

# Many-Lined Sun Skinks (*Mabuya multifasciata*) Do not Compensate for the Costs of Tail Loss by Increasing Feeding Rate or Digestive Efficiency

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**ABSTRACT** We used the many-lined sun skink (*Mabuya multifasciata*) as a model system to evaluate the energetic and locomotor costs of tail loss, and to examine whether tailless skinks compensate for the costs of tail loss by increasing feeding rate or digestive efficiency. We successively removed three tail segments from each of the 20 experimental skinks initially having intact tails. Energy content in each removed tail segment was measured, and swimming performance was measured for each experimental skink before and after each tail-removing treatment. Another independent sample of 19 skinks with intact tails were measured for swimming performance to serve as controls for successive measurements taken for the experimental skinks. Tailless experimental skinks and control skinks were then measured for food intake and digestive efficiency. Tail loss affected swimming speed, but the adverse influence was not significant until more than 55% of the tail (in length) was lost. Our data show that partial tail loss may not severely affect energy stores or locomotor performance in *M. multifasciata*. However, as tail breaks occurred more frequently in the proximal portion of the tail in skinks collected from the field, we conclude that caudal autotomy occurring in nature often incurs substantial energetic and locomotor costs. As tailless and tailed skinks did not differ in food intake, apparent digestive coefficient and assimilation efficiency, we conclude that tailless individuals do not compensate for the costs of tail loss by increasing feeding rate or digestive efficiency in *M. multifasciata*. *J. Exp. Zool.* 311A:125–133, 2009. © 2008 Wiley-Liss, Inc.

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Most lizards use caudal autotomy as a defensive tactic to evade potentially fatal predatory encounters after other antipredation strategies such as crypsis, fight and flight have failed (Bellairs and Bryant, '85; Arnold, '88). Although offering an immediate survival benefit by facilitating escape from a predator, tail loss entails several costs subsequent to escape (Arnold, '88; Wilson, '92; Downes and Shine, 2001; Cooper, 2003). For example, tailless lizards may have reduced abilities to escape from predators (Dial and Fitzpatrick, '84; Wilson, '92; Niewiarowski et al., '97; Fox and McCoy, 2000; Lin et al., 2006), modified foraging tactics (Martin and Salvador, '93a), activity patterns (Martin and Salvador, '95; Martin and Avery, '98; Zhao et al., 2008) and

microhabitat use (Ballinger, '73; Martin and Salvador, '92), decreased home range size and access to females (Martin and Salvador, '93b; Salvador et al., '95) and diminished social status (Ruby, '81; Fox and Rostker, '82; Tokarz, '85; Fox et al., '90). Many lizards carry a substantial portion of their total energy reserves in the form of fatty tissue in the tail (Derickson, '76;

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Greer, '86; Ji and Wang, '90; Ji et al., '94; Lin and Ji, 2005). Therefore, loss of tail energy reserves makes lizards more susceptible to starvation, and in temperate regions they are less likely to survive overwinter (Avery, '70; Bauwens, '81; Daniels, '84). Moreover, the loss can slow the lizard's growth (Derickson, '74; Ballinger and Tinkle, '79; Smith, '96; Niewiarowski et al., '97; Goodman, 2006) and, in the case of females, reduce reproductive investment (Congdon et al., '74; Smyth, '74; Dial and Fitzpatrick, '81; Taylor, '86; Vitt and Cooper, '86; Wilson and Booth, '98).

Many lizards with the mechanism of caudal autotomy have evolved specialized behavioral and physiological adaptations to compensate for any negative consequences of tail loss. In most cases a successful autotomous escape is followed by regeneration of the lost tail and, in general, tail regeneration is the most effective way to counteract the costs of tail loss. Tail regeneration may be energetically expensive and may, therefore, require the division of energetic resources from other functions such as growth or reproduction (Congdon et al., '74; Ballinger and Tinkle, '79; Dial and Fitzpatrick, '81; Bellairs and Bryant, '85; Martin and Salvador, '93b). Regeneration costs may also be met by increasing food intake. In the Texas banded gecko *Coleonyx brevis*, for example, tailless individuals increase feeding rates to meet increased energetic demands during tail regeneration (Dial and Fitzpatrick, '81). However, not all lizards do the same as *C. brevis* when undergoing tail loss. For example, tailless individuals do not increase feeding rates in the Iberian rock lizard *Lacerta monticola* (Martin and Salvador, '93a) and the Mongolian racerunner *Eremias argus* (Zhao et al., 2008). This inconsistency raises a question of whether lizards always compensate for costs of tail loss by increasing feeding rate.

In this study, we used the many-lined sun skink (*Mabuya multifasciata*) as an experimental model to evaluate the costs of tail loss by examining the effects of tail loss on energy stores and locomotor performance and, more specifically, to examine whether tailless skinks compensate for any negative consequences of tail loss by increasing feeding rate or digestive efficiency. We successively removed at 3-day interval three tail segments from each experimental skink initially having an intact tail. This approach allows us to examine the distribution of caudal energy along the tail and the differences in locomotor performance among skinks that differ in tail length (TL). Furthermore, to establish whether costs associated with tail loss in *M. multifasciata* are ecologically

relevant, we determined the frequency and relative position of tail loss in the sampled population.

## MATERIALS AND METHODS

### *Study animals*

The many-lined sun skink (*M. multifasciata*) is a medium sized (to 117 mm snout–vent length, SVL; Ji et al., 2006), viviparous scincid lizard that has an exclusively tropical distribution ranging from southern China and Indo-China to India, south to Malaysia, Singapore, Indonesia, the Philippines, Indo-Australian Archipelago and New Guinea (Huang, '99). Adults are sexually dimorphic in body and head size, with males being the larger sex (Ji et al., 2006). Females larger than 90 mm SVL usually produce a single litter of 2–7 offspring per breeding season stretching from May to June, with larger females generally producing more and larger offspring than do smaller ones (Ji et al., 2007). Energy reserves in the skink are located in both the tail and abdomen (Lin et al., 2005).

We collected 244 adults (>92 mm SVL) and 18 juveniles (81–89 mm SVL) in November 2006 from a population in Ledong (18°46'N, 109°10'E), Hainan, southern China. The captured skinks were individually sexed, measured for SVL and TL, and checked for signs of previous tail loss. The location of the tail break was noted for each skink with a regenerated tail, which could be easily distinguished because of the presence of irregular scales at the site where caudal autotomy occurred. Most of these skinks were then released at their point of capture, and the remaining 39 individuals (20 ♀♀/19 ♂♂) without any previous experience of caudal autotomy were transported back to our laboratory in Hangzhou, where they were used as either experimental [10 ♀♀ (93.6–115.1 mm SVL; 143.0–183.0 mm TL)/10 ♂♂ (92.5–112.2 mm SVL; 152.0–188.0 mm TL); hereafter E0 skinks] or control [10 ♀♀ (95.1–111.5 mm SVL; 145.0–178.0 mm TL)/9 ♂♂ (94.2–117.0 mm SVL; 141.0–178.0 mm TL); hereafter C skinks] animals. The mean values for SVL and TL did not differ between the experimental and control skinks and between sexes (two-way ANOVA for SVL, and two-way ANCOVA with SVL as the covariate for TL; all  $P > 0.05$ ). The E0 and C skinks were maintained ten or nine in one of the four 0.95 m × 0.65 m × 0.5 m (length × width × height) plastic cages, which contained a substrate of soil, with rocks, pieces of clay tiles and straws provided as cover; previous research with this skink has

revealed no agonistic interactions between individuals. These cages were placed in a room at  $23 \pm 2^\circ\text{C}$ . A 100-W light bulb, suspended at one end of each cage, created a thermal gradient from the room temperature to  $55^\circ\text{C}$  for 12 hr daily. Skinks were exposed to a natural daylight cycle and some direct sunlight, and could regulate body temperature behaviorally during the photophase. Skinks were fed mealworms (larvae of *Tenebrio molitor*), house crickets (*Achetus domesticus*) and water enriched with vitamins and minerals *ad libitum* and, 2 weeks later, they were used to examine energetic and locomotor costs of tail loss and the effect of tail loss on feeding rate and digestive efficiency.

### Methods

Terrestrial racetracks were not used because *M. multifasciata* relies heavily on swimming to escape predators (Lin et al., 2008). We therefore evaluated locomotor performance by measuring swimming rather than running performance of skinks inside a  $1.2\text{ m} \times 0.5\text{ m} \times 0.4\text{ m}$  bath filled with 25 cm of water. The water temperature was maintained at  $32^\circ\text{C}$  via a water bath heater fixed to a metal stand. A WMZ-3 electronic thermometer (Shanghai Medical Instrument, China) confirmed that the water temperature did not vary more than  $0.3^\circ\text{C}$  during trials. We individually placed skinks, of which body temperatures had been controlled at the test level using an incubator, into the bath, and then gently tapped on the mid-body with a paintbrush to encourage them to swim. We filmed them with a Panasonic NV-GS408 digital video camera (Panasonic Co., Japan), and examined tapes with a computer using MGI ViedoWave III software (MGI Software Co., Canada) for swimming speed in the fastest 25-cm interval and the maximum distance traveled without stopping (hereafter maximum distance). To minimize the possible influence of diel variation in swimming performance, we began measurements on any given day at 09:00 hr (Beijing time) and ended within 2 hr.

After obtaining data on swimming performance for the E0 and C skinks, we successively removed (pinched off) at 3-day intervals three tail segments of nearly the same length (mean = 46.0 mm, range = 37.7–52.7 mm) from each E0 skink, thereby producing skinks in E1, E2 and E3 conditions, respectively. The E3 skinks had a ~31-mm (mean = 31.1 mm, range = 30–32 mm) tail stump, and none of these skinks exhibited any ill effects

from our procedures. The E1–E3 skinks were allowed to heal the wound for 3 days following each tail-removing event to minimize the possible influence of handling stress, and were thereafter measured for swimming performance following the procedures described above. The C skinks were also measured for swimming performance to serve as controls for the three subsequent measurements taken for the experimental skinks. All removed tail segments were weighed and then dried in an oven at  $65^\circ\text{C}$  until a constant mass could be obtained. Dried samples of tail segments were individually burnt in a ZWR-1 adiabatic calorimeter (Changsha Instruments, China), and data were automatically downloaded to a computer.

The E3 and C skinks were moved into a  $4\text{ m} \times 3\text{ m}$  artificial atmospheric phenomena simulator room at  $32 \pm 0.5^\circ\text{C}$  following the measurements of swimming performance. The fluorescent tubes in the room were on a 12 light: 12 dark cycles, and the photophase started at 07:00 hr. Skinks were housed individually in  $0.25\text{ m} \times 0.25\text{ m} \times 0.25\text{ m}$  glass cages. We fasted skinks at the test temperature for 3 days earlier to feeding to ensure postabsorptive conditions (Lin et al., 2008), and then fed them mealworms and provided water *ad libitum*. We collected feces and urates at least four times daily. Trials lasted for 3 weeks (between January 15 and February 6, 2007) so that sufficient feces and urates could be collected for calorimetry. At the end of the experiment the E3 skinks were remeasured for TL to determine the amount (in length) of tail regeneration accomplished along the 3-week period. Feces, urates and mealworms corresponding to each skink were dried to constant mass at  $65^\circ\text{C}$  and weighed. Dried samples were burnt in the same adiabatic calorimeter described above. The assimilation efficiency was calculated as  $\text{AE} = 100 \times (I - F - U)/I$ , where  $I$  = total energy consumed,  $F$  = energy in feces and  $U$  = energy in urates; the apparent digestive coefficient was calculated as  $\text{ADC} = 100 \times (I - F)/I$  (Xu and Ji, 2006).

### Statistical analyses

All data were tested for normality (Kolmogorov–Smirnov test) and homogeneity of variances ( $F$ -max test), and arc-sine (for ADC and AE) and  $\log_e$  (for other traits when necessary) transformations were performed to achieve the conditions for using parametric analyses. We used  $G$  test

(for the between-sex difference in the frequency distribution of locations of the tail break), one-way ANOVA (for the between-sex difference in the amount of tail regeneration), two-way ANOVA (for the variables associated with food intake and food assimilation), repeated measures ANCOVA (for dry mass and energy content of the removed tail segments, with SVL as the covariate), repeated measured ANOVA (for swimming performance) and Tukey's post hoc comparison to analyze the corresponding data. Descriptive statistics are presented as mean  $\pm$  standard error, and the significance level is set at  $\alpha = 0.05$ .

## RESULTS

### *Caudal autotomy occurring in nature*

Of the 244 adults collected from the field, 139 (~57%; 70 ♀♀ and 69 ♂♂) had autotomized some portion of the tail at least once. Nine (50%; 4 ♀♀ and 5 ♂♂) of the 18 juveniles had signs of tail loss. Tail breaks at the extreme base (<10 mm from the vent) of the tail were absent. Of the 139 adults with previous bouts of caudal autotomy, 63 (45.3%) had shed their tails in the proximal portion (<50 mm, from the vent to where the tail was autotomized) of the tail, 53 (38.1%) in the middle portion (50–100 mm) and 23 (16.5%) in the distal portion (>100 mm) (Fig. 1). The frequency distribution of locations of the tail break differed between the sexes ( $G = 26.83$ ,  $df = 15$ ,  $P < 0.05$ ), with females (54.3%) shedding tails more frequently than did males (36.2%) in the proximal portion of the tail (Fig. 1).

### *Dry materials and energy contents in the removed tail segments*

Between-sex differences in dry mass and energy content were not found in the removed tail segments (Table 1). The proximal, middle and distal portions of the removed tail differed significantly in both dry mass and energy content (Fig. 2, Table 1). The proximal tail segments contained more energy and dry materials than did the middle tail segments, whereas the middle tail segments contained more energy and dry materials than did the distal tail segments (Fig. 2). The proximal, middle and distal tail segments also differed from each other with respect to energy content per unit of tail dry mass (repeated measures ANOVA:  $F_{2,38} = 527.64$ ,  $P < 0.0001$ );

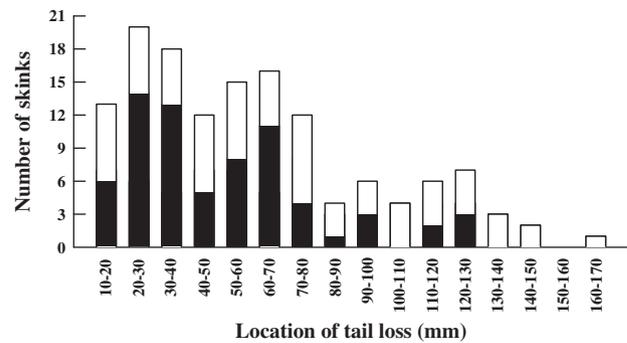


Fig. 1. The frequency distribution of locations where caudal autotomy occurred in nature. Data are based on 139 adult *Mabuaya multifasciata* collected from the field. Numbers in the horizontal axis indicate the distances from the vent. Solid bars: females ( $N = 70$ ); open bars: males ( $N = 69$ ).

TABLE 1. Results of repeated-measures ANCOVAs for dry mass and energy content of the removed tail segments, with SVL as the covariate, tail-removing order as the within-subject factor, and sex as the between-subject factor

	Dry mass	Energy content
Tail-removing order	$F_{2,36} = 338.93$ , $P < 0.0001$ ; E1 <sup>c</sup> , E2 <sup>b</sup> , E3 <sup>a</sup>	$F_{2,36} = 339.37$ , $P < 0.0001$ ; E1 <sup>c</sup> , E2 <sup>b</sup> , E3 <sup>a</sup>
Sex	$F_{1,17} = 0.92$ , $P = 0.353$	$F_{1,17} = 0.60$ , $P = 0.450$
Interaction	$F_{2,36} = 0.69$ , $P = 0.506$	$F_{2,36} = 0.03$ , $P = 0.974$

Tukey's post hoc comparisons were performed when differences in the examined variables were significant ( $a > b > c$ ). E1, E2 and E3: experiments in which the distal, middle and proximal tail segments were removed, respectively.

mass-specific energy content was greatest in the proximal portion of the tail (mean = 20.7 kJ, range = 13.9–28.0 kJ) and lowest in the distal portion (mean = 15.6 kJ, range = 11.4–24.7 kJ), with the middle portion in between (mean = 16.9 kJ, range = 12.2–25.5 kJ).

### *Locomotor performance, food intake and food assimilation*

A series of preliminary analyses revealed that, within each tail condition (tailless vs. tailed)  $\times$  sex combination, swimming speed and maximum distance were both independent of body size (SVL) and that sex was not a significant source of variation in the two locomotor variables (all  $P > 0.25$ ). We, therefore, used repeated measures ANOVA to analyze data. Overall, swimming speed was greater in the control than in the

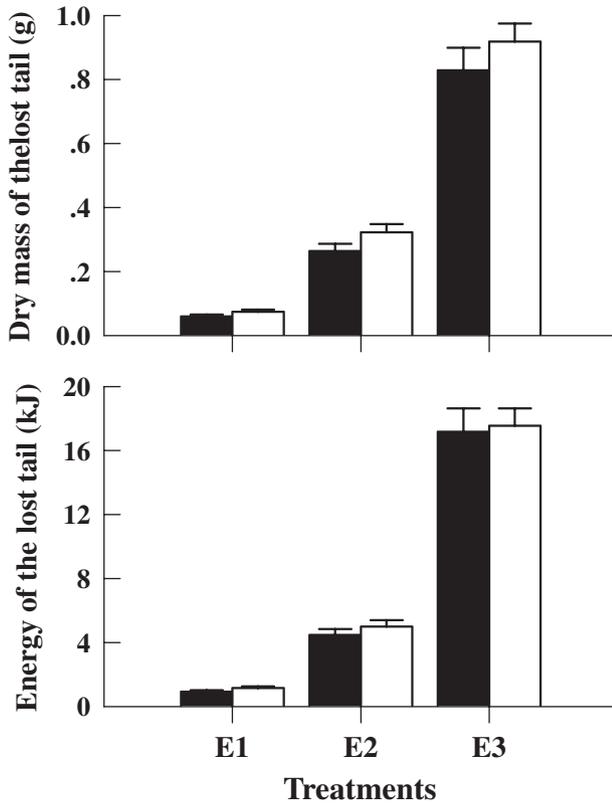


Fig. 2. Mean values (+SE) for dry mass and energy content of the three tail segments successively removed from each of the 20 experimental skinks. E1, E2 and E3 skinks were produced by successively removing three tail segments of the same length (mean = 46.0 mm, range = 37.7–52.7 mm) from each experimental skink initially having an intact tail, with all E3 skinks having a ~31-mm tail stump.

experimental skinks, but maximum distance did not differ between them (Table 2). Tail loss affected swimming speed but not maximum distance, with the E0 and E1 skinks swimming faster than did the E2 and E3 skinks (Fig. 3, Table 2).

Daily food intake, daily production of feces and daily production of urates, ADC and AE were all independent of SVL within each tail condition × sex combination (all  $P > 0.10$ ), so we used a series of two-way ANOVAs to analyze data. This series of analyses revealed that (1) none of the examined feeding variables differed between tail-less and tailed skinks, and between the sexes; and (2) the interaction between tail condition and sex was significant for none of these variables (Table 3). The amount of tail regeneration accomplished along the 3-week period, which did not differ between sexes (one-way ANOVA:  $F_{1,18} = 0.10$ ,  $P = 0.755$ ), was  $40.8 \pm 2.0$  (13.0–52.0 mm).

TABLE 2. Results of repeated-measures ANOVAs for swimming performance (maximum distance and swimming speed), with tail-removing order as the within-subject factor, and animal category (control vs. experimental skinks) as the between-subject factor

	Swimming performance	
	Maximum distance	Swimming speed
Tail-removing order	$F_{3,111} = 1.11$ , $P = 0.274$	$F_{3,111} = 15.02$ , $P < 0.0001$ E0 <sup>a</sup> , E1 <sup>a</sup> , E2 <sup>b</sup> , E3 <sup>b</sup>
Control vs. experimental skinks	$F_{1,37} = 0.22$ , $P = 0.642$	$F_{1,37} = 5.55$ , $P = 0.024$ C > E
Interaction	$F_{3,111} = 2.45$ , $P = 0.068$	$F_{3,111} = 2.70$ , $P = 0.049$

Tukey's post hoc comparisons were performed when differences in the examined variables were significant ( $a > b > c$ ). E0: experimental skinks initially having intact tails; E1, E2 and E3: see Table 1 for explanation of E1–E3 skinks.

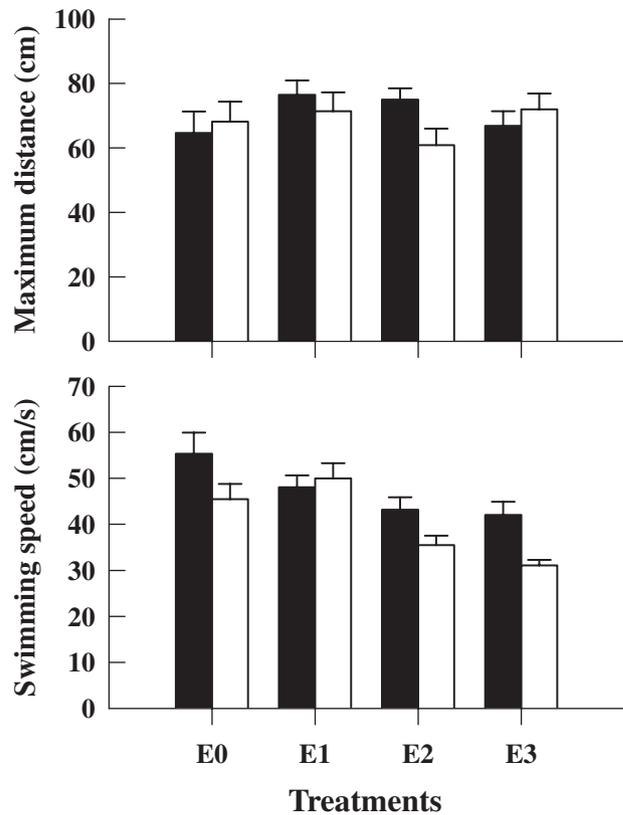


Fig. 3. Mean values (+SE) for locomotor variables before and after tail removing treatments. Black bars: control skinks; open bars: experimental skinks; E0: experimental lizards initially having intact tails; E1, E2 and E3: See Figure 2 for explanation of E1, E2 and E3 skinks.

TABLE 3. Descriptive statistics for food intake, production of feces, production of urates, ADC and AE

		N	Energy in food (kJ)	Energy in feces (kJ)	Energy in urates (kJ)	ADC (%)	AE (%)
Females	C	10	134.4 ± 9.7 (90.4–190.3)	7.9 ± 0.8 (5.2–11.4)	9.8 ± 0.7 (4.4–13.1)	94.1 ± 0.3 (92.2–95.2)	86.8 ± 0.4 (84.3–88.6)
	E3	10	136.3 ± 13.8 (75.9–209.8)	7.5 ± 0.8 (2.7–12.0)	10.0 ± 1.1 (4.6–15.9)	94.4 ± 0.4 (91.7–96.4)	87.1 ± 0.6 (84.5–90.3)
Males	C	9	155.1 ± 16.6 (48.0–226.0)	9.1 ± 0.8 (3.9–11.9)	10.4 ± 1.0 (3.8–14.1)	93.9 ± 0.3 (91.9–95.0)	87.1 ± 0.5 (84.0–88.5)
	E3	10	167.1 ± 15.0 (109.1–261.1)	9.7 ± 1.1 (5.2–17.3)	11.2 ± 1.2 (7.2–18.8)	94.2 ± 0.3 (93.1–95.9)	87.5 ± 0.5 (85.6–90.5)
Tail condition			$F_{1,35} = 0.25$ , $P = 0.619$	$F_{1,35} = 0.01$ , $P = 0.919$	$F_{1,35} = 0.31$ , $P = 0.584$	$F_{1,35} = 0.92$ , $P = 0.344$	$F_{1,35} = 0.50$ , $P = 0.486$
Sex			$F_{1,35} = 3.44$ , $P = 0.072$	$F_{1,35} = 3.97$ , $P = 0.054$	$F_{1,35} = 0.67$ , $P = 0.417$	$F_{1,35} = 0.45$ , $P = 0.505$	$F_{1,35} = 0.44$ , $P = 0.513$
Interaction			$F_{1,35} = 0.13$ , $P = 0.718$	$F_{1,35} = 0.37$ , $P = 0.548$	$F_{1,35} = 0.09$ , $P = 0.766$	$F_{1,35} = 0.004$ , $P = 0.951$	$F_{1,35} = 0.003$ , $P = 0.955$

## DISCUSSION

The portion of tail breaks was slightly greater in adults (~57%) than in juveniles (50%). Because we only collected a limited number ( $N = 18$ ) of juveniles from the field, whether a large portion of tail breaks observed in adults occurred when they were juveniles remains unknown. However, as tail regeneration was very evident in adult *M. multifasciata*, adults are well suited to our investigation.

The tail is one of the major sites of energy storage and represents a considerable portion of body mass in *M. multifasciata* (Lin et al., 2005). The E1 skinks that lost distally ~27% of the tail (in length) could on average retain more than 95% of the caudal energy, and the E2 skinks that lost cumulatively ~55% of the tail could on average retain more than 75% of the caudal energy (Fig. 2). Thus, as in the metallic skink *Niveoscincus metallicus* (Chapple and Swain, 2002a), the southern water skink *Eulamprus tympanum* (Doughty et al., 2003), the northern grass lizard *Takydro-mus septentrionalis* (Lin and Ji, 2005), the Chinese skink *Eumeces chinensis* (Lin et al., 2006) and the brown forest skink *Sphenomorphus indicus* (Sun et al., 2007), caudal energy stores are proximally aggregated in *M. multifasciata*. Such aggregation might represent an energy conserving mechanism evolved in the species to offset the high frequency (~57%) of tail autotomy. Alternatively, the limited space in the more distal portion of the tail may function as a physical constraint on energy stores. Based on our data, we conclude that tail breaks occurring in the distal portion of the tail may not

severely reduce energy stores in *M. multifasciata*. This conclusion is in agreement with studies of the lizards mentioned above (Chapple and Swain, 2002a; Doughty et al., 2003; Lin and Ji, 2005; Lin et al., 2006; Sun et al., 2007).

It is common in lizards that caudal vertebrae near the tailbase lack fracture planes through which tail autotomy can occur (Bellairs and Bryant, 1985). This anatomical feature explains why tail breaks at the extreme base of the tail are absent in lizards including *M. multifasciata*. The effectiveness of the shed tail depends on its size and movement (Dial and Fitzpatrick, '83; Chapple and Swain, 2002a). With species that have nearly full sets of autotomy planes in their tail vertebrae, there is considerable variation in the ease with which they shed their tails. Often, this seems to be determined by the equilibrium between the costs and benefits of shedding tails (Lin et al., 2006). Tail breaks at the extremely distal portion of the tail are rare in *M. multifasciata*, presumably because leaving a limited tail segment to predators is not enough to stop their predation attempts on the "body" part of the skink. In our sample, tail breaks occurred more frequently within the proximal half of the tail (Fig. 1). This observation indicates that, as in *T. septentrionalis* (Lin and Ji, 2005), *E. chinensis* (Lin et al., 2006) and *S. indicus* (Sun et al., 2007), tail breaks occurring in nature often incur substantial energetic costs in *M. multifasciata*.

Caudal autotomy reduces locomotor performance in many species of lizards (Lin et al., 2006 and included references). The impairment of locomotor performance resulting from tail loss

may increase vulnerability of tailless lizards to predation and consequently increase mortality (Congdon et al., '74; Dial and Fitzpatrick, '84; Daniels et al., 1986; Chapple and Swain, 2002b). Our results show that tail loss affects swimming speed but not maximum distance in *M. multifasciata* (Fig. 3, Table 2). The mean swimming speed of the E3 skinks was reduced by approximately 32% of the mean speed of the E0 skinks (Fig. 3). This degree of locomotor impairment associated with tail loss falls within the values (12–48%) reported for other species of lizards measured for sprint speed (Ballinger et al., '79; Punzo, '82; Arnold, '84; Formanowicz et al., '90; Martin and Avery, '98; Downes and Shine, 2001; Chapple and Swain, 2002b; Lin and Ji, 2005; Lin et al., 2006), thus signifying that *M. multifasciata* is among lizard species where tail loss may entail locomotor costs. Because swimming speed was dramatically reduced in the E2 skinks that lost about 55% of the tail and because more than 45% of skinks with previous bouts of caudal autotomy shed their tails in the proximal portion of the tail, we conclude that tail breaks occurring in nature often entail substantial locomotor costs in *M. multifasciata*.

The result that E3 skinks did not consume more food than the C skinks indicates that, as in *L. monticola* (Martin and Salvador, '93a) and *E. argus* (Zhao et al., 2008), tailless individuals do not increase feeding rates in *M. multifasciata*. In combination with the result that the E3 skinks did not assimilate food more efficiently than the C skinks, we conclude that many-lined sun skinks do not compensate for the costs of tail loss by increasing feeding rate or digestive efficiency. The absence of differences in ADC and AE between the E3 and C skinks is not surprising as both ADC and AE are primarily determined by activities of digestive enzymes, food passage time and the type and amount of food consumed, and significant differences in the two variables often cannot be detected between lizards of the same species unless they forage or are maintained under very different thermal conditions (Xu and Ji, 2006).

In this study, the finding that tailless skinks did not increase feeding rates is of particular interest, because it might suggest a behavioral mechanism adopted by tailless *M. multifasciata* to minimize the risks of predation in nature. Assuming a linear relationship between foraging time and food ingested, one may expect that to compensate for the negative consequences of tail loss tailless

lizards should forage longer than tailed ones. In *C. brevis*, for example, tailless individuals may have to remain more active to increase feeding rates (Dial and Fitzpatrick, '81). Because tailless lizards must forage without their primary defense mechanism and because locomotor efficiency is often adversely affected by tail loss, the risks of predation to tailless lizards can be concomitantly greater. Thus, if being active is costly for a lizard, tailless lizards that do not increase feeding rates are more likely to minimize the risks of predation while simultaneously saving energy that could be devoted to tail regeneration by reducing activity levels (Martin and Salvador, '93a; Zhao et al., 2008). Alternatively, it is possible that the lack of change in feeding rate or digestive efficiency in experimental animals simply reflects the fact that *M. multifasciata* has not responded evolutionarily, perhaps owing to weak selection or an unidentified trade-off. Finally, it is conceivable that our experimental design, in which the lizards were fed ad libitum, did not allow us to detect a reduction in the time devoted to foraging by experimental individuals even while they maintained a similar food intake rate.

In summary, caudal autotomy occurring in the distal portion of the tail has little effect on energy stores and locomotor performance in *M. multifasciata*, but caudal autotomy occurring in the proximal portion of the tail may greatly reduce the skink's fitness. As tail breaks occurred more frequently in the proximal portion of the tail in skinks collected from the field, we conclude that caudal autotomy often entails substantial energetic and locomotor costs in *M. multifasciata*. As tailless and tailed skinks did not differ in food intake, ADC and AE, we conclude that tailless individuals do not compensate for the negative consequences of tail loss by increasing feeding rate or digestive efficiency in *M. multifasciata*.

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