Tail Autotomy Plays No Important Role in Influencing Locomotor Performance and Anti-Predator Behavior in a Cursorial Gecko

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Abstract

We used the frog-eyed sand gecko (*Teratoscincus scincus*) as a model system to evaluate the locomotor costs of tail loss, and to examine whether tailless geckos use alternative anti-predator behavior to compensate for the costs of tail loss. Of the 16 field-captured geckos, eight were used as experimental animals and the remaining ones as controls. Locomotor performance, activity level and anti-predator behavior were measured for experimental geckos before and after the tail-removing treatment. Control geckos never undergoing the tail-removing manipulation were measured to serve as controls for the measurements taken at the same time for experimental geckos. Experimental geckos did not differ from controls in activity level before they underwent the tail-removing manipulation, but became less active thereafter. The mean locomotor stamina of tailless geckos was reduced by about 30% of the mean value for tailed ones. However, as the maximum stamina predicted from the laboratory trials is seldom required in nature, we expect that the costs associated with the reduced locomotor stamina may be relatively minor in *T. scincus*. All other examined locomotor (overall speed, maximal speed and stride length) and behavioral (distance to refuge, approach distance and flight distance) traits were not affected by the tail-removing manipulation. Overall, our results suggest that tail autotomy plays no important role in influencing locomotor performance and anti-predator behavior in lizards where the tail has no direct role in locomotion but is used to direct predatory strikes away from the torso.

Introduction

Many lizards use tail autotomy to evade fatal predatory encounters after other anti-predation strategies such as crypsis and flight have failed (Arnold 1988). While providing an immediate survival benefit by facilitating escape from predators, tail autotomy entails a number of costs that may affect the individual's subsequent fitness (Arnold 1988; Bernardo & Agosta 2005; Clause & Capaldi 2006; Bateman & Fleming 2009). For example, the loss of energy stored in the tail may retard growth (Ballinger & Tinkle 1979; Niewiarowski et al. 1997; Goodman 2006), reduce reproductive output (Smyth 1974; Dial & Fitzpatrick 1981; Taylor 1986; Wilson & Booth 1998) and increase mortality during hibernation (Bauwens 1981; Daniels 1984). Tailless lizards may also have reduced abilities to survive subsequent predatory encounters (Dial & Fitzpatrick 1984; Niewiarowski et al. 1997; Fox & McCoy 2000; Downes & Shine 2001), decreased home range size and access to females (Martin & Salvador 1993a; Salvador et al. 1995) and diminished social status (Fox & Rostker 1982; Fox et al. 1990; Martin &

Salvador 1993a). Many lizards have evolved specialized behavioral shifts to compensate for the costs associated with tail loss. For example, tailless lizards may rely more on crypsis, stay closer to refuges, and flee earlier from predators (Formanowicz et al. 1990; Downes & Shine 2001; Cooper 2003a, 2007). However, these behavioral adjustments often entail additional costs (Martín & Salvador 1993a; Downes & Shine 2001).

Of the costs associated with tail autotomy, changes in locomotor performance and anti-predator behavior have received the most attention. The effects of tail autotomy on locomotor performance may vary among lizard species. For example, while reducing running speed in many lizards (Fleming et al. 2009 and references therein), tail loss increases running speed in other lizards such as the Texas banded gecko *Coleonyx brevi* (Dial & Fitzpatrick 1981), the marbled gecko *Christinus* (*Phyllodactylus*) *marmoratus* (Daniels 1983) and the common wall lizard *Podarcis muralis* (Brown et al. 1995) because of reduced weight, reduced friction with the substrate or altered anti-predator behavior. In species where the tail has no direct role in locomotion, the locomotor costs associated with tail loss are relatively minor or even negligible (Kelehear & Webb 2006; Medger et al. 2008). The effects of tail loss on behavioral performance may also vary among lizard species. For example, tailless Texas banded geckos increase foraging activities to meet the increased energetic demands during tail regeneration (Dial & Fitzpatrick 1981). However, as increasing activity level may potentially increase the risks of predation, not all lizards do the same as *C. brevi* after undergoing tail loss. For example, Iberian rock lizards (*Lacerta monticola*; Martín & Salvador 1993b), Mongolian racerunners (*Eremias argus*; Zhao et al. 2008) and many-lined sun skinks (*Mabuya multifasciata*; Sun et al. 2009) do not increase foraging activities after undergoing tail autotomy. Taken together, previous studies of lizards show that tail autotomy often affects locomotor and behavioral performances, but not always.

In this study, we investigated the impact of tail loss on locomotor performance and anti-predator behavior in a psammophilous cursorial gecko, *Teratoscincus scincus*. We address four questions: (1) does tail loss affect locomotor performance in cursorial geckos? (2) if so, how are different locomotor variables affected by tail loss? (3) do tailless geckos compensate for any negative effects of tail loss by using alternative anti-predator behaviors? (4) if so, how are different aspects of anti-predator behavior affected by tail loss?

Materials and Methods

Study Animals

The frog-eyed sand gecko (*Teratoscincus scincus*) is a medium-sized (to 93 mm snout-vent length, SVL), nocturnal gekkonid lizard that is widely distributed in desert regions in central Asia (westwards to Iran), including Northwest China (Liu 1999). In daytime, it hides in burrows in the sand, leaving them after dark to forage outside (Liu 1999). Despite the fact that it is taxonomically and biogeographically well known (Macey et al. 1997, 1999; Hiller 2005), the ecology and biology of *T. scincus* remain poorly known (but see Marcellini 1977; Szél et al. 1986; Loewe et al. 1996; Seligmann et al. 2007).

We collected 16 adult males (SVL > 70 mm) in late Apr. 2008 from a population in Jinghe (44°40′N, 82°55′E), Xinjiang, north-west China. Each individual was intact and showed no evidence of previous tail autotomy. Geckos were placed singly in cloth bags and transported to our laboratory in Hangzhou, where they were weighed, measured for SVL and tail length, and marked by a non-toxic waterproof label for future identification. We housed four geckos in each of four cages (length × width × height: 50 cm × 20 cm × 25 cm) that contained a substrate of sand (10 cm in depth), with rocks and pieces of clay tiles provided as the cover. The cages were placed in an indoor animal holding facility where temperatures varied from 22°C to 28°C. Geckos 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*. Geckos were held in captivity 3 wk prior to experimentation and were released at the site of capture soon after the experiments.

Experimental Procedures

Eight geckos were used as experimental animals, and the remaining ones as controls. Experimental geckos did not differ from controls in SVL, body mass and tail length (ANOVA for SVL and ANCOVA with SVL as the covariate for the other two variables; all p > 0.264). We measured locomotor performance of control and experimental geckos having intact tails at a body temperature of 28°C, which was achieved by placing geckos into an incubator at the corresponding temperature for about 2 h prior to each trial. Geckos were individually chased down the length of a 1.2 m racetrack with one transparent side through which they were filmed with a

PCO1200 high-speed digital camera (100 frames per second; Cooke Corporation, Romulus, MI, USA) connected to a PC computer. Each gecko was chased twice, with a minimum of 30 min rest between the two trials. The clips were examined on a frame-by-frame basis using MaxTRAQ 2D software (Innovision Systems Inc., Columbiaville, MI, USA) for the overall speed (the maximal length traveled without stopping divided by the time taken), maximal speed (the maximal stride speed calculated as stride length divided by stride duration) and stride length (the interval between consecutive footfalls of the right hindfoot). The stride length was repeatedly measured for each gecko, with the mean value used for statistical analyses. The locomotor stamina was measured on a TSE treadmill (TSE Systems International Group, Bad Homburg, Germany) at a speed of 22 cm/s. We individually introduced geckos into the treadmill, and then tapped on the mid-body with a paintbrush to encourage them to run. The time it took for each gecko to run until exhaustion, as estimated from the loss of any locomotor ability after strong stimulation on the head with the same paintbrush, was considered as its locomotor stamina.

Following the measurement of locomotor performance, we moved all geckos into a 4 m × 4 m enclosure built in a 60 m² room where temperatures were controlled at 22.0 ± 1.0°C. The enclosure contained a substrate of sand (15 cm in depth), with nine plastic pipes (30 cm in length and 15 cm in diameter) half-buried in the substrate in a random way. Three 200 W ceramic heaters suspended above the enclosure created thermal gradients ranging from the room temperature to about 55°C for 24 h daily, so that geckos had an ample opportunity to regulate body temperature. We recorded activity level (the number of geckos that could be seen) and behavioral responses (distance to nearest refuge, approach distance and flight distance) to an approaching person (always the first author beginning at a fixed point 5 m away from the centre of the enclosure) at a speed of ~60 m/min during the period of 20:00–23:00 hours (Liu 1999) for 7 d. Distance to refuge was the distance between a sighted gecko and the nearest plastic pipe. Approach distance was the distance between the approaching person and a gecko when it began to flee. Flight distance was the distance between a gecko's initial position and its first stop position after fleeing.

After obtaining data for experimental geckos having intact tails, we removed their tails by grasping the tail base with forceps, thereby producing tailless geckos. All these individuals were not anesthetized for the autotomy so that tail separation always occurred at natural fracture planes. Tailless geckos were allowed to heal the wound for 7 d to minimize the possible influence of handling stress, and were thereafter examined following the procedures described above. Control geckos were also examined to serve as controls for the measurements taken at the same time for tailless geckos.

Statistical Analyses

All data were tested for normality (Kolmogorov–Smirnov test) and homogeneity of variances (F-max test). No data needed to be transformed to meet the assumptions of parametric analyses. We used Wilcoxon matched pairs test to examine whether the tail-removing manipulation induced variation in activity level. None of the examined locomotor and behavioral variables was dependent on body size (SVL) (linear regression analysis; all $p > 0.15$), so we used repeated measures ANOVA to analyze the corresponding data, with tail-removing manipulation as the between-subject factor and time step (before and after the manipulation) as the within-subject factor. Descriptive statistics are presented as mean ± SE, and the significance level is set at $\alpha = 0.05$.

Results

Experimental geckos did not differ from control ones in activity level before they underwent the tail-removing manipulation ($Z = 1.83$, $p = 0.068$), but became less active when their tails were removed ($Z = 2.37$, $p < 0.02$) (Fig. 1). Activity levels did not differ in control geckos measured before and after the tail-removing episode ($Z = 0.27$, $p = 0.787$) (Fig. 1).

The tail-removing manipulation reduced locomotor stamina, but had no influence on the other three locomotor variables (Fig. 2; Table 1). Mean values for the three behavioral variables (distance to refuge, approach distance and flight distance) were apparently greater in tailed geckos (Fig. 3) but, statistically, these values did not differ between experimental and control geckos, and between geckos measured before and after the tail-removing episode (Table 2).

Discussion

Our sample size was relatively low (eight geckos in each group), and this limitation might hamper detection of differences. However, as the observed
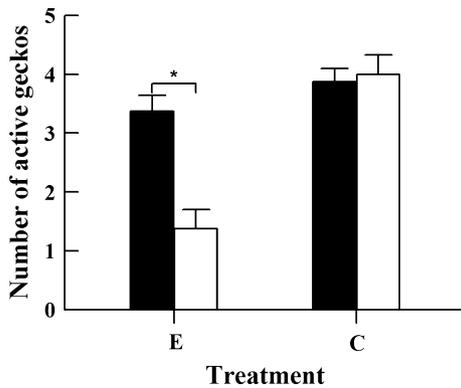
Fig. 1: Mean values (+SE) for activity levels of tailed and tailless frog-eyed sand geckos. E, experimental geckos; C, control geckos; solid bars: activity levels measured before the tail-removing treatment; open bars: activity levels measured after the tail-removing treatment. The asterisk denotes a significant difference (p < 0.05) in activity level between tailed and tailless geckos.

non-significant differences are so small, we believe that our conclusions (acceptance or rejection of the null hypothesis) are likely to be identical even when sample size would be much larger.

The tail is one of the major sites of energy storage and represents a considerable portion of body mass in *T. scincus* (Liu 1999). We predicted that *T. scincus* would become faster after undergoing tail loss as a result of reduced weight or friction with the substrate, as for *C. brevi* (Dial & Fitzpatrick 1981) and *C. marmoratus* (Daniels 1983). Contrary to our expectation, tailless frog-eyed sand geckos did not differ from tailed ones in running speed (Fig. 2; Table 1),

thus suggesting that the tail may not be a major physical burden for *T. scincus* to carry over short distances (such as those tested in this study). On the racetrack and during encounters with an approaching human predator, tailed frog-eyed sand geckos always raised their tails to run. Moreover, tailed and tailless geckos never run the entire length of the racetrack but exhibited intermittent locomotion, with movement sequences interrupted by frequent short pauses. During short pauses, tailed geckos raised or vigorously waggled their tails. What can be inferred from these observations are: (1) the tail plays no important role in influencing locomotor speed in *T. scincus*; and (2) the frog-eyed sand gecko is among lizard species that use tail displays to attract predatory strikes away from the torso (Bustard 1965; Congdon et al. 1974; Daniels et al. 1986; McConnachie & Whiting 2003; Kelehear & Webb 2006).

In this study, tail loss impacted only one aspect of locomotion by reducing locomotor stamina. The negative impact of tail loss on locomotor stamina has also been found in the eastern water skink *Sphenomorphus* (*Eulamprus*) *quoyii* (Daniels 1985), the metallic skink *Niveoscincus metallicus* (Chapple & Swain 2002) and the Cape dwarf gecko *Lygodactylus capensis* (Fleming et al. 2009). It is hypothesized in *N. metallicus* that the increase of stride frequency due to tail loss may reduce locomotor stamina (Chapple & Swain 2002). Our data do not support this idea, because tailed geckos did not differ from tailless ones in both stride length and locomotor speed (Fig. 2; Table 1), and thus stride frequency. Fleming et al.
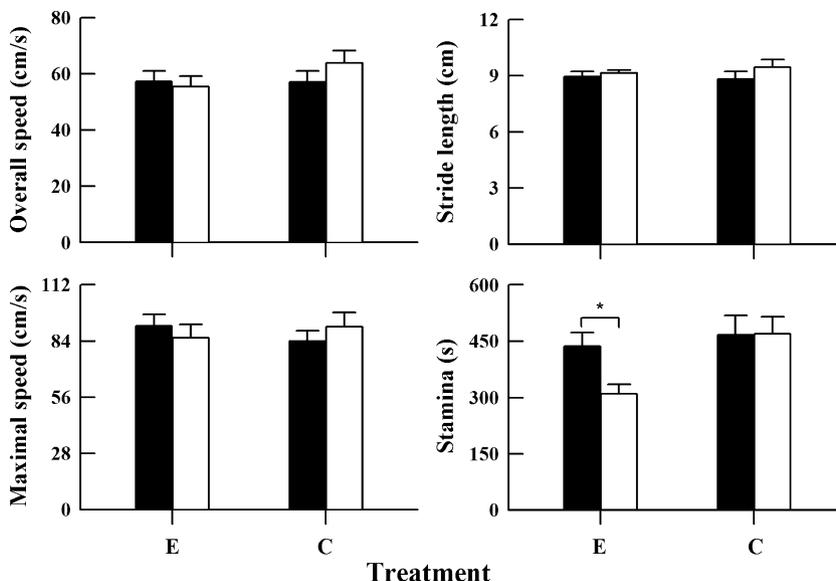
Fig. 2: Mean values (+SE) for the four locomotor variables (overall speed, maximal speed, stride length and locomotor stamina) of tailed and tailless frog-eyed sand geckos. E, experimental geckos; C, control geckos; solid bars: measurements taken before the tail-removing treatment; open bars: measurements taken after the tail-removing treatment. The asterisk denotes a significant difference (p < 0.05) in locomotor stamina between tailed and tailless geckos.

Table 1: Results of repeated-measures ANOVAs on the four locomotor variables (overall speed, maximal speed, stride length and locomotor stamina) measured for tailed and tailless frog-eyed sand geckos, with animal category (control vs. experimental geckos) as the between-subject factor and time step (measurements taken before and after the tail-removing treatment) as the within-subject factor

	Locomotor variables			
	Overall speed	Maximal speed	Stride length	Locomotor stamina
Control vs. experimental geckos	$F_{1,14} = 0.99$, $p = 0.337$	$F_{1,14} = 0.04$, $p = 0.840$	$F_{1,14} = 0.05$, $p = 0.828$	$F_{1,14} = 3.13$, $p = 0.099$
Time step	$F_{1,14} = 0.43$, $p = 0.522$	$F_{1,14} = 0.01$, $p = 0.927$	$F_{1,14} = 0.002$, $p = 0.967$	$F_{1,14} = 9.27$, $p < 0.01$ T1 > T2
Interaction	$F_{1,14} = 1.28$, $p = 0.277$	$F_{1,14} = 0.94$, $p = 0.348$	$F_{1,14} = 1.02$, $p = 0.331$	$F_{1,14} = 9.91$, $p < 0.01$

T1, measurements taken before the tail-removing treatment; T2, measurements taken after the tail-removing treatment.

(2009) interpret a reduction in locomotor stamina in tailless *L. capensis* as reflecting a reduction in active metabolic rate after tail autotomy. However, we are

Fig. 3: Mean values (+SE) for the three anti-predator behavioral variables (distance of refuge, approach and flight distance) of tailed and tailless frog-eyed sand geckos. E, experimental geckos; C, control geckos; solid bars: measurements taken before the tail-removing treatment; open bars: measurements taken after the tail-removing treatment.

currently unable to test whether this interpretation also applies to *T. scincus* because our experiment was not designed to look at the effects of tail loss on locomotor energetics. The mean locomotor stamina of tailless geckos was reduced by about 30% of the mean value for tailed ones (Fig. 2). However, as free-ranging frog-eyed sand geckos are able to assess predation risks and react accordingly by modulating approach distance, speed and pauses (Liu 1999), the maximum stamina predicted from the laboratory trials may be seldom required in nature. We therefore expect that the costs associated with the reduced locomotor stamina may be relatively minor in *T. scincus*.

Tail regeneration is the most effective way to counteract the costs of tail loss. Thus, in most cases a successful autotomous escape is followed by regeneration of the lost tail. Tail regeneration is energetically expensive and may, therefore, require the diversion of energetic resources from other functions such as growth and reproduction (Congdon et al. 1974; Ballinger & Tinkle 1979; Dial & Fitzpatrick 1981; Bellairs & Bryant 1985; Martin & Salvador 1993b). Regeneration costs may also be met by increasing food intake (Dial & Fitzpatrick 1981). Assuming a positive correlation between foraging activity and food intake, one may expect that to increase food intake tailless lizards would forage longer than tailed ones. For example, tailless Texas banded geckos have to be more active to increase foraging time (Dial & Fitzpatrick 1981). However, as tailless lizards must forage without their primary defense mechanism, the risks of predation to tailless lizards may be concomitantly greater. Thus, if being active is costly for a lizard species, tailless lizards that reduce activity levels could be more likely to minimize predation risks while simultaneously saving energy that can be shunt to tail regeneration (Formanowicz et al. 1990; Martin & Salvador 1993b; Salvador et al. 1995; Downes & Shine 2001; Cooper 2007; Zhao et al. 2008). Our finding that tailless
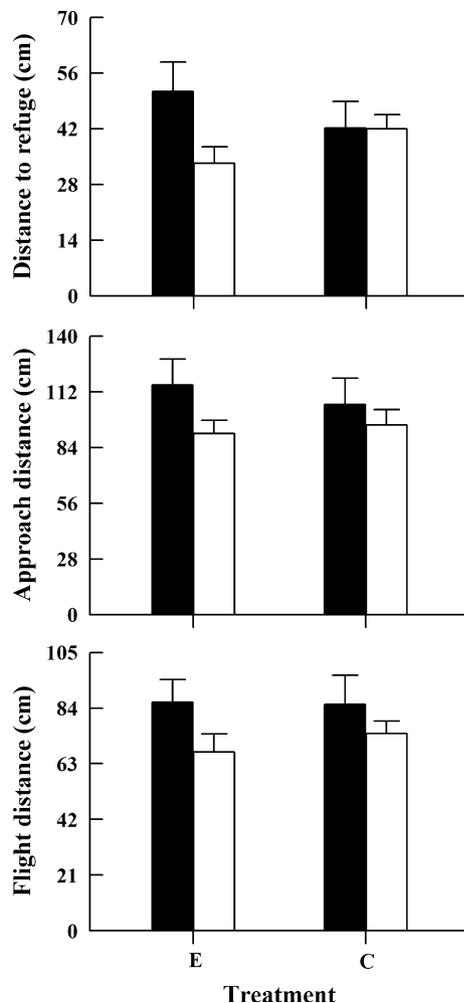
Table 2: Results of repeated-measures ANOVAs on the three anti-predator behavioral variables (distance of refuge, approach and flight distance) measured for tailed and tailless frog-eyed sand geckos, with animal category (control vs. experimental geckos) as the between-subject factor and time step (measurements taken before and after the tail-removing treatment) as the within-subject factor

| | Anti-predator behavioral variables | | |
	Distance to refuge	Approach distance	Flight distance
Control vs. experimental geckos	$F_{1,14} = 0.003$, $p = 0.959$	$F_{1,14} = 0.05$, $p = 0.822$	$F_{1,14} = 0.12$, $p = 0.734$
Time step	$F_{1,14} = 2.01$, $p = 0.178$	$F_{1,14} = 3.20$, $p = 0.095$	$F_{1,14} = 4.24$, $p = 0.059$
Interaction	$F_{1,14} = 1.90$, $p = 0.189$	$F_{1,14} = 0.53$, $p = 0.477$	$F_{1,14} = 0.29$, $p = 0.600$

geckos reduced activity levels is of interest, because it might suggest that tailless frog-eyed sand geckos use this behavioral adjustment to minimize predation risks in nature. More interestingly, a reduction of activity level following tail autotomy appears to be common in lizards that use tail displays to direct predatory strikes away from the torso (Bustard 1965; Congdon et al. 1974; Daniels et al. 1986; Kelehear & Webb 2006).

Lizards often use alternative anti-predator behaviors when undergoing tail autotomy (Martín & Salvador 1993b; Cooper 2003b; 2007). However, the effects of tail autotomy on aspects of anti-predator behavior may vary among species. For example, tailless keeled earless lizards (*Holbrookia propinqua*) tend to stay closer to refuges, and take a greater flight distance but a similar approach distance (Cooper 2003a). In the striped plateau lizard (*Sceloporus virgatus*), however, tailless lizards do not change the distance to refuges, but run sooner and flee further during encounters with predators (Cooper 2007). Our finding that none of the three examined aspects of anti-predator behavior is affected by tail loss in *T. scincus* is of interest, because it suggests that the effects of tail autotomy on anti-predator behavior may be more diverse in lizards than thought before. There are three possible explanations for this finding. First, because locomotor speed is not negatively affected by tail autotomy, it is not necessary for tailless frog-eyed sand geckos to alter their anti-predator behaviors because their ability to flee from an approaching predator is apparently unaffected by tail autotomy. Secondly, field (Liu 1999) and laboratory (Fig. 3) studies show that both tailed and tailless frog-eyed sand geckos both stay quite close to refuges. Hence, we expect that changes in anti-predator behavior may contribute little (if any) to the survival benefit, because tailless geckos may not take a longer time than tailed ones to enter available retreat sites during encounters with predators. Finally, it is conceivable that our experimental design, in which behavioral trials were carried out in a small

laboratory enclosure, did not allow us to detect changes in a gecko's ability to use alternative anti-predator behaviors to compensate for the costs associated with tail loss. Consistent with the results reported for *O. lesueurii* (Kelehear & Webb 2006) where the tail also has no direct role in locomotion but is used to attract predatory strikes away from the torso, our data show that tail autotomy has no important role in influencing locomotor performance and anti-predator behavior in *T. scincus*.

Acknowledgements

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