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Energetic and locomotor costs of tail loss in the Chinese skink, *Eumeces chinensis*

Zhi-Hua Lin [a,c], Yan-Fu Qu [b], Xiang Ji [b,c,*]

[a] *Department of Biology, Lishui University, Lishui 323000, Zhejiang, China*
[b] *Jiangsu Key Laboratory for Biodiversity and Biotechnology, College of Life Sciences, Nanjing Normal University, Nanjing 210097, Jiangsu, China*
[c] *Hangzhou Key Laboratory for Animal Sciences and Technology, School of Life Sciences, Hangzhou Normal College, Hangzhou 310036, Zhejiang, China*

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Abstract

Caudal autotomy is a defense mechanism used by numerous lizards to evade predators, but this entails costs. We collected 294 adult Chinese skinks (*Eumeces chinensis*) from a population in Lishui (eastern China) to evaluate energetic and locomotor costs of tail loss. Of the 294 skinks, 214 (c. 73%) had previously experienced caudal autotomy. Neither the proportion of individuals with regenerated tails nor the frequency distribution of locations of the tail break differed between sexes. We successively removed four tail segments from each of the 20 experimental skinks (adult males) initially having intact tails. Lipid content in each removed tail segment was measured, and locomotor performance (sprint speed, the maximal length traveled without stopping and the number of stops in the racetrack) was measured for each skink before and after each tail-removing treatment. Another independent sample of 20 adult males with intact tails was measured for locomotor performance to serve as controls for successive measurements taken for the experimental lizards. Caudal lipids were disproportionately stored along the length of the tail, with most lipids being aggregated in its proximal portion. Tail loss significantly affected sprint speed, but not the maximal length of, or the number of stops during the sprint. However, the adverse influence of tail loss on sprint speed was not significant until more than 51% of the tail (in length) was lost. Our data show that partial tail loss due to predatory encounters or other factors may not severely affect energy stores or locomotor performance in *E. chinensis*. 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 in *E. chinensis*.

Keywords: Reptilia; Scincidae; Chinese skink; *Eumeces chinensis*; Tail autotomy; Energy stores; Locomotor performance; Costs of tail autotomy

1. Introduction

Caudal autotomy is a defense mechanism employed by numerous lizards to evade potentially fatal predatory encounters (Arnold, 1984, 1988; Bellairs and Bryant, 1985). Caudal autotomy provides an immediate survival benefit by facilitating release from a predator, but this entails several costs and consequences subsequent to escape (Arnold, 1988; Wilson, 1992; Downes and Shine, 2001; Chapple and Swain, 2002; Cooper, 2003; Lin and Ji, 2005a,b). For example, the loss of stored energy due to tail loss may decrease growth rate, delay reproduction, reduce reproductive output and increase failure of winter dormancy (Smyth, 1974; Dial and Fitzpatrick, 1981; Wilson and Booth, 1998). Caudal autotomy also reduces locomotor performance in many (Pond, 1978; Ballinger et al., 1979; Punzo, 1982; Zani, 1996; Martin and Avery, 1998; Downes and Shine, 2001; Shine, 2003; Lin and Ji, 2005a,b) but not all (Daniels, 1983; Huey et al., 1990; Brown et al., 1995) species of lizards. The impairment of locomotor performance resulting from tail loss may also increase vulnerability of tailless lizards to predation and consequently increase mortality (Congdon et al., 1974; Dial and Fitzpatrick, 1984; Daniels et al., 1986; Chapple and Swain, 2002). Although tailless lizards may compensate for reduced locomotor performance to some extent by modifying activity, habitat use and antipredator

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* Corresponding author. Hangzhou Key Laboratory for Animal Sciences and Technology, School of Life Sciences, Hangzhou Normal College, Hangzhou 310036, Zhejiang, China. Tel.: +86 571 28865337; fax: +86 571 28865331.
E-mail address: xji@mail.hz.zj.cn (X. Ji).

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behavior, such behavioral shifts often reduce their fitness (Fox and Rostker, 1982; Dial and Fitzpatrick, 1984; Fox et al., 1990; Martin and Salvador, 1993; Salvador et al., 1995; Downes and Shine, 2001; Chapple and Swain, 2002; Cooper, 2003). The energetic and locomotor costs of tail loss are an interesting topic but remain explored in a few species of lizards.

In this study we used the Chinese skink (*Eumeces chinensis*), a medium-large sized [to 134 mm snout-vent length (SVL)] oviparous scincid lizard (Lin and Ji, 2000), as a model animal to study energetic and locomotor costs of tail loss in lizards. This skink is ideally suited for such a study, because its tail is a major site of energy storage, and can be easily induced to autotomize (Ji et al., 1994; Wu and Xu, 2000). We collected a large number of skinks from the field and successively removed at intervals of 3 days four tail segments from each experimental skink initially having intact tails. This approach allowed us to estimate the frequency of tail loss for the sampled population and to examine the distribution of caudal lipids and the differences in locomotor performance among skinks differing in tail lengths. Our purpose was not to undertake only an assessment of the energetic and locomotor costs of tail loss, but also to look at whether caudal autotomy occurring in nature entails substantial energetic and locomotor costs in *E. chinensis*.

2. Materials and methods

A total of 294 adults (♀♀: ♂♂ = 134: 160; SVL > 90 mm) were collected by hand in late April 2005 from a population in Lishui (28° 46′ N, 119° 92′ E), eastern China. The captured skinks were transported to our laboratory at Lishui University, where they were sexed, weighed, measured [for SVL, tail length (from the posterior edge of the cloaca to the tail tip) and tailbase width (the maximal width of the tailbase)] and checked carefully for signs of previous tail loss. The regenerated part of the tail could be easily distinguished because of the presence of irregular scales at the site where caudal autotomy occurred. The location of the tail break was noted for each skink with a regenerated tail. Twenty adult males (hereafter E0 skinks) without previously having experienced caudal autotomy were used as experimental animals (Table 1), and another independent sample of 20 adult males (hereafter C skinks) with intact tails were maintained under the same conditions as controls for locomotor performance, never undergoing the tail-removing manipulation. Control skinks did not differ from experimental skinks in SVL, tail length, body mass or tailbase width (ANOVA for SVL, and ANCOVA with SVL as the covariate for the other three variables; all $P > 0.075$). We released the remaining skinks at the site of collection. Prior to collection of data, skinks were maintained as groups of 10 in each of the four glass cages (aquaria) [90 × 65 × 50 cm (length × width × height)] for one month to allow them to habituate the laboratory conditions. The cages were maintained in a temperature controlled room at 26 ± 0.5 °C, so that the mean body temperature of the skinks was maintained at 26 °C, which is within the range of optimal body temperatures for this species (Ji et al., 1995). Skinks were fed mealworms (larvae of *Tenebrio molitor*) and water enriched with vitamins and minerals (Nekton-Rep, Nekton-product) ad libitum.

Table 1
Descriptive statistics of the 20 experimental male *Eumeces chinensis* used to examine the effects of tail loss on energy stores and locomotor performance

	Mean	SE	Range
Snout-vent length (mm)	111.2	2.0	98.0–127.0
Body wet mass (g)	29.2	1.7	18.4–39.8
Body dry mass (g)	9.5	0.6	5.4–13.8
Tail length (mm)	164.7	4.7	118.0–193.0
Tailbase width (mm)	10.4	0.2	9.0–12.1
Tail wet mass (g)	7.3	0.5	3.9–11.8
Tail dry mass (g)	2.90	0.21	1.38–4.93
Lipid content in the tail (g)	0.36	0.02	0.20–0.59
Lipid content in the carcass (g)	0.47	0.03	0.29–0.66
Lipid content in the liver (g)	0.04	0.01	0.02–0.09
Lipid content in the fatbody (g)	0.05	0.02	0–0.28

We measured locomotor performance of control and experimental skinks initially having intact tails at a body temperature of 26 °C. Skinks were individually chased down the length of a 2 m racetrack with one transparent side through which they were filmed using a Panasonic NV-MX3 digital video camera. Each skink was run twice, with a minimum of 30 min rest between the two trials (Braña and Ji, 2000; Lin and Ji, 2005a,b). The sequences were examined with a computer using MGI VideoWave III software (MGI Software Co., Canada) for sprint speed in the fastest 250 mm interval, the maximal distance traveled without stopping (hereafter the maximal length), and the number of stops in the trial. Maximal values for sprint and distance, and minimum values for stop number were considered as representative of locomotor performance at the test body temperature (Braña and Ji, 2000).

After obtaining data for the C and E0 skinks, we successively removed four tail segments by cutting at points a given distance from the cloaca of each E0 skink at intervals of 3 days, thereby producing E1, E2, E3 and E4 skinks with 80, 40, 10, and 0 mm (the tail was completely removed) tail length, respectively. The E1–E3 skinks were allowed to heal the wound for three days after each tail-removing episode to control for the influence of handling stress, and were thereafter measured for sprint speed following the procedures described above. The E4 skinks were killed by freezing to −15 °C, permitted by the Zhejiang Provincial Bureau of Forestry. Upon thawing, they were separated into five components, carcass (containing liver-free viscera), liver, abdominal fat bodies and tail, so that the total amount of lipids could be determined.

All removed tail segments and body components separated from the E4 skinks were individually weighed and then dried in an oven at 65 °C until a constant mass could be obtained. We extracted non-polar lipids from dried samples in a Soxhlet apparatus for a minimum of 10 h using absolute ether as solvent. The amount of lipids in each sample was determined by subtracting the lipid-free dry mass from the total sample dry mass.

All data were tested for normality (Kolmogorov–Smirnov test) and homogeneity of variances (*F*-max test). No data needed to be transformed to obey the assumptions of parametric analyses. We used the log-likelihood ratio test (*G*-test), linear

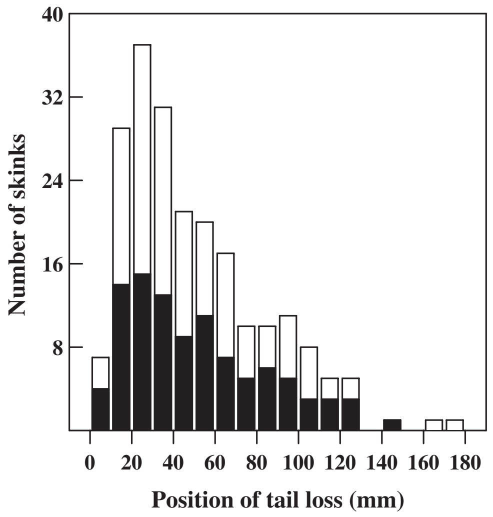

Fig. 1. Frequency distribution of locations at which caudal autotomy occurred. Data are based on 214 adult *Eumeces chinensis* collected from the field. Numbers in the horizontal axis indicate the distances from the vent. Solid bars: females ($N=96$); open bars: males ($N=118$).

correlation (regression) analysis, repeated measures ANOVA and Tukey's post hoc tests to analyze the corresponding data. Descriptive statistics are presented as mean ± SE, and the significance level is set at $\alpha=0.05$.

3. Results

3.1. Tail autotomy in the skinks collected from the field

Of the 294 skinks (134 females and 160 males) collected from the field, 214 (c. 73%) had autotomized some portion of the tail at least once. The proportion of individuals with regenerated tails did not differ between sexes (females vs. males = 71.9 vs. 73.9%; $G=0.148$, $df=1$, $P>0.90$). Tail breaks at the extreme base (<5 mm from the vent) of the tail were absent. Of the skinks having previous bouts of tail autotomy, 104 (48.5%) had shed their tails in the proximal portion (<40 mm, from the vent to where the tail was autotomized) of the tail, 68 (31.8%) in the middle portion (40–80 mm), and 42 (19.6%) in the distal portion (>80 mm). The frequency distribution of locations of the tail break did not differ between females and males ($G=7.85$, $df=15$, $P>0.90$; Fig. 1). When pooling data for sexes, we found that the numbers of skinks shedding tails in the proximal, middle and distal portions of the tail differed significantly ($G=27.40$, $df=2$, $P<0.001$), with

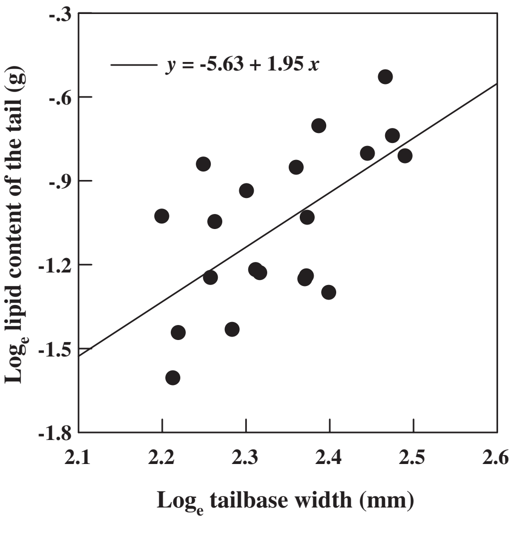

Fig. 2. The linear regression of lipid content of the removed tail plotted against tailbase width. The regression equation is indicated in the figure.

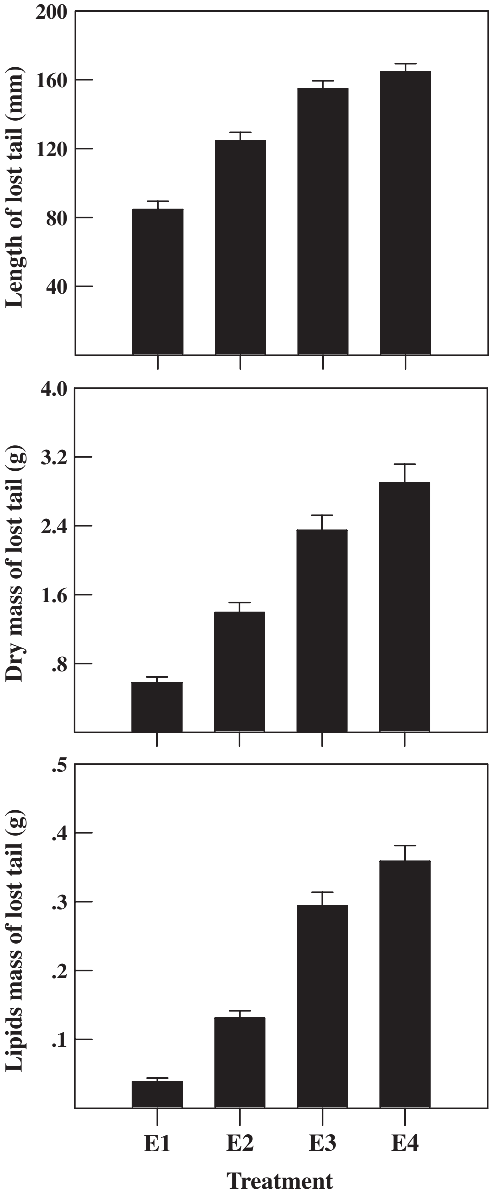

Fig. 3. Mean values (+SE) for cumulative values of length, dry mass and lipid content of the four tail segments successively removed from each of the 20 experimental skinks. E1: skinks produced by removing the distal portion of the tail (mean = 84.7 mm, range = 38.0–113.0 mm), thus being differentiated from the E0 skinks initially having intact tails; E2: skinks produced by removing a 40-mm tail segment from the E1 skinks; E3: skinks produced by removing a 30-mm tail segment from the E2 skinks; E4: skinks produced by removing a 10-mm tail segment from the E3 skinks.

more tail breaks occurring at points of 20–30 mm from the vent (Fig. 1).

3.2. Lipid content in different segments of the tail

Tail segments removed from the E0 skinks varied from 38.0 to 113.0 mm, and averaged 84.7 (SE=4.7) mm; tail segments removed from the E1, E2 and E3 skinks were 40, 30 and 10 mm, respectively (Table 1). Lipids in the tail, carcass, liver and fatbody accounted for proximately 40%, 52%, 4% and 4% of the total lipids, respectively (Table 1). The total amount of lipids in the tail was positively correlated with the tailbase width ($r=0.62$, $F_{1,\ 18}=11.01$, $P<0.004$; Fig. 2), but not with the tail length ($r=0.06$, $F_{1,18}=0.06$, $P=0.815$).

Proximal (0–40 mm, from the vent to where the tail was autotomized), middle (40–80 mm) and distal (>80 mm) portions of the tail differed significantly in both dry mass (repeated measures ANOVA: $F_{2,38}=85.96$, $P<0.0001$) and lipid content (repeated measures ANOVA: $F_{2,38}=115.62$, $P<0.0001$; Fig. 3). The proximal tail segments contained more lipids and dry materials than did the middle tail segments (Tukey's, both $P<0.05$), whereas the middle tail segments contained more lipids and dry materials than did the distal tail segments (Tukey's, both $P<0.05$). The proximal tail segments only accounted for 24% of the total tail length, but accounted for its 52% dry materials and 63% lipids. Proximal, middle and distal tail segments also differed from each other with respect to lipid content per unit of tail length (repeated measures ANOVA: $F_{2,38}=143.37$, $P<0.0001$) or per unit of tail dry mass (repeated measures ANOVA: $F_{2,38}=66.82$, $P<0.0001$), with length- and mass-specific lipid contents being both greatest in the proximal portion of the tail and lowest in the distal portion of the tail.

3.3. Locomotor performance

Sprint speed, the maximal length and the number of stops were all independent of body size (SVL) (all $P>0.10$), so we used repeated measures ANOVA to analyze data. Sprint speed was overall greater in control than in experimental lizards, but the number of stops and the maximal distance both did not differ significantly between experimental and control lizards (Table 2). Tail loss affected sprint speed but not the maximal length and the number of stops (Table 2), with the E0 skinks running faster than did the E2 and E3 skinks (Fig. 4).

Table 2
Results of repeated-measures ANOVAs with animal category (experimental and control lizards) as between-subject factor and the corresponding performance trait as within-subject factor

	Locomotor performance		
	Sprint speed	Number of stops	The maximal distance
Between subjects	$F_{1,38}=8.35$, $P=0.006$ Experimental<Control	$F_{1,38}=47$, $P=0.495$	$F_{1,38}=0.001$, $P=0.979$
Within subject	$F_{3,114}=4.78$, $P=0.004$ E0^{a}, E1^{ab}, E2^{b}, E3^{b}	$F_{3,114}=0.78$, $P=0.505$	$F_{3,114}=0.37$, $P=0.775$
Interaction	$F_{3,114}=5.67$, $P=0.001$	$F_{3,114}=0.28$, $P=0.840$	$F_{3,114}=0.48$, $P=0.694$

Superscripts identify significant differences between treatments (Tukey's test, $\alpha=0.05$, $a>b$).

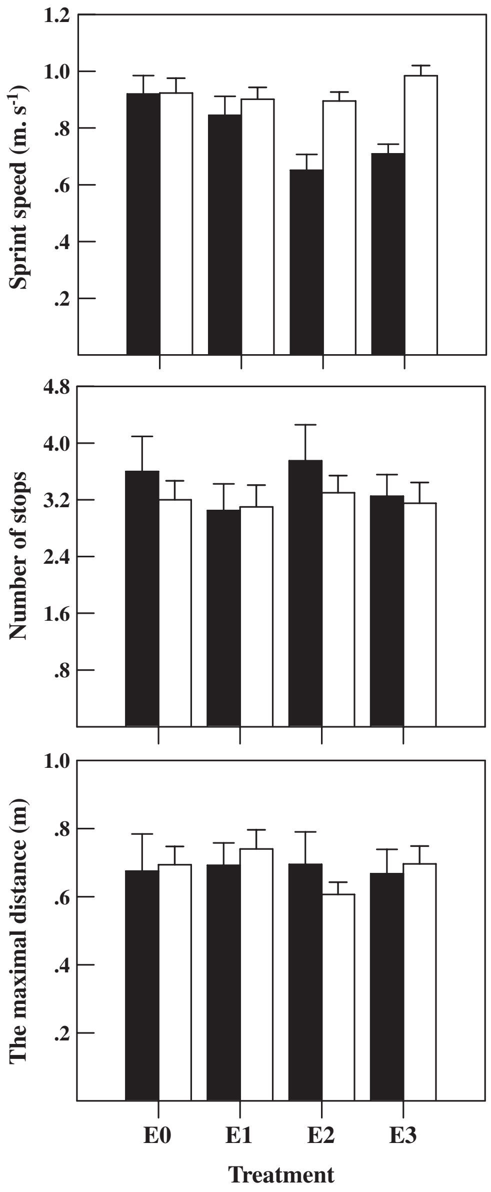

Fig. 4. Mean values (+SE) for locomotor variables before and after tail-removing treatments. Black bars: experimental skinks; open bars: control skinks; E0: experimental lizards initially having intact tails; E1, E2 and E3: See Fig. 3 for explanation of E1–E3 skinks.

4. Discussion

As in other lizards (e.g. Derickson, 1976; Dial and Fitzpatrick, 1981; Vitt and Cooper, 1986; Ji and Wang, 1990; Ji et al., 1994; Wu and Xu, 2000; Chapple and Swain, 2002; Doughty et al., 2003), the tail is an important storage organ for lipids in *E. chinensis* (Ji et al., 1994). Moreover, throughout the year the tail is much more important than abdominal fat bodies in *E. chinensis* with respect to the amount energy stored (Ji et al., 1994). Our data demonstrate that caudal lipids are disproportionately stored along the length of the tail. For example, the E1 skinks that on average lost distally 51% of the tail could retain 89% of its caudal lipid stores, and the E2 skinks that lost cumulatively 76% of the tail still retained 63% of its caudal lipid stores (Fig. 3). Clearly, caudal lipid stores are proximally aggregated in *E. chinensis*. Such aggregation might represent a lipid conserving mechanism adopted by skinks to offset the high frequency (c. 73%) of tail autotomy. Alternatively, the limited space in the more distal portion of the tail may function as a physical constraint on lipid stores. Based on our data, we conclude that partial tail loss (tail breaks occurring in the distal portion of the tail) may not severely influence energy stores in *E. chinensis*. This conclusion is consistent with that recently reported for the metallic skink *Niveoscincus metallicus* (Chapple and Swain, 2002), the water skink *Eulamprus tympanum* (Doughty et al., 2003) and the northern grass lizard (Lin and Ji, 2005b).

Caudal vertebrae near the tailbase lack fracture planes through which tail autotomy can occur (Bellairs and Bryant, 1985). This explains why tail breaks at the extreme base (<5 mm from the vent) of the tail are absent in *E. chinensis*. In lizards that enjoy survival benefit by using caudal autotomy as a defense mechanism, the effectiveness of the shed tail depends on its size and movement (Dial and Fitzpatrick, 1983; Chapple and Swain, 2002). Tail breaks at the tip of the tail are rare in *E. chinensis* (Fig. 1), presumably because partial tails do not distract predators enough to stop the predation attempt on the "body" part of the skink. It is noteworthy, however, that the position of tail breaks was not normally distributed along the length of the tail in our sample, but occurred most frequently within the range of 20 to 40 mm from the vent (Fig. 1). This observation presumably suggests that tail breaks occurring in nature often entail substantial energetic costs in *E. chinensis*.

The effects of tail loss on locomotor performance vary among species. For example, tail loss reduces sprint speed in many lizards (Pond, 1978; Ballinger et al., 1979; Punzo, 1982; Arnold, 1984; Martin and Avery, 1998; Downes and Shine, 2001) but increases sprint speed in other lizards such as *Christinus* (*Phyllodactylus*) *marmoratus* (Daniels, 1983) and *Podarcis muralis* (Brown et al., 1995). In the species in which sprint speed increases after tail loss, the tail appears to impede locomotion because of its mass and its friction with the substrate (Martin and Avery, 1998). In this study, tail loss produced only one locomotor impact: reducing sprint speed. The mean sprint speed of tailless skinks was reduced by 29% of the mean value of the E0 skinks (Fig. 4). This value falls within of the values (12–48% of the normal value) reported for other species of lizards (Pond, 1978; Ballinger et al., 1979; Punzo, 1982; Arnold, 1984; Martin and Avery, 1998; Downes and Shine, 2001), and therefore shows clearly that *E. chinensis* is among the species in which the tail plays a vital role in locomotor performance. Because the skinks (the E1 skinks per se) that lost the distal 51% of the tail still maintained almost normal sprint speeds, we conclude that partial tail loss may not substantially increase locomotor costs in the species.

Collectively, caudal autotomy occurring in the distal portion of the tail has little effect on energy stores and locomotor performance in *E. chinensis*, 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 *E. chinensis*.

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