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Does tail regeneration following autotomy restore lizard sprint speed? Evidence from the lacertid *Psammodromus algirus*

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Tail autotomy is a widespread antipredator strategy among lizards, which consists of the capability of willingly detaching a portion of the tail in order to escape predator attacks. Nonetheless, tail autotomy has a number of costs, including reduced sprint speed which increases predation risk. However, lizards regenerate the tail following autotomy, although a regenerated tail is usually shorter and histologically different from the original tail. In the present work, we assess the effect of tail regeneration on sprint speed by comparing *Psammodromus algirus* lizards with intact and regenerated tails under controlled laboratory conditions. We found that sprint speed was similar in lizards with intact and regenerated tails. Therefore, tail regeneration following autotomy effectively restored sprint speed, although regenerated tails were shorter than intact ones. Thus, regenerating shorter tails could diminish anabolic costs with no negative consequences on flight ability.

Key words: intact tail, lizard, regenerated tail, sprint speed, tail autotomy

INTRODUCTION

Predation is one of the strongest selective forces on prey (Caro, 2005). Predators reduce prey future fitness drastically by ending prey's life (Abrams, 2000). Most antipredator strategies are behavioural and/or physiological, and are energetically costly (Lima, 1998). Moreover, different antipredator strategies often cannot be simultaneously enhanced due to energetic trade-offs or physical limitations (Witter & Cuthill, 1993; Bourdeau, 2009).

Because lizards are often victims of predation, they use numerous antipredator strategies, mainly relying on sprint speed and tail autotomy (Brock et al., 2015). Fleeing is considered the most important antipredator strategy, since most lizards escape when attacked (Martín & López, 2000a; Higham et al., 2013). High sprint speed to reach safe refuges increases survival and reproductive output, and is thus under strong selection (Husak et al., 2006; Calsbeek & Irschick, 2007; Irschick & Meyers, 2007; Vervust et al., 2007).

Tail autotomy allows lizards to escape predator attacks by detaching (a portion of) their tails. The breakage occurs at preformed horizontal fracture planes (Sanggaard et al., 2012), and is induced by physical contact (Maginnis, 2006). While high predation pressure selects more brittle tails in lizards (Cooper et al., 2004), tail autotomy is not devoid of costs. Besides compromising the immune system and fat storage (Chapple & Swain, 2002; Kuo et al.,

2013), tailless lizards experience impaired mobility and sprint speed since tails stabilise locomotion (Ballinger, 1973; Gillis et al., 2009; Cromie & Chapple, 2012). Sprint speed is vital for antipredator strategies of most lizards (Gifford et al., 2008; Bateman & Fleming, 2009), and tail autotomy negatively affects home range area (Salvador et al., 1994), foraging ability (Martín & Salvador, 1993a), social dominance (Fox et al., 1990), mating success (Dial & Fitzpatrick, 1981; Martín & Salvador, 1993b), and ultimately, survival (Fox & McCoy, 2000; Downes & Shine, 2001).

Lizards have the ability to regenerate the tissues lost as a consequence of autotomy, although regenerated tails are usually shorter than intact ones and have vertebrae bone tissue replaced with cartilage (Fisher et al., 2012; Higham et al., 2013). Tail regeneration is faster in larger individuals, who are better facing the metabolic costs (Naya et al., 2007; Marvin, 2011). That lizards invest energy in regenerating tails suggests the importance of having a complete tail, but the consequences of tail regeneration on lizard biology have so far received little attention. For example, as far as we know, no study has analysed whether regenerated tails allow lizards to run as fast as lizards with intact tails. Given that regenerated tails are shorter than, and histologically different from, intact tails, sprint speed of lizards with regenerated tails could be slower than that of lizards with intact tails.

In the present paper we explore the effect of tail regeneration on sprint speed in the lizard *Psammodromus*

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algrus. As in many other species, tail autotomy impairs their mobility (Martín & Avery, 1998), but whether full mobility is recovered in lizards with regenerated tails is unknown. To this end, we compare sprint speed of lizards with complete intact tails with lizards with regenerated tails, in order to infer whether tail regeneration restores sprint speed.

MATERIALS AND METHODS

Psammodromus algirus is a medium-sized, oviparous, generalist lacertid lizard that inhabits shrubby areas in south-western Europe and north-western Africa from the sea level to above 2600 m.a.s.l. (Salvador, 2011). Lizards can either use a sit-and-wait or, more frequently, an active search strategy, to prey on diverse invertebrates, usually not far from the bushes they use as shelters from potential predators (Salvador, 2011). *Psammodromus algirus* has a tail length which more than twice exceeds the snout-vent length (SVL), making it particularly susceptible to impaired sprint speed as a consequence of tail autotomy (McElroy & Bergmann, 2013).

We captured *P. algirus* individuals by hand during their reproductive season in 2012 (April–July) on the south face of the Sierra Nevada (SE Spain) from six populations at 300, 700, 1200, 1700, 2200, and 2500 m.a.s.l. as part of a long-term research project, although previous studies have shown that sprint speed does not vary with elevation (Zamora-Camacho et al., 2014). Since habitat characteristics can have an effect on escape behaviour (Martín & López, 1995; Iraeta et al., 2010), we selected plots as similar as possible in vegetation structure (see Appendix A in Zamora-Camacho et al., 2013).

Captured lizards were transported to the laboratory in individual cotton bags. We considered three reproductive conditions: males, gravid females and non-gravid females. Males were identified through their wider heads, orange spots in the commissures of their mouths, and more abundant and prominent femoral pores. Gravid females evidenced developing eggs by manual abdomen palpation. We categorized three tail states: intact, if tail showed no damage; incomplete, if tail had been autotomised and new tissue regeneration had not started or was in progress; and regenerated, if tail had been broken but a new tail had been completely restored. We could recognise regenerated tails because

breakage points remain visible, and tissue morphology and colouration which clearly differ from intact tails (Fisher et al., 2012). We discarded lizards with an incomplete or growing tail. The group with regenerated tails only included individuals that had lost at least 75% of their original tail length as compared with average intact tails in the species. In all cases, we measured SVL, hind-limb length (since it is particularly involved in this lizards' sprint speed; Bauwens et al., 1995; Zamora-Camacho et al., 2014), and tail length with a millimetre-marked ruler, as well as body mass with a balance (model CDS-100, precision 0.01 g). Lizards were marked by toe clipping as part of a long-term research project, avoiding the fourth toe in the hind limbs since it could play a particular role in lizard mobility; toe clipping has been proven not to affect lizard sprint performance (Huey et al., 1990; Dodd, 1993; Husak, 2006). During their captivity, lizards were kept in individual terraria (20 x 13 x 9 cm) nearby to a window allowing lizards to maintain natural circadian rhythms, and a heat cable activated during daytime to facilitate thermoregulation. Lizards were fed *ad libitum* with mealworm (*Tenebrio molitor*) larvae and nutritious aqueous gel as a water source. After the experiments, we released lizards in the same location where they were captured. No lizard suffered any damage or died as a consequence of this study.

Two days after capture, lizards ran in a wooden, linear raceway (320 x 20 x 40 cm), whose bottom was lined with artificial cork to provide a traction surface (Bauwens et al., 1995). The bottom of the raceway was divided into 25 cm stretches delimited by transversal marks, since this is the distance that lizards approximately run to reach their natural refuges (Martín & López, 2000b). At the end of the raceway, a dark background simulated a shelter. Whenever lizards stopped running, a researcher chased them in order to stimulate the run. Each lizard ran three consecutive trials since they exhibited no sign of fatigue, and trials were performed individually. Sprint performance is temperature-sensitive in ectotherms (Pérez-Tris et al., 2004; Iraeta et al., 2010), and individuals were trialled at a body temperature of 32°C, which is within the species' thermal preference (Díaz & Cabezas-Díaz, 2004) and achieved by 10 minutes in an incubator and measured by inserting a thermocouple (1mm diameter) connected to a thermometer (Hibok18; 0.1°C precision) 8 mm inside the cloaca. Runs were videotaped

Table 1. Linear Mixed Models testing the effects of tail state, reproductive condition, and their interaction on body mass, snout-vent length, hind-limb length, and tail length in *Psammodromus algirus*. Population of origin was introduced as random factor. Values are *F*-values. Degrees of freedom (df) are shown for each model. Significant results are in *italic*. Symbols indicate: [ns] for non-significant; [§] for marginally non-significant ($0.05 < p < 0.10$); * for $p < 0.05$; *** for $p < 0.001$.

Variable	Tail state	Reproductive condition	Tail state * Reproductive condition
df	1, 63	2, 63	2, 63
Body mass	0.516[ns]	*13.859***	0.743[ns]
Snout-vent length	0.597[ns]	4.900 [§]	1.351[ns]
Hind-limb length	0.003[ns]	*23.516***	4.082[ns]
Tail length	*37.878***	*6.685**	0.658[ns]

Table 2. Average values±standard error (SE) of biometric variables analysed in Table 1, compared between *Psammodromus algirus* with intact and regenerated tails.

Variable	Intact tailed lizards (*n*=50) Mean±SE	Regenerated-tailed lizards (*n*=19) Mean±SE
Body mass (g)	7.61±0.33	8.46±0.54
Snout-vent length (mm)	66.90±0.89	70.00±1.44
Hind-limb length (mm)	35.09±0.33	35.98±0.53
Tail length (mm)	158.16±2.20	118.16±3.57

with a Canon EOS 550D camera. We calculated the time that each lizard spent in covering each stretch with the software Movavi v. 11 (Chen et al., 2003) to the nearest ms, obtaining the speed each lizard developed in each stretch. Maximum sprint speed was defined as the speed in each lizard's fastest stretch. Clutch size or days until oviposition have no effect on gravid female sprint speed (Zamora-Camacho et al., 2014).

Since data met the criteria of residual homoscedasticity and normality, we performed parametric statistics (Quinn & Keough, 2002). Several Linear Mixed Models of Restricted Maximum Likelihood (REML-LMM) were performed, including population of origin as a random factor (Zuur et al., 2009). This way, we tested the effect of tail state, reproductive condition, and their interaction on morphological variables: body mass, SVL, hind-limb length, and tail length. Moreover, we tested the effect of tail length (the only morphological variable affected by tail state), tail state, and reproductive condition on sprint speed. The effects of predictors were examined with sum of squares type III. Statistical analyses were conducted with the software R v. 3.1.1 (R Core Development Team 2014). Raw data are provided in the Online Appendix.

RESULTS

Body mass, SVL, and hind-limb length did not differ between lizards with intact and regenerated tails (Tables 1 and 2), but regenerated tails were significantly shorter than intact tails (Tables 1 and 2). Tail state*reproductive condition interaction was not significant (Table 1). On the other hand, we found morphological differences among reproductive conditions (male tail and hind-limb lengths were higher, while gravid females were heavier; Table 1). Nevertheless, reproductive condition had no effect on sprint speed (Table 3). Sprint speed was not affected by tail length nor tail state (sprint speed of intact-tailed lizards mean±SE=141.81±11.67cm/s, *n*=50; sprint speed of regenerated-tailed lizards mean±SE=197.43±28.62 cm/s, *n*=19; Table 3). When interactions (none of which significant; Table 3) were removed from the model, all effects remained non-significant (data not shown).

DISCUSSION

Tail autotomy is a common antipredator strategy among lizards, and involves the capability of shedding a portion of the tail in order to escape a potential predator attack (Lima & Dill, 1990). Nonetheless, tail autotomy has a number of costs (reviewed in Bateman & Fleming, 2009), including reduced speed sprint which facilitates a further capital antipredator defence in lizards (Gifford et al., 2008; Cooper & Smith, 2009). Lizards regenerate lost tails at energetic costs (Maginnis, 2006; Naya et al., 2007). Tails are fundamental for mobility (Ballinger, 1973), but it is unknown whether lizards with regenerated tails achieve a sprint speed similar to lizards with intact tails. Our findings suggest that tail regeneration restores sprint speed, although our results do not include data on individual speed prior to tail loss. As victims of a predator attack, individuals with regenerated tails could be characterised by slower sprint speed than individuals with an intact tail. In such a scenario we would expect them to be slower also after tail regeneration, which is not supported by our data. Tail loss may also be a consequence of intraspecific agonistic encounters (Jennings & Thompson, 1999).

Table 3. Linear Mixed Models testing the effects of tail length, tail state, reproductive condition, and their interactions on sprint speed in *Psammodromus algirus*. df: degrees of freedom. Population was included in the models as random factor. Sum of squares was type III.

Variable	df	*F*-statistic	*p*-value
Tail length	1, 57	0.655	0.418
Tail state	1, 57	0.003	0.954
Reproductive condition	2, 57	1.298	0.523
Tail length * Tail state	1, 57	0.032	0.859
Tail length * Reproductive condition	2, 57	1.102	0.576
Tail state * Reproductive condition	2, 57	0.471	0.790
Tail length * Tail state * Reproductive condition	2, 57	0.309	0.857

The reduction in sprint speed following tail autotomy can make lizards more prone to be preyed upon (Downes & Shine, 2001; Calsbeek, 2008). Tailless lizards may lack mechanisms to metabolically compensate the costs of tail loss (Sun et al., 2009), or to efficiently shift antipredator behaviour (Kelehear & Webb, 2006). For example, tailless *Anolis carolinensis* are unable to improve in-air stability during escape leaps in repeated trials, suggesting that they cannot learn to jump efficiently without a tail (Kuo et al., 2012). Moreover, some autotomised lizards exhibit a more cautious behaviour including reduced feeding (Cooper, 2003). Our results show that *P. algirus* with regenerated tails were not slower than those with intact tails, whilst tailless individuals of this species are slower (Martín & Avery, 1998; for other species see also Brown et al., 1995; Gillis et al., 2009). Therefore, sprint speed retrieval could be one reason why energy investment in tail regeneration outweighs its costs (Naya et al., 2007). Tail regeneration improves sprint speed by the recovery of the stabilising role of the tail during locomotion (Ballinger et al., 1979). Tailless leopard geckos (*Eublepharis macularius*) experience a displacement of the centre of mass and the relative position of the hindlimb joint angle, but return to their original position after tail regeneration (Jagnandan et al., 2014).

We also found that regenerated tails were significantly shorter than intact tails, however with no effect on sprint speed. Regeneration of shorter tails could require a lower energy investment (Naya et al., 2007), allowing lizards to divert energy to other life-history traits which enhance the ability to flee from predators. The proportion of the tail lost is related to the cost of tail loss (Sun et al., 2009; Cromie & Chapple, 2013), and specific thresholds exist for effects on locomotory speed (Marvin, 2013). Therefore, fully intact tails are not needed for optimal locomotor performance. The specific length of intact tails could also be advantageous for attracting predator attention towards a detachable body part (Dial, 1986). In conclusion, tail regeneration following autotomy proved effective in retrieving sprint speed in *P. algirus.* Regenerating shorter tails could diminish regeneration costs with no negative consequences on sprint speed and, thus, on capability of fleeing from potential predators.

ACKNOWLEDGEMENTS

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