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ORIGINAL PAPER

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Partial tail loss has no severe effects on energy stores and locomotor performance in a lacertid lizard, *Takydromus septentrionalis*

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Abstract Many species of lizards use caudal autotomy as a defense strategy to avoid predation, but tail loss entails costs. These topics were studied experimentally in the northern grass lizard, *Takydromus septentrionalis*. We measured lipids in the three-tail segments removed from each of the 20 experimental lizards (adult females) initially having intact tails to evaluate the effect of tail loss on energy stores; we obtained data on locomotor performance (sprint speed, the maximal length traveled without stopping and the number of stops in the racetrack) for these lizards before and after the tail-removing treatments to evaluate the effect of tail loss on locomotor performance. An independent sample of 20 adult females that retained intact tails was measured for locomotor performance to serve as controls for successive measurements taken for the experimental lizards. The lipids stored in the removed tail was positively correlated with tailbase width when holding the tail length constant, indicating that thicker tails contained more lipids than did thinner tails of the same overall length. Most of the lipids stored in the tail were concentrated in the proximal portion of the tail. Locomotor performance was almost unaffected by tail loss until at least more than 71% 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 and locomotor performance in *T. septentrionalis*.

Keywords Lacertidae · *Takydromus septentrionalis* · Tail autotomy · Energy stores · Locomotor performance · Costs of tail autotomy

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Introduction

Caudal autotomy is an effective defense tactic used by many species of lizards to escape from predators when other strategies such as crypsis and fleeting have failed (e.g., Arnold 1984, 1988; Bellairs and Bryant 1985). The frequency of tail loss in a lizard population has been reported to be indicative of predation pressure and/or of the efficiency of autotomy as a defense (Arnold 1988). Nonetheless, numerous other independent factors also account for tail loss in lizards, suggesting that the frequency of tail loss cannot be considered simply as a direct result of predation (e.g., Arnold 1988; Bauer and Russell 1994). The frequency of tail breaks varies among species as a trait co-evolved with morphology, locomotor performance, habitat use and foraging behavior (Vitt 1983; Zani 1996). For example, widely foraging lizards have lower frequencies of tail breaks than do sit-and-wait foraging lizards (Vitt 1983). Caudal autotomy provides an immediate survival benefit by facilitating escape, but this benefit is associated with several costs and consequences subsequent to escape (Arnold 1988; Wilson 1992; Downes and Shine 2001; Cooper 2003). The tail is an important storage organ for lipids (energy) in many species of lizards (Bustard 1967; Congdon et al. 1974; Daniels 1984; Ji and Wang 1990; Ji et al. 1994b). For example, tail loss reduces energy stores and, consequently, delays the animal's next reproductive episode, reduces size and number of offspring and increases failure of winter dormancy (Smyth 1974; Dial and Fitzpatrick 1981; Wilson and Booth 1998; Wu and Xu 2001). Tail loss in lizards is also associated with the reduced locomotor performance and mobility (Punzo

1982; Zani 1996; Martin and Arvey 1998; Downes and Shine 2001; Shine 2003; Lin and Ji 2005; see also Daniels 1983; Huey et al. 1990; Brown et al. 1995). Impairment of locomotor performance resulting from tail loss may contribute to the increased vulnerability of tailless lizards to predation and consequently increase mortality (Congdon et al. 1974; Dial and Fitzpatrick 1984; Daniels et al. 1986; Downes and Shine 2001; Chapple and Swain 2002). Modification of activity, habitat use and antipredator behavior may compensate for the absence of the tail and the reduced locomotor performance (Dial and Fitzpatrick 1984; Downes and Shine 2001; Chapple and Swain 2002; Cooper 2003), but such behavioral shifts often reduce fitness of tailless lizards (Fox and Rostker 1982; Fox et al. 1990; Martin and Salvador 1993; Salvador et al. 1995; Chapple and Swain 2002).

In this study, we used the northern grass lizard (*Takydromus septentrionalis*) as an experimental model to evaluate costs of tail loss by examining the effects of tail loss on energy stores and locomotor performance. The lizard is particularly suitable for such work, because its tail of which the length is often three times longer than its snout–vent length (SVL) can be easily induced to autotomize (Chen 1991). Our study differed from previous studies in that three-tail segments were successively removed from each experimental lizard having an intact tail at intervals of 3 days. This approach allows us to examine the distribution of caudal lipids and the differences in locomotor performance among lizards with different tail lengths. Specifically, we address the two questions: (1) Does partial tail loss severely reduce energy stores? (2) Does partial tail loss severely reduce locomotor performance?

Materials and methods

Animals

Takydromus septentrionalis is a small (up to 76 mm SVL) multiple-clutched oviparous lacertid lizard, which is endemic to China and is distributed in the southern provinces of the country, northward to Gansu (Chen 1991). This widely foraging lizard spends much of its daily active time on grasses and shrubs (Ji et al. 1994a, 1998). Prey items mostly belong to arthropods found in leafy vegetation (Zhang and Ji 2000). Adults are sexually dimorphic in head size but not in SVL, and larger females can lay up to seven clutches per breeding season (Zhang and Ji 2000). The tail constitutes one of the major energy storage systems in the species (Wu and Xu 2001; Xu et al. 2002).

A total of 92 adults (> 55 mm SVL, Wang 1966) were collected by noose or by hand in September 2004 from a population in Lishui (28°46′N, 119° 92′E), eastern China. The captured lizards were transported to our laboratory at Lishui University, where they were individually sexed, weighed and measured for SVL, TL and tailbase width (the maximal width of the tail base). The sign of previous tail loss was carefully identified for each lizard. Twenty adult females that had no evidence of previous caudal autotomy were used as experimental animals (Table 1). The experimental lizards were maintained 10 in each of the two glass cages [1,000×800×500 mm (length × width × height)]. The cages were placed in a controlled temperature room at 26 ± 0.5°C, so that the mean body temperature of these lizards could be controlled at 26°C (Wang and Xu 1987). The lizards were provided with mealworms (larvae of *Tenebrio molitor*) and water enriched with vitamins and minerals and, 1 month later, they were used for data collection. An independent sample of 20 adult females with intact tails that were maintained under the same conditions but never underwent the tail-removing manipulation served as controls for measurements of locomotor performance. These lizards did not differ from experimental lizards in SVL, TL, body mass and tailbase width (ANOVA for SVL, and ANCOVA with SVL as the covariate for the other three variables; all $P > 0.205$).

Methods

We measured locomotor performance of the experimental lizards initially having intact tails (hereafter E0 lizards) at the body temperature of 26°C. Lizards were chased down the length of a 2 m racetrack with one side transparent, which allows lateral filmation with a Panasonic NV-MX3 digital video camera (e.g., Braña and Ji 2000; Zhang and Ji 2004; Lin and Ji 2005). Each lizard was run two times with a minimum of 30 min rest between the two trials. The tapes were examined with a computer using MGI VideoWave III software (MGI Software Co., Canada) for sprint speed in the fastest 250 mm interval, maximal distance traveled without stopping (hereafter the maximal length) and number of

Table 1 Descriptive statistics of the 20 experimental female *Takydromus septentrionalis* used to examine the effects of tail loss on energy stores and locomotor performance

	Mean	SE	Range
Snout–vent length (mm)	64.1	0.7	57.5–71.0
Body mass (g)	4.78	0.16	3.5–6.1
Total length of the removed tail (mm)	163.0	5.9	124.0–204.0
Tailbase width (mm)	4.9	0.1	4.1–5.5
Total wet mass of the removed tail (g)	1.34	0.06	0.77–1.85
Total dry mass of the removed tail (g)	0.47	0.02	0.22–0.67
Total lipid content in the removed tail (g)	0.13	0.01	0.06–0.19

stops in the trial. Maximal values for sprint and distance and minimum ones for stop number were considered as representative of locomotor performance at the test body temperature (Braña and Ji 2000; Braña 2003).

After obtaining data on locomotor performance for E0 and control lizards, we successively removed three-tail segments from each E0 lizard at intervals of 3 days, thereby inducing E1, E2 and E3 lizards with 100 mm, 50 mm and 10 mm TL, respectively. Lizards were allowed to heal the wound for three days after each tail-removing episode to control for the direct influence of handling stress, and were thereafter measured for sprint speed following the procedures described above. The control lizards were also measured for locomotor performance to serve as controls for the three subsequent measurements taken for the experimental lizards.

All removed tail segments 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 tail segments 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.

Statistical analyses

All data were tested for normality (Kolmogorov–Smirnov test) and homogeneity of variances (*F* max test). No data were needed to be transformed to achieve the conditions for using parametric analyses. We used *G* test, paired-sample *t* test, linear correlation (regression) analysis, partial correlation 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 $\alpha = 0.05$.

Results

Tail autotomy in the lizards from the field

Of the 92 adults collected from the field, 38 (41.3%) had autotomized the tail for at least one time. Caudal autotomy did not occur at the extreme base of the tail (< 10 mm from the vent to where the tail was autotomized). Of the lizards having previous experience with tail autotomy, 22 (57.9%) shed their tails at the proximal portion (10–50 mm from the vent) of the tail, 12 (31.6%) at the middle portion (50–100 mm), and 4 (10.5%) at the distal portion (100–175 mm). The number of lizards shedding their tails at the three different portions of the tail differed significantly ($G = 13.77$, $df = 2$, $P < 0.005$), but the location of naturally occurring tail breaks was normally distributed along the length of the tail (Kolmogorov–Smirnov test, $P > 0.236$), with most around 53 mm (approximately 31% of the tail length) from the vent and fewer proximal and distal breaks (Fig. 1).

Lipid content in different segments of the tail

A paired-sample *t* test on experimental lizards showed that the two measures of tail width were the same ($t = 0.43$, $df = 19$, $P = 0.673$). Tail segments removed from E0 lizards varied from 34.0 to 114.0 mm, and averaged 73.0 ($SE = 5.9$) mm; Tail removed from E1 and E2 lizards were 50 mm and 40 mm, respectively. The total lipid content in three segment of removed tail was independent of the animal's body size (SVL) ($r = 0.21$, $F_{1,18} = 0.85$, $P = 0.369$), but it was positively correlated

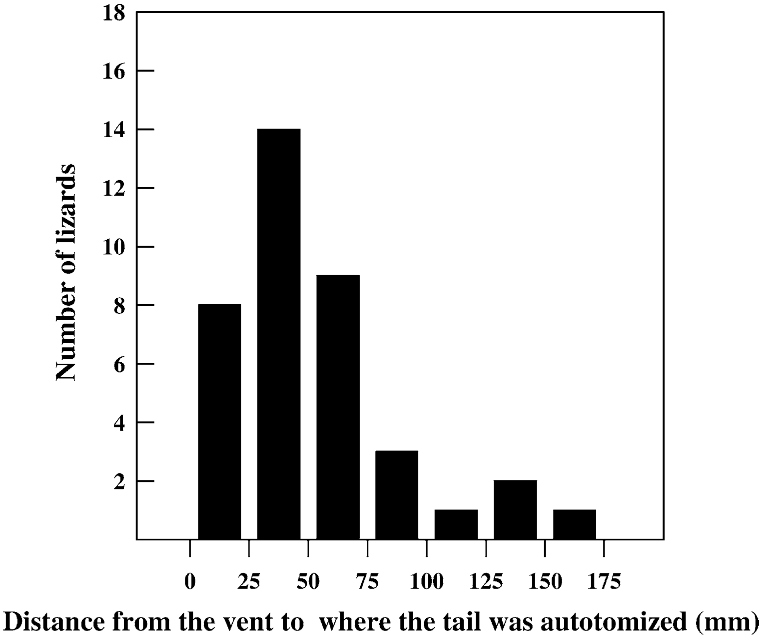

Fig. 1 Frequency distribution of locations where caudal autotomy occurred. Data are based on 38 adult *Takydromus septentrionalis* collected from the field

with the tailbase width ($r = 0.49$, $F_{1,18} = 5.82$, $P = 0.027$) (Fig. 2). The total lipid content in the removed tail was positively correlated with its length ($r = 0.53$, $F_{1,18} = 7.17$, $P = 0.015$), its wet mass ($r = 0.89$, $F_{1,18} = 68.19$, $P < 0.0001$) and its dry mass ($r = 0.97$, $F_{1,18} = 264.83$, $P < 0.0001$). When holding the length of the removed tail constant using a partial correlation analysis, the total lipid content in the removed tail was also positively correlated with the tailbase width ($r = 0.50$, $t = 2.37$, $df = 17$, $P = 0.031$). This analysis confirmed that thicker tails contained more lipids than did thinner tails of the same overall length.

Tail segments removed from E0, E1 and E2 lizards differed significantly in both dry mass (repeated measures ANOVA: $F_{2,38} = 166.69$, $P < 0.0001$) and lipid content (repeated measures ANOVA: $F_{2,38} = 451.64$, $P < 0.0001$) (Fig. 3). Tail segments removed from E2 lizards contained more lipids and dry materials than did those removed from E1 lizards (Tukey's, both $P < 0.05$); tail segments removed from E1 lizards contained more lipids and dry materials than did those removed from control lizards (Tukey's, both $P < 0.05$). Tail segments removed from E2 lizards only accounted for approximately 25% length of the removed tail, but accounted for its 49% dry materials and 60% lipids. There were also significant differences among tail segments removed from control, E1 and E2 lizards with respect to lipid content per unit of tail length (repeated measures ANOVA: $F_{2,38} = 483.30$, $P < 0.0001$) or per unit of tail dry mass (repeated measures ANOVA: $F_{2,38} = 8070.63$, $P < 0.0001$). Tail segments removed from E2 lizards contained relatively (to either tail length or tail dry mass) more lipids than did those removed from E1 lizards (Tukey's, both $P < 0.05$); tail segments removed from E1 lizards contained relatively more lipids than did those removed from control lizards (Tukey's, both $P < 0.05$).

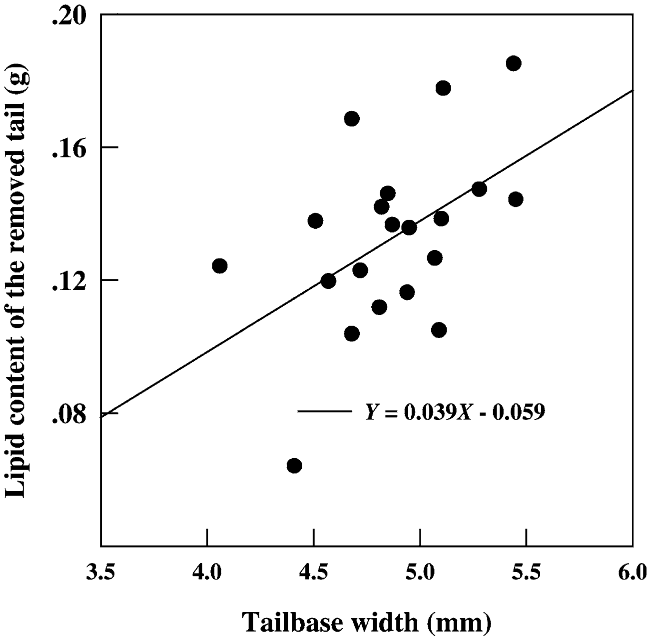

Fig. 2 The linear regression of lipid content of the removed tail on the tailbase width. The removed tail was constituted by three-tail segments which were sequentially removed from each of the 20 experimental lizards having no previous experience with caudal autotomy

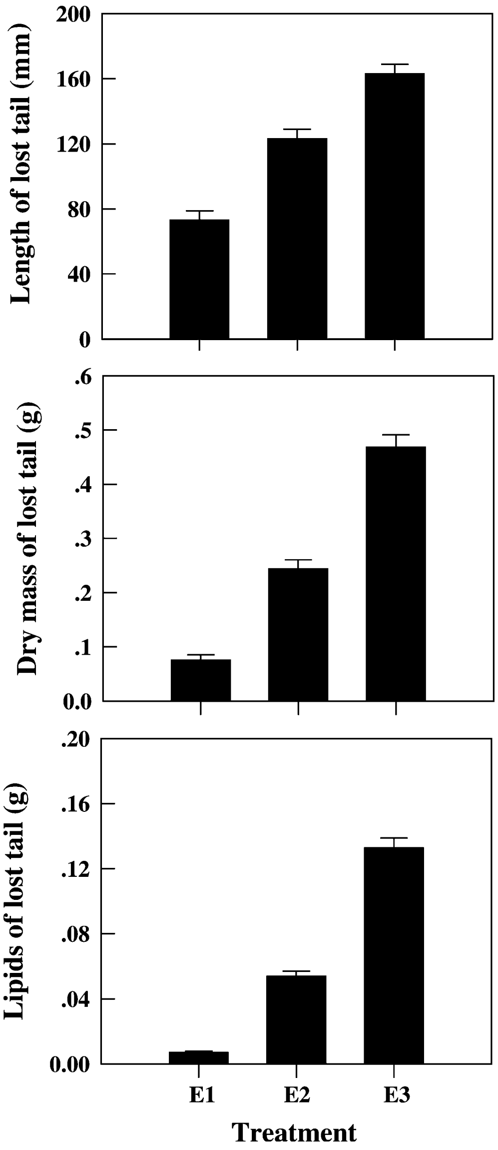

Fig. 3 Mean values (+ SE) for accumulative values of the length, dry mass and lipid content of the three-tail segments successively removed from each of the 20 experimental lizards. E1: the distal portions (mean = 73.0 mm, range = 34.0–114.0 mm) of the tail were removed from E0 lizards initially having intact tails; E2: the middle portions (50 mm) of the tail were removed from E1 lizards; E3: the proximal portions (40 mm) of tail were removed from E2 lizards

Locomotor performance

The three examined locomotor variable were all independent of body size (SVL) (all $P > 0.497$), so we used repeated measures ANOVA to analyze data. The number of stops was overall greater in experimental lizards than in control lizards, but sprint speed and the maximal distance both did not differ between experimental and control lizards (Table 2, Fig. 4). The effects of tail loss on sprint speed, the maximal length and number of stops were all significant, but these differences primarily resulted from much worse locomotor performance in E3 lizards (Table 2, Fig. 4). E0, E1 and E2 lizards did not differ significantly from each other in all examined locomotor variables (Table 2).

Discussion

Caudal lipid reserves represent the major site of energy storage in many species of lizards (e.g., Derickson 1976; Dial and Fitzpatrick 1981; Vitt and Cooper 1986; Ji and Wang 1990; Ji et al. 1994b; Chapple and Swain 2002; Doughty et al. 2003). Total lipids in the entire individual were not measured in this study, so we are unable to discuss the amount of lipids in the different tail segments relative to the total lipid stores. However, in *T. septentrionalis*, caudal fat bodies and abdominal fat bodies are the two major energy storage systems but, throughout the year, caudal fat bodies comprise the majority (>55%) of these fat reserves (Wu and Xu 2001; Xu et al. 2002). Thus, the tail is more important than abdominal fat bodies in the species with respect to the amount energy stored. Our data further demonstrates that lipids are disproportionately stored along the length of the tail. For example, E1 lizards that lost distally approximately 42% of the tail could retain at least 95% of its caudal lipid stores, and E3 lizard that lost three-fourths of the tail still retained at least 60% of its caudal lipid stores (Fig. 3). Thus, the energy consequences of partial tail loss are less significant to *T. septentrionalis*. This conclusion is consistent with that recently reported for the metallic skink *Niveoscincus metallicus* (Chapple and Swain 2002) and the water skink *Eulamprus tympanum* (Doughty et al. 2003).

The effects of tail loss on locomotor performance vary among species. Whereas, sprint speed decreases after tail loss in most species of lizards (Pond 1978; Ballinger et al. 1979; Punzo 1982; Arnold 1984; Martin and Arvey 1998; Downes and Shine 2001; Lin and Ji 2005), the locomotor variable increases after tail loss in

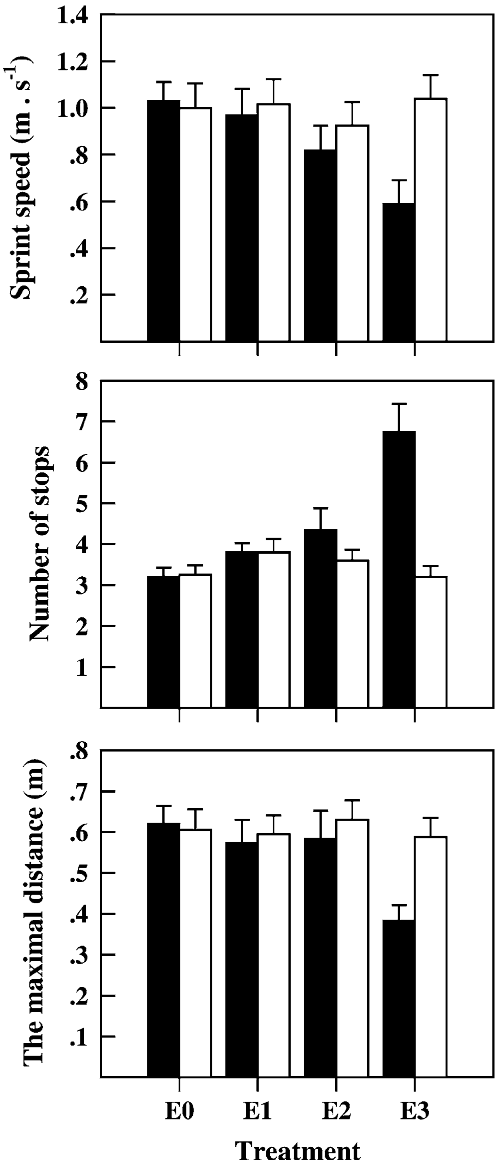

Fig. 4 Mean values (+ SE) for locomotor variables before and after tail-removing treatments. Means with different superscripts differ significantly (Tukey's test, $\alpha = 0.05$). *Black bars* experimental lizards; *Open bars* control lizards; E0: experimental lizards initially having intact tails; E1, E2 and E3: see Fig. 3 for key to symbols

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	$F_{1,38} = 1.51$, $P = 0.227$	$F_{1,38} = 7.23$, $P = 0.011$; Experimental > control	$F_{1,38} = 2.27$, $P = 0.140$
Within subject	$F_{3,38} = 3.63$, $P = 0.015$E0^{a}, E1^{ab}, E2^{ab}, E3^{b}	$F_{3,38} = 5.47$, $P = 0.011$E0^{b}, E1^{ab}, E2^{ab}, E3^{a}	$F_{3,38} = 3.19$, $P = 0.027$E0^{a}, E1^{ab}, E2^{ab}, E3^{b}
Interaction	$F_{3,38} = 4.37$, $P < 0.006$	$F_{3,38} = 8.37$, $P < 0.0001$	$F_{3,38} = 2.13$, $P = 0.100$

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

some lizards such as *Phyllodactylus marmoratus* (Daniels et al. 1983) and *Podarcis muralis* (Brown et al. 1995). In the species with increased sprint speed after tail loss, the tail appears to impede locomotion because of its mass and because of friction with the substrate (Martin and Arvey 1998). At least one species of lizard (*Sceloporus merriami*) was reported that sprint speed was unaffected by tail loss because of its relatively short and slender tail (Huey et al. 1990). In the species with reduced locomotor performance after tail loss, sprint speed of tailless lizards was reduced by 12–48% of the normal value (Pond 1978; Ballinger et al. 1979; Punzo 1982; Arnold 1984; Martin and Arvey 1998; Downes and Shine 2001; Shine 2003; Lin and Ji 2005). In this study, the mean sprint speed of tailless lizards (i.e., E3 lizards) was reduced by 43% of the mean value of E0 lizards (Fig. 4), with the reduced proportion of sprint speed falling within the range reported for other species of lizards. Thus, *T. septentrionalis* is among species of lizards whose tails play an important role in such activities as locomotion and/or climbing (Pond 1978; Ballinger et al. 1979; Punzo 1982; Arnold 1984; Martin and Avery 1998; Lin and Ji 2005). However, as E2 lizards of which the tail length was 50 mm still maintained almost normal values of the three locomotor variables (Fig. 4), the adverse effect of tail loss on locomotor performance was not significant until the length of the removed tail was at least longer than 71% [(173–50)/173] of the original tail length. This result provides evidence that partial tail loss may not have an important effect on locomotor performance in *T. septentrionalis*.

The frequency of naturally occurring tail breaks varies among populations of *T. septentrionalis* that differ in predation pressure (Ji et al. 1994a). In our sample, 41% of the 92 adults collected from the field had evidence of previous caudal autotomy. The proportion was greater than those (4–23%) reported previously for *T. septentrionalis* collected from different localities on the Zhoushan Islands (Ji et al. 1994a), presumably reflecting that predation pressure was higher in Lishui than in Zhoushan. It is worth noting that the majority (58%) of the lizards having previous experience with tail autotomy shed their tails at points within the range 10–50 mm from the vent (Fig. 1). This result suggests that most of tail breaks involve major tail loss in the population that we studied. Thus, although partial tail loss may not have important effects on energy stores and locomotor performance, the energy and locomotor consequences of autotomy events occurring in nature may be often more significant than expected.

In summary, partial tail loss in *T. septentrionalis* may not have severe effects on energy stores and locomotor performance. Given that energy stores and locomotor performance are greatly reduced in tailless lizards, caudal autotomy occurring at the extreme base of the tail may greatly reduce fitness of lizards.

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