Jusufi et al., 2008; Bateman & Fleming, 2009; Gillis et al., 2009). However, the locomotor costs of tail autotomy vary among species and between sexes (Chapple & Swain, 2002a; Clause & Capaldi, 2006; Bateman & Fleming, 2009). For example, tail loss can significantly impair a variety of locomotor performances including speed, stamina and climbing ability in *Niveoscincus metallicus* (Chapple & Swain, 2002a), but only reduces the swimming ability in *Eulamprus quoyii* (Daniels, 1985), and the climbing ability in *Podarcis muralis* (Brown et al., 1995).

The impairment of locomotor ability after tail loss may be the result of altered running dynamics or a loss of the energy available to support locomotion (Clause & Capaldi, 2006). During terrestrial locomotion, lateral bending of the trunk and tail helps to increase stride length (Ritter, 1992). Animals can also use harmonic motion of the tail to aid femoral retraction, and regulate stride frequency by adjusting the frequency of tail oscillation (Hamley, 1990). In lizards, the changes in stride length and stride frequency often occur after tail autotomy. For example, tail loss substantially reduces locomotor speed and stride length, but increases stride frequency in *Psammodromus algirus* (Martin & Avery, 1998). The reduction in locomotor stamina is hypothesized to be caused by the increase in stride frequency in *N. metallicus* (Chapple & Swain, 2002a), or to be linked to the decrease in active metabolic rate in *Lygodactylus capensis* (Fleming et al., 2009). However, those studies involved only a few species of lizards; more data from a number of different species are needed to draw general conclusions.

In most cases, tail autotomy is followed by regeneration, which may be relatively effective in countering the costs of tail loss. However, this process is energetically expensive and may, therefore, result in a reallocation of energetic resources (Congdon et al., 1974; Chapple & Swain, 2002b). Within an individual, available energy must be partitioned between maintenance, growth and reproduction. In order to fuel tail regeneration, tailless individuals may reduce the energetic cost of maintenance or divert energetic resources from other functions such as somatic growth and reproduction, which increase respiratory metabolism (Bellairs & Bryant, 1985; Clause & Capaldi, 2006). However, caudal lipid reserves represent the major site of energy storage in many species of lizards (Chapple & Swain, 2002b; Lin et al.,

2006; Sun et al., 2007). Tail loss may cause a substantial decrease in metabolically active tissue, thus reducing metabolic rate. The changes in overall metabolic rate after tail autotomy may be determined by the balance between the amount of tissue loss and the energy required for regeneration. The metabolic cost of tail autotomy has only been examined in a few species of lizards, and the results varied among studies (Congdon et al., 1974; Naya & Božinović, 2006; Naya et al., 2007).

Tail autotomy is very common among scincid lizards. For example, 67% of *Lampropholis guichenoti* (Downes & Shine, 2001), 78% of *N. metallicus* (Chapple & Swain, 2002b), 73% of *Plestiodon* (*Eumeces*) *chinensis* (Lin et al., 2006) and 57% of *Eutropis* (*Mabuya*) *multifasciata* (Sun et al., 2009) in natural populations have evidence of previous tail autotomy. In these species, the tail is an important organ for energy storage and locomotion, and autotomy will incur substantial energetic and locomotor costs (Chapple & Swain, 2002a, b; Shine, 2003; Lin et al., 2006; Sun et al., 2009; Cromie & Chapple, 2012). However, there has been no examination of whether the impaired locomotor performance after tail loss is related to changes in running dynamics or metabolic rate. In this study, we investigated the impact of tail loss on locomotor performance and standard metabolic rate (SMR) in a viviparous skink, *Sphenomorphus indicus*. This skink is widely distributed in the southern part of China, India (Darjeeling & Sikkim), Indochina and the Malay Peninsula. A previous study has shown that, in the Hangzhou population (30°16′N, 120°12′E, Zhejiang, eastern China) of *S. indicus*, 77% of adults have signs of tail loss, with 55% of tail breaks occurring in the proximal portion of the tail, and nearly 35% of the total lipids are stored in the tail (Sun et al., 2007). Given that the locomotor speed and stamina of tailless *S. indicus* is reduced, we predicted a change in gait characteristics and SMR. Our study aims were to: (1) assess the locomotor and metabolic costs of tail loss in *S. indicus*; (2) evaluate the potential effects of changes in running dynamics and energy allocation on locomotor performance; and (3) compare our data with those reported for other lizard species.

Materials and methods

Experimental design

In early April 2011, 24 adult males with original intact tails were collected from the suburb of Hangzhou and transferred to our laboratory. Each individual was measured for body mass, snout-vent length (SVL) and tail length, and marked by a non-toxic waterproof label for future identification. Prior to collection of data, all individuals were maintained in one of four cages (60 cm × 30 cm × 30 cm) that contained a substrate of sand (10 cm in depth), with rocks and pieces of clay tiles provided as the cover, for 2 weeks to let them habituate to laboratory conditions. The cages were placed in a room at an ambient temperature of 24 ± 3°C and a 12 light (L):12 dark (D) photoperiod. The skinks were fed a combination of mealworms (larvae of *Tenebrio molitor*) and house crickets (*Acheta domesticus*), and water enriched with vitamins and minerals was provided *ad libitum*.

Two weeks after arrival in the laboratory, the skinks were allocated at random to two groups (12 experimental animals and 12 control animals). There was no difference in SVL between the experimental (73.2 ± 0.5 mm) and control skinks (71.9 ± 0.9 mm) (*t*-test, $t_{22} = 1.18$, $P = 0.250$). All individuals were fasted for 2 days, and then measured for locomotor performance (sprint speed and stamina) and SMR. Next, tail autotomy was induced in experimental animals by grasping the base of the tail, approximately 2 cm from the vent, thereby producing tailless skinks. Stress and blood loss during the procedure were minimal. Tailless skinks were allowed to heal the wound for 1 week, to minimize the possible influence of handling stress. Tailless and tailed (control) skinks were then fasted again for 2 days, and measured for locomotor performance and SMR for a second time.

Measurements of locomotor performances

All measurements (locomotor performance and respiratory metabolism) were conducted in a temperature-controlled room at 28 ± 0.5°C. Prior to each measurement of locomotor performance, the skinks were kept in the room for about 2 h, then chased individually down the length of a 1.2-m racetrack and filmed simultaneously using a PCO1200 high-speed digital camera (Cooke Corporation, USA; 100 frames per second) aligned perpendicularly over the middle portion of the racetrack. Each skink was chased two or three times, with a minimum of 30 min rest between the two trials. Film clips that included two to four consecutive strides at a steady speed were examined on a frame-by-frame basis using MaxTRAQ 2D software (Innovision Systems Inc., USA). Sprint speed was taken to be the greatest running speed over a distance of 25 cm in each locomotor trial, while stride speed (forward speed of each stride) was the distance traveled divided by the time between successive footfalls of the same foot (stride duration). Stride frequency is the reciprocal of stride duration. Accounting for the differences in body size and limb length, the angle through which a fore- or hind-limb moved was used as a relative measure of stride length (Martín & Avery, 1998). Stride length and speed were measured repeatedly for each skink, with the mean value being used for statistical analyses. Locomotor stamina was measured on a TSE treadmill (TSE Systems International Group, Germany) at a speed of 22 cm/s. Skinks were introduced individually into the treadmill, and encouraged to run by tapping on the tail and hindlimbs with a paintbrush. The time it took for each skink to run until exhaustion (no longer keeping pace with the moving belt) was considered to be its locomotor stamina.

Measurement of standard metabolic rate

Carbon dioxide production (V_{CO_2}) was measured in an open-flow respirometry system (Qubit Systems, Kingston, ON, Canada) using an acrylic metabolic chamber of 220 ml. The air flow rate was set at 200 ml/min. Incoming air flowed through a decarbite (Baralyme) before entering the chamber and then through a desiccant (Drierite) after passing the chamber. The air then entered a CO_2 analyzer. Each

skink was put on its own inside the metabolic chamber 30 min before the beginning of the metabolic recording. While a skink was resting, CO_2 production was measured continuously for 30 min. Baseline measurements for each run were made using the same experimental chamber at the end of each measurement period. Each record was transformed automatically and recorded with Logger Pro 3.7 analysis software (Vernier, Inc., Beaverton, OR, USA). SMR was estimated as the average of the 3-5 min stable state of CO_2 production during periods of inactivity. To minimize the potential temporal effect on metabolism, all metabolic rates were measured between 12:00 and 15:00 h, and individuals belonging to different groups were measured sequentially.

Data analysis

All data were tested for normality using the Kolmogorov-Smirnov test, and for homogeneity of variances using Bartlett's test before statistical analysis. Locomotor speed, stamina and SMR were all independent of body size (SVL) (linear regression analysis, all $P > 0.05$), so we used repeated-measures ANOVA to analyze the corresponding data, with animal category (control and experimental skinks) as the between-subject factor and time step (measurements taken before and after tail removal) as the within-subject factor. Running speed is a result of stride length × stride frequency, so we used two-way ANCOVA with stride speed as the covariate to detect differences in stride frequency and length between the experimental and control animals, and between the two trials.

Results

Sprint speed differed significantly between the experimental and control skinks and between trials, while stamina differed only between trials. The group × time interaction exerted a significant effect on sprint speed, but not on stamina (table 1). There was a significant decline in locomotor speed after tail removal in the experimental skinks, but no change in the control skinks (fig. 1). Stamina

Table 1.
Results of repeated-measures ANOVAs on locomotor speed and stamina measured for tailed and tailless brown forest skinks, with animal category (control and experimental skinks) as the between-subject factor and time step (measurements taken before and after tail removal) as the within-subject factor.

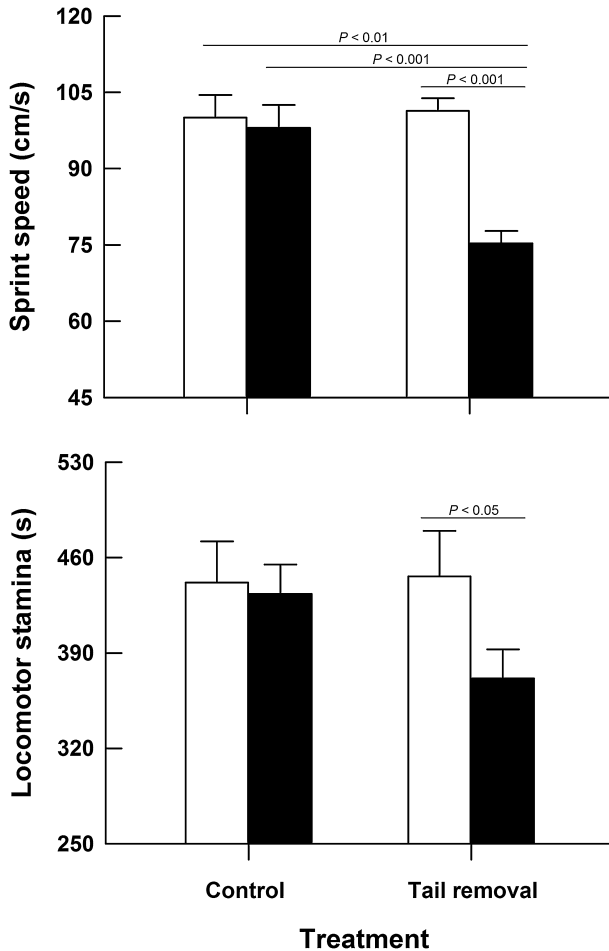| | Locomotor variables | |
	Sprint speed	Stamina
Control vs. experimental skinks	$F_{1,22} = 11.89$, $P < 0.01$	$F_{1,22} = 0.78$, $P = 0.388$
Before vs. after tail removal	$F_{1,22} = 12.07$, $P < 0.01$	$F_{1,22} = 4.32$, $P < 0.05$
Interaction	$F_{1,22} = 8.85$, $P < 0.01$	$F_{1,22} = 2.79$, $P = 0.109$

Figure 1. Mean values (+ SE) for locomotor speed and stamina of *Sphenomorphus indicus*. Open bars: measurements taken before tail removal; solid bars: measurements taken after tail removal.

was also reduced after tail removal in the experimental skinks (fig. 1). Stride frequency and relative stride length (the angle through which the limbs moved) were positively correlated with locomotor speed (linear regression analysis, stride frequency, $r^2 = 0.30$, $F_{1,46} = 19.91$, $P < 0.0001$; relative stride length for hindlimb, $r^2 = 0.27$, $F_{1,46} = 16.68$, $P < 0.001$; relative stride length for forelimb, $r^2 = 0.11$, $F_{1,46} = 5.81$, $P < 0.02$). The ANCOVA results revealed significant differences between the experimental and control skinks and between trials in relative stride length for hindlimb, but only a slight difference in stride frequency. There were no differences between the experimental and control skinks and between trials in relative stride length for forelimb. The group × time interaction had a significant effect on relative stride length for hindlimb (table 2). At any given speed, experimental skinks took shorter but more strides in the tailless condition than in the tailed

Table 2.

Results of two-way ANCOVAs on gait characteristics (relative stride length and stride frequency) for tailed and tailless brown forest skinks, with stride speed as the covariate.

	Gait characteristics		
	Relative stride length for forelimb	Relative stride length for hindlimb	Stride frequency
Control vs. experimental skinks	$F_{1,43} = 0.06$, $P = 0.800$	$F_{1,43} = 23.87$, $P < 0.001$	$F_{1,43} = 4.41$, $P = 0.042$
Before vs. after tail removal	$F_{1,43} = 0.79$, $P = 0.380$	$F_{1,43} = 7.03$, $P < 0.05$	$F_{1,43} = 3.76$, $P = 0.059$
Interaction	$F_{1,43} = 1.67$, $P = 0.203$	$F_{1,43} = 8.23$, $P < 0.01$	$F_{1,43} = 1.08$, $P = 0.304$

condition, while control skinks did not change stride length and frequency (fig. 2). There were no significant differences between the experimental and control skinks ($F_{1,22} = 0.29$, $P = 0.597$) and between trials ($F_{1,22} = 0.77$, $P = 0.391$) in standard metabolic rate (fig. 3).

Discussion

A decrease in locomotor performance after tail autotomy has been demonstrated in many lizard species. In this study, the mean sprint speed of tailless *S. indicus* was reduced by 26% compared with the mean value of tailed skinks (fig. 1). This proportion is similar to the values reported for scincid species [23% for *Plestiodon* (*Eumeces*) *fasciatus*, Goodman, 2006; 29% for *P. chinensis*, Lin et al., 2006; 31% for *Lampropholis guichenoti*, Shine, 2003; 32% for *Eutropis* (*Mabuya*) *multifasciata*, Sun et al., 2008; 35% for *Scincella lateralis* and *Niveoscincus metallicus*, Formanowicz et al., 1990; Chapple & Swain, 2002a], but lower than the values reported for teiid, phrynosomatid and lacertid species (36% for *Cnemidophorus sexlineatus*, Ballinger et al., 1979; 32% for *Cophosaurus texanus*, 42% for *Uma notata*, Punzo, 1982; 48% for *Psammodromus algirus*, Martin & Avery, 1998; 28% for *Podarcis lilfordi*, Cooper et al., 2004; 43% for *Takydromus septentrionalis*, Lin & Ji, 2005). However, not all data indicate such adverse effects. For example, tail autotomy has no effect on speed in some gekkonid species (Daniels, 1983; Kelehear & Webb, 2006; Medger, 2008; Lu et al., 2010). Such variation might be related to the difference in function of a lizard's tail during terrestrial locomotion, such as walking and running. The detrimental impact of tail autotomy on speed generally was obvious in species with functionally 'active' tails, but was not as noticeable in species with 'passive' tails (Vitt et al., 1977). Stride length was positively correlated with locomotor speed in *S. indicus*, suggesting that these skinks increase speed by increasing stride length. Tailless *S. indicus* had a shorter stride length and thus higher stride frequency compared with tailed skinks at any given speed, which
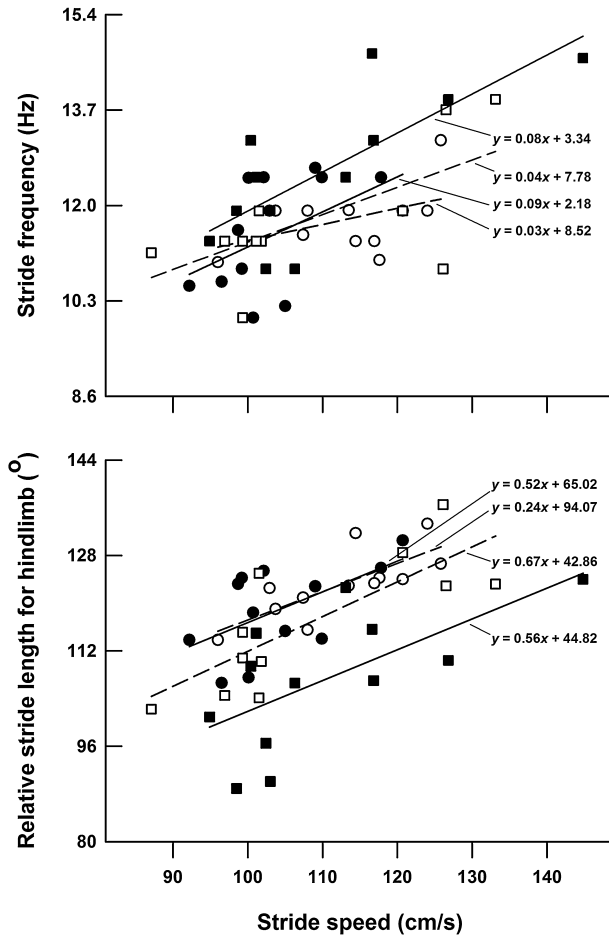
Figure 2. Linear regressions of stride frequency and length for hindlimb against stride speed in *Sphenomorphus indicus*. Open dots and dashed line: control skinks, measurements taken before tail removal; solid dots and solid line: control skinks, measurements taken after tail removal; open squares and dashed line: experimental skinks, measurements taken before tail removal; solid squares and solid line: experimental skinks, measurements taken after tail removal.

is consistent with the result from a previous study on *P. algirus* (Martin & Avery, 1998). Stride length is significantly reduced after a large portion of the tail being autotomized, and stride frequency has to increase if the lizard is to maintain the same speed. However, increasing stride frequency will directly increase the energetic cost of locomotion (Heglund & Taylor, 1988). Because of the energetic constraints, the increase in stride frequency is generally limited, and therefore, it is hard for tailless lizards to attain the same maximum speed as before tail loss. Such an explanation, however, might seem inapplicable in some gekkonid species. Tail autotomy did not cause a decrease in stride length or an increase in stride frequency in *Lygodactylus capensis* (Medger, 2008) and *Teratoscincus scincus* (Lu et al., 2010). Moreover,
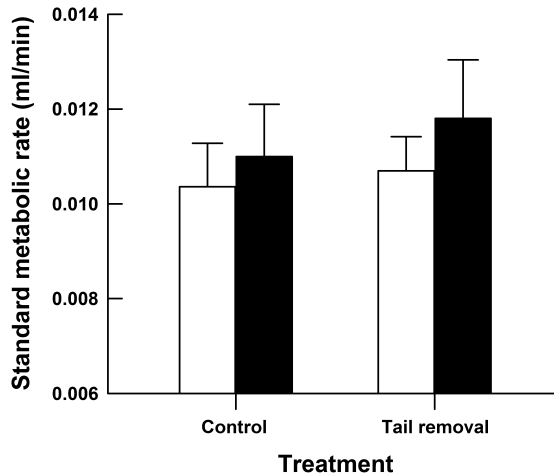
Figure 3. Mean values (+ SE) of standard metabolic rate for *Sphenomorphus indicus*. Open bars: measurements taken before tail removal; solid bars: measurements taken after tail removal.

a lizard's tail may provide momentum and balance during terrestrial locomotion (Bateman & Fleming, 2009). The potential disequilibrium caused by tail loss can also result in a lower sprint speed (Brown et al., 1995; Martin & Avery, 1998).

Tail loss caused a 17% reduction in stamina in *S. indicus*, an effect also found in *Eulamprus quoyii* (Daniels, 1985), *N. metallicus* (Chapple & Swain, 2002a), *L. capensis* (Fleming et al., 2009) and *T. scincus* (Lu et al., 2010). A decrease in locomotor stamina following tail autotomy may result from the loss of caudal lipid reserves, which might be important in providing fuels for locomotion in lizards (Fleming et al., 2009). A reduced stamina after tail autotomy might be closely linked to changes in metabolic rate. However, we found no significant difference in SMR measured in the skinks before and after tail removal (fig. 3). In fact, SMR is often measured as an indicator of the energetic cost of maintenance (Naya et al., 2007). The loss of lipid reserves may primarily reduce activity-related energy expenditure including the energy expended during exercise and recovery periods, but not significantly affect energy expenditure for maintenance. Consequently, tailless animals should exhibit a reduced active metabolic rate rather than SMR, which has been demonstrated in *L. capensis* (Fleming et al., 2009). Unfortunately, we did not measure CO_2 production or O_2 consumption during locomotion, therefore we are currently unable to test whether this interpretation applies to *S. indicus*. Moreover, Chapple & Swain (2002a) have hypothesized that the increase in stride frequency as a result of tail loss might reduce locomotor stamina in female *N. metallicus*. Our results provide an example of a similar shift in stride frequency in another scincid species and may support this idea.

Tailless *S. indicus* exhibited slightly higher metabolic rates than tailed skinks, but the difference was not significant (fig. 3). No obvious shift in O_2 consump-

tion or CO_2 production after tail autotomy has been found in two other species of lizards, *Coleonyx variegates* and *L. capensis*, nor in one species of salamander, *Oedipina uniformis* (Congdon et al., 1974; Smits & Brodie, 1995; Fleming et al., 2009). However, tail autotomy imposed a substantial increase in SMR in other species of lizards. For example, after tail autotomy, metabolic rate was increased by approximately 25% in *C. brevis*, 26% in *Liolaemus nitidus* and 36% in *L. bellii* (Dial & Fitzpatrick, 1981; Naya & Božinović, 2006; Naya et al., 2007). Tailless animals might have lower metabolic rates as a result of the loss of metabolically active tissue (Fleming et al., 2009) and a change in corticosteroid level (Miles et al., 2007). The tails of *S. indicus* represent about 24% of total body mass (Sun et al., 2007), and autotomy may cause a substantial reduction in tail musculature. However, the anticipated decrease in SMR did not occur in *S. indicus*, nor in other species of lizards and salamanders. As mentioned earlier, no change in SMR after tail autotomy may reflect a minor effect on maintenance energy expenditure. On the other hand, in most cases tail regeneration normally occurs following autotomy to counteract subsequent costs, and this process is energetically expensive (Meyer et al., 2002; Simou et al., 2008). An increase in SMRs after tail autotomy may arise from the intensive cellular and physiological activity during the tissue repair process (Bellairs & Bryant, 1985).

Acknowledgements

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