ORIGINAL ARTICLE

The movement dynamics of autotomized lizards and their tails reveal functional costs of caudal autotomy

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Abstract

Autotomy has evolved independently several times in different animal lineages. It frequently involves immediate functional costs, so regeneration evolved in many instances to restore the functionality of that body part. Caudal autotomy is a widespread antipredator strategy in lizards, although it may affect energy storage, locomotion dynamics, or survival in future encounters with predators. Here, we assessed the effect of tail loss on the locomotor performance of wall lizards (*Podarcis muralis*), as well as the recovery of locomotor functionality of lizards with regenerated tails, and the movement dynamics of shed tails that were either intact or having regenerated portions. Tail loss had no effect on locomotion over unhindered spaces, possibly due to compensation between a negative effect on the stride of front limbs, and a positive effect of losing mass and friction force. We found a clear negative impact of tail loss on locomotion in spaces with interspersed obstacles, in which tailed lizards jumped larger distances when leaving the obstacles. Besides, lizards that used the tail to push off the ground were able to approach the obstacles from further, so that the tail seemed to be useful when used during jumping. Regeneration fully restores lizard's locomotor capacities, but tail antipredator value, as indicated by the intensity of post-autotomic movements, is only partially retrieved. From these results, we propose that, together with the recovery of post-autotomy antipredator capacities, the restoration of the organismal locomotor performance may have been an important, yet frequently neglected factor in the evolution of lizard's regeneration ability.

Key words: autotomy, locomotor performance, regeneration, tail, wall lizard

INTRODUCTION

Many animals, both vertebrates and invertebrates, are able to self-induce the shed of an expendable appendage as a reflex response to threats. This phenomenon, called "autotomy" (Fredericq 1892), does not represent the

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accidental loss of a body part, but an innate response integrated in the behavior and physiology of the animal (Bely & Nyberg 2010) that has evolved independently several times in different lineages (Fleming *et al.* 2007; Emberts *et al.* 2019). Autotomy may have evolved since it provides benefits, such as avoiding predation (Cooper *et al.* 2004), solving molting complications (Maginnis 2006), eliminating toxins from a certain body part (Moore *et al.* 1989), or allowing survival after physical damages (Wulff 2006). However, autotomy frequently involves immediate functional costs, as it represents the loss of a useful appendage (such as the tail of a lizard or the arm of a starfish) which

may be important, for instance, for feeding, locomotion or reproduction (for a review, see Bateman & Fleming 2009). Besides, the loss of a body part often involves social costs, which may affect the social status (Fox & Rostker 1982) or habitat selection (Fox *et al.* 1981) and, as a result, it might decrease survivorship (Fox & McCoy 2000). Consequently, autotomy is often followed by some behavioral changes aiming to compensate the functional losses, such as modifications of the locomotor dynamics and the escape strategies (Dial & Fitzpatrick 1981; Clause & Capaldi 2006), changes in feeding behavior (Ramsay *et al.* 2001) or in activity time and patterns (Díaz-Guisado *et al.* 2006; Barrios *et al.* 2008). However, behavioral adjustments are often costly and fail to fully restore the impaired function, and subsequently regeneration often evolved to recover lost parts that are not vital but increase survivorship and fitness (Goss 1969; Lin *et al.* 2017). In turn, regeneration implies an energy cost, thereby involving allocation trade-offs that may negatively affect somatic growth (Ballinger & Tinkle 1979), reproductive investment (Bellairs & Bryant 1985; Barrios *et al.* 2008) or immune function (Argaez *et al.* 2018), likely having physiological and evolutionary consequences (Stearns 1992).

The post-anal tail is a characteristic structure of chordates (and particularly of vertebrates) that assumes important functions (Kardong 2014); for example, lizards' tails often act as a counterbalance influencing the distribution of body weight (Arnold 1988) and providing stability during climbing (Jusufi *et al.* 2008; Medger *et al.* 2008), so it is an essential element for jumping dynamics and efficient landings (Gillis *et al.* 2009; Gillis *et al.* 2013). Even so, in many species of lizards, more than a half of the adult population have mutilated or regenerated tails, so they have undergone caudal autotomy at least once (e.g. Downes & Shine 2001; Cooper *et al.* 2004; this study). According to Arnold (1988), the benefits of caudal autotomy regarding predation avoidance are associated to two different escape strategies: (i) breaking away from a predator when the lizard is seized by the tail (in this case the smallest possible fragment of the tail is shed), and (ii) breaking the tail as a distraction to escape from the predator prior to capture (which in most cases implies basal autotomy). Vigorous post-autotomy movements, along with bright ventral colors (Castilla *et al.* 1999), make the tail more visible, setting the attention of predators and thus facilitating escape (Dial & Fitzpatrick 1983). Basal autotomy, although implies a less economical detachment, offers a large fragment to distract the predator, therefore increasing the probability of escape (Bellairs & Bryant 1985).

Locomotion is a function of widespread use for many kind of activities in a variety of ecologically relevant contexts (feeding, escape from predators, mating, social interactions, etc; see, e.g. Huey & Pianka 1981; Webb 1986; Robson & Miles 2000; Husak *et al.* 2006), and is accordingly closely related to fitness (Garland & Losos 1994; Miles 2004; Bauwens *et al.* 1995). The value of autotomy and regeneration relies on the balance between the costs and benefits of losing a body part (Arnold 1988).Given that locomotor performance may be important for survival under predatory pressure (e.g. Jayne & Bennett 1990; Braña 2003), it is probable that some mechanisms have evolved to counter the functional costs associated to caudal autotomy. Therefore, assessing the magnitude of the costs of tail loss and underlying possible mechanisms that evolved to minimize its consequences is essential to reach an accurate understanding of the evolutionary scenarios in which autotomy evolved.

Considering the value of caudal autotomy as a generalized antipredator strategy in lizards, the main aim of this study was to assess the effect of tail loss on locomotor performance of wall lizards (*Podarcis muralis*; Laurenti 1968), in order to understand the functional costs of tail loss, together with the potential of the regeneration to achieve the functional recovery of lost capacities. On the other hand, since the antipredatory effectiveness of caudal autotomy depends on the ability of the tail to attract and maintain the predator's attention, we have furthermore examined the movement dynamics of autotomized tails in order to assess their function as a predator distraction. At this respect, we have compared tails having signs of previous regeneration with apparently intact tails. Finally, we propose some scenarios in which autotomy and regeneration may have evolved in lacertid lizards.

MATERIAL AND METHODS

Laboratory trials and measurements

The common wall lizard, *Podarcis muralis,* is a small lacertid lizard (Reptilia: Lacertidae) inhabiting rocky habitats of both natural and urban areas from South Europe, from 0 to 2400 m of elevation (Salvador 2014). Adult individuals of *P. muralis* (i.e. larger than 4.8 cm in snout-vent length (SVL), see Salvador 2014) were captured by noose from May to July of 2017 ($N = 67$; 36 males and 31 females), in several close localities of central Asturias (northern Spain). Autotomy is frequent in this population, as 65.54% of sighted adults in our study area had mutilated or regenerated tails ($N = 148$). Lacertid lizards are able to autotomize their tail through

intra-vertebral fracture planes, and the proportion of tail that is shed depends on the position where the lizard is seized. Although the regenerated fragment of the tail lacks fracture planes, the tail can be detached once again through an anterior vertebral fracture plane (Bellairs & Bryant 1985). Lizards were transported to the Zoology laboratory (University of Oviedo), measured for snout-vent length and tail length (TL) to the nearest 0.01 cm, and weighed to the nearest 0.001 g. Lizards were kept in terrariums with 35 W lamps, supplied ad libitum with water containing supplementary vitamins and calcium, and fed daily with mealworms, grasshoppers or crickets. These procedures were ethically reviewed and approved by the Principality of Asturias Regional Government and the University of Oviedo.

A before-after design was used to test the differences between tailed and tailless individuals. Lizards were divided into a control (tailed) group ($N = 32$, 17 males and 15 females; mean $\pm$ SD SVL: 5.99 ± 0.41 cm; tail length: 8.03 ± 1.88 cm; body weight: 4.49 ± 1.23 g) and an experimental (hereafter tailless) group ($N = 35$, 19 males and 16 females; mean $\pm$ SD SVL: 5.97 ± 0.48 cm; tail length: 7.98 ± 1.51 cm; body weight: 4.44 ± 1.00 g). Groups were homogeneous with respect to body length (SVL), tail length and mass (ANOVA, $p > 0.5$ in all cases). Because animals live in a tridimensional habitat (vertical walls and stone clusters in the case of wall lizards) and spatial complexity often interferes with maximal locomotor performance (Braña 2003), lizards were subjected to two different locomotor trials (with 5 min resting time between them), one on a smooth corridor without obstacles and the other one with two obstacles of 3.2 cm high located at 20 cm and 47 cm, respectively from the beginning of the track. First, all the lizards of both the control and experimental group performed these two locomotor trials ("before" trials), having long tails (intact or completely regenerated). After this, we induced caudal autotomy (i.e. the self-detachment of the tail) to the experimental group (hereafter tailless) by grasping each lizard firmly from the base of the tail, between thumb and index fingers. To avoid behavioral biases during the locomotor trials after autotomy, lizards of the control group were handed and manipulated in a similar way than were experimental individuals, but preventing tail loss. After that, all the lizards were allowed to rest for two days so that they could recover from the physical trauma and (for the tailless lizards) get used to move in their new tailless condition; then we repeated the same two locomotor trials again for all the individuals from both the tailed and the tailless groups ("after" trials). The shed tails were measured (length and width) and weighed, and

its condition (totally intact or with regenerated portions) was registered. Autotomized individuals were left a tail stub of almost 1 cm long (mean $\pm$ SD tail stub: 0.87 ± 0.16 cm), and the detached piece of tail represented a mean of 1.34 times SVL and 91% of the complete tail. After autotomy, the detached tail moves vigorously to attract the attention of the predator: both duration of movement and distance travelled by the detached tails in each of the successive movements were measured, recording sequential positions every time the tail made a perceptible movement, until the tail stopped moving.

Before conducting all the locomotor tests and before inducing tail autotomy, lizards were placed in an incubator at 35 °C for 30 min to set body temperature close to the optimal temperature for maximum locomotor performance (Braña & Ji 2000). Locomotor trials were conducted inside a room with controlled temperature at 30 °C, corresponding to a frequent environmental temperature for the studied population. Lizards were placed for running in a racetrack of 1.2 m long and 4.5 cm wide, with a transparent sidewall and provided with a coarse surface to ensure a proper traction, and the race was recorded with a video camera (PANASONIC Lumix DMC-TZ10), filming at constant 30 frames s^{-1}. Videos of the races performed on smooth, unhindered substrates, were examined for maximum speed (calculated with the fastest four consecutive frames), average speed during the whole race (calculated without considering the frames in which the animal did not move) and number of stops during the race (considering a stop as at least three consecutive frames without moving). The videos of the races on the track with obstacles were examined for the total race time, distance from which the animal jumps to the first obstacle (preobstacle distance), distance covered by the animal when jumping to leave the first obstacle (post-obstacle distance), and total time stopped over the obstacle. Behavioral observations were made on whether lizards use or not the tail to push off the ground before jumping to the first obstacle (tail push), on whether they approach to the obstacle jumping or running, on how they pass over the obstacle (jumping the obstacle/running over it), on how they get off the obstacle (falling from it or jumping) and on whether they stop over the obstacle or not.

Statistical analysis

A Kolmogorov–Smirnov test was used to check the assumption of normality in the locomotor variables studied, and the variables that did not show normal distribution were $\log_{10}$-transformed in order to achieve normality. Linear regressions were conducted to dilucidate whether

the locomotor variables measured before inducing caudal autotomy were dependent on tail length and SVL. To evaluate the effect of tail loss on locomotion, a repeated measures ANOVA (with tailed group and sex as inter-subject factors) was carried out with the locomotor performance variables (SVL was not included as the covariate for any of the locomotor variables studied, as size was not significantly related to any of the performance traits). One way ANOVA with tail push (i.e. whether lizards use or not the tail to push off the ground when jumping to the obstacle) as the categorical predictor variable was done to test its influence on the total running time in obstacle races and on the preobstacle distance (only with variables measured before inducing autotomy, to evaluate all the individuals with tail). A Pearson's Chi-square test was carried out to check for differences between tailed and tailless individuals in the qualitative locomotor variables. Some individuals captured in the field had complete regenerated portions of the tail, while others had entire intact tails ($N_{intact} = 24$; $N_{regenerated} = 43$); the influence of tail condition (i.e. intact or completely regenerated) on locomotor performance was evaluated for all the individuals before inducing autotomy to the experimental group, by a one way ANOVA with the locomotor variables measured (in the "before" trials) and the tail condition as factor. Besides, a two-way ANOVA was done with the locomotor performance variables from the trials after autotomy, considering tail condition and tail group as categorical predictor variables, to search for possible effects of previous autotomy experiences on locomotor performance.

Linear regressions were used to test whether the length and the mass of the shed tails were related to the movement performance of autotomized tails. Tail robustness was calculated as the residuals from the regression of tail mass on tail length. Before doing parametric analyses, a Kolmogorov–Smirnov test was used to check the assumption of normality in the post-autotomy variables. Two out of 35 detached tails barely moved (less than 2 s), so they were considered as outliers and were not included in the analysis. Since the total number of movements was quite different among tails, we analyzed only the first 20 movements for all the tails that reached that number (25 out of a total of 33 detached tails), grouping movements in successive intervals of 5 each one. A repeated measures ANOVA was done to test possible differences in movement dynamics (in successive intervals) between regenerated and intact tails. Two-way ANOVA was used to examine differences in time of movement and distance covered by tails after autotomy between tails with regenerated portions and intact ones, and between sexes. Intact tails were slightly longer than regenerated

ones, so two-way ANCOVA including tail length as the covariate was also done. Two-way ANCOVA was done for distance moved by the tail, with time of tail movement as the covariate and tail condition and sex as the factors. Due to the presence of the hemipenes at the base of the tail, males have greater robustness and some morphological specializations in that region; for example, the first complete fracture plane occurs in the 6th–7th vertebra in males, while in females occurs in the 5th–6th vertebra (Barbadillo *et al.* 1995; Barbadillo & Bauwens 1997). For these reasons, we tested for possible differences between males and females in the performance of the detached tails, including sex as factor in the previous two-way ANOVAs and ANCOVAs. For all the analyses carried out in this study, significant level was set at $p < 0.05$.

RESULTS

Effect of tail loss on locomotor performance

The main locomotor performance traits for all lizards before and after autotomy are summarized in Table 1. Tailless and tailed individuals did not show significant differences in maximum speed, average speed, or number of stops in races on smooth, unhindered substrates, nor in preobstacle distance and stop time over the obstacle in obstacle races. On the contrary, tailless individuals performed the obstacle race in a longer time than the tailed ones (repeated measures ANOVA: $F_{1,63} = 10.581$, $p = 0.002$) (Fig. 1A), and jumped a shorter distance when getting off the obstacle (repeated measures ANOVA: $F_{1,63} = 6.4201$, $p = 0.014$) (Fig. 1B). Sex of lizards was never a significant factor on the measured locomotor variables (data not shown).

Tailed lizards tend to jump more frequently than the tailless ones, rather than run when approaching the obstacle ($X^2_1 = 5.558$, $p = 0.018$) or fall when leaving it ($X^2_1 = 6.777$, $p = 0.009$) (Fig. 2), but there were no differences between tailed and tailless individuals regarding how they overcome the obstacles (i.e. if they jump the obstacle or they run over it; $X^2_1 = 2.251$, $p = 0.134$) or whether they stop over the or not ($X^2_1 = 0.239$, $p = 0.625$). Besides, among tailed lizards, those that used the tail to push off the ground jumped to the obstacles from a longer distance (preobstacle distance, $F_{1,65} = 9.170$, $p = 0.004$) and performed the races in a shorter time ($F_{1,65} = 4.525$, $p = 0.037$) than those that did not use the tail.

Tail length positively influenced the preobstacle distance (total length measured before inducing autotomy; $R^2 = 0.056$, $p = 0.053$), but not maximum speed ($R^2 = 0.002$, $p = 0.728$), average speed in the straight

Table 1 Descriptive statistics from the main variables measured in the locomotor performance trials (with and without obstacles) done before and after inducing caudal autotomy to the experimental (tailless) group. Repeated measures ANOVA were carried out with tail group as the categorical predictor variable in all cases. $N_{tailed} = 32$; $N_{tailless} = 35$. Values are means $\pm$ SE

		Before		After		ANOVA	
		Tailed	Tailless	Tailed	Tailless	F	P
Without obstacles	Max speed (cm s^{-1})	1,31 $\pm$ 0,06	1,32 $\pm$ 0,05	1,44 $\pm$ 0,06	1,39 $\pm$ 0,05	0,390	0,535
	Average speed (cm s^{-1})	0,92 $\pm$ 0,06	0,87 $\pm$ 0,04	0,90 $\pm$ 0,04	0,90 $\pm$ 0,04	0,455	0,502
With obstacles	Time (s)	1,50 $\pm$ 0,12	1,42 $\pm$ 0,10	1,26 $\pm$ 0,06	1,64 $\pm$ 0,09	10,581	0,002**
	Preobst. dist. (cm)	5,30 $\pm$ 0,79	5,49 $\pm$ 0,73	5,20 $\pm$ 0,84	4,09 $\pm$ 0,83	0,554	0,460
	Post-obst. dist. (cm)	15,22 $\pm$ 1,02	15,87 $\pm$ 0,80	15,64 $\pm$ 0,88	12,19 $\pm$ 1,05	6,420	0,014*

race ($R^2 = 0.001$, $p = 0.822$), running time in obstacles race ($R^2 = 0.024$, $p = 0.207$) or post-obstacle distance ($R^2 = 0.005$, $p = 0.587$). There were no differences in the locomotor performance after autotomy between tailless and tailed individuals depending on their previous tail condition (i.e. if they had intact or previously regenerated tails) (two-way ANOVA for max. speed and average speed in straight race, running time in obstacles race, preobstacle distance and post-obstacle distance; $p > 0.300$ in all cases for the interaction between tail group and tail condition).

Functionality of regenerated tails

Individuals with previously completely regenerated tails did not show differences when compared to individuals with entire intact tails in the locomotor variables measured before inducing tail loss to the experimental group (one factor ANOVA, max. speed in straight race: $F_{1,65} = 0.128$, $p = 0.722$; average speed in straight race: $F_{1,65} = 0.010$, $p = 0.921$; running time in obstacles race: $F_{1,65} = 0.712$, $p = 0.402$; preobstacle distance: $F_{1,65} = 0.031$, $p = 0.862$; post-obstacle distance: $F_{1,65} = 1.304$, $p = 0.258$). Autotomized tails moved at a non-linear decreasing rate until they stopped moving, dropping substantially during the first movements and then decreasing slowly until definitive stop. Intensity of movement in the initial 20 intervals (i.e. accumulated distance moved) was significantly higher for intact tails than for the regenerated ones (repeated measures ANOVA, $F_{1,23} = 9.317$; $p = 0.006$; Fig. 3). Intact tails were slightly longer than the regenerated ones (intact TL: 8.38 $\pm$ 0.98 cm; regenerated TL: 7.28 $\pm$ 1.17 cm; ANOVA, $F_{1,23} = 7.581$; $p = 0.017$), so we analyzed tail movement intensity using tail length as the covariate, resulting again that intact tails moved further than the regenerated ones (repeated measures ANOVA with TL as the covariate, $F_{1,23} =$

4.739; $p = 0.041$). Total time of movement and total distance travelled by shed tails were lower for tails having regenerated portions than for the intact ones (two-way ANOVA for time of movement: $F_{1,31} = 5.875$, $p = 0.022$; distance travelled: $F_{1,31} = 12.863$, $p = 0.001$), but such differences were mainly due to differences in tail length, and disappeared when including it as covariate (two-way ANCOVA with tail length as the covariate for time of movement: $F_{1,31} = 0.214$, $p = 0.648$; distance travelled: $F_{1,31} = 1.292$, $p = 0.265$). Distance moved by intact tails was higher than for regenerated ones (two-way ANCOVA with tail movement time as the covariate; $F_{1,31} = 6.132$, $p = 0.020$). Total movement time of autotomized tails depended on tail length ($R^2 = 0.286$, $p = 0.001$), but not on tail robustness (tail mass residuals: $R^2 = 0.023$, $p = 0.397$), and the same happened for the total distance travelled by the tail until definitive stop (tail length: $R^2 = 0.414$, $p < 0.001$; tail mass residuals: $R^2 = 0.016$, $p = 0.479$). Females' autotomized tails moved during significantly more time than those of males (two-way ANOVA; $F_{1,31} = 4.380$, $p = 0.045$; $N = 33$; mean $\pm$ SD males: 2.48 $\pm$ 0.73 s; mean $\pm$ SD females: 3.27 $\pm$ 1.36 s), but no significant between sex differences were found in the total distance covered by their tails before stopping (two-way ANOVA; $F_{1,31} = 1.222$, $p = 0.352$).

DISCUSSION

Effect of tail loss on locomotor performance

It is well known the role of the post-anal tail in the locomotion of terrestrial vertebrates, providing stability during running and climbing, and influencing jumping dynamics (Arnold 1988; Jusufi *et al.* 2008). Consequently, tail loss can be expected to affect the performance of ecologically relevant tasks, such as pursuit and capture
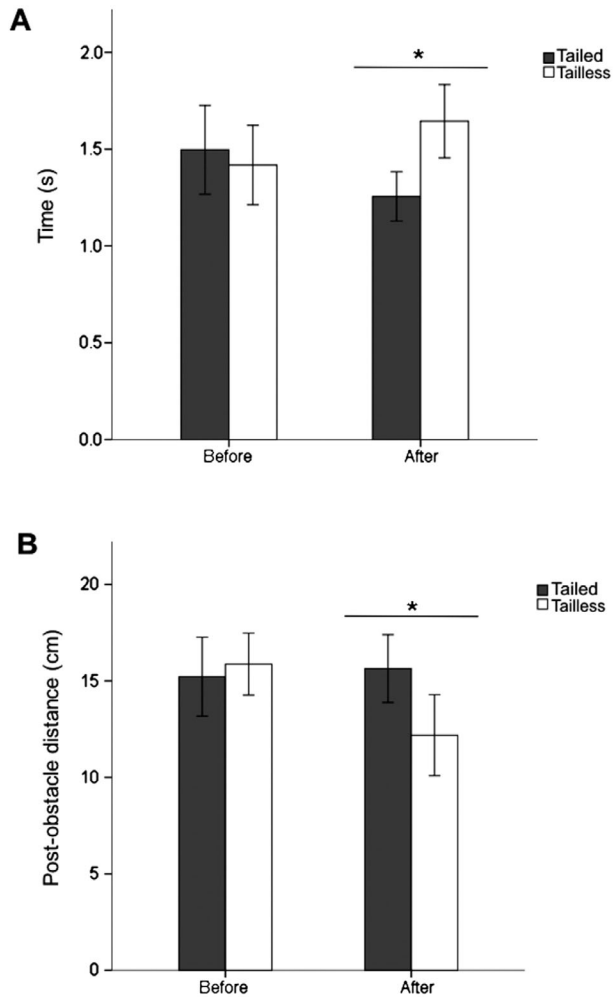
Figure 1 Locomotor performance of control (tailed, gray bars; $N = 32$) and experimental (tailless, white bars; $N = 35$) lizards, before and after inducing caudal autotomy to the experimental group. (A) Time of running for races with obstacles. (B) Mean post-obstacle distance reached by tailed and tailless lizards. Values are means ± SE; $*p < 0.05$.

Figure 2 Behavior of tailed (gray bars; $N = 32$) and tailless (white bars; $N = 35$) lizards when approaching an obstacle ("preobstacle") and when leaving it ("post-obstacle"). Values are percentage of individuals that jump instead of running toward the obstacle or falling from it. $*p < 0.05$.

of prey, territorial patrolling, or escape from predators, that depend on mobility and are closely related to fitness (e.g. Garland & Losos 1994; Bauwens *et al.* 1995; Braña 2003; Miles 2004; Husak 2006). Several studies have been conducted to test the effect of tail loss on locomotion in different lizard species, and their results have shown considerable variation: in most studies, lizards experienced a reduction in maximum burst speed after autotomy (Daniels 1985; Chapple *et al.* 2004; Fleming *et al.* 2009), while in some others there was apparently no effect (Medger *et al.* 2008; Gillis *et al.* 2009) and even in a few
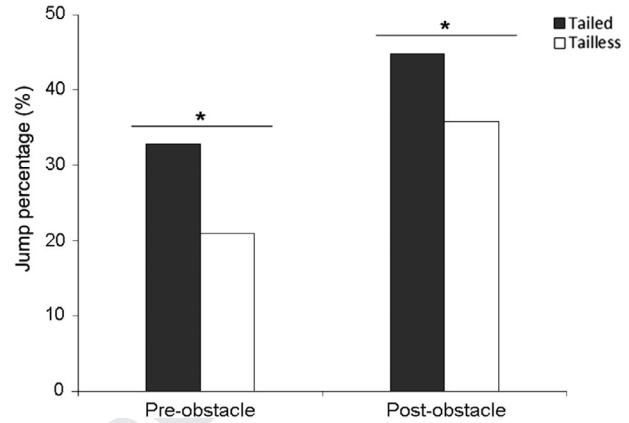
cases tailless lizards exhibited an increase in maximum sprint speed (Brown *et al.* 1995; Ekner-Grzyb *et al.* 2013). Apart from methodological differences among these studies, changes in sprint speed after caudal autotomy vary among the different lizard families, each having different morphological and behavioral specificities: it usually decreases in skinks and iguanids, while there is a larger variation in lacertids and geckos (McElroy & Bergmann 2013). Such variability may be partially explained by differences in body shape (Bergmann & Irschick 2012) and in the biomechanics of locomotion, including the function of the tail and limbs (McElroy & Bergmann 2013).

Our study on wall lizards showed that autotomy has no effect on locomotor performance over unhindered spaces, but has a clear negative impact on locomotion in spaces with obstacles, which represents a more realistic approach to locomotion in natural conditions. Our results suggested two possible causal mechanisms for the higher locomotor performance of tailed lizards in habitats with higher structural complexity: (i) non-mutilated lizards that used the tail to push off the ground were able to approach the obstacle from a larger distance, and (ii) tailed individuals jumped a larger distance when leaving the obstacles. Besides, tailed lizards were more prone to jump when approaching the obstacle and when leaving it, rather than run toward it or fall from it, while mutilated individuals tended to run/fall more frequently than the tailed ones.

It is well known that the tail may be important for several aspects of lizards' locomotion, such as impulse and balance (Gillis & Higham 2016), and it seems to play a key role in physical interactions with the substrate, which
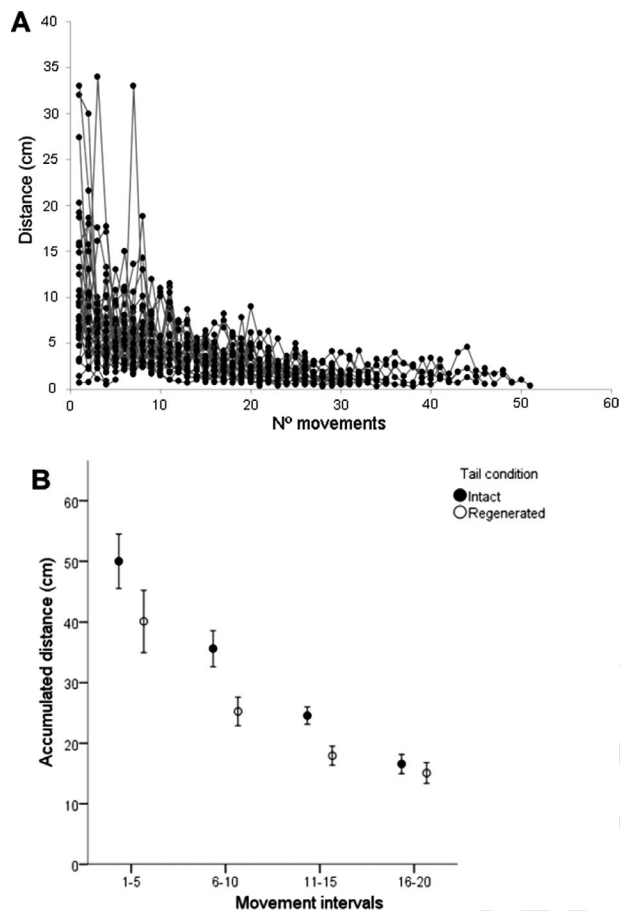
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Figure 3 (A) Distance moved by each tail in successive movements after autotomy ($N = 33$). (B) Accumulated distance moved by intact (black, $N = 12$) and regenerated (white, $N = 13$) tails in successive movements after autotomy, grouped in four intervals, for tails that performed at least 20 movements. Values on B are means ± SE of the total distance moved in each interval.

may also influence trajectory and body posture (Gillis *et al.* 2013) and stability while climbing (Jusufi *et al.* 2008). As a consequence, tail loss decreases escape speed of the Cape dwarf gecko *Lygodactylus capensis* (Smith 1849) over a leaning surface (Medger *et al.* 2008), and has a desestabilizing effect in *Anolis carolinensis* (Voigt 1832) during running (Hsieh 2016). Thereby, caudal autotomy affects physiology and biomechanics, and therefore locomotor performance and behavior, which will finally affect the fitness of the individual (Gillis & Higham 2016). In our study, tail removal in fact had biomechanical and behavioral effects on jumping dynamics. For example, when leaving the obstacle, 68.57% of tailless individuals (i.e. 24 out of a total of 35) jumped rather than fell from it, in contrast with the 93.75% of tailed lizards (i.e. 30 out of 32). This difference seems to be the main explanation for the distance reached when leaving the obstacle, which was significantly larger for tailed lizards. In addition, locomotor biomechanics may be affected after tail loss, producing a reduction in jumping and climbing effectiveness. Many cursorial lizards raise their tail during running, acting like a counterpoise to the head and body, and thus the body weight is mainly concentrated on the hind limbs. The loss of a long and heavy tail displaces to the front the body mass center (Snyder 1949; Arnold 1984), which results in more weight being transferred to the fore limbs, as it has been shown for *Podarcis sicula* (Rafinesque 1810) or *A. carolinensis* (Arnold 1984; Gillis *et al.* 2013). According to the biomechanical models proposed by Ballinger *et al.* (1979) and Punzo (1982), we assume that such displacement of the body mass center to the fore limbs after tail loss would decrease efficiency of propulsive force in the lizards we tested, affecting their jumping distance and total race time, which may result in a decrease of locomotor effectiveness.

On the contrary, we did not find clear negative effects of tail loss on locomotor performance of lizards when tested in open, obstacle-free spaces. As said before, tail loss may have different effects on locomotion depending on lizards' morphology and the role of their tails, either increasing or reducing locomotor performance. Tail often acts as a counterbalance for lateral bendings of the spinal cord, which influence stride length and frequency. Sprint speed is mainly determined by stride length and frequency (see Braña 2003, for wall lizards), and the lack of tail may have a negative effect on those kinematic parameters, thus decreasing sprint speed (Martin & Avery 1998; Cromie & Chapple 2012). On the other hand, long and heavy tails are often dragged during the race, increasing friction force and total body mass, thus acting as a mechanical impairment, and in such case caudal autotomy should imply a positive effect on burst speed (Arnold 1997; Willey *et al.* 2004). The absence of effect of caudal autotomy on velocity over a smooth horizontal surface found in our experiments could be the result of compensation between the negative effect of tail loss on stride length of front limbs, and the positive effect of losing mass and tail friction force after autotomy, as suggested by Medger *et al.* (2008).

Functionality of regenerated tails

Regeneration evolved to minimize the negative effects of the loss of a valuable appendage (Goss 1969), so the regenerated appendage should restore at least partially the

functional role of the lost appendage (Clause & Capaldi 2006), thus providing some benefits to the animal (Arnold 1988). We found that the functionality of fully regenerated tails was equivalent to that of the intact ones in terms of locomotor performance, and that tailless animals that had suffered previous autotomy events did not exhibit better locomotor performance than the tailless ones without previous experience. Lin *et al.* (2017) found that lizards with regenerated tails had similar survivorship than those with intact tails but higher than tailless individuals, so that regeneration seemed to restore the functionality of the tails. Brown *et al.* (1995) working on a population of *P. muralis* introduced in Ohio (United States) found that individuals with regenerated tails were slower than those with intact tails. Besides, they found that tailless individuals that had previously experienced caudal autotomy, ran faster than tailless individuals that had intact tails just before the experimentally induced caudal autotomy, attributing these findings to learning effects and previous experience. On the contrary, our results suggest that lizards suffer temporary effects on locomotor performance after autotomy, regardless of their previous experience, which could be compensated by behavioral changes, as proposed by Dial and Fitzpatrick (1981), Downes and Shine (2001), or Chapple and Swain (2002). These differences between studies may be due to methodological differences and also maybe to the fact that intact and previously regenerated tails have large size differences in the sample studied by Brown and coworkers, unlike in ours.

Caudal autotomy in lizards can be considered as a defensive response to attempted predation (Arnold 1988), and its success will depend on the ability to distract the predator until the lizard manages to escape, which depends largely on tail color and mobility (Castilla *et al.* 1999; Cooper *et al.* 2004; Kuriyama *et al.* 2016). Post-autotomy performance of mutilated tails exhibited a significant positive correlation with its length in our experiments. Studies carried out with *Lampropholis* sp. (Fitzinger 1843) and *Trachylepis maculilabris* (Gray 1845) showed that the longer the shed tail, the longer the distance it covered after autotomy, but in contrast to our results, those studies did not show any correlation between tail length and movement time (Cooper & Smith 2009; Cromie & Chapple 2012). Our results evidenced a longer duration of tail movement after autotomy in females and, in contrast, a larger distance travelled by males' tails in relation to the total time of movement. Males have more robust base tail to accommodate hemipenes (Barbadillo *et al.* 1995), and this could allow more energetic initial movements of the detached tail, which might constrain their total duration. A long tail

probably increases the probability of performing flips when bending as a consequence of the violent movements that immediately follows autotomy. Complex movements and flips of the autotomized tail are common in species that live in an exposed habitat because they involve unpredictable trajectories that increase the probability of distracting the predator (Higham & Russell 2010). Our results show that movements of shed tails after autotomy were stronger at the beginning, and their strength (measured as the mean distance travelled in each of the first 20 movements immediately after autotomy) experienced an exponential decrease with time. A forceful initial response may ensure predator's distraction (Bellairs & Bryant 1985) and could be in many cases decisive for the success of the escape response, and therefore movements during the first seconds after autotomy would be under a strong selective pressure. In our study, shed tails with regenerated portions performed weaker movements and during a shorter time than intact tails, but these differences were mainly explained by tail length, which was slightly longer for intact tails. Moreover, intensity of the first movements was significantly stronger for intact tails than for the regenerated ones, even after correction for differences in length. These findings may be explained by some structural differences between intact and regenerated tails. Skeleton of regenerated portions of the tails consists on a continuous, unsegmented cartilage axis, rather than a succession of articulated vertebrae (Hughes & New 1959). Besides, arrangement of regenerated muscle bundles is less regular than in intact tails, and they are not attached to the cartilage tube (Bellairs & Bryant 1985). In addition, according to Higham *et al.* (2013), muscles of intact tails were more resistant to fatigue. As a consequence of these different anatomic and physiological features, intensity of the initial movements, which is crucial for the escape success and determines the antipredator value of autotomy, would be diminished in regenerated tails.

In conclusion, our results evidenced that tail loss impairs locomotor performance, and that tail regeneration fully restores locomotor capacities. However, given that regenerated tails exhibit clearly diminished intensity of movement after autotomy, even after removing the effect of its different size, it seems likely that the antipredator post-autotomy value of tails is only partially retrieved after regeneration. These findings shed light on the possible adaptive scenarios in which autotomy and regeneration could have evolved, suggesting that the restoration of the antipredator post-autotomy function (i.e. another tail shed to increase the survival probability in future encounters with predators) has not been the only selective pressure

that led to the evolution of regenerative abilities in lacertid lizards. The restoration of the efficiency of locomotion, a function of widespread use for many kind of activities in a variety of ecologically relevant contexts and that is accordingly closely related to fitness, may have been equally important in the evolution of lizard's regeneration ability.

ACKNOWLEDGMENTS

FUNDING

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Cite this article as: