Tail Autotomy Does Not Increase Locomotor Costs in the Oriental Leaf-toed Gecko *Hemidactylus bowringii*

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Abstract Tail autotomy is a defense mechanism used by many lizards to evade predators, but it entails costs. We used the oriental leaf-toed gecko *Hemidactylus bowringii* as a model animal to evaluate locomotor costs of tail autotomy. We removed the tail about 5 mm from the tail base from each of the experimental geckos (adult males) initially having intact tails. Tailless experimental geckos and tailed control geckos were measured for overall speed and sprint speed in both vertical and horizontal directions. Overall speed and sprint speed did not differ between tailless and tailed geckos. The influence of locomotor direction on both overall speed and sprint speed was significant, with horizontal speed being greater than vertical speed. The interaction between tail condition and locomotor direction was not significant in overall speed, but was significant in sprint speed. Tailless geckos had faster vertical sprint speed than the tailed individuals. Of the 130 field-caught adults, 59 had previously lost their tails, with most (about 61%) of them shedding their tails near the tail base. Neither the proportion of geckos with tail autotomy nor the frequency distribution of locations of the tail break differed between the sexes. Our data show that tail loss of *H. bowringii* occurs frequently in nature. However, tail loss does not incur locomotor costs in this gecko.

Keywords Gekkonidae, *Hemidactylus bowringii*, tail autotomy, locomotor performance, cost of tail autotomy

1. Introduction

Tail autotomy is a common phenomenon in many lizard species (Vitt *et al*., 1977; Arnold, 1984). When other anti-predation strategies such as crypsis, fight and flight have failed, lizards may escape by deflecting a predatory attack to an autotomous tail (Arnold, 1984, 1988; Bellairs and Bryant, 1985; Clause and Capaldi, 2006; Maginnis, 2006; Bateman and Fleming, 2009). This defense mechanism increases the survival probability of tailed lizards from predatory attacks. Consequently, tailed lizards may have higher survival probability than tailless individuals when they encounter predators (Congdon *et al*., 1974). Tail autotomy is a spontaneous behavioural response of lizards to escape from predators, but it is also a costly behaviour for numerous lizards where the tail functions as a weapon

of defense, signals an individual's social status, stores fat, and has a balance function for locomotion (Arnold, 1984; Clause and Capaldi, 2006; Maginnis, 2006; Bateman and Fleming, 2009). Tailless lizards exploit habitats differently (Martín and Salvador, 1992; Cooper, 2003), reduce their activity range (Salvador *et al*., 1995), develop anticipatory escape behaviours (Cooper, 2003), and implement furtive anti-predation behaviour (Martín and Salvador, 1993; Zhao *et al*., 2008), to compensate the impairment from tail autotomy. All of the post-autotomy behaviours potentially lower individual fitness.

In species where locomotor ability is impaired by tail autotomy, tailless lizards may have reduced escape opportunity from predators (Arnold, 1984). However, the locomotor costs vary among species. For example, there is no locomotor cost from tail loss in some lizards such as *Teratoscincus scincus*, where the tail has no important role in influencing locomotor performance (Lu *et al*., 2010). In *Sphenomorphus quoyii*, tail loss can significantly decrease swimming ability, but not running speed (Daniels, 1985). Previous studies show that tail autotomy reduces

locomotor ability in most lizards (Martín and Avery, 1998; Chapple and Swain, 2002; Shine, 2003; Chapple *et al*., 2004; Lin and Ji, 2005; Goodman, 2006; Lin *et al*., 2006; Medger *et al*., 2008; Sun *et al*., 2009), makes no difference in others (Daniels, 1983, 1985; Huey *et al*., 1990; McConnachie and Whiting, 2003; Chapple *et al*., 2004; Kelehear and Webb, 2006; Lu *et al*., 2010), or even increases locomotor speed in only a few species (Daniels, 1983; Brown *et al*., 1995).

Studies on the effects of tail autotomy on locomotor performance in lizards have focused mainly on cursorial lizards, with fewer on climbing lizards (Daniels, 1983; Brown *et al*., 1995; Kelehear and Webb, 2006; Medger *et al*., 2008; Gillis *et al*., 2009). While it is known that tail autotomy decreases the locomotor performance in scincid lizards (Formanowicz *et al*., 1990; Chapple and Swain, 2002; Shine, 2003; Goodman, 2006; Lin *et al*., 2006; Sun *et al*., 2009), it is yet unclear if the same result is true in gekkonid lizards, of which most are climbing species. Thus, the study on the influence of tail autotomy on locomotor performance in climbing lizards will be positive in revealing the adaptation significance of tail autotomy in gekkonid lizards.

In this study, we recorded the frequency of tail loss in a population of the oriental leaf-toed gecko (*Hemidactylus bowringii*) to estimate the intensity of predation pressure on the species. We also studied the horizontal and vertical locomotor performances of lizards after tail loss to test the effects of tail autotomy on the locomotor performance in a wall-climbing lizard.

2. Materials and Methods

2.1 Animal collection and care The oriental leaf-toed gecko (*H. bowringii*) is a small [up to 60 mm snout-vent length (SVL), and 75 mm tail length], nocturnal gekkonid lizard that is widely distributed in tropical and subtropical regions in southeastern Asia, including southern China (Zhou and Liu, 1999; Xu *et al*., 2007). In the daytime, the gecko hides in crevices in the walls of houses, but at night it climbs walls of houses and other buildings in search of insects attracted by lights (Zhou and Liu, 1999). Male and female reproductive cycles (Zhang *et al*., 1999, 2000), thermal physiology (Xu *et al*., 2007), postprandial thermophily (Xu *et al*., 2006), ontogenetic shifts in sexual dimorphism, female reproductive traits and egg incubation (Xu and Ji, 2007), and variation in locomotor performance induced by proximate factors (Xu *et al*., 2009) have been examined, whereas other biological and ecological aspects of the species remain unknown.

A total of 130 adult geckos (> 39 mm SVL) were collected by hand in early May 2009 from a population in Zhaoqing (23º02'N, 112º27'E), Guangdong, China. The collected geckos were transported to our laboratory in Nanjing, where the individuals were sexed, measured for SVL and tail length, checked for signs of previous tail loss, and marked by a nontoxic waterproof label for future identification. The position of the tail break was determined for each gecko with previous signs of tail loss. We housed 10 geckos, with 4–6 of each sex, together in each 600 mm × 400 mm × 400 mm (length × width × height) mesh cage placed in an indoor animal holding facility where temperatures were never outside the range of 23–28°C. Geckos were exposed to a natural daylight cycle, and were fed on mealworms (larvae of *Tenebrio molitor*), house crickets (*Achetus domesticus*) dusted with multivitamins, minerals and water, and enriched with vitamins and minerals *ad libitum*.

2.2 Experimental design Twenty-five adult males (42–54 mm SVL) with no evidence of tail regeneration were selected and randomly divided into an experimental group (n = 11) and a control group (n = 14). The experimental geckos autotomized their tails when they were grasped 5 mm near the tail base with forceps, thereby producing tailless individuals. The experimental and control groups were maintained under the same laboratory conditions, and tailless geckos were given two days for their wounds to heal to minimize any possible effects of handling stress on subsequent measurements of locomotor costs associated with tail autotomy. Two tailless geckos were excluded from statistical analyses because they died at the wound recovery stage.

We measured the horizontal locomotor performance and the vertical locomotor performance two days after tail autotomy. We conducted all measurements in a temperature-controlled room at 30 ± 0.5°C, and kept the geckos there for 2 hours prior to each measurement. Body (cloacal) temperature (to the nearest 0.01°C) was taken for each gecko using a UT325 digital thermometer (Shanghai Medical Instruments, China) before the measurement of locomotor performance. We chased the geckos along the length of a 1-m wooden racetrack set horizontally or vertically. For each individual, trials in the two directions were conducted on two successive days. One sidewall of racetrack was the transparent, which allowed video recording with a Panasonic NV-GS400 digital video camera. It was always the first author who chased the geckos to standardize the stimulus. The videotapes were later examined for sprint

speed in the fastest 25 cm interval and overall speed (the maximal length traveled without stopping divided by the time taken) in the whole racetrack with a computer, using Windows Movie Maker 2.6 software (Microsoft Co., USA).

2.3. Statistical analyses We used Statistica software package (version 6.0 for PC, Tulsa, OK, USA) to analyze data. All data were tested for normality using the Kolmogorov-Smirnov test, and for homogeneity of variances using the Bartlett's test. The data were normally distributed. Body size (SVL) was not a significant source of variation in the locomotor variables examined (linear regression analysis; all $P > 0.341$). We used log-likelihood ratio test (G-test) to examine whether the proportion of individuals with previous bouts of tail loss differed between the sexes, whether the frequency of locations of tail loss differed between the sexes, and whether the number of individuals shedding tails in the proximal, near proximal, middle and distal portions of the tail differed significantly. We used repeated-measures ANOVA with locomotor direction as the within-subject factor and tail condition as the between-subject factor to examine whether locomotor performance differed between tailed and tailless geckos, and between horizontally- and vertically-running geckos. Descriptive statistics are presented as mean ± 1 standard error (SE), and the significance level is set at α = 0.05.

3. Results

Of the 130 geckos (64 females and 66 males) collected from the field, 59 (c. 45.4%) had autotomized some portion of the tail at least once. The proportion of individuals with regenerated tails did not differ between sexes (females versus males = 45.3% versus 45.5%; G = 0.0003, df = 1, $P > 0.90$; Figure 1). Of the geckos with previous bouts of tail autotomy, 36 (61.0%) had shed their tails in the proximal portion (< 10% tail length, from the vent to where the tail was autotomized) of the tail, 17 (28.8%) near the proximal portion (10%–40% tail length), 6 (10.2%) in the middle portion (40%–70% tail length), and 0 (0%) in the distal portion (> 70% tail length). The frequency distribution of locations of the tail break did not differ between sexes (G = 10.8, df = 6, $P > 0.05$). When data for the sexes were pooled, we found that the number of geckos shedding tails in the proximal, near proximal, middle, and distal portions of the tail differed significantly (G = 26.6, df = 3, $P < 0.0001$), with more tail breaks occurring near the base of the tail (Figure 1).
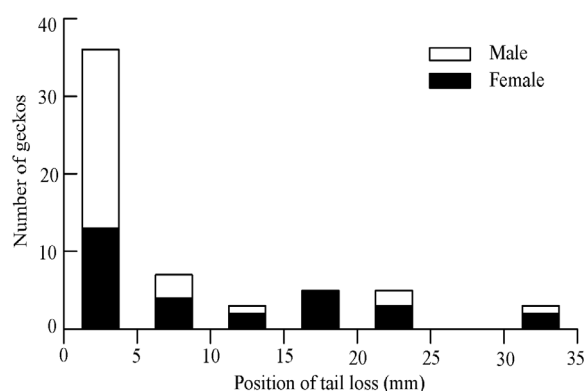

Figure 1 Frequency distribution of locations at which tail autotomy occurred. Data are based on 130 adults of *H. bowringii* collected from the field. Solid bars: Females; Open bars: Males; 0: Tailbase (i. e., cloaca); 35: 35 mm from the tailbase.

Figure 2 shows locomotor performance of experimental (tailless) and control (tailed) geckos in horizontal and vertical directions. Overall speed and sprint speed did not differ between tailless and tailed geckos (Table 1). The influences of locomotor direction on overall speed and sprint speed were both significant, with horizontal speeds being greater than vertical speeds; the interaction between tail condition and locomotor direction was not significant in overall speed, but was significant in sprint speed (Table 1).
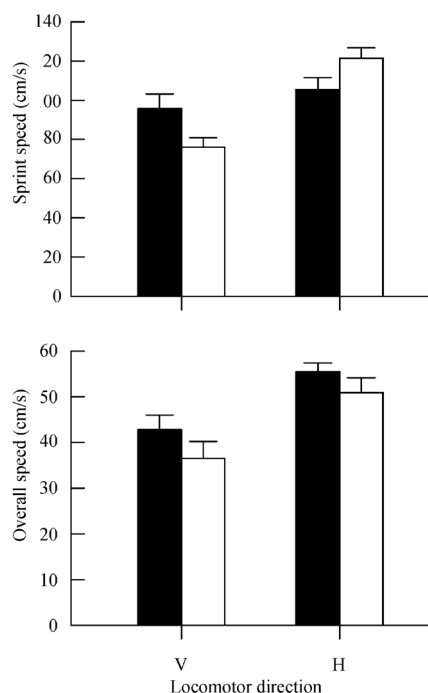

Figure 2 Mean values (+ SE) for the two locomotor variables (sprint speed and overall speed) of tailed and tailless geckos in the vertical and horizontal locomotor directions. V: Vertical locomotor direction; H: Horizontal locomotor direction; Solid bars: Tailless geckos; Open bars: Tailed geckos.

Table 1 Results of repeated-measures ANOVA with tail condition (tailed versus tailless geckos) as the between-subject factor and locomotor direction (horizontal versus vertical) as the within-subject factor for locomotor performance.

Effect	Locomotor performance	
	Sprint speed	Overall speed
Tail condition	$F_{1, 21} = 0.08, P = 0.781$	$F_{1, 21} = 2.00, P = 0.172$
Locomotor direction	$F_{1, 21} = 36.56, P < 0.0001$; H > V	$F_{1, 21} = 19.93, P < 0.0005$; H > V
Interaction	$F_{1, 21} = 15.37, P < 0.001$	$F_{1, 21} = 0.078, P = 0.782$

H: Horizontal direction; V: Vertical direction

4. Discussion

Tail autotomy is widespread in lizards, but the frequency and degree of tail loss differ among species. The frequency of tail breaks in the natural population of *H. bowringii* is about 45%, falling within the range (3%–82%) reported for most lizards with the mechanism of caudal autotomy (Bateman and Fleming, 2009). The frequency of tail breaks is indicative of the intensity of interspecific predation in natural populations of lizards. The frequency of tail breaks is lower in *H. bowringii* than in other ground-dwelling diurnal lizards such as *Eumeces chinensis* (73%; Lin *et al*., 2006), *Sphenomorphus indicus* (77%; Sun *et al*., 2007) and *Eutropis* (*Mabuya*) *multifasciata* (57%; Sun *et al*., 2009) that can be found within the range of *H. bowringii*, presumably suggesting that the intensity of predation pressure differs among lizards that differ in habitat preference and temporal activity pattern. Tail autotomy in *H. bowringii* (about 61%; Figure 1) occurred largely close to the tail base, suggesting that, as in *Takydromus septentrionalis* (Lin and Ji, 2005), *E. chinensis* (Lin *et al*., 2006), *S. indicus* (Sun *et al*., 2007) and *E. multifasciata* (Sun *et al*., 2009), most of tail breaks occurring in nature involve major tail loss in the gecko.

Tail loss adversely affects horizontal locomotion in several species of lizards (Martín and Avery, 1998; Shine, 2003; Chapple *et al*., 2004; Lin and Ji, 2005; Goodman, 2006; Sun *et al*., 2009). Our study shows that there is no significant effect in either sprint speed or overall speed after tail loss (Figure 2). So, we suggest that the tail does not play an important role in horizontal locomotion of *H. bowringii*, which is also true in the velvet gecko *Oedura lesueurii* (Kelehear and Webb, 2006), the Cape dwarf gecko *Lygodactylus capensis* (Medger *et al*., 2008) and the frog-eyed sand gecko *Teratoscincus scincus* (Lu *et al*., 2010).

Xu *et al*. (2009)'s finding that tail loss in *H. bowringii* can decrease the locomotor ability on a horizontal surface, and complete tail loss can significantly affect its sprint speed, is a direct contradiction to our result. So, why does tail loss affect locomotor performance of *H. bowringii* in Xu *et al*. (2009)'s study? It may be caused by the different tail breaking method. Xu *et al*. (2009) cut the gecko's tail using a scalpel, which resulted in more trauma than tail autotomization. The tail base stores hemipenes in male lizards, and the method Xu *et al*. (2009) used caused much more injuries to the experimental geckos than tail autotomy did. So we believe that the result will be more reliable if a less harmful method had been taken.

Hemidactylus bowringii uses its adhesive toes to walk on vertical or sloping surface, and our results indicate that the tailless individuals were over 20.6% faster than the tailed individuals (Figure 2). The force of gravity acting on geckos in vertical motion can affect its locomotion (Medger *et al*., 2008). Tail loss may decrease the body burden in *H. bowringii*, and hence tailless individuals can move at a faster sprint speed to increase the probability of successful escapes from predators. This locomotory advantage following tail autotomy is also observed in *Phyllodactylus marmoratus* (Daniels, 1983), but not in *L. capensis* (Medger *et al*., 2008), and may be attributed to the differences in species-specific traits.

The horizontal speed was always faster than the vertical locomotory speed in *H. bowringii*. For the tailed geckos, the horizontal sprint speed was 37% faster than the vertical speed, and for the tailless individuals, this value was 9% (Figure 2). For the tailed geckos, the horizontal overall locomotory speed was 28% faster than the vertical speed, and for the tailless ones, this value was 23% (Figure 2). These results are similar to those from *L. capensis* (Medger *et al*., 2008), and a possible explanation for why speed increases may lie in that less weight makes the vertical speed faster. However, there was no significant effect with the horizontal and vertical sprint speed in tailless geckos, which may be related with the reducing self burden. Sprint speed is a key index of functional performance in lizards, the increase of vertical sprint speed is very important for tailless geckos escaping from a vertical surface.

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