

Losing stability: tail loss and jumping in the arboreal lizard *Anolis carolinensis*

Gary B. Gillis^{1,*}, Lauren A. Bonvini^{1,†} and Duncan J. Irschick²

¹Department of Biological Sciences, Mount Holyoke College, South Hadley, MA 01075, USA and ²Department of Biology and Organismal and Evolutionary Biology Graduate Program, University of Massachusetts, Amherst, MA 01003, USA

*Author for correspondence (e-mail: ggillis@mtholyoke.edu)

†Present address: Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA

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SUMMARY

Voluntary loss of an appendage, or autotomy, is a remarkable behavior that is widespread among many arthropods and lower vertebrates. Its immediate benefit, generally escape from a predator, is balanced by various costs, including impaired locomotor performance, reproductive success and long-term survival. Among vertebrates, autotomy is most widespread in lizards, in which tail loss has been documented in close to 100 species. Despite numerous studies of the potential costs of tail autotomy in lizards, none have focused on the importance of the tail in jumping. Using high-speed video we recorded jumps from six lizards (*Anolis carolinensis*) both before and after removing 80% of the tail to test the hypothesis that tail loss has a significant effect on jumping kinematics. Several key performance metrics, including jump distance and takeoff velocity, were not affected by experimental tail removal, averaging 21 cm and 124 cm s⁻¹, respectively, in both tailed and tailless lizards. However, in-air stability during jumping was greatly compromised after tail removal. Lizards without tails rotated posteriorly more than 30 deg., on average, between takeoff and landing (and sometimes more than 90 deg.) compared with an average of 5 deg. of rotation in lizards with intact tails. Such exaggerated posterior rotation prevents coordinated landing, which is critical for animals that spend much of their time jumping to and from small branches. This work augments recent experiments demonstrating the importance of the tail as a mid-air stabilizer during falling in geckos, and emphasizes new and severe functional costs associated with tail autotomy in arboreal lizards.

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Key words: jumping, kinematics, autotomy, anolis.

INTRODUCTION

A post-anal tail is a defining characteristic of chordates and represents the ancestral state for vertebrate animals (Kardong, 2005). Among vertebrates, tails are functionally critical and versatile, serving primary roles in locomotion, balance and sexual display from fish to primates. Nevertheless, in many amphibians and reptiles, tails can be voluntarily shed as a remarkable, if drastic, means of escaping predators. Among lizards, this phenomenon is particularly widespread, and in diverse species representing nearly 2/3 of lizard families, the tail can be lost *via* self-amputation or caudal autotomy (Downes and Shine, 2001). This remarkable ability has evolved multiple times within lizards and different species exhibit a range of mechanisms enabling tail loss, such as fracture planes between or within vertebrae, and a host of modifications to other tail tissues, including blood vessels and musculature (Etheridge, 1967). After separation, the muscles of the autotomized tail can continue to contract and these movements act to distract a predator long enough for the lizard to escape (Dial and Fitzpatrick, 1983; Naya et al., 2007; Rumping and Jayne, 1996).

Although the immediate benefits of caudal autotomy are obvious, potential costs are numerous, if less clear, and may include energetic constraints (Ballinger and Tinkle, 1979; Congdon et al., 1974; Dial and Fitzpatrick, 1981; Naya et al., 2007), loss of social status (Fox et al., 1990; Fox and Rostker, 1982), decrements in locomotor speed and endurance (Ballinger et al., 1979; Brown et al., 1995; Chapple et al., 2004; Daniels, 1985; Lin et al., 2006; Martin and Avery, 1998; Punzo, 1982) and reductions in territory size and access to females (Martin and Salvador, 1993; Salvador et al., 1995; Salvador et al.,

1996). Given the high frequency with which lizards lose and regenerate parts of their tails in natural populations (in some studies greater than 50%) (Vitt et al., 1977) and the potential range of costs imposed, the functional consequences of tail loss are ecologically important.

For many lizards, particularly arboreal species, jumping is a locomotor mode frequently used for habitat navigation, capturing prey and evading predators (Irschick and Losos, 1998; Losos and Irschick, 1996; Moermond, 1979; Pounds, 1988). However, no studies have examined the potential costs of caudal autotomy in relation to jumping, despite a number of detailed studies examining the kinematics and kinetics of jumping lizards (e.g. Bels et al., 1992; Lailvaux and Irschick, 2007; Toro et al., 2003; Toro et al., 2004). Work by Higham and colleagues demonstrated the use of tail movements in relation to in-air body turning during jumping in various anole species (Higham et al., 2001) and recent work by Jusufi and colleagues showed that the tail plays an active role in controlling the body orientation of falling geckos (Jusufi et al., 2008). We hypothesized that tails are essential for in-air body movement and coordination in lizards and that autotomy would have detrimental effects on jumping behavior.

We tested for the effects of tail loss on jumping in the arboreal green anole (*Anolis carolinensis*, Voigt 1832) by using high-speed video to compare takeoff, in-air and landing kinematics of animals before and after experimental tail removal. The green anole lizard is a medium-sized (~2–6 g) arboreal lizard that has been widely used for jumping studies (Bels et al., 1992; Lailvaux and Irschick, 2007; Toro et al., 2003); therefore, it is a good model system for testing

the effects of tail loss on jumping. We measured simple jump kinematics (body angle, tail base angle) as well as several common measures of jump performance on the same set of lizards before and after tail removal. We focused on three key aspects of performance (jump distance, takeoff duration and takeoff velocity) that are likely to be important to green anoles when evading a predator (Toro et al., 2003; Toro et al., 2004).

MATERIALS AND METHODS

Two female and four male *Anolis carolinensis* were obtained commercially in Hadley, MA, USA (see Table 1 for measurements of each of the lizards). Animals were numbered on their ventral surface using permanent marker and housed in pairs in glass aquaria. Tanks were furnished with sticks and plastic leaves, which were sprayed with tap water twice daily. Lizards were fed 4–6 mealworms 2–3 times each week and provided with a 12 h:12 h light:dark cycle.

To track body and tail movements during jumping, individuals were marked using Bic Wite-Out® (BIC Corporation, Shelton, CT, USA). Small dots were placed on the lateral and dorsal surface of each animal at points representing the pectoral girdle, pelvic girdle, center of the trunk (intermediate between girdles), vent and at 20% intervals along the tail. All jumping events took place within a cardboard arena with raised edges to reduce the likelihood of lizard escape. Jumping trials consisted of placing a lizard onto a platform constructed out of a small cardboard box with the jumping surface covered with fine sandpaper. The jumping surface was 11 cm above the landing area and both were illuminated using 500 W Lowel Omni lights (Lowel Lighting, Brooklyn, NY, USA). Once on the platform, lizards generally walked to the edge facing the landing area and were encouraged to jump using hand movements or by tapping the platform or their tail. A Photron 1280 PCI high-speed video camera (Photron, San Diego, CA, USA) was placed above the setup and was used to record all lizard jumps at 500 frames per second. A mirror placed at 45 deg. adjacent to the jumping platform allowed both dorsal and lateral views of the animals to be recorded using a single camera. Individual lizards were allowed to jump from the platform to the landing area for approximately 5 min and each jump was saved onto a personal computer as an AVI file. The four longest and straightest jumps from each lizard were identified and used for kinematic analysis.

Twenty-four hours following these initial jumps, tails were manually removed from the same six individuals. To induce caudal autotomy, tails were grasped with blunt, curved forceps at a point approximately 20% from the base of the tail. Lizards were given a surface to grasp while the tail was tugged until it was dropped. In all lizards, 80% of the tail was removed, accounting for 5–7% of the animal's body mass (Table 1). Lizards then rested for approximately 5–10 mins before post-autotomy jump trials began. Again, animals were encouraged to jump for several minutes and the four longest and straightest jumps were identified from each

lizard after tail loss for kinematic analysis. In total, 48 jumping movies were analyzed, four from each of the six lizards before and after tail removal.

To analyze in-air body movements during jumping, every fourth frame from each of the movies was saved from takeoff to landing. From the lateral perspective, the lizards' snout tip, pectoral girdle, center of trunk, pelvic girdle, vent and tail marks were digitized in each frame with the custom-digitizing program Didge (courtesy of Alistair Cullum, Creighton University, Omaha, NE, USA). Using the coordinates overlying the pectoral and pelvic girdles, we calculated body angle relative to the horizontal in each of the saved frames throughout the jump (Fig. 1). Tail base angle was also calculated throughout each jump using the markers at the pectoral girdle, vent and 20% mark on the tail (Fig. 1). In addition, in the 20 frames preceding takeoff in each movie, the front edge of the mark at the center of the trunk was digitized, and by dividing the distance traveled by that mark by the time between frames, the body's instantaneous velocity between each pair of frames was calculated and smoothed using a 5-point running average to determine velocity throughout the takeoff phase. We chose 20 frames because in all jumps, this interval included the majority of the takeoff phase; ultimately we chose only to analyze the instantaneous velocity at takeoff (i.e. the last frame in which the animal is still contacting the jumping platform). Finally, the distance traveled during each jump was determined by calculating the horizontal distance traveled by the mark at the center of the trunk between takeoff and landing. Measured distances between the points on each lizard's body were used for scale.

To test for the effects of tail loss on jumping we used two-way, mixed-model analyses of variance (ANOVA) on several variables of interest: jump distance, takeoff velocity, takeoff duration and body and tail base angle at takeoff and landing and at three equally spaced times during the aerial phase. Presence or absence of the tail was a fixed factor; individual was a random factor. The fixed factor was tested over the interaction mean square whereas the random factor and interaction term were tested over the error mean square. To account for multiple ANOVA, a sequential Bonferroni correction was used (Rice, 1989).

RESULTS

Jumping in *Anolis* lizards is generally stereotyped and our animals exhibited the same basic movements described by Bels and colleagues (Bels et al., 1992) and Toro and colleagues (Toro et al.,

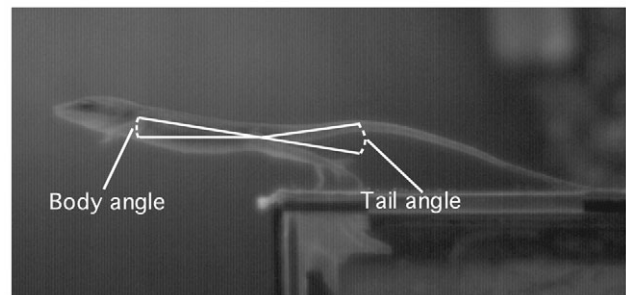


Fig. 1. Method for measuring body and tail base angle during jumping. Body angle was measured relative to the horizontal using a line connecting points on the lateral surface of the animal's body at the level of the pectoral and pelvic girdles. Tail base angle was measured relative to the body angle and was measured using a line connecting points on the lateral surface of the animal's body at the level of the vent and at 20% tail length (also the point of tail removal).

Table 1. Basic morphometrics of individual lizards used in this study

Individual	Body mass (g)	Snout–vent length (cm)	Tail length (cm)	Mass of tail removed (g)
1	3.14	5.1	9.4	0.18
2	2.86	5.4	10.0	0.17
3	3.79	6.1	11.2	0.19
4	4.00	6.3	11.5	0.24
5	2.36	5.1	8.9	0.16
6	3.38	5.7	10.1	0.19
Mean	3.26	5.6	10.2	0.19

2004). Jumps typically began with preparatory limb movements to position the hindfeet as far forward as the forefeet. This was followed by takeoff, which was propelled entirely by the hindlimbs, then an aerial phase and finally, a landing phase when the animal's limbs re-established contact with the substrate.

Before tail removal, animals took off at an average velocity of $1.2 \pm 0.05 \text{ m s}^{-1}$ (mean \pm s.e.m.) with an angle of 16 ± 2 deg. to the horizontal and essentially maintained this angle throughout the jump, landing with their bodies at an average angle of 21 ± 7 deg. Horizontal jump distances ranged between 14.9 and 29.9 cm and averaged 21.1 ± 1.3 cm. Following experimental tail removal, preparatory and takeoff kinematics of jumping lizards were unaffected; neither the duration of the takeoff phase ($F_{1,5}=0.54$, $P=0.47$) nor the body's angle ($F_{1,5}=3.89$, $P=0.06$) nor velocity at takeoff ($F_{1,5}=0.02$, $P=0.88$) differed significantly from jumps before tail loss (Fig. 2; Table 2). Furthermore, the horizontal distance traveled during jumps was also not significantly affected by tail loss ($F_{1,5}=0.545$, $P=0.46$) (Fig. 2; Table 2).

The importance of the tail was obvious; however, only once the animals took off and their limbs left the ground. Lizards without tails had an average takeoff angle of 12 ± 2 deg. to the horizontal and typically underwent substantial posterior rotation in the air before landing (Fig. 3; Movie 1 vs Movie 2 in supplementary material). The degree of rotation became significantly different between tailed and tailless animals 50% of the way through the aerial phase ($F_{1,5}=13.96$, $P=0.001$) and remained significant at 75% ($F_{1,5}=31.17$, $P<0.001$) of the aerial phase and at 100% or landing ($F_{1,5}=25.73$, $P<0.001$) (Fig. 3; Table 2). Indeed, half of the recorded jumps for lizards without tails ended with animals landing with body angles greater than 45 deg. whereas fewer than 10% of jumps from the same animals before tail removal had landing angles of this magnitude. Individual variation in most kinematic variables was high, and significant individual \times tail loss interactions were found for body rotation during most of the jump (Table 2) because four lizards exhibited the pattern of rotation described above but two did not.

To better understand the possible role of the tail we also characterized tail base kinematics during jumping. The movement of the tail base during takeoff was very consistent in tailed lizards

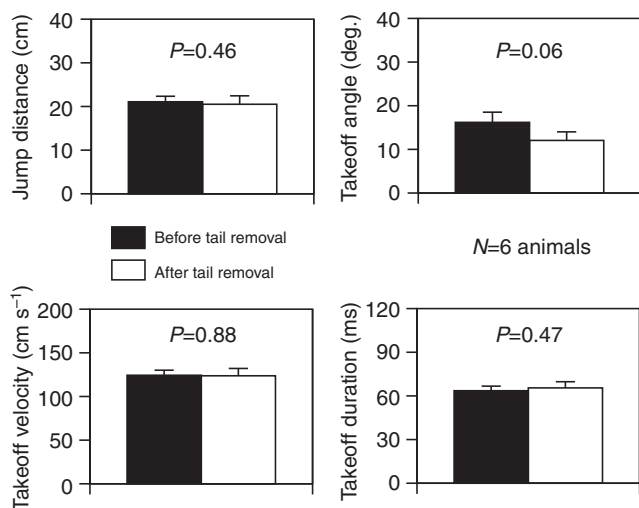


Fig. 2. Four key jump variables (takeoff velocity, takeoff duration, takeoff angle and jump distance) do not differ significantly between lizards before and after tail removal. Values shown are the average of individual means \pm s.e.m. ($N=6$ individuals).

Table 2. F -values (with associated significance levels) for different jump variables comparing lizards before and after tail removal

Variable	Tail loss d.f.=1, 5	Individual d.f.=5, 36	Tail loss \times Individual d.f.=5, 36
Jump distance	0.545 (0.465)	16.61 (<0.001)	1.05 (0.402)
Takeoff duration	0.54 (0.466)	6.93 (<0.001)	1.34 (0.272)
Takeoff velocity	0.02 (0.884)	10.88 (<0.001)	0.59 (0.707)
Body angle 0%	3.89 (0.056)	3.35 (0.014)	0.80 (0.557)
Body angle 25%	1.46 (0.235)	7.34 (<0.001)	2.78 (0.032)
Body angle 50%	13.96 (0.001)	7.76 (<0.001)	7.63 (<0.001)
Body angle 75%	31.17 (<0.001)	12.39 (<0.001)	12.20 (<0.001)
Body angle 100%	25.73 (<0.001)	10.15 (<0.001)	12.53 (<0.001)
Tail angle 0%	0.03 (0.869)	6.08 (<0.001)	3.78 (0.008)
Tail angle 25%	2.35 (0.134)	6.03 (<0.001)	1.66 (0.169)
Tail angle 50%	10.19 (0.003)	1.22 (0.320)	2.93 (0.025)
Tail angle 75%	11.69 (0.002)	1.75 (0.151)	1.37 (0.259)
Tail angle 100%	1.48 (0.232)	1.62 (0.184)	2.23 (0.074)

0%, 25%, 50%, 75% and 100% represent the relative time in the aerial phase of the jump (where 0% is takeoff and 100% is landing).

and in all jumps animals rapidly elevated the base of the tail throughout the takeoff phase. The largest angle between the tail base and body during this interval averaged 24 ± 4 deg. and was achieved at takeoff (Figs 4 and 5). In the initial portion of the aerial phase following takeoff, more posterior portions of the tail typically dragged or 'slapped' against the takeoff platform (Fig. 5; Movie 1 in supplementary material). Following this and during most of the aerial phase, the tail generally underwent little active movement, although it was often the first part of the animal to touchdown during landing, leading to a change in the angle between the body and tail base near the end of the jump (Fig. 4; Movie 1 in supplementary material).

Following the removal of most of the tail, lizards still underwent a consistent pattern of raising what remained of the tail during the takeoff phase. As observed in tailed animals, the tail base reached its largest angle relative to the body at takeoff, averaging 24 ± 2 deg. (Fig. 4). As tailless animals began to rotate posteriorly after takeoff, they vigorously swung their tail 'stump' (Fig. 4), and the angle subtended by the tail base relative to the body (as measured in the vertical plane) was significantly greater in lizards after tail removal at 50% ($F_{1,5}=10.19$, $P=0.003$) and 75% ($F_{1,5}=11.69$, $P=0.002$) of the aerial phase, reflecting the exaggerated tail base movements generated as the animals lost control in flight.

DISCUSSION

Despite the widespread capacity for caudal autotomy among diverse lizards and the common use of jumping, particularly in arboreal species, to our knowledge no studies have directly examined the effects of tail loss on jumping behavior. Our *a priori* prediction that tail removal would affect jumping in green anoles was supported; tailless lizards exhibited significant levels of posterior rotation of the body in mid-air (Movies 1 and 2 in supplementary material; Fig. 2), sometimes tumbling backwards 'head over heels' before landing.

Previous work on the kinematics of jumping in *A. carolinensis* indicates that animals generally takeoff at velocities near $1-1.5 \text{ m s}^{-1}$ and angles between 10 and 50 deg. relative to the horizontal (Bels et al., 1992; Toro et al., 2004; Toro et al., 2006); values comparable with those found in this study. After takeoff, lizards travel maximum distances of 20–50 cm before landing (Bels et al., 1992; Losos and Irschick, 1996; Toro et al., 2004) and this variation can be explained,

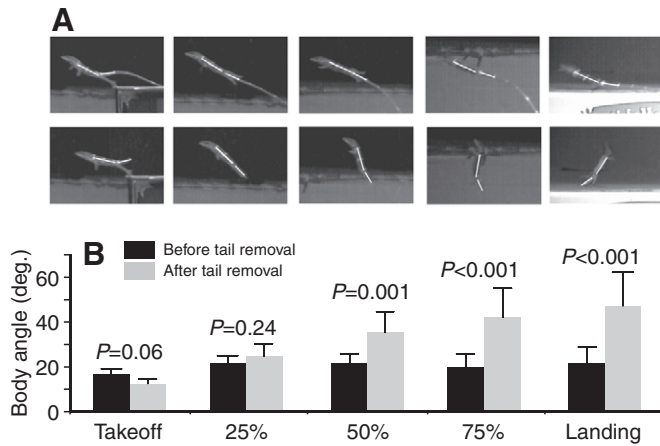


Fig. 3. Body angles during jumping before and after tail removal. (A) Movie stills taken from the same lizard before and after tail removal at five points during a jump: takeoff, 25%, 50% and 75% during the aerial phase and at landing. White lines are drawn to highlight the orientation of the body and tail base. Note the 'head over heels' pitch in the lower panel showing the tailless lizard. (B) Mean body angles, relative to the horizontal, from all jumps in all lizards. Body angle diverges significantly in tailless lizards by the halfway point of the aerial phase. Values shown are the average of individual means \pm s.e.m. ($N=6$ individuals).

in part, by the height of the jump surface and by animal size. Larger lizards have longer maximal jumps (Bels et al., 1992) and the relatively long 50 cm jumps recorded by Losos and Irschick (Losos and Irschick, 1996) were from animals on perches elevated 28 cm above the landing surface, compared with 11 cm elevation in this study (maximum jump distances ranged from 20–30 cm) and no elevation in the work of Bels and colleagues (Bels et al., 1992) (maximum distances ranged from 20–35 cm) and Toro and colleagues (Toro et al., 2004) (mean maximum distance of 32 cm).

Numerous studies have examined the consequences of tail loss on running and many have shown significant effects, including 15–50% reductions in maximum speed (Chapple et al., 2004; Formanowicz et al., 1990; Lin et al., 2006; Martin and Avery, 1998; Punzo, 1982), although this was not shown in all studies (Daniels, 1983; Kelehear and Webb, 2006). Thus, as during running, the loss of a large fraction of the tail also has significant effects on jumping behavior in lizards. However, unlike in running, tail removal has little effect on performance, as traditionally measured by takeoff duration and jump distance, as animals jumped similar distances and used similar amounts of time to takeoff before and after tail removal (Fig. 2). Jump distance is not affected by tail removal because the tail probably plays no active role in propulsion during jumping in *A. carolinensis*, as neither takeoff angle nor takeoff velocity differed significantly between tailed and tailless lizards (Fig. 2). Furthermore, because the takeoff provides all of the power for jumping (Marsh, 1994), it makes sense that animals jumped similar distances given their similar takeoff kinematics. Although lizards are lighter following caudal autotomy (the tail accounted for approximately 5% of body mass in our animals), this difference appears to be negligible in terms of its effect on jump distance, as was any potential change in the drag experienced by the animal due to alterations in mid-air kinematics, although further research would be useful in this regard. Other metrics of jump performance, such as jump height and accuracy, are likely to be important in certain circumstances (e.g. an animal in dense vegetation trying to get to

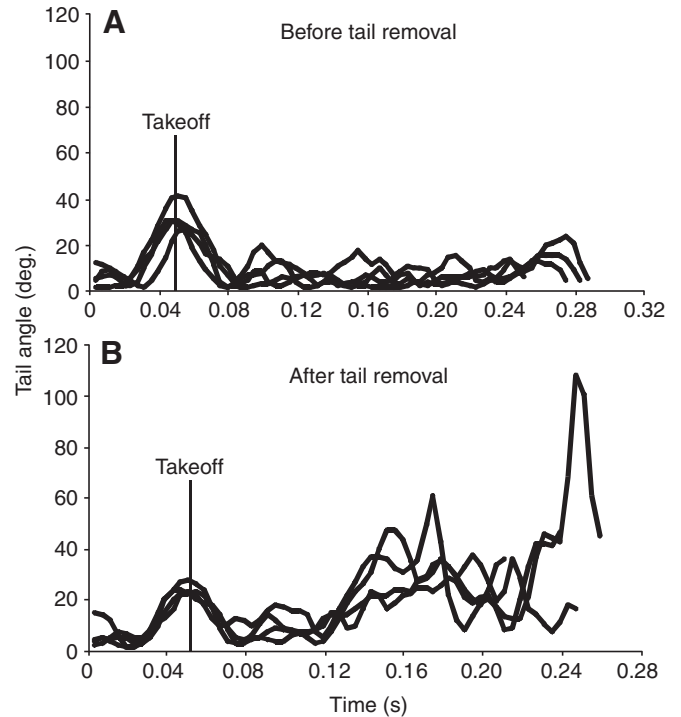


Fig. 4. Tail base angles during jumping before and after tail removal. (A) Representative data from four jumps (each jump is represented by a different line) of a single lizard showing patterns of tail base movement during jumping. Note how the tail base is raised as the animal approaches takeoff, after which it returns to lower values for the rest of the jump (typically <20 deg.). (B) Data from the same lizard following tail removal. The pattern is similar until shortly after takeoff when the tail angle gets consistently higher, reflecting vigorous rotation of the tail base, presumably to try to correct body orientation as the animal pitches out of control.

a specific perch above it) and we look forward to future work addressing the effects of tail loss on these variables.

By tracking the kinematics of jumping animals during the aerial phase, we detected a curious effect of tail loss in most individuals, namely exaggerated posterior rotation of the body after takeoff (Fig. 3; Movie 2 in supplementary material). The main discernible difference between trials before and after tail removal that might account for this result is the interaction between the tail and jumping surface shortly after takeoff in tailed animals. In most jumps, distal portions of the tail slide along or slap down onto the jump surface after the animal's hindfeet leave the ground (Fig. 5; Movie 1 in supplementary material). Given the tendency for tailless lizards to rotate posteriorly, we hypothesize that this tail–substrate interaction provides forces to counteract this motion, much as a 'wheelie-wheel' prevents a motorcyclist from toppling over backwards when performing a wheelie. Force plate recordings are required to demonstrate this interaction directly, as they would permit quantification of the forces exerted by the tail against the jump surface after takeoff. Regardless, the three-dimensional nature of arboreal habitats necessitates that lizards must jump downward from elevated locations regularly. Our work on animals jumping from a slightly elevated platform suggests that following caudal autotomy, coordinated landing during jumps from higher to lower perches would be nearly impossible in this species because of the typical loss of control of body position in such descending jumps.

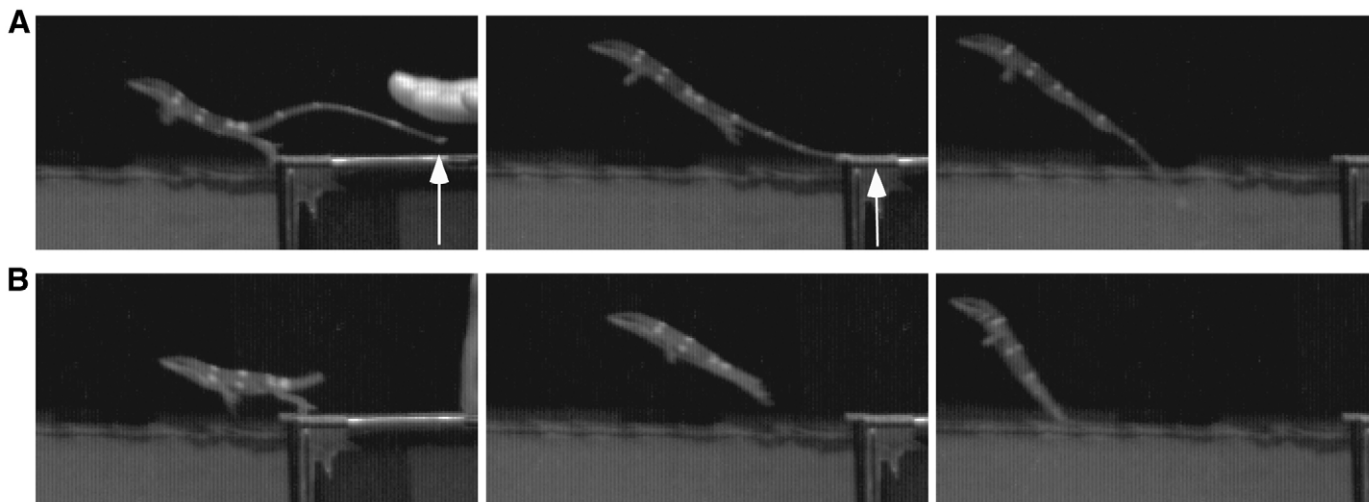


Fig. 5 Tail-substrate interactions after takeoff. (A) Movie stills of a lizard with its tail intact at three points early in a jump: takeoff, shortly after takeoff and in mid-air. At takeoff, the base of the lizard's tail is raised and in this jump the entire tail is lifted off of the jump platform (white arrow in left-most image). Shortly after takeoff, the tail slaps down onto the platform and drags along it for a brief period (white arrow in center image). We hypothesize that such tail-substrate interactions generate forces that counteract posterior rotation of the body. (B) High-speed video images of the same lizard at similar points in a jump after tail removal. Shortly after takeoff, the body is in a comparable orientation; however, without the tail-substrate interactions, once the animal is in mid-air, exaggerated posterior rotation of the body begins.

We also hypothesize that the tail plays a role in mediating body orientation in mid-air, where its momentum can be used to twist and turn the body. Previous work in various anole species during body turning by Higham and colleagues (Higham et al., 2001), as well as personal observations with *A. carolinensis* (G.B.G.), suggest the tail can be used actively in the aerial phase to correct body position in three dimensions. Moreover, the vigorous actions of the tail stump exhibited by tailless lizards pitching backwards in mid-air suggest attempts by the animals to right themselves as they are losing control (Fig. 4). Thus, we predict that the tail is not only important for body stabilization just after takeoff, *vis-à-vis* interactions with the jumping surface but also in mid-flight for regaining control of body position. Such active use of the tail as a mid-air stabilizer is consistent with recent work showing that geckos actively use their tails to right themselves when falling (Jusufović et al., 2008).

Elongated tails are common in many arboreal animals and our work, along with the recent work on falling geckos, reveals an interesting twist to the use of tails as in-air stabilizers. Specifically, tail loss, although natural and widespread among lizard species (Maginnis, 2006), can pose a significant hindrance to mid-air stability and subsequent landing and therefore could impose a remarkable cost on effective locomotion in arboreal lizards. The detailed role(s) of the tail as a stabilizer in jumping lizards should be further tested using force plate recordings. Furthermore, because lizards often lose different amounts of their tail in the wild, examining the effects of different degrees of tail loss (e.g. 25% vs 50% of tail) will also be an important step toward a more ecologically relevant understanding of autotomy in relation to jumping behavior. We note that many lizards commonly lose parts of tails naturally (Vitt et al., 1977) and recover them relatively quickly by regeneration (Hughes and New, 1959; Rumping and Jayne, 1996) and therefore such manipulations do not cause long-term damage to the animals.

Finally, our results underscore a fascinating feature of the evolutionary process; in evolving a radical functional morphological

mechanism to elude predators, green anole lizards also seem to suffer a substantial cost that may affect many aspects of their arboreal activities (i.e. avoiding areas that might require coordinated jumps to escape). And because of the link between mating success and territory quality in lizards (Fox et al., 2003; Stamps and Krishnan, 1997), tailless lizards may suffer a temporary reproductive decrement. Despite the potentially severe nature of this tradeoff, the ultimate benefits of tail loss must outweigh the costs, as the capacity for caudal autotomy is maintained in many arboreal lizards. Indeed, the ease of autotomy may even evolve within species to be sexually dimorphic when there are different costs associated with tail loss between sexes (Fox et al., 1998).

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