Autotomy, tail regeneration and jumping ability in Cape dwarf geckos (*Lygodactylus capensis*) (Gekkonidae)

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Many studies have examined the effect of caudal autotomy on speed and behaviour of lizards escaping over horizontal surfaces, but there have been few studies on lizards escaping over vertical surfaces and, in particular, species that jump between surfaces. We examined jumping by the Cape dwarf gecko (*Lygodactylus capensis*) in terms of individuals' varying states of tail autotomy and regeneration. Although longer jumps were less likely to be successful (i.e. the animal would not successfully grip the surface and fell to the ground), there was no difference in the distance over which animals with full and partial tails would attempt to jump. Both recently autotomized individuals and individuals with intact tails successfully jumped up to nine times their body length (snout–vent length). The jumping ability of *L. capensis* was therefore clearly not negatively impaired by tail loss, presumably because the geckos are using their hind legs to propel their jump. Their tails may, however, be important to control their landing as well as their locomotion on vertical surfaces. The high observed frequency of tail loss, coupled with rapid and complete regeneration (including the scansorial tail tip), suggests that caudal autotomy is an important survival tactic in this species.

Key words: caudal autotomy, defence, escape behaviour, leaping, lizard, tail loss.

INTRODUCTION

Many species of lizard escape by running and jumping away from predators. Caudal autotomy is an extreme defence tactic where lizards shed their tail to escape predators (Arnold 1984, 1988; Bateman & Fleming 2009). As a consequence of shedding their tail, lizards can experience compromised locomotion. Reduction of speed has been demonstrated for most species examined; however, there are some notable exceptions, suggesting that for some species, reduction in body mass as a consequence of tail loss may actually be beneficial for escape speed (reviewed by Bateman & Fleming 2009). A number of species have also been recorded as having decreased endurance after tail autotomy (reviewed by Bateman & Fleming 2009).

In addition to speed and stamina, a tail may be important for agility, particularly for arboreal or vertical surface-dwelling lizards where it may be used as a prop to brace against the substrate, or to propel the body during movements. For example, *Podarcis muralis* can run faster on horizontal surfaces post-autotomy but much slower on an arboreal substrate when tailless (Brown *et al.* 1995). Jumping can be as important as running if the lizard's escape route can take them between trees, branches and other surfaces (e.g. Losos & Irschick 1996), and for *Anolis carolinensis* (a tree-branch ecomorph anole), the accuracy of jumps is compromised by tail autotomy (Gillis *et al.* 2009).

Arguably, one of the best-studied species for the effects of autotomy on vertical and horizontal escape ability is the small diurnal Cape dwarf gecko (*Lygodactylus* capensis). Medger *et al.* (2008) found that autotomy had little effect on horizontal escape speed (although initial speed was faster for autotomized geckos), but vertical escape speed was significantly reduced in this species, with increased likelihood of the geckos falling off the vertical surface. The tail tip of *Lygodactylus* spp. has a scansorial pad, similar to those on the feet, which acts as a fifth point of attachment, while the tail itself appears to act as a brace to prevent the animal falling backwards (Bauer & Russell 1994; Medger *et al.* 2008). Fleming *et al.* (2009) reported that autotomized *L. capensis* incur energetic costs on horizontal surfaces, expending less effort in running, moving both slower and for a shorter distance than intact geckos and having lower excess CO_2 production (CO_2 production in excess of normal resting metabolic rate) when running.

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Decreased stamina may be due to the loss of adipose tissue (fuelling metabolism) in the tail; although we do not know the tissue composition of tails in this species, the tails of these animals are between 9 and 13% of body mass (Medger *et al.* 2008; Fleming *et al.* 2009) and therefore are likely to represent a substantial portion of their body reserves.

Although their tails are therefore important for locomotion, a high proportion (over 50%) of natural populations of *L. capensis* have regenerated tails (Medger *et al.* 2008; Fleming *et al.* 2009), suggesting that caudal autotomy is an important defence tactic in these animals. The tail regenerates quickly in *Lygodactylus* spp. (first visible approximately 11 days post autotomy, Medger *et al.* 2008), and the scansorial pad has regenerated after about four weeks (Maderson 1971; Vitt & Ballinger 1982). This rapid regrowth may counter the locomotory costs associated with tail loss.

Preliminary observations of *Lygodactylus capensis* in the field, both in urban and undeveloped sites, indicate that vertical running is only part of the escape behaviour and that, when running up one surface, geckos orient their head and body towards a separate vertical surface (wall or branch), bring their feet together, pause briefly and then jump across the interstice to the targeted surface. *Lygodactylus capensis* also jumps (i.e. all legs off the ground) when sprinting on horizontal surfaces, but jumping was only noted for intact individuals (Medger *et al.* 2008). As autotomy has a significant effect on vertical escape running in this species, we were interested in examining the effect of autotomy and regrowth of the tail on jumping ability, the other component of escape behaviour.

We made two predictions:

i) Intact geckos or geckos with fully regenerated tails would be prepared to jump farther than geckos with partial tails (lacking the distal scansorial pad) or no tails; and that

ii) Intact geckos or geckos with fully regenerated tails were more likely to jump successfully (would land on and stick to the vertical surface) than geckos with partial or no tails.

METHODS

The Cape dwarf gecko (*Lygodactylus capensis*) is a small (mean SVL 34.6 ± 3.0 mm, n = 39: this study; approx. 1.0 g mass) diurnal gecko, widely distributed across eastern and southern Africa where it is common in urban areas on walls and posts, and on scrub and high in dead trees in undeveloped areas (Pianka & Huey 1978; Simbotwe 1983a; Branch 1998). We captured 39 *L. capensis* by hand at several sites in southern Zimbabwe in May 2010. Animals on a branch or pole were captured by approaching the animal from the other side of the pole and, under direction from a second observer, swiftly covering the animal with both hands. In this way we were able to catch geckos without running them to exhaustion, which might affect their subsequent locomotion (Fleming *et al.* 2009).

We tested geckos within 10 min of capture and released them immediately after testing. Animals were never removed from their point of capture. Animals were measured (snout–vent length (SVL) and tail length), the state of the tail was recorded (intact or autotomized) and the original and regenerated portions of the tail were measured. We also recorded whether the animal had regenerated the adhesive pad on the distal tip of the tail. Animals were classified as having a partial tail (17 individuals with incomplete regeneration) or a full tail (16 intact animals and six animals that had regrown their tail, complete with the distal tail pad). Animals were marked with a non-toxic temporary marker to ensure that they would not be resampled.

We then recorded a simple but realistic metric of jumping ability. *Lygodactylus capensis* held (not restrained) on the fingers of an open hand of a person jump towards adjacent objects to escape in the same way as they do on natural surfaces: they orient their head and eyes towards a target landing spot, shuffle their feet together and launch towards it. Starting from a distance of 0.5 m, the experimenter slowly (approximately 3 cm/s) advanced the hand with the gecko towards a vertical surface (a wooden pole cleared of bark, 15–20 cm diameter) at chest height.

We recorded the distance from the target surface when the gecko jumped (cm).

Jumps were categorized as 'successful' where:

W = The animal walked off finger onto the vertical surface (scored as 1 cm from target)

A = The animal jumped from finger and landed on the vertical surface at a point directly adjacent launch point

B = The animal jumped from finger and landed on the vertical surface at a point more than two body lengths below launch point

Or 'unsuccessful', where

C = The animal fell to the ground

The distance over which animals jumped was

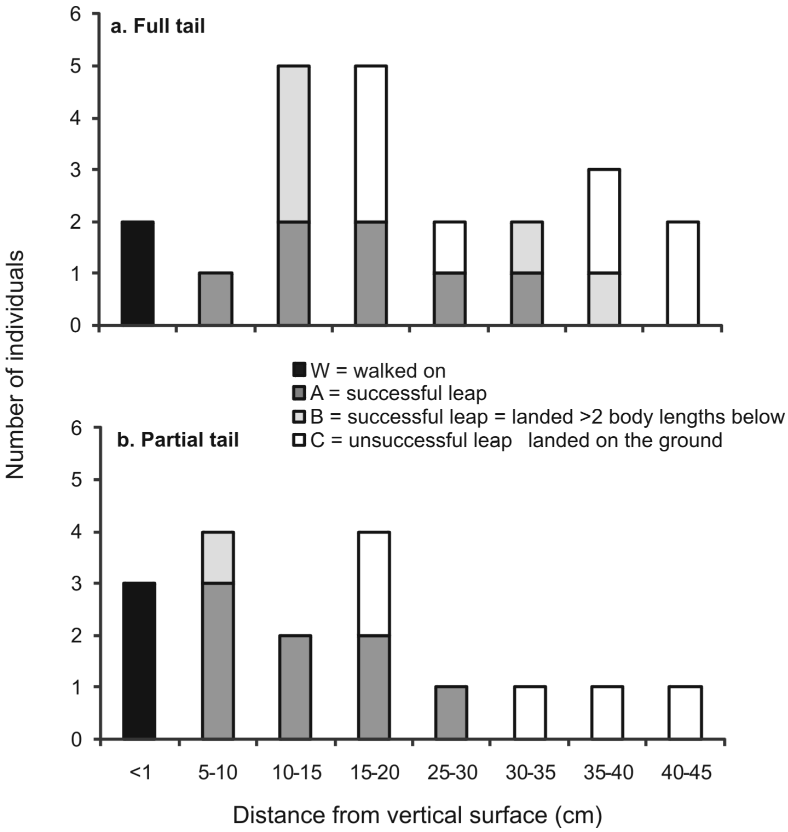

Fig. 1. The distribution of individual animals that jumped across a distance between the experimenter's finger tip and an adjacent vertical target surface (recorded as the jump distance). *Lygodactylus capensis* with either an intact tail (**a**): 'full tail', including animals that had regenerated their tail complete with the scansorial tail tip), or only a partial tail (**b**), are shown and are coded by the outcome of each jump.

compared between animals with a full or partial tail by *t*-test. The fate of a jump (dependent variable, classified as either 1 = successful or 0 = unsuccessful) was tested for the effects of having a tail or not (1 = full tail or 0 = partial tail), tail length (as a percentage of SVL) and the distance from which the animal jumped (cm) as a logistic regression.

RESULTS

Of the 39 individual *L. capensis* captured, 59% (n = 23) had lost their tails previously. Eight of these animals had lost their tails recently (the wound had sealed off but regeneration had barely commenced) while six animals had fully regrown tails complete with the distal tail pad.

Five of the 39 (13%) geckos tested did not attempt to jump but walked off the experimenter's finger onto the vertical surface (Fig. 1). The majority of animals (54%) made a successful jump (landing directly opposite or <2 body lengths below) while a third of the animals tested (33%) made unsuccessful jump attempts.

There was no significant difference in the distance over which geckos with either a full (n = 16) or a partial (n = 23) tail attempted to jump (t_{37} = 0.82, P = 0.419) (Fig. 2). There was also no significant difference in the distance of successful jumps for geckos with either a full (n = 9) or a partial (n = 17) tail (t_{24} = 1.16, P = 0.257).

The fate of a jump (successful or unsuccessful) was also not dependent on whether the animal had a full or partial tail (Wald Statistic$_{df=1}$ = 1.69, P = 0.193) or the length of the tail (as a proportion of SVL; Wald Statistic$_{df=1}$ = 1.75, P = 0.186), but jumps over shorter distances were more likely to be successful (Wald Statistic$_{df=1}$ = 9.06, P = 0.003) (Fig. 2). All jumps that were ≤3 times SVL (jump distance ≤15 cm) were successful, while the longest successful jump was for an intact animal that jumped from 35 cm away (9.3 times SVL). The

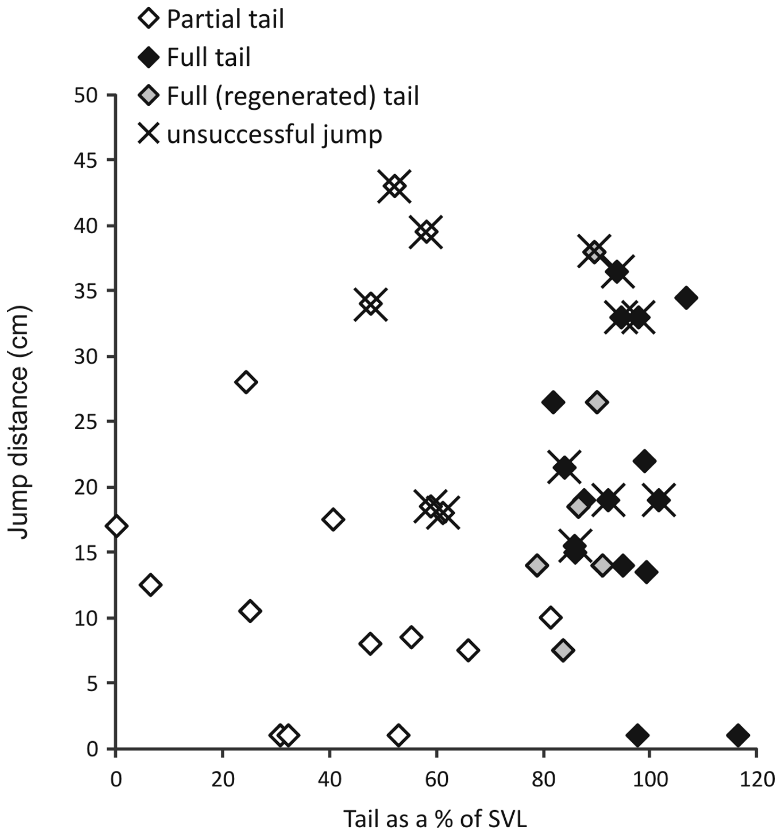

Fig. 2. Correlation between jump distance and relative tail length of *Lygodactylus capensis.* Tail length averages 95 ± 9% of snout–vent length (SVL) in intact individuals.

longest successful jump for an animal with a partial tail (remaining tail only 24% of SVL) was for an individual with a fresh autotomy (evident as recent healing of the tail, with only ~0.5 mm regrowth evident). This animal successfully jumped 28 cm (8.9 times SVL).

DISCUSSION

We found that autotomized *Lygodactylus capensis* resorted to escape jumping as often as animals with a full tail, and there was no significant difference in the distance over which these animals could successfully jump. We also found no significant effect of tail loss on jumping success (i.e. whether the gecko made it to the point more or less opposite its launching point). *Lygodactylus capensis* with or without a full tail (complete with scansorial tail tip) were capable of jumping up to nine times their body length (SVL) (this jumping ability is comparable to data from anoles: Losos & Irschick 1996; Gillis *et al.* 2009).

There have been analyses of jumping in intact individuals of various anole species that suggest this behaviour in lizards is quite stereotyped: jumps begin with positioning the hind feet close to the forefeet (which we observed in *L. capensis*), followed by takeoff powered by the hind limbs, trajectory through the air, then landing on the target surface (e.g. Toro *et al.* 2004). However, despite there being many arboreal, saxicolous and synanthropic wall-climbing lizard species that jump between surfaces, changes in jumping behaviour with autotomy have only been examined in detail once. Gillis *et al.* (2009) found that *Anolis carolinensis* that had undergone autotomy suffered no effect on jump velocity or jump distance through autotomy but were less stable when in mid-jump, rotating posteriorly in the air (i.e. becoming more 'upright' or even tumbling head over heels) to such a degree that accurate landing was compromised. The tail appears to act as a brake to this rotation through contact with the substrate during the launch phase.

Although we found no difference in jump ability of tailless and intact *L. capensis,* there may be an effect of autotomy on other variables that we could not measure. We did not have footage of our animals to compare their mid-air movements with *A. carolinensis.* We had no evidence to suggest that the loss of their tail compromised their landing, but recovery from jumps before continuing to run might also be affected, since a tailless lizard that tumbled head over heels in flight would likely have had to reorient itself before continuing to flee. Also we did not consider the effect of the substrate on which they landed: big trunks *vs* narrow twigs. Losos & Irschick (1996) found that decreasing perch diameter (i.e. a more 'twiggy' substrate) reduced sprint speed in five anole species and in the field, anoles jumped more frequently when escaping over small diameter substrates. The energetic costs of maintaining fleeing activity on *L. capensis* (Fleming *et al.* 2009) suggest that tailless geckos may be more susceptible to persistent predators; although Simbotwe (1983b) found that *L. capensis* and *L. chobiensis* in Kafue (Zambia) that had lost tails did not demonstrate heightened wariness over intact individuals. These aspects warrant further investigation.

In conclusion, tail loss and regeneration appeared to have little effect on the jumping ability of *L. capensis.* Medger *et al.* (2008) recorded a relatively high incidence of autotomy (57%) in their study population, very similar to that recorded in this study (59%) (between 3 and 82% across published data for other lizard species, Bateman & Fleming 2009). The rapid and complete (including scansorial pads and cutaneous glands) tail regeneration in a small, short-lived gecko (approximately 18 months, Branch 1998) with low survivorship (Simbotwe 1983a) suggests that the tail is important both for predator escape and for other functions. Future work should, however, consider whether recently autotomized *L. capensis* individuals alter their activity and microhabitat use adaptively to reflect their reduced escape capacity on vertical surfaces.

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