



Take this broken tail and learn to jump: the ability to recover from reduced in-air stability in tailless green anole lizards [*Anolis carolinensis* (Squamata: Dactyloidae)]

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Locomotion is involved in various fitness-related tasks, such as foraging, acquiring mates, and escaping from predators. Despite the importance of locomotor performance in determining fitness, animals often encounter situations in nature during which their locomotor performance is severely compromised. For animals that actively discard appendages as an anti-predator strategy, the loss of appendages can cause a severe reduction in locomotor performance. However, whether animals can compensate for the impact on locomotor performance after autotomy is still unclear. A previous study has shown that tailless green anole lizards suffered from reduced in-air stability during jumping. In this study, we monitored jump kinematics in three groups of *Anolis carolinensis* for five consecutive weeks to test two hypotheses: first, whether tailless green anoles can recover from reduced in-air stability before their tails can regenerate; and second, whether gaining locomotor experience facilitates locomotor recovery. Our results revealed extensive individual variation in the ability to compensate for reduced in-air stability. Some individuals did improve in-air stability during the study period, whereas others showed no sign of improvement. Moreover, the acquisition of locomotor experience did not facilitate the recovery process. Our findings suggested that tail autotomy in green anoles probably imposes a long-term fitness disadvantage. The utility of other compensatory mechanisms, such as altering behaviour, might play a role in natural populations to minimize the impact of autotomy on individual fitness. Our findings also shed light on the independent evolutionary losses of the ability to autotomize within lizards. Comparative studies which test whether species that autotomize more frequently/easily can better compensate for the effect of autotomy would be a fruitful direction of future research. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, ••, ••–••.

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INTRODUCTION

Locomotion is involved in almost every aspect of an animal's daily life and forms a central part of various ecologically relevant activities such as foraging, acquiring mates, and escaping from predators. As a consequence, natural selection often favours high

locomotor performance in the wild (reviewed by Irschick *et al.*, 2008). However, animals often encounter situations in nature during which their locomotor performance is severely compromised. For example, in many animal species, females are encumbered with offspring during gravidity and therefore suffer from reduced movement speed and endurance (e.g. Lee *et al.*, 1996; Shaffer & Formanowicz, 1996; Wapstra & O'Reilly, 2001). Locomotor performance may also be greatly reduced when the appendages involved

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in locomotion are injured or even lost altogether (Fleming, Muller & Bateman, 2007; Bateman & Fleming, 2009; Gillis, Bonvini & Irschick, 2009), although it may require the loss or injury of multiple appendages to cause a significant reduction in locomotor abilities (e.g. Guffey, 1999; Brueseke *et al.*, 2001). The situation of appendage loss is particularly common in animals that can voluntarily discard certain body parts as a strategy to distract or break free from predators (autotomy, McVean, 1975). Autotomy is widespread in the animal kingdom and occurs in a diverse array of invertebrates and some vertebrates (Fleming *et al.*, 2007; Bateman & Fleming, 2009). Moreover, the frequency of autotomy within natural populations can be extremely high [more than 80% of the individuals in some amphipod and lizard populations (Needham, 1953; Van Sluys & Vrcibradic, 2002)]. The widespread occurrence and high incidence of autotomy in natural populations suggest that the reduction in locomotor performance after autotomy can pose a challenge to those species that exhibit this behaviour. Although the lost appendage(s) will regenerate in most animals, the rate of the regeneration process varies extensively among taxa, ranging from a few weeks (most invertebrates) to months (most vertebrates) to around a year in a starfish species (Vitt, Congdon & Dickson, 1977; Pomory & Lares, 2000; Fleming *et al.*, 2007). Therefore, one might expect natural selection to favour mechanisms that enable individuals to rapidly overcome any deficits in reduced locomotor performance after appendage loss. If animals that autotomize can restore impaired locomotor performance before the lost appendages can regenerate, the impact of autotomy on locomotion will only impose a short-term cost to fitness. Conversely, autotomy might incur costs that cannot be quickly remedied, thus resulting in a more substantial impact on locomotor performance and fitness.

One potential short-term solution for animals to compensate for reduced locomotor performance is by making kinematic adjustments. For example, many animals can adjust their kinematics in response to increased loads (Chai & Dudley, 1995; Hoyt, Wickler & Cogger, 2000; Wickler *et al.*, 2001). Humans with muscle injuries also alter the kinematics of other uninjured muscle groups when performing a locomotor task to compensate for reduced overall muscle strength (e.g. Kvist, Good & Tagesson, 2007; Gutierrez *et al.*, 2012). Although it is not clear whether other vertebrates can alter kinematics under similar circumstances in response to injury or the loss of a body part, many non-human vertebrates possess the ability to use muscles differently depending on the context of the locomotor task. For example, toads, cats, and monkeys are all capable of activating forelimb

muscles in anticipation to the timing of landings during jumps (Prochazka *et al.*, 1977; Dyhre-Poulsen & Laursen, 1984; Gillis, Akella & Gunaratne, 2010). Therefore, it is reasonable to hypothesize that animals are capable of perceiving appendage loss and compensate for reduced locomotor performance by changing kinematics accordingly.

Several different factors could influence the ability to make effective kinematic adjustments. The amount of experience that an animal has for undertaking a particular task following autotomy. In humans and some other mammals, training has been shown to have striking effects on the ability to perform effectively (e.g. Barbeau & Rossignol, 1987; Dean & Richards, 2000; Tsauo, Cheng & Yang, 2008, but see Fouad *et al.*, 2000), but for most non-mammalian vertebrates, especially for reptiles, the role of training is far more ambiguous (Gleeson, 1979; Tipton *et al.*, 1979; Liu *et al.*, 2009; Busquets *et al.*, 2011). Because strong similarities exist in the sensorimotor mechanisms of locomotion across vertebrates (Rossignol, Dubuc & Gossard, 2006), we can expect that the acquisition of more locomotor experience might facilitate the restoration of locomotor performance following autotomy. On the other hand, humans and some animals show improved locomotor performance following a severe injury simply because the sensorimotor motor system can adjust to the new physical arrangement over time (e.g. Barbeau & Rossignol, 1987). We tested how both factors (locomotor experience and time) influenced the ability of green anole lizards (*Anolis carolinensis* Voigt, 1832) to jump following tail autotomy, a common occurrence in lizards that has been shown to alter in-air stability during jumping (Gillis *et al.*, 2009).

Anolis carolinensis represents an excellent system to test whether animals that autotomize can compensate for compromised locomotor performance after losing appendages. As a member of the trunk–crown ecomorph (Williams, 1983), *A. carolinensis* use jumping as their primary means of locomotion (Losos & Irschick, 1996; Irschick & Losos, 1998). Numerous studies have used *A. carolinensis* to address questions related to locomotor performance and kinematics (e.g. Bels *et al.*, 1992; Toro *et al.*, 2003; Toro, Herrel & Irschick, 2004; Gillis *et al.*, 2009; Kuo, Gillis & Irschick, 2011). As with many other lizards, *A. carolinensis* commonly autotomize their tails as a way to distract predators or break free from their grasp. The tail is critical in controlling in-air body movement in lizards (e.g. Gillis *et al.*, 2009; Libby *et al.*, 2012), as tailless individuals often exhibited unstable jump kinematics and even awkward landings (Fig. 1; Supporting Information, Fig. S1). Consequently, lower in-air stability and a higher risk of unsuccessful landings after tail loss might create problems for *A. carolinensis*. For example, an unsuc-

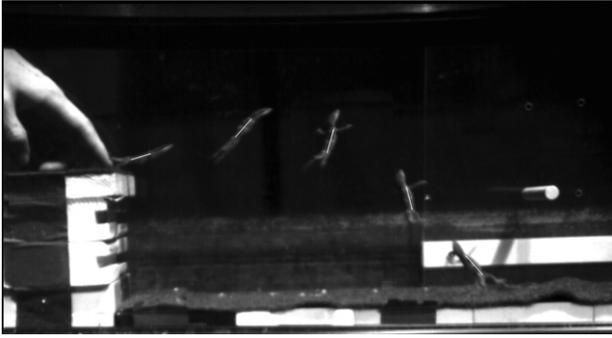


Figure 1. The course of a jump made by a tailless green anole lizard. Note the extensive body rotation during the aerial phase and a high landing angle.

Successful landing may cost a lizard extra time and energy to return to its habitat, or may cause physical injury or render the lizard vulnerable to predators when it misses the target of landing. Because it can take several months for the tail to fully regenerate (Cox, 1969), lowered in-air stability and its potential fitness consequences suggest that *A. carolinensis* may possess behavioural mechanisms for minimizing the impact of tail autotomy.

In this study, we investigated whether tailless *A. carolinensis* can recover from reduced in-air stability as a function of both time (5 weeks) and the amount of locomotor experience. We hypothesized that both time and locomotor experience after tail loss will facilitate locomotor recovery. Our findings will allow us to better understand whether animals can compensate for impaired locomotor performance after autotomy before the lost appendage can regenerate. More importantly, our results will shed light on whether the costs of autotomy, an important anti-predator strategy, can be ameliorated over relatively short time intervals.

MATERIAL AND METHODS

We commercially obtained 21 lizards (17 males, four females) with intact and original tails from NC Enterprises (Brooklyn, NY, USA) for our experiment. Lizards were housed individually in terrariums ($42.9 \times 15.2 \times 21.6$ cm length \times width \times height) with mulch bedding and provided sufficient lighting with 60-W white light bulbs. The size of the terrariums allowed the lizards to move freely but was not large enough for performing full jumps. We sprayed the lizards with water daily and provided them with crickets twice a week (Flukers Farms, Port Allen, LA, USA). We painted white dots (~ 0.3 cm in diameter, ~ 1 – 1.5 cm apart depending on body size) at the positions of pectoral girdle, centre of the trunk, and pelvic girdle on both dorsal and left lateral surfaces of the

lizards for digitizing locomotion and extracted performance and kinematic data using computer software (see below).

As male and female *A. carolinensis* do not differ in their jumping abilities once size is taken into account (Lailvaux & Irschick, 2007), we pooled lizards of both sexes and assigned them randomly into three groups while making the mean snout-to-vent length (SVL) roughly the same across groups. Lizards in the first group (hereafter the tailless-weekly jumping group, mean SVL = 52.9 mm, $N = 9$) had 80% of their tails removed by grasping the tails with blunt forceps to induce caudal autotomy (Gillis *et al.*, 2009). Lizards in this group were subject to weekly jumping trials for five consecutive weeks. The second group (hereafter the tailless-no weekly jumping group, mean SVL = 53.3 mm, $N = 6$) had their tails removed in the same manner as in the tailless-weekly jumping group but were only subject to jumping trials in the first and the fifth weeks. The third group (hereafter the control group, mean SVL = 54.31 mm, $N = 6$) had intact tails and also experienced weekly jumping trials. The control group allowed us to observe any negative effect that our weekly jumping trials might have induced on jump performance (e.g. fatigue and stress). We finished data collection within 5 weeks so that changes in tail length during the study period would not be a confounding factor in this experiment [about 1 cm (10–15% tail length in week 1) by the end of the study period].

In a week, lizards were subject to two rounds of tests, each of which consisted of no more than two consecutive jumping trials. We did not test the animals more frequently because we were concerned about the potential stress to the animals associated with the experimental procedure, especially when data collection had to continue for 5 weeks. The two rounds of tests were at least 60 min apart. Before performing jumping trials, lizards were heated to average body temperatures of 30–32 °C by placing them in a cloth bag in a bucket with a heat lamp located above for 45–60 min. This range of body temperatures has been shown to elicit maximal jumping in *A. carolinensis* (Lailvaux & Irschick, 2007). At the beginning of each jumping trial, we placed the lizards on a platform (11 cm in height) in an arena with raised edges and presented the lizards with a perch 40 cm from the platform as an incentive to jump. The distance of 40 cm was beyond the reach of all lizards and did not interfere with the courses of jumps. Immediately after placing the lizards on the platform, we induced jump behaviour by gently tapping their tails. We filmed all trials at 500 frames s^{-1} with a Photron 1280 PCI high-speed video camera (Photron, San Diego, CA, USA) and saved each video into separate AVI files for further analyses.

To analyse jump kinematics, we recorded the body angles at the point of takeoff, 25, 50, and 75% during the aerial phase and at landing, following Gillis *et al.* (2009). Body angles were measured as the angle between the horizontal and a line connecting the white dots on the side of a lizard. At least two out of three dots were visible at any point of a jump, so we were able to measure all body angles without ambiguity. As *A. carolinensis* exhibited little body bending during the aerial phase of jumps, we believed that this method introduced negligible error to the measurement of body angles. We also calculated the difference between body angles at takeoff and at landing and used it to measure in-air body rotation in a jump. As there was normally three to four jumps for an individual in a given week, we used the mean of each variable from all jumps in the same week to represent the data of individuals for that week. By doing so, each individual had only one value for each variable in any given week.

Table 1. Factor loadings of the first two principal components and the cumulative amount of variation explained

Variable (body angles)	Loadings	
	PC1	PC2
Takeoff	0.356	0.744
25% aerial phase	0.473	0.320
50% aerial phase	0.491	-0.133
75% aerial phase	0.474	-0.298
Landing	0.430	-0.488
Eigenvalue	1.996	0.928
Cumulative variation (%)	79.6	96.8

We first reduced the number of variables by performing a principal component analysis (PCA) on the five body angles (takeoff, 25%, 50%, and 75%, and landing) and used the first principal component (PC1) as a descriptor for overall jump kinematics (see Results). Apart from the first principal component, we also compared landing angle and in-air body rotation among the three groups of *A. carolinensis* individuals, as high values of those two variables signified instability in the air and were two diagnostic features of unsuccessful landings. To see whether the three groups differed in jump kinematics at the beginning of the study period, we used separate one-way analysis of variance (ANOVA) to compare the means of the three variables among the three groups using the data from the first week. We performed the same analysis using the data from the last week to see whether the three groups still differed in jump kinematics at the end of the study period. To determine how jump kinematics changed across the 5-week period, we tested the effect of week on the first principal component, landing angle and in-air body rotation using separate repeated-measures ANOVAs within each group. In our models, individual was treated as a random factor and week as a fixed factor to account for within-individual variation.

RESULTS

PC1 accounted for 79.6% of total variation and loaded strongly for all five body angles (takeoff, 25%, 50%, and 75%, and landing). Therefore, it represented a useful general description of jump kinematics in *A. carolinensis* (Table 1). Data for all variables are summarized in Table 2. In week 1, the mean of the first principal component did not differ significantly

Table 2. Descriptive statistics of jump performance and kinematic variables for the three groups at the beginning (week 1) and the end (week 5) of the study period; values are means \pm SEM

	Week 1			Week 5		
	Control	Tailless-weekly jumping	Tailless-no weekly jumping	Control	Tailless-weekly jumping	Tailless-no weekly jumping
Body angles (degrees)						
Takeoff	13.41 \pm 1.96	10.70 \pm 0.56	15.12 \pm 1.97	9.00 \pm 2.67	6.68 \pm 0.96	8.14 \pm 1.01
25% aerial phase	17.14 \pm 2.09	23.52 \pm 1.08	29.77 \pm 2.22	12.83 \pm 2.50	16.80 \pm 1.66	16.62 \pm 0.87
50% aerial phase	15.89 \pm 2.26	36.85 \pm 1.79	40.20 \pm 2.67	12.40 \pm 2.61	30.47 \pm 2.57	26.63 \pm 1.44
75% aerial phase	16.36 \pm 2.56	46.02 \pm 2.41	46.26 \pm 3.38	11.44 \pm 3.46	37.70 \pm 3.25	31.30 \pm 1.70
Landing	5.43 \pm 1.97	51.72 \pm 2.93	39.27 \pm 3.20	5.89 \pm 2.72	41.96 \pm 3.63	30.51 \pm 2.30
In-air body rotation (degrees)*	16.99 \pm 0.74	39.87 \pm 0.91	35.52 \pm 1.03	8.87 \pm 0.45	37.19 \pm 0.92	27.68 \pm 0.81

*The difference in body angles between takeoff and landing.

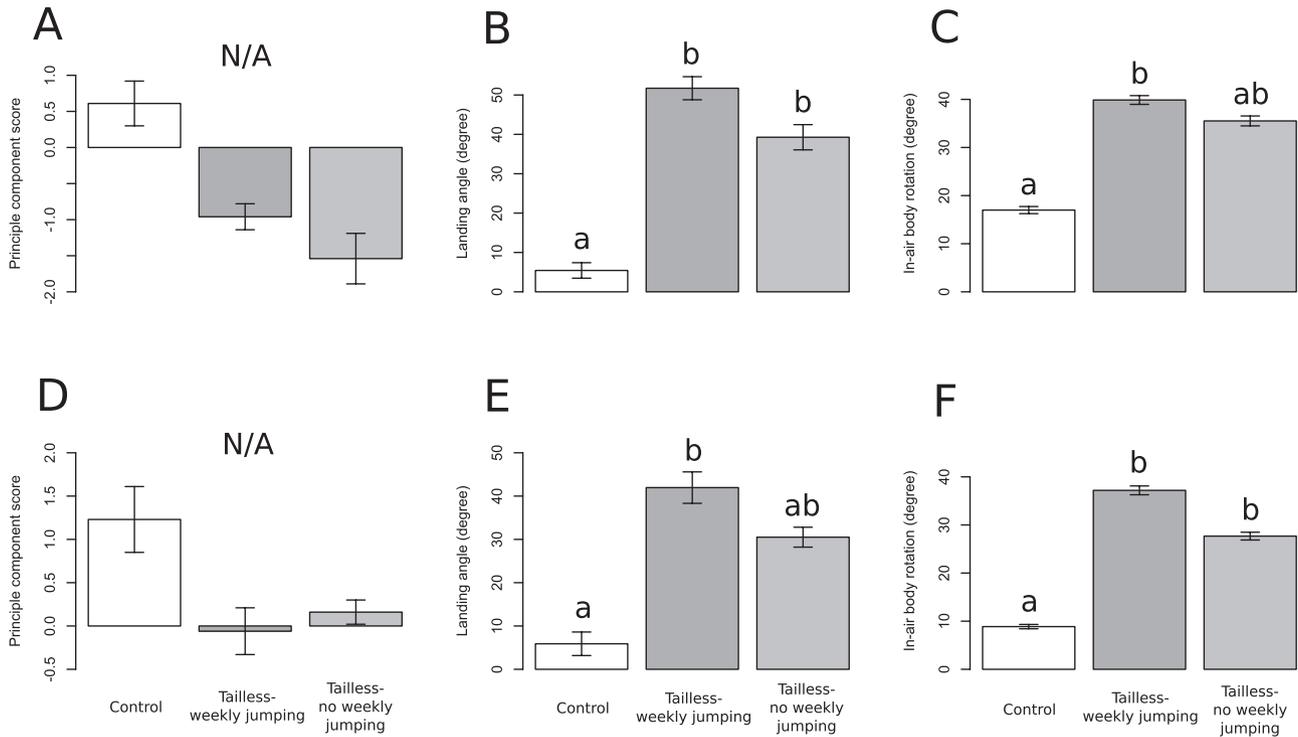


Figure 2. Comparisons of mean values for the first principal component (A and D), landing angle (B and E), and in-air body rotation (C and F) among the three groups of lizards: A–C, from data obtained in week 1; D–F, from week 5. Error bars represent standard errors. Within each figure, groups with the same letter did not differ significantly in post-hoc pairwise comparisons. N/A denotes overall lack of statistical significance in the ANOVA model.

among the three groups ($F_{2,18} = 2.25$, $P = 0.13$, Fig. 2A). Not surprisingly, there was no significant difference in any of the variables between the two groups of tailless lizards in week 1. However, the control group had significantly lower landing angles and less in-air body rotation (landing angle: $F_{2,18} = 8.72$, $P = 0.002$, Fig. 2B; in-air body rotation: $F_{2,18} = 3.91$, $P = 0.04$; Fig. 2C). Lizards with intact tails on average had a landing angle of less than 10° and body rotation of less than 20° , whereas the values of tailless lizards were on average two- to seven-fold higher (Table 2). It is worth noting that the variation in body angles also increased towards later phases of jumps in tailless lizards (supporting Fig. S1). Our findings were consistent with those of Gillis *et al.* (2009). Tailless lizards were in general unable to maintain a constant body angle in the air, resulting in more in-air body rotation and higher landing angles.

The difference in jump kinematics and in-air stability among lizards with and without tails still persisted through week 5. Although the mean values of all variables decreased in both the tailless-weekly jumping and tailless-no weekly jumping groups, tailless lizards on average still had more than three-fold higher landing angles and more in-air body rotation than the control group (landing angle: $F_{2,17} = 4.23$,

$P = 0.03$, Table 2, Fig. 2E; in-air body rotation: $F_{2,17} = 10.03$, $P = 0.001$, Table 2, Fig. 2F). The first principal component, on the other hand, still did not differ among the three groups in week 5 ($F_{2,17} = 0.71$, $P = 0.51$, Fig. 2D). One individual died after being tested in week 4, which resulted in the difference in the denominator degrees of freedom of F -tests between week 1 and 5. One interesting observation from our data was that the difference in body angles between tailed and tailless lizards became more striking towards later phases of a jump (Table 2), which was also observed by Gillis *et al.* (2009). As in the means, the difference in the variation in body angles between the control and the other two groups was still substantial in week 5 (Table 2).

The effect of week was not significant for the first principal component, landing angle or in-air body rotation in all linear models, suggesting that the means of the three variables did not differ statistically from week to week in any group (Table 3). However, a closer examination of our data revealed extensive individual variation in not only in-air stability itself after tail loss but also the ability to improve in-air stability (Fig. 3). The variation among individuals was more notable in the two tailless groups. Some individuals did not seem to suffer from

Table 3. Summary of statistics from generalized linear models that tested for the effect of week on the first principal component (PC1), landing angle (θ_L) and in-air body rotation ($\Delta\theta$) within each group; the effect of week was not significant for all three variables in all groups

	Control			Tailless-weekly jumping			Tailless-no weekly jumping		
	PC1	θ_L	$\Delta\theta$	PC1	θ_L	$\Delta\theta$	PC1	θ_L	$\Delta\theta$
F	3.15	0.07	2.56	3.83	3.20	< 0.001	3.46	0.44	0.01
d.f.	1, 27	1, 27	1, 27	1, 43	1, 43	1, 43	1, 10	1, 10	1, 10
P	0.08	0.79	0.12	0.06	0.08	0.99	0.09	0.52	0.92

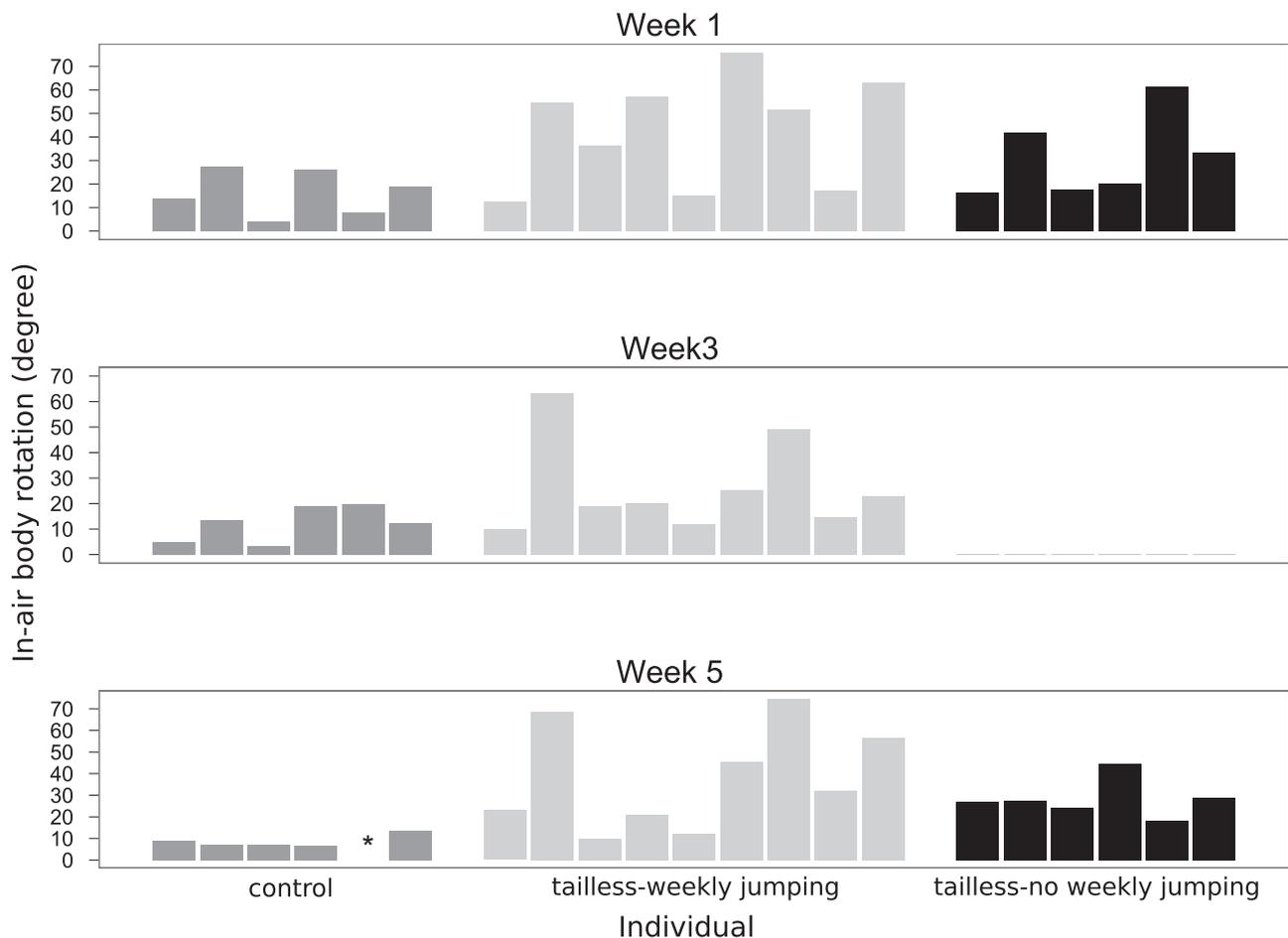


Figure 3. Changes in the degree of in-air body rotation in all individuals during the study period. Each bar in the graph represents the same individual in week one, three and five. Note the extent of individual variation in two tailless groups. The asterisk denotes missing data for one individual in week five.

lower in-air stability even in week 1 (e.g. the first individual of the tailless-weekly jumping group), whereas some individuals were more severely affected (e.g. the second to last individual in the tailless-no weekly jumping group). Similarly, some individuals exhibited a gradual decrease in both landing angle and in-air body rotation (e.g. the fourth individual of

the tailless-weekly jumping group), whereas some did not show any sign of improvement (e.g. the sixth individual in the tailless-weekly jumping group). The existence of extensive individual variation probably contributed to the lack of statistical difference in the mean values of landing angle and in-air body rotation across weeks.

DISCUSSION

In general, we found little evidence for improvement in in-air stability during jumping either as a function of the amount of locomotor experience or as a function of time. Indeed, at the conclusion of 5 weeks, tailless lizards still showed significantly lower in-air stability. At the individual level, however, it appeared that some tailless *A. carolinensis* individuals did improve their in-air stability substantially (Fig. 3). Our findings thus suggest some ability of some individuals to make kinematic adjustments following autotomy, but that overall, *A. carolinensis* do not seem to recover fully in their jumping ability, even after 5 weeks. This suggests that the loss of a large portion of tail could represent a relatively long-term fitness consequence in *A. carolinensis*.

The fact that more locomotor experience did not facilitate locomotor recovery in *A. carolinensis* differs from what has been generally established in humans and other mammals (e.g. Tsauo *et al.*, 2008). This finding is consistent with other studies, which show that training effects for locomotion in lizards are not highly effective, and can even have negative effects (Gleeson, 1979; Garland *et al.*, 1987). However, it is important to consider how our study differs from other studies of injury in mammals and humans. In most studies on mammals, the reduction in locomotor performance was due to neural injuries or illness that damaged sensorimotor pathways. The acquisition of more locomotor experience in those cases helped to enhance muscle strength and/or endurance. In our studies, however, lowered in-air stability was probably the consequence of disrupted jump dynamics after tail loss, with sensorimotor circuits being unaffected (Gillis *et al.*, 2009). Recovering from compromised locomotor performance in tailless *A. carolinensis* individuals therefore might be more directly related to motor coordination capacity than the amount of acquired locomotor experience. As individuals vary in motor coordination capacity (e.g. Getchell, Forrester & Whitall, 2001; Richards, Mulara & Bloomberg, 2007), it might explain why individual variation turns out to be the most relevant factor that determines the extent of locomotor recovery in our study.

Animals may experience costs under various circumstances. Costs may arise as a consequence of possessing certain traits (e.g. the conspicuousness costs of aposematic coloration; Speed & Ruxton, 2010) or may be imposed on the animals by the sociobiological environments (e.g. females in different mating systems; Martin & Hosken, 2003). Costs can also result when animals adopt certain behavioural strategies, such as autotomy (Naya *et al.*, 2007). Regardless of the circumstance, it is reasonable to expect

species to have developed compensatory mechanisms to mitigate the most frequently encountered costs. The fact that *A. carolinensis* seemed unable to recover from reduced in-air stability following tail loss is therefore somewhat surprising, as jumping following tail autotomy should be a fairly common situation in this species. The findings in our study are not only relevant to how *A. carolinensis* deals with autotomy but may also offer some insight into the distribution of autotomy among vertebrates (see below).

The apparent inability of *A. carolinensis* to cope with tail loss causes the effect of autotomy to last at least until the tail has re-grown significantly, which may require up to 6 months (Cox, 1969). Poor jump performance, even for a few weeks, thus might have considerable impact on their fitness. For instance, tailless *A. carolinensis* males might be unable to forage or defend territories as well as individuals with intact tails due to impaired locomotor performance, which could result in reduced mating opportunities. In fact, studies on other lizard species have shown that males suffered from reduced territory size and less mating opportunities after tail loss (e.g. Martin & Salvador, 1993). As anole lizards are short-lived [rarely more than 4 years in nature (Scott, 1984)], forfeiting mating opportunities in even one breeding season could lower their fitness. While our study examined whether *A. carolinensis* can compensate kinematically for tail loss, there remain other behavioural adjustments that could be important for these lizards. For example, female lizards often change their behaviour to become more cryptic during gravidity to compensate for impaired locomotor performance (e.g. Cooper *et al.*, 1990). It is possible that *A. carolinensis* will behaviourally compensate for the impact of tail loss by moving less often and allowing predators to approach closer before fleeing (reviewed by Bateman & Fleming, 2009). Another possibility would be a modification in habitat use after tail autotomy. For example, it is possible that *A. carolinensis* would use those parts of the microhabitat that would not require long jumps. All of the above possibilities could be tested with manipulative field studies that follow *A. carolinensis* individuals before and after tail loss. It would also be interesting to examine if the extensive individual variation in locomotor performance following autotomy also occurs in nature, and whether some individuals might be able to recover more quickly than others, thus resulting in lessened impact on fitness.

The results from our study also offer some useful information regarding the occurrence of autotomy among vertebrates. Despite the utility of autotomy during predatory encounters, losing appendages can impose various costs, which may include the loss of energy storage, impaired organismal functions

associated with appendage loss, the need of additional energy for regeneration, and altered behaviour, to name just a few (see Fleming *et al.*, 2007 for a detailed review). Under those circumstances, a reduction in fitness often results as a consequence of reduced foraging ability and the impaired ability to compete with conspecifics, a lower likelihood to attract mates, higher vulnerability to predators, and even reduced longevity and survival. Thus, the sooner the animals are able to fully regenerate the lost appendages, the sooner those costs will be ameliorated. Therefore, it is not surprising that most species that exhibit autotomy are invertebrates, whose regeneration rate tends to be more rapid (Fleming *et al.*, 2007). Within vertebrates, salamanders and lizards are the two lineages that contain the majority of autotomous species (Fleming *et al.*, 2007). Interestingly, within each lineage autotomy has been lost multiple times (Wake & Dresner, 1967; Arnold, 1984), especially in species which possess other traits that are advantageous during predatory encounters (e.g. larger body size). This trend suggests that autotomy, with its high costs, might be an evolutionary 'last resort' for predator defence in salamanders and lizards. Our study lends some support to this view by showing that even for a vertebrate species that commonly autotomizes, the costs of autotomy are not easily remedied. Comparative studies which test whether species that autotomize more frequently/easily can better compensate for the effect of autotomy would be especially interesting.

Our study demonstrated a general lack of ability to compensate kinematically for reduced in-air stability in tailless *A. carolinensis* individuals but also revealed extensive individual variation in the ability to cope with the locomotor challenge posed by tail autotomy. Thus, it appears that tail autotomy represents a significant and relatively long-term (relative to the lifespan of *A. carolinensis*) cost that is not easily ameliorated. Whether this same pattern holds for locomotor performance for a wide variety of ecologically diverse lizard species is a fruitful avenue for future research. Our findings underline the importance of individual variation in response to a traumatic injury, and in recovery from such an injury.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Mean body angles (takeoff, 25%, 50%, 75% of aerial phase and landing) in the three groups of lizards across five weeks. Figures in the same row belong to the same group. (A) the control group (B) the tailless-weekly jumping group and (C) the tailless-no weekly jumping group. Each error bar represented one standard deviation around the mean. Note the differences in mean and variation between the control and the other two groups throughout the weeks. There was no data for the tailless-no weekly jumping group from week two to four because we only collected data from this group in week one and five (see text).

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