Sci Nat (2017) 104:3
DOI 10.1007/s00114-016-1425-5

ORIGINAL PAPER

Tail autotomy affects bipedalism but not sprint performance in a cursorial Mediterranean lizard

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Received: 13 May 2016 / Revised: 29 November 2016 / Accepted: 7 December 2016

Abstract Running is essential in all terrestrial animals mainly for finding food and mates and escaping from predators. Lizards employ running in all their everyday functions, among which defense stands out. Besides flight, tail autotomy is another very common antipredatory strategy within most lizard families. The impact of tail loss to sprint performance seems to be species dependent. In some lizard species, tail shedding reduces sprint speed, in other species, increases it, and, in a few species, speed is not affected at all. Here, we aimed to clarify the effect of tail autotomy on the sprint performance of a cursorial lizard with particular adaptations for running, such as bipedalism and spike-like protruding scales (fringes) on the toepads that allow high speed on sandy substrates. We hypothesized that individuals that performed bipedalism, and have more and larger fringes, would achieve higher sprint performance. We also anticipated that tail shedding would affect sprint speed (though we were not able to define in what way because of the unpredictable effects that tail loss has on different species). According to our results, individuals that ran bipedally were faster; limb length and fringe size had limited effects on sprint performance whereas tail autotomy affected quadrupedal running only in females. Nonetheless, tail loss significantly affected bipedalism: the ability for running on hindlimbs was completely lost in all adult individuals and in 72.3% of juveniles.

Communicated by: Fritz Geiser

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Keywords Locomotion · Antipredator · Interactions · Lizards · *Acanthodactylus* · Cyprus

Introduction

Running is an essential skill that serves many different functions such as defense, foraging, mating, and territoriality (Elliot et al. 1977; Amaya et al. 2001; Alexander 2003). Not all animals have the same potential for running (Garland 1983). Some of them are excellent sprinters (Sharp 1994) while others are endurance runners (Saltin et al. 1994); some run for long distances (Bramble and Lieberman 2004) whereas others can barely cover few centimeters (Denny 1980). In any case, running is of pivotal importance for the majority of terrestrial animals, and lizards are no exception (Garland and Losos 1994).

Lizards have an impressive, species dependent, locomotor repertoire (Bauwens et al. 1995; Vanhooydonck et al. 2001), as they can climb, swim, glide, and run (Vitt and Caldwell 2014). Many lizards are capable runners (Van Damme and Vanhooydonck 2001), and their locomotor performance may affect dominance (faster males may control larger territories, sire more offspring, and perform better in intraspecific agonistic encounters, Perry et al. 2004; Husak et al. 2006), foraging mode (McElroy et al. 2008), and escape from predators (Losos and Irschick 1996). Locomotion is a fundamental link between an animal and its environment (Miles 2004), and thus the sprint performance of a lizard marks out the ability to survive in a given habitat. As a general rule, faster lizards tend to be more fit (Miles 2004).

Sprint performance may vary according to sex, age, substrate, and even phylogenetic history (Miles 1994, 2004; Tulli et al. 2012; Vanhooydonck et al. 2015). The most decisive factor, though, is morphology (Van Damme et al. 2003).

Numerous morphological features, including leg length (Losos and Sinervo 1989; Melvile and Swain 2000), body length, width and mass (Losos 1990; Bauer et al. 1996; Van Damme and Vanhooydonck 2001; Bergmann and Irschick 2010), hindlimb length (Bonine and Garland 1999; Stiller and McBrayer 2013; Sathe and Husak 2015), and toepad characteristics (Bauer and Russell 1991; Macrini et al. 2003; Russell and Johnson 2007) have been reported influencing locomotor performance. Two important mechanisms may act as modulating agents in the morphology-locomotor performance relationship: bipedalism and tail autotomy. Bipedalism changes this relationship without affecting morphology, whereas autotomy potentially affects the same relationship through alterations in morphology (Aerts et al. 2003; McElroy and Bergmann 2013).

The ability for bipedal locomotion seems to have evolved within different lizard families (Clemente 2014). During bipedalism, lizards shift their body's center of mass backwards and run on their hindlimbs. According to Aerts et al. (2003), this center of mass shift may be merely the result of acceleration. Even though bipedal locomotion is thought to confer certain advantages, such as higher speed (Snyder 1949, 1962) or better acceleration (Clemente et al. 2008), it is not clear whether it is positively related to sprint performance (Irschick and Jayne 1999a, b; Clemente 2014).

Tail autotomy is a common defensive strategy among many lizard families. Lizards shed their tail in response to mechanical stimuli, and afterwards, the detached tail thrashes to distract predators (Arnold 1988). Tailless lizards usually experience energetic and social costs (Pafilis and Valakos 2008; Pafilis et al. 2008; Bateman and Fleming 2009; Cooper et al. 2009), while tail autotomy may affect locomotion as well. The tail plays a functional role in locomotion in most lizards (Gillis et al. 2009; Libby et al. 2012; McElroy and Bergmann 2013), so tail loss should affect sprint performance. However, the effects of autotomy on locomotor performance are dependent on a number of factors, and as such, the responses to tail shedding may vary. In most lizards, post-autotomy locomotion is slower (Punzo 1982; Martin and Avery 1998; Cromie and Chapple 2012), in others faster (Daniels 1983; Brown et al. 1995), while in some species, no effect was detected (Huey et al. 1990; Kelehear and Webb 2006). These unpredictable post-autotomic effects can be attributed to the different morphological tail traits (size, girth, shape) among species as well as to the impact of various substrates on the performance and interspecific variation of behavioral responses to autotomy (McElroy and Bergmann 2013).

Body mass and the position of body center of mass also hold an important role in locomotion performance (Van Damme and Vanhooydonck 2001; McElroy et al. 2008; Higham et al. 2013). The center of mass influences body balance and the propulsive system (the hindlimbs, Russell and Bels 2001) and, thus, has direct effects on locomotion performance (Foster and Higham 2012; Gillis et al. 2013). Tail shedding affects both body mass and center of mass, whereas bipedalism has an impact only on the latter. Tail autotomy results in weight loss through tail loss and as such causes a direct decrease of body mass, as well as shift of the center of mass (Higham et al. 2013; Jagnandan et al. 2014). Bipedalism can also induce changes to the center of mass (Aerts et al. 2003) but the displacement is to the opposite direction.

In this study, we aimed to assess the interactions between toepad morphology, tail autotomy, and bipedalism in a highly cursorial species, *Acanthodactylus schreiberi*. As the Greek etymology of its Latin name denotes, the toes of this genus have numerous fringes, similar to small spines (Salvador 1982; Baier et al. 2009). Toe fringes represent a pedal specialization of several lizard genera for running in sandy habitats (Higham 2015). They are clearly projecting, elongated scales that maximize the surface area that is in contact with the substrate, thus allowing the lizards not to sink into the sand (Salvador 1982; Luke 1986). Though it is believed that lizards achieve considerable speeds on the sand surface, thanks to the fringes (Carothers 1986), recent research questions their role (Irschick and Jayne 1999a; Korff and McHenry 2011). Another particular feature of this lizard is bipedalism that is performed when running in high speeds. We predicted that the particular microarchitecture of the toes together with bipedalism would affect the center of mass and, ergo, sprint performance (maximum speed and maximum instant acceleration). We measured several limb morphological parameters, recorded sprint performance before and after tail shedding, and formulated three hypotheses: First, we predicted that longer toepads would have more and larger fringes providing higher sprint performance. Second, we anticipated that when lizards perform bipedalism, they would run faster. Third, we predicted that tail autotomy would cause shifts in the ability for bipedal locomotion and total body mass and consequently would affect sprint speed, though in a way we could not prefigure because of the high variation in post-autotomic effects.

Materials and methods

Study species

The Schreiber's spiny-footed lizard (*A. schreiberi* Boulenger, 1878; Lacertidae) is a medium-sized lizard with a snout-vent length (SVL) ranging between 73 and 93 mm for males and 55–76 mm for females (Baier et al. 2009). The tail is particularly long (two thirds of the total body length), and lizards use it as a counterbalance when running: after the first one or two meters, when lizards achieve high speed, they raise their tail to the level of the body (Baier et al. 2009, and pers. observ.).

When lizards perform bipedal running, they somehow curve their tail (pers. observ.).

We captured 35 individuals near Geri (Cyprus, 35° 05′ 50″ N, 33° 26′ 21″ E). Sampling was performed from April to August 2015. We only captured individuals with intact tails and separated them into three groups according to age and sex (14 males, 10 females, and 11 juveniles).

The lizards were kept in the laboratory under a stable temperature of 26 °C in individual terraria (30 × 30 × 30 cm) with an incandescent heating lamp (100 W) suspended over the terraria providing a controlled photoperiod (12-h light and 12-h dark). We provided the lizards with food (*Tenebrio molitor* larvae) every day and fresh water ad libitum. Lizards were kept in the laboratory up to 2 weeks and after the completion of the experiment were released at the sampling site.

Morphological measurements

Before any trial, we measured with a digital caliper (Silverline 380244, accurate to 0.01 mm) the following morphometric characters: SVL, tail length, fore- and hindlimb length, distance between fore- and hindlimb length, pelvis breadth, and fore and hind toepad length (all above measurements in centimeters). In order to test whether longer toepads carry more developed fringes, we counted the total number of fringes and measured the length of the two longest fringes (mm) on the longest toe (mm) (left hindlimb). Finally, to check for possible effects of body temperature on locomotor performance trials, we measured body temperature before and after autotomy (using a Miller & Weber, Inc. cloacal thermometer).

Sprint performance

Experimental design was based on previous studies of locomotor performance (Huey and Hertz 1984; Avery et al. 1987a, b; Irschick and Jayne 1998; Martin and Avery 1998; Kaliontzopoulou et al. 2012; Vanhooydonck et al. 2015). We used a custom racetrack (250 × 12 cm) with a cork substrate, scaling marks on its underside at 10-cm increments, and a clear acrylic glass at the front. Each lizard ran five times on the track with hourly breaks in-between. Sprint was stimulated by tapping the lizard with a paintbrush on the base of the tail. With a digital camera (Olympus SH-60), we recorded each trial at 240 frames per second (fps) to calculate maximum speed and maximum instant acceleration. All individuals were allowed to thermoregulate at a thermal gradient, implied in a specifically designed terrarium with a heating lamp on one end and ice bags on the other (Van Damme et al. 1986). All lizards were thermoregulated for 1 h prior to each trial, because maximum performance is expected at the preferred temperature (Irschick and Losos 1998).

Trials were evaluated as “good” (the lizard covered at least a 50-cm distance with a constant sprint performance) or “bad,” in order to obtain only data close to the maximum performance abilities (Losos et al. 2001). Trials (or individuals with less than two good trials) that did not meet these criteria were eliminated. Maximum speed was calculated as meters per second (m/s) for 20-cm distances (using the scale on the racetrack’s backside). We chose the fastest 20-cm pass from all five trials, based on the number of frames needed to cover each 20-cm distance and the known frame rate (240 fps) (Avery et al. 1987a, b). In the case of instant acceleration, we digitized the position of the lizard’s snout on every frame of each trial on *x*- and *y*-axes with a digitizing tool (MATLAB DLTdataviewer3, Hedrick 2008). Then, we calculated the Euclidean distance as the displacement of the snout among all sequential frames and used a scaling factor in order to transform the obtained displacement from pixel distance into meters. Next, we filtered the data using a fourth-order zero-phase shift Butterworth low-pass data noise filter in VBA for EXCEL (Van Wassenbergh 2007) and calculated the instant acceleration in meters per second as the second derivative of the scaled filtered displacement against time. We kept the highest value from all trials per individual, as their maximum instant acceleration. Last, we marked the trials where the lizards performed bipedalism.

The abovementioned procedures were performed before and after autotomy. To stimulate tail autotomy, we used the methodology proposed by Pérez-Mellado et al. (1997). Briefly, we grasped the tail with a digital vernier caliper 20 mm behind the cloaca until it was autotomized. Next, we placed the lizards in a terrarium with a heating lamp (100 W) with food and water for at least 3 days before any post-autotomy trials, in order to let the animal recover and thus measure the maximal sprint values. Nonetheless, we have to acknowledge that this acclimatization period might give lizards the time to become habituated to their new locomotor condition, thus alleviating somewhat the direct effects of tail loss on sprint performance.

Statistical analyses

In order to remove possible influence of body size on sprint performance, we used the following formula, proposed by Lleonart et al. (2000):

$$Y_{\mathrm{i}}^{*} = Y_{\mathrm{i}}\left(\frac{X_{\mathrm{m}}}{X_{\mathrm{i}}}\right)^{b}$$

where Y_{i} is the observed value (morphological characteristic) for each individual, X_{m} is the average SVL for each group, X_{i} is the SVL of each individual, and b is the slope of the regression of each morphological characteristic measurement against SVL.

Normality of data (morphometric variables and temperature) was tested by Shapiro-Wilk test and homogeneity of variances with Levene's test before any statistical analyses. All individuals ($N = 35$) were included in statistical analyses of characters and performance, except for maximum speed (in this case, one male and two females were excluded) and for acceleration after autotomy (also one male was excluded).

To test body temperature before and after autotomy for each individual, we used a paired *t* test. We also tested for differences in body temperature before and after autotomy among the three groups using one-way ANOVA. We also used Spearman's rank correlation coefficient to test whether sprint performance was correlated with body temperature and to test for correlation among toepad length, total number of fringes, and the length of the two longest fringes. Effects of morphometric values on performance were identified using a multimodel inference approach introduced by Burnham and Anderson (2002). First, we used linear multiple regression models incorporating all characters, after checking for multicollinearity (elimination threshold VIF >0.10). Then, we ranked all possible subset models for each dependent variable (e.g., max. speed) according to their AICc values. Next, we selected only the models with a ΔAICc value lower than two. We averaged the selected subset models, and, based on their averaged coefficients (*b*), we assessed the effect for each remaining character. The predictive power of each model was evaluated based on the adjusted R^2 value from a subset model that incorporates only the characters found in the models with ΔAICc value lower than two (Burnham and Anderson 2002, Mammides et al. 2016). Weight loss percentage (WLP) was also included in the analysis for model testing performance after tail autotomy. MANOVA was used to check for differences in morphometric characters (dependent variables) among the three groups (grouping factor). Differences in sprint performance before and after autotomy were evaluated with paired *t* tests. We also applied ANOVA to test for differences among groups in the ratio of tail length to SVL, in order to evaluate possible effects of tail length on performance.

Results

Body temperature before and after autotomy did not differ among individuals (paired *t* test; $N = 35$; $t_{(34)} = -1.32$; $P = 0.193$) or groups (ANOVA; temperatures before: $F_{(2,32)} = 2.586$, $P = 0.091$; temperatures after: $F_{(2,32)} = 0.959$, $P = 0.394$) (Table 1). The overall performance was not correlated with temperature variation during treatments (Table 1).

All morphometric measurements, even after correcting for body size, differed among the three groups, except for fore toepad length and pelvis breadth (Table 2). SVL was linearly correlated to body mass both before and after autotomy in all groups (Table 3). Fringe features had a rather low variation (number of fringes: 20–25, longest fringe: 0.55–0.75 mm, second longest fringe: 0.5–0.75 mm, toepad length: 1.8–2.5 mm). Fringe length was positively related to toepad length, among six individuals (first longest fringe: $r_s = 0.955$, $P = 0.003$, second longest fringe: $r_s = 0.938$, $P = 0.006$). Number of fringes on the longest toe was negatively correlated with toepad length ($r_s = -0.885$, $P = 0.019$).

Juveniles performed higher maximum speed than males before autotomy (ANOVA; $F_{(2,32)} = 3.660$, $P = 0.037$, post hoc Tukey honest significant difference (HSD) test: males-juveniles: $P = 0.029$), and that was the only significant difference for the performance among groups, either pre- or post-autotomy. Average maximum speed and maximum instant acceleration for the three groups are given in Fig. 1.

Performance was affected by different morphometric characters in each group (Fig. 2 and Table 4). For males, maximum speed before autotomy was negatively affected by hindlimb length and distance between limbs and positively by hind toepad length. Maximum speed after autotomy was negatively affected by fore toepad length and pelvis breadth, but the model had low predictive power. Maximum instant acceleration before autotomy was negatively affected by distance between limbs and positively by hind toepad and hindlimb length. Maximum instant

Table 1 Mean temperatures and standard deviation (SD) among individuals and groups, and correlation between selected body temperature (T_b) and performance before and after tail autotomy

Mean temperatures among individuals (°C)				Mean temperatures among groups (°C)											
Ba	SD	Aa	SD	Males ($N = 14$)				Females ($N = 10$)				Juveniles ($N = 11$)			
33.06	1.47	33.41	1.50	Ba	SD	Aa	SD	Ba	SD	Aa	SD	Ba	SD	Aa	SD
				33.71	1.38	33.55	1.33	32.75	1.31	32.87	1.74	32.5	1.52	33.72	1.46
				Spearman's rank correlation coefficient. None was statistically significant ($a = 0.05$)											
								T_b—speed				T_b—acceleration			
				Ba				−0.054				−0.078			
				Aa				0.231				0.273			

Ba before autotomy, *Aa* after autotomy

Table 2 MANOVA results for morphometric measurements (after normalizing against body size) among the three groups

Character	$F_{(2,32)}$	$P<$	Males ($N = 14$)				Females ($N = 10$)				Juveniles ($N = 11$)			
			$P<$				$P<$				$P<$			
			Mean	SD	Females	Juveniles	Mean	SD	Males	Juveniles	Mean	SD	Males	Females
Snout-vent length	29.8	0.001	7.57	0.26	0.001	0.001	6.90	0.56	0.001	0.001	5.90	0.53	0.001	0.001
Forelimb length	524.4	0.001	0.028	0.02	0.001	0.001	1.752	0.24	0.001	0.001	0.423	0.02	0.001	0.001
Hindlimb length	1024.4	0.001	0.639	0.63	0.001	0.001	3.960	0.39	0.001	0.001	0.215	0.01	0.001	0.001
Pelvis breadth (PBR)	430.7	0.001	0.010	0.007	0.001	0.225	0.405	0.06	0.001	0.001	0.034	0.006	0.225	0.001
Distance between limbs	330.3	0.001	0.124	0.12	0.001	0.001	0.514	0.06	0.001	0.001	0.311	0.01	0.001	0.001
Fore toepad length	591.7	0.001	0.026	0.002	0.001	0.989	0.738	0.10	0.001	0.001	0.023	0.002	0.989	0.001
Hind toepad length	878.8	0.001	0.329	0.009	0.001	0.001	1.210	0.10	0.001	0.001	0.258	0.01	0.001	0.001

Mean values (cm) and results of post hoc Tukey HSD tests for all combinations are also given

acceleration before autotomy was negatively affected by pelvis breadth and weight loss percentage.

In females, maximum speed before autotomy was affected negatively by SVL and positively by hind toepad length. Furthermore, maximum instant acceleration after autotomy was affected negatively by SVL and positively by pelvis breadth. We found no effect of these characteristics on maximum speed after autotomy or maximum instant acceleration before autotomy.

In juveniles, no morphometric characteristic did affect maximum speed before or after autotomy, whereas maximum instant acceleration before autotomy was affected by the distance between limbs (negatively) and pelvis breadth (positively). After autotomy, maximum instant acceleration of juveniles was affected negatively by pelvis breadth and distance between limbs and positively by fore and hind toepad length.

Individuals from all groups exerted bipedalism before tail autotomy, with juveniles using bipedalism in higher frequency than males and females (percentage of individuals performing bipedalism before tail autotomy: males 64%, females 60%, and juveniles 91%). Also, during the pre-autotomic trials, all individuals that practiced bipedalism performed at their highest level (see Table 3; only maximum acceleration in females did not differ significantly during bipedalism). Only juveniles exhibited bipedalism after tail autotomy, but to much lower frequency compared to pre-autotomy situation (percentage of individuals performing bipedalism after tail autotomy: males 0%, females 0%, and juveniles 27.3%).

Table 3 Results of correlations (Spearman's rank correlation coefficient) between snout-body length (SVL) and body mass before and after tail autotomy for each group

	Males	Females	Juveniles
Before autotomy	0.840	0.798	0.989
After autotomy	0.810	0.760	0.954

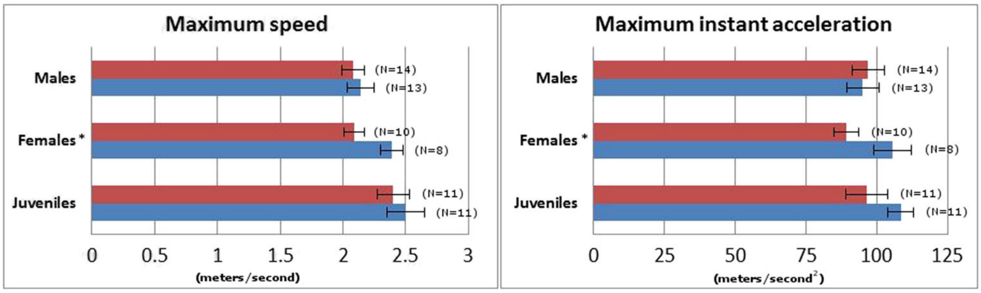
All correlations are significant ($P < 0.01$)

Maximum speed and maximum instant acceleration before and after autotomy differed only in females (paired t test; speed: $N = 8$, $t_{(31)} = 3.172$, $P = 0.016$; mean before = 2.39, SD = 0.32; mean after = 2.09, SD = 0.39; acceleration: $N = 10$, $t_{(31)} = 3.354$, $P = 0.008$; mean before = 105.63, SD = 18.3; mean after = 89.22, SD = 23.58). Even though body weight reduction after autotomy was significant in all groups (males: $N = 14$, $t_{(13)} = 12.644$, $P = 0.00$, reduction mean = 1.41, SD = 0.41; females: $N = 10$, $t_{(9)} = 14.230$, $P < 0.001$, reduction mean = 0.90, SD = 0.20; juveniles: $N = 11$, $t_{(10)} = 10.844$, $P < 0.001$, reduction mean = 0.76, SD = 0.23), this weight loss did not seem to affect their overall performance levels (except for females as mentioned previously) (Fig. 1). Females had a significantly lower tail length/SVL ratio than both males and juveniles (ANOVA; $F_{(2,33)} = 11.216$, $P < 0.001$, post hoc Tukey HSD test: males-females: $P < 0.001$, females-juveniles: $P = 0.007$) (mean ratios: males = 1.75, SD = 0.11; females = 1.44, SD = 0.20; juveniles = 1.69, SD = 0.18).

Discussion

Locomotor performance is influenced by numerous factors. Here, we studied how morphology and shifts in center of mass, imposed by bipedalism and tail loss, affected sprint performance in a skillful lizard runner. Our initial predictions were only partially verified. Limb and toepad length had limited but obvious effects on sprint performance. Tail autotomy affected only females, in which tail loss caused a significant deceleration in maximum speed and decreased maximum instant acceleration. However, tail loss impact was more important in regard to bipedalism: adult lizards that shed their tail were incapable of bipedalism after autotomy, whereas juveniles continued to perform bipedal locomotion, though in

Fig. 1 Average sprint performance and standard errors (*black bar*) for males, females, and juveniles before (*blue*) and after (*red*) autotomy. Sample size after standard errors and significant differences are given with *asterisks*



much lower percentages. Bipedalism had a favorable effect on sprint performance: all individuals that exerted bipedalism were much faster compared to their peers that used the typical quadrupedal locomotion.

Males did not perform at their highest levels (they did more bad trials than females and juveniles) both before and after autotomy (before autotomy, males: 43 good and 27 bad trials, females: 37 good and 13 bad trials, and juveniles: 45 good and 10 bad trials; after autotomy, males: 42 bad and 28 good trials, females: 34 good and 16 bad trials, and juveniles: 49 good and 6 bad trials). Given that experimental treatment was identical for all groups, this lack of ability to achieve high performance could be attributed to different male antipredator responses. In most lizards, males are highly territorial and often engage to aggressive encounters with conspecifics (Lailvaux and Irschick 2007; McEvoy et al. 2012; Cooper et al. 2015). At the same time, though, they have to be alert for possible predators. In other words, they have to defend themselves against a predator on the one hand and to protect their territory from a rival on the other. This demanding situation might turn males bolder and less responsive to external stimuli (Cooper 1997; Martin and López 1999). Another factor that may affect male response is predator size (Cooper and Stankowich 2010), which in our case was not tested, as "predator" was simulated by the use of pincers and was the same in all treatments.

Morphometric characters differed significantly among the three groups, even after removing the effect of body size (Table 2), and appeared to affect sprint performance in various ways. A notable point from our results is the limited (negative) effect of hindlimb length (only in the male's speed and acceleration before autotomy) that contradicts most previous studies reporting that hindlimb length affects sprint performance (e.g., Stiller and McBrayer 2013; Sathe and Husak 2015). Interestingly, hind toepad length had a positive effect on speed and/or acceleration in all groups. This finding agrees with our first hypothesis (longer toepads would have longer and more fringes that would increase sprint performance). Longer toepads had indeed longer (but not more) fringes. Thus, it seems that the decisive factor here was the length and not the number of fringes. These longer fringes seem to provide better traction and, consequently, support higher sprint performance. Toe fringes are an adaptation to sandy substrates (not restricted to these though), and, besides locomotion, they are associated with other activities such as "swimming" through sand and digging (Higham 2015). The potential alternative uses of fringes in *A. schreiberi* remain to be investigated.

Even though our findings did not corroborate the hypothesized positive effect of limb morphology on sprint performance, they shed light on the alterations that tail autotomy may cause in body balance. According to our results, fore toepad length and pelvis breadth became significant predictors of speed and/or acceleration in males after autotomy, whereas hindlimb-related features were significant before autotomy. A similar situation was found in females, where hind toepad length and SVL were significant predictors of speed before autotomy, while pelvis breadth and SVL became significant predictors of acceleration after autotomy. These changes should be attributed to the anterior displacement of the body's center of mass after tail loss. The effects of tail shedding on body mechanics yielded interesting findings and represent a promising research avenue (Arnold 1984; Martin and Avery 1998; Fleming et al. 2009; McElroy and Bergmann 2013).

In full agreement with our second hypothesis, bipedalism led to a generally higher sprint performance in all groups (Table 5). Bipedalism was quite common in adults (over 60%) and certainly the rule for juveniles that performed bipedalism in 91% of the cases, before tail autotomy. During bipedalism, the body's center of mass is displaced to the rear, thus lizards can better accelerate and increase maximum speed (Irschick and Jayne 1999b; Aerts et al. 2003; Dhongra 2004). Like its congeneric *Acanthodactylus erythrurus* (Aerts et al. 2003), *A. schreiberi* exerts bipedalism to improve its locomotor performance, as do species that live in open habitats (Vanhooydonck and Van Damme 2003). Bipedalism is quite rare among lacertid lizards and thus remains largely

Fig. 2 Radar charts showing the effect of each character according to ▶ their beta values in the significant models found for sprint performance in each group. **a** Max. speed before and after autotomy in males. **b** Max. speed before autotomy in females. **c** Max. instant acceleration before autotomy in males. **d** Max. instant acceleration after autotomy in males. **e** Max. instant acceleration after autotomy in females. **f** Max. instant acceleration before and after autotomy in juveniles. *Blue color* refers to the models before autotomy and *red color* to the models after autotomy. Codes for *characters* as in Table 3

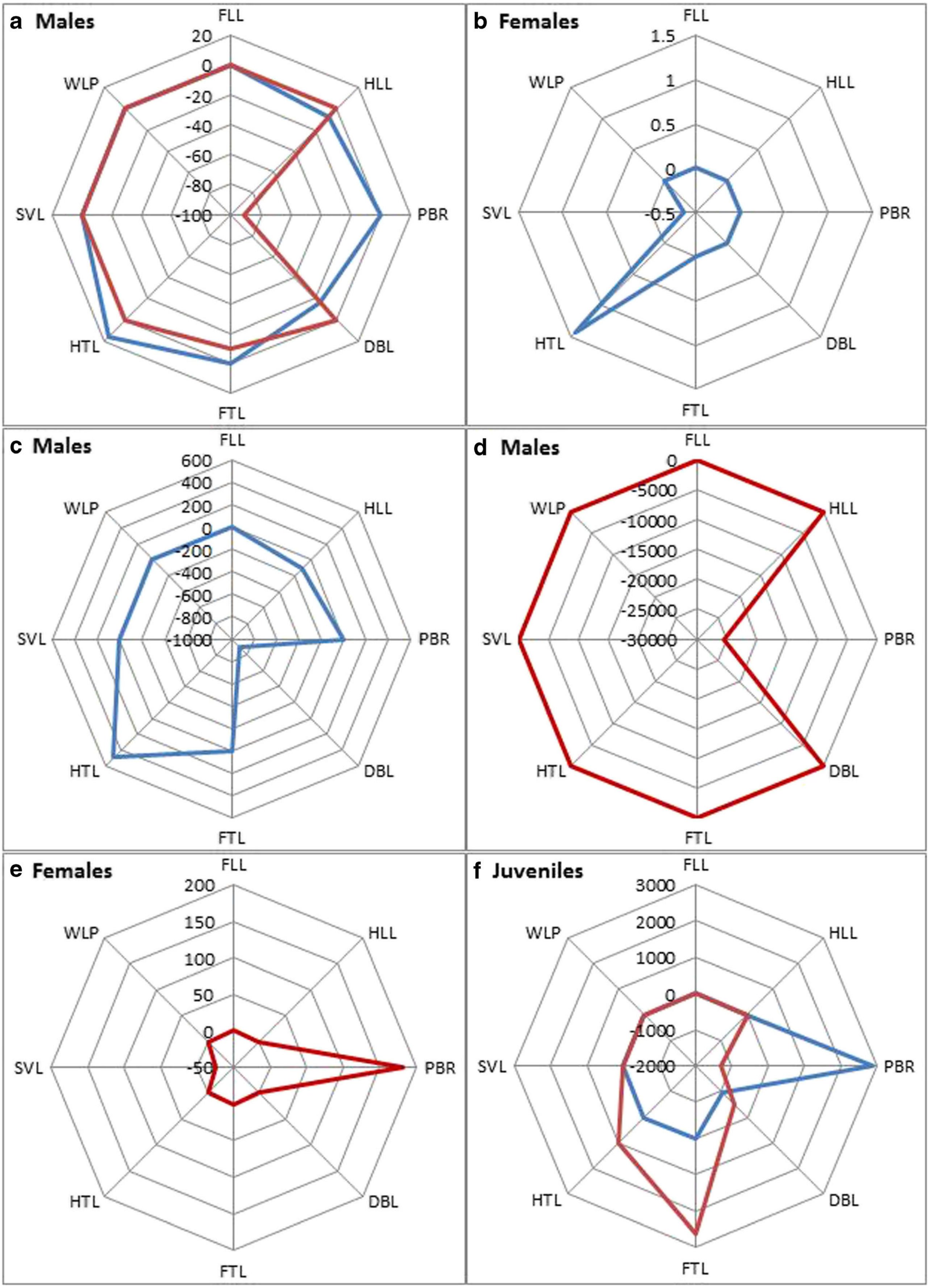

a Males
FLL
HLL
PBR
DBL
FTL
HTL
SVL
WLP
20
0
-20
-40
-60
-80
-100
b Females
FLL
HLL
PBR
DBL
FTL
HTL
SVL
WLP
1.5
1
0.5
0
-0.5
c Males
FLL
HLL
PBR
DBL
FTL
HTL
SVL
WLP
600
400
200
0
-200
-400
-600
-800
-1000
d Males
FLL
HLL
PBR
DBL
FTL
HTL
SVL
WLP
0
-5000
-10000
-15000
-20000
-25000
-30000
e Females
FLL
HLL
PBR
DBL
FTL
HTL
SVL
WLP
200
150
100
50
0
-50
f Juveniles
FLL
HLL
PBR
DBL
FTL
HTL
SVL
WLP
3000
2000
1000
0
-1000
-2000

Table 4 Results of multiple regression of morphometric characters on locomotor performance after model averaging

Males			
	Maximum speed before autotomy—linear model, $R^2 = 0.538$		
Character	beta	*b*	*i*
HLL	−0.37465	−7.7494	0.67
HTL	0.1755	15.545	0.41
DBL	−0.0909	−16.313	0.22
	Maximum speed after autotomy—linear model, $R^2 = 0.273$		
	beta	*b*	*i*
PBR	−0.21423	−91.350	0.43
FTL	−0.06152	−9.817	0.17
	Maximum instant acceleration before autotomy—linear model, $R^2 = 0.617$		
	beta	*b*	*i*
DBL	−0.4099	−901.1	0.72
HTL	0.2437	488.5	0.53
HLL	−0.1597	−116.2	0.34
	Maximum instant acceleration before autotomy—linear model, $R^2 = 0.691$		
	beta	*b*	*i*
PBR	−0.81086	−25,624.69	1
WLP	−0.08312	−69.27	0.3
Females			
	Maximum speed before autotomy—linear model, $R^2 = 0.636$		
Character	beta	*b*	*i*
SVL	−0.4635	−0.3642495	0.72
HTL	0.1168	1.4152143	0.25
	Maximum instant acceleration after autotomy—linear model, $R^2 = 0.533$		
	beta	*b*	*i*
SVL	−0.3704	−25.37634	0.60
PBR	0.1924	180.71498	0.38
Juveniles			
	Maximum instant acceleration before autotomy—linear model, $R^2 = 0.482$		
Character	beta	*b*	*i*
DBL	−0.3337	−932.5397	0.28
PBR	0.3740	2866.9728	0.28
	Maximum instant acceleration after autotomy—linear model, $R^2 = 0.921$		
	beta	*b*	*i*
FTL	0.4574	2620.124	1
HTL	0.9493	989.3565	1
PBR	−0.1988	−1293.2941	0.34
DBL	−0.3873	−472.2211	0.66

Only characters with significant effects are shown. Percentage of variance explained (R^2) is given for the linear model including only the significant characters

HLL hindlimb length, *HTL* hind toepad length, *DBL* distance between limbs, *PBR* pelvis breadth, *FTL* fore toepad length, *HTL* hind toepad length, *SVL* snout-vent length, *WLP* weight loss percentage, *beta* standardized regression coefficient, *b* unstandardized regression coefficient, *i* percentage of models in which the respective character is significant

understudied. The few published papers reported that lacertids could run on their hindlimbs from the first meters after the initiation of the motion (Aerts et al. 2003; Vanhooydonck and Van Damme 2003), in contrast to agamids that perform bipedalism simply as a result of exceeding acceleration threshold, something that does not affect the overall performance of the lizard (Clemente et al. 2008).

Tail shedding induced dramatic shifts in the extent of bipedalism. No adult was able to run on their hindlimbs after autotomy, and the percentage of juveniles decreased to only

Table 5 Comparison of bipedal and quadrupedal sprint performance for individuals that performed bipedalism

Sprint performance			
Maximum speed (m/s)		Maximum instant acceleration (m/s^2)	
No bipedalism	Bipedalism	No bipedalism	Bipedalism
Males			
Paired t test: −3.68, P = 0.006		*Paired t test: −3.28, P = 0.011*	
2.17	2.77	89.7	106.6
1.85	2.17	76	83.4
1.85	2.27	84.3	88.1
1.72	2.5	80.9	118.5
1.61	1.47	57.8	60.2
1.85	1.92	94.3	102.8
1.92	2.22	66.4	100.4
2.22	2.43	103.4	139.4
1.92	2.5	92	94.5
Females			
Paired t test: −3.99, P = 0.010		Paired *t* test: −1.92, *P* > 0.05	
2	2.7	89.2	90.3
2.12	2.32	90.9	92.2
2.32	2.63	107.2	125.4
2.17	2.5	97.3	99.1
1.72	2.22	69	103
2.08	2.17	110	116
Juveniles			
Paired t test: −6.03, P < 0.001 (before autotomy)		*Paired t test: −3.77, P = 0.009* (before autotomy)	
1.78	2.63	56.4	110.4
–/2.85[a]	2.77/3.22[a]	–/63.8[a]	89.4/102.8[a]
–	2.63	–	106.7
2.38	2.7	102.5	108.3
2.32	2.5	104.6	128.6
2.56/2.70[a]	3.03/2.94[a]	123.8/112.3[a]	132.3/119[a]
2.00	2.5	89.5	114.9
1.72	2.17	74.9	117.8
–/2.17[a]	2.12/2.27[a]	–/105.6[a]	95.4/106.6[a]
1.66	2.17	72.1	88.1

Significant results of paired *t* tests in ital

[a] Before/after autotomy

27.3%. This limited ability of bipedalism in juveniles, even after tail autotomy, can explain the synergistic positive effect of fore and hind toepad length on acceleration. The loss of the tail results in anterior displacement of the body's center of mass and thus reduces the ability of bipedal run in post-autotomic trials (McElroy and Bergmann 2013). The fact that juveniles expressed this ability to a higher extent than adults, even after autotomy, might be due to ontogenetic differences in the overall distribution of body mass. Such differences can decrease the effects of the displacement of the body's center of mass in smaller and lighter individuals. Our results are in full accordance with Snyder's classical study (1949), which found that basilisk lizards lost their bipedal ability when their tail was removed and attributed that alteration to the importance of the tail as counterbalance.

Tail shedding did not have the same effect on sprint performance in all groups, despite the loss of mass that it implies. Sprint performance in males and juveniles did not change prior to, and after, autotomy. The ratio tail length/SVL was lower in females, advocating a higher deceleration in males and juveniles since they lose a larger part of their tail and total body length. On the contrary, females demonstrated slower maximum speed and maximum instant acceleration after autotomy (Fig. 1). The tail autotomy's effects on locomotion do not conform to a general, universal rule. Tailless lizards may increase, decrease, or maintain their sprint performance unchanged (McElroy and Bergmann 2013). Nonetheless, all individuals of a given species follow the same pattern, regardless of sex or age. Our results differ from previous research in the sense that tail autotomy did not have the same impact on all groups. Our data could not explain the observed exception in the case of the slower females. This issue invites further research in the future.

Locomotion enables animals to explore and exploit their environment (Vanhooydonck et al. 2006). This study comes to enhance the growing literature on lizard locomotion (Vanhooydonck et al. 2014). Our results elucidate the interactions among toe fringes, bipedalism and tail autotomy, and their impact on sprint performance. Fine-tuned studies that investigate microarchitecture and behavioral particularities (Irschick 2000; Bartlett et al. 2012; Higham 2015) will provide new evidence for the better understanding of locomotion patterns.

Acknowledgements For this study, we followed all international, national (Cyprus Law on the use of Animals in Scientific Experiments, 133(I)/2005), and institutional guidelines for the care and use of animals. We are grateful to Mrs. H. Mair for the linguistic editing of the text.

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