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Locomotor performance of sand lizards (*Lacerta agilis*): effects of predatory pressure and parasite load

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Abstract Locomotor performance affects foraging efficiency, predator avoidance and consequently fitness. Agility and speed determine the animal's social status and reflect its condition. In this study, we test how predatory pressure and parasite load influences locomotor performance of wild specimens of the sand lizard *Lacerta agilis*. Animals were chased on a 2-metre racetrack. Lizards with autotomy ran significantly faster than lizards with an intact tail, but there was no significant difference in running speed between individuals with fresh caudal autotomy and regenerated tails. Parasite presence and load, age and sex had no significant effect on speed. Our results indicate that autotomy either alters locomotory behaviour or that individuals with autotomised tails were those that previously survived contact with predators, and therefore represented a subgroup of the fastest individuals. Therefore, in general, predatory pressure but not parasites affected locomotor performance in lizards.

Keywords Tail loss · Anti-predator behaviour · *Ixodes ricinus* · Caudal autotomy · Running speed · *Lacerta agilis*

Introduction

Locomotor performance is of primary importance for lizard survival while escaping (Husak 2006). Successful escape from predators, foraging and mating ability may be strongly dependant on individual's capacity to accelerate or to achieve a certain speed (Tsuji et al. 1989; Clobert et al. 2000; Vanhooydonck and Van Damme 2003). Being such an important feature, running speed in lizards is also commonly used as a predictor of animal's health, body condition and potential survival under predatory pressure (Hertz et al. 1988; Huey et al. 1990; Jayne and Bennett 1990).

The locomotor performance of lizards is influenced by many factors, such as tail length, body mass, snout-vent length (SVL) (Du et al. 2005; Lin and Ji 2005; Vervust et al. 2008; Li et al. 2011) and caudal autotomy (Martin and Avery 1998; Chapple and Swain 2002; Shine 2003; Chapple et al. 2004; Cooper et al. 2009). Tail autotomy is a widespread predator avoidance strategy among lizards (Arnold 1988), providing a visual stimulus for the predator to focus its attention on the tail and increase the chances of the lizard's escape (Bateman and Fleming 2009; Lu et al. 2010). However, autotomy may also have negative consequences, such as lower social status (Fox et al. 1990), smaller territory size (Salvador et al. 1995) or low reproductive success (Martín and Salvador 1993). In many lizard species, the tail is an important organ for lipid storage, which is mainly concentrated in its proximal part (Lin and Ji 2005), and lipids

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are the main source of energy for many lizard species (Doughty et al. 2003). Therefore, autotomised lizards may be more vulnerable to predation than lizards with intact tails (Dial and Fitzpatrick 1984; Wilson 1992). Autotomy may also modify locomotor performance in various ways. Most of the previous studies showed that caudal autotomy often impaired the sprint performance in lizards (Martin and Avery 1998; Shine 2003; Chapple et al. 2004; Cooper et al. 2009). Tailless individuals may lose equilibrium, thus leading to irregularities of trajectories of the central point of the pelvis during movements (Martin and Avery 1998). However, other research has demonstrated that tailless lizards run faster (Daniels 1983; Brown et al. 1995) or did not differ from the intact ones (Huey et al. 1990; Kelehear and Webb 2006; Lu et al. 2010). The effect of caudal autotomy on locomotor performance seems to be species specific (Van Damme and Vanhooydonck 2001) and depends on the amount of tail loss and the time since autotomy (Downes and Shine 2001; Chapple and Swain 2002; Lin and Ji 2005).

The effect of parasites on locomotor performance is barely understood. Parasites strongly negatively affect life-histories (review by Møller 1997), fitness (review by Møller 1990) and survival (Sorci et al. 1996) of their host. Further negative effects include physiological, ecological and behavioural alternations of the host animal organism (Schall et al. 1982; Main and Bull 2000; Reavis and Barrett 2001; Bouma et al. 2007; Fenner and Bull 2008; Martín et al. 2008). A few published results on parasites in lizards showed that Shingleback (*Tiliqua rugosa*) infected with the haemogregarine blood parasite *Hemolivia mariae* had smaller home ranges (Bouma et al. 2007), and parasitized females of the common lizard *Zootoca vivipara* had lower activity levels (Sorci et al. 1996). The common lizards infected with haemogregarines (Oppliger et al. 1996) were characterised by slower running speed. On the other hand, malaria caused lizards to have better endurance, but did not influence their speed during sprints (Schall et al. 1982; but see Schall 1990). Sorci et al. (1994) suggested that parasites may not only modify locomotor performance of their lizard hosts but also of their offspring. Some parasites caused weight loss (Lavoie et al. 2000), which may contribute to greater capacity for rapid speed (Cooper et al. 1990).

One of the most common worldwide parasites that live on lizards are ticks (Barnard and Durden 2000). Despite a few studies which indicated a possible positive correlation between tick load and some life history traits of the sleepy lizard (*T. rugosa*), such as body mass and mating probability (Bull and Burzacott 1993), the majority of authors have reported a negative impact of ticks on their hosts (Lehmann 1993). Lizard infested with ticks may have slower running speeds, lower endurance and consequently different home range than individuals without ticks (Main and Bull 2000). Lizards with ticks may also have reduced activity and a lower chance of

finding suitable food resources or refuges (Main and Bull 2000). The negative effects of ticks in relation to the lizard's locomotor performance may be manifested in several ways: (1) pathogen transmission, i.e. *Borrelia burgdorferi* s.l. and *Anaplasma* spp. (Ekner et al. 2011), which, among others, are also human infecting bacteria, affecting nervous and immunological systems (Svetina et al. 1999; Dumler et al. 2001), (2) lower haemoglobin concentration leading to anaemia in their hosts (Oppliger et al. 1996; Schall et al. 1982; Schall 1990; Wikelski 1999) and (3) mechanical alternations to lizard's mobility by altering mechanisms of running, by occupying joints, mostly around forelimbs (Bauwens et al. 1983; Fig. 1).

The sand lizard *Lacerta agilis* is one of the most abundant lizard species across Europe (Sura 2003). However, according to our knowledge, there have been only a few studies on its locomotor performance (Nemes 2002), and none of them relates to the problem of how animal's performance is affected by body condition, tick load and former contacts with predators. To date, only a few studies have tested the effect of parasites on lizard running speed (Main and Bull 2000). Moreover, recent studies on the lizard's movement have only been done under laboratory conditions. Therefore in our experiment, we have only included wild caught lizards soon after they have been captured in the field, which provided the best reflection of the natural variation in the tick load and autotomy on the running performance. We predict that parasites should alter the locomotor performance of sand lizards.

We hypothesised that parasites should alter the locomotor performance of sand lizards. In the present study, we investigated the influence of the castor bean tick *Ixodes ricinus* and autotomy on running speed of *L. agilis*. Moreover, we also tested for sex and age differences on locomotor performance of the lizards when controlled for body temperature.

Materials and methods

Study area and the species studied

The study was carried out in April–June in 2009 and 2010 in the Barycz valley, in Poland (51°34′ N, 17°40′ E, elevation

Fig. 1 Ticks, *I. ricinus* concentrated around the forelimb joints of a sand lizard, *Lacerta agilis*

110–170 m). This study area is characterised by extensively farmed land with a varied mosaic of arable fields, meadows, small woodlots and scattered trees and shrubs of different ages, dominated by white willow (*Salix fragilis*), silver birch (*Betula pendula*), black poplar (*Populus nigra*) and Scots pine (*Pinus silvestris*). It contains both dry sandy areas and moist areas (for details see Antczak et al. 2004).

L. agilis is a short-legged, rather robust, small to medium sized lizard (ranging from 121 (100 for juveniles) to 235 mm SVL) from the family Lacertidae (Juszczyk 1987). It is a ground-dwelling and strongly diurnal species with one of the widest distribution ranges of all reptiles (Bischoff 1984). In the study area, *L. agilis* is a common species, and an average of 0.37 individuals were noted on a 200 m transect route (Ekner et al. 2008).

Experimental procedures

Lizards were captured using special herpetology nets (fabric net attached to a metal circle on the end of a metal stick) or by hand. Animals were placed separately in cotton bags to avoid interaction between them. They were kept for 1 h before the experiment (Vervust et al. 2008). Pregnant females were excluded from the experiment because too few were caught. Afterwards, lizards were chased on a 2-metre racetrack, consisting of a floor (made of a porous surface to ensure appropriate grip), three lateral walls and a shaded shelter at the end of the track, which was supposed to induce the reptiles to run in that direction (Farley 1997). Animals were placed on the track and were encouraged to run by hand tapping on the floor, just behind the tail (Pérez-Tris et al. 2004). To avoid experimenter effects, only one person (A.E.G.) ran the experiment. We treated all individuals in the same way we chased all of them, not only those which did not want to run. The experiment was filmed using a digital camera, placed on a tripod behind the simulated trap. The recording was analysed using the AxioVision (Zeiss) computer programme.

We analysed running speed of the lizards. Most lizards stopped during running, and those with more than three stops during this phase were omitted from analysis. Where stops occurred, we averaged running speed between the stops.

Immediately after the experiment, cloaca temperature was checked, using a pyrometer. Next, lizards were aged (adult, sub-adult and juvenile), sexed and measured (SVL). Animals were examined for the presence of ticks, which were removed with forceps and stored in 70 % ethanol. Next, in a laboratory, ticks were identified to species and aged using a binocular microscope, according to Siuda (1993). All were identified as *I. ricinus*. Autotomy was checked for tail length; original or regenerated was measured.

To avoid pseudoreplication, lizards were permanently marked using medical cautery units (Ekner et al. 2011), and hence each individual was used only once in the experiment.

Statistics

General linear mixed models (GLMM) were built to test the effects of age, sex, autotomy (comparison of lizards with and without tail autotomy), tick presence and load (square root transformed) and cloacal temperature on mean lizard speed. Tick presence was an explanatory variable, coded as 0 (ticks absent) and 1 (at least one tick present), and it was tested in a separate model from that in which tick load (number of ticks per lizard) was analysed. In the latter model, only lizards with at least one tick were included. Because the sex of sub-adult and juvenile lizards could not be determined during this study, three different GLMM were built. The first model contained all the factors above except sex. In the second model, we compared the effect of the factors above on mean speed, ignoring age of lizards but including the effect of sex. Because the effects of age and sex were non-significant in both models, we joined these variables into one categorical variable (with the following levels: adult females, adult males, sub-adults and juveniles) and included it in the final GLMMs. We present results of these latter models only because their results were convergent with the former ones. In each model, we included interaction terms between the categorical and continuous variables. We removed all interaction from the final model because none were statistically significant. In every model, site identity (place where lizards were captured and tested) was included as a random effect.

Statistical analyses were performed using JMP 9 and SPSS 18.0 PL software. Data are summarised as means with a 95 % confidence limit for binary (presence–absence) data and ± standard deviation or standard error otherwise.

Results

We analysed 142 *L. agilis* lizards (26 females, 41 males, 42 sub-adults and 33 juveniles). One hundred and two individuals had an intact tail (71.8 %, 95 % CL 63.7–79.1), and 40 were autotomised (28.2 %, 95 % CL 21.0–36.3). Among the autotomised individuals, 10 had fresh autotomy (25.0 %, 95 % CL: 12.7–41.2), and 30 had regenerated tails (75.0 %, 95 % CL 58.8–87.3).

In total, 341 ticks were found in 55 of the 142 (38.7 %, 95 % CL 30.7–47.3) examined lizards. On average, there were (x ± SD) 2.4±7.1 ticks per host. The maximum number of ticks on a lizard was 66 (on an adult male). Most parasites were concentrated around axilla (Fig. 1).

Table 1 Statistical results from a general linear mixed model examining the effects of age, sex, tail autotomy (comparison of individuals with versus without tail autotomy), tick presence and cloacal temperature on mean speed of the sand lizard (*Lacerta agilis*)

Fixed effect tests

Source	DF numerator	DF denominator	F	P
Age sex	3	53.6	0.34	0.797
Autotomy	1	57.2	5.36	0.024*
Ticks' presence	1	55.1	0.05	0.823
Temperature	1	21.0	0.58	0.455

Table 2 Statistical results from a general linear mixed model examining the effects of age, sex, autotomy (comparison of individuals with and without tail autotomy), tick load and cloacal temperature on mean sand lizard (*Lacerta agilis*) speed–results run with data on lizards with at least one tick

Fixed effect tests

Source	DF numerator	DF denominator	F	P
Age sex	3	14.1	0.13	0.938
Autotomy	1	13.2	0.85	0.372
Tick load (Sqrt)	1	15.9	1.88	0.189
Temperature	1	13.9	0.07	0.802

Autotomy positively influenced the speed of *L. agilis* (Table 1, Fig. 2). There were no significant effects of tick presence, tick load, cloaca temperature, age or sex on speed (Tables 1 and 2). When we compared lizards with fresh caudal autotomy and those with regenerated tails, we found no statistical difference in the mean speed between these two groups (Table 3, Fig. 2). There was also no statistical difference in tail length between lizards with autotomised (fresh or regenerated) and intact tails (mean ± SD; 88.5± 40.7 and 77.8±27.6, respectively; Mann–Whitney *U* test, Z = −1.31, asymptotic significance (two-tailed) = 0.189). There were no significant effects of SVL on speed, in both cases.

Discussion

Locomotor performance is important for lizards, when they are escaping from predators or when hunting (Clobert et al. 2000; Vanhooydonck and Van Damme 2003). The results of our study indicate that the lizards with autotomy ran faster. The results are similar to those obtained in previous research (Daniels 1983; Brown et al. 1995), which was probably a result of the marginal role that body part plays in movement
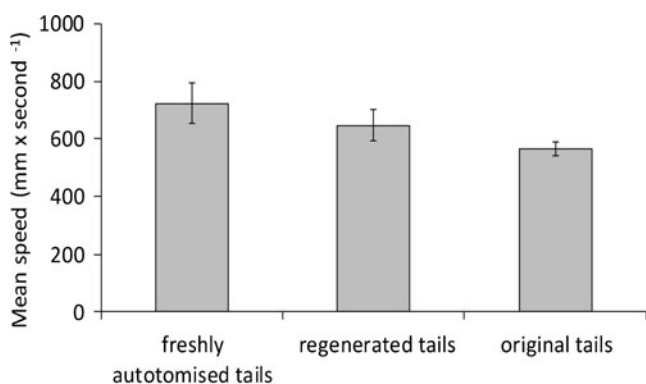
in some species, e.g. the frog-eyed sand gecko, *Teratoscincus scincus* (Lu et al. 2010). Locomotor performance could also be influenced by the length of the original tails, where shorter tail increases the running speed (Garland 1985; Li et al. 2011). The higher speed of short-tailed individuals could also be a result of their lower body weight (Martin and Avery 1998) or lower ground contact while running (Daniels 1983). However, in our study, most (75 %) autotomised lizards had already regenerated tails, and the length of the tails of lizards with autotomy (fresh or regenerated) did not differ from the intact individuals. Moreover, when we compared lizards with fresh and with regenerated autotomy, there was no difference in speed between them. This interesting result suggests that, in this case, tail length, or other factors mentioned above, did not influence locomotor performance, but the effect of autotomy is important. Our findings support a previous study on the common wall lizard, *Podarcis muralis*, where individuals with regenerated tails ran faster than individuals with intact tails (Brown et al. 1995). However, in the metallic skink *Niveoscincus metallicus* and the Cape dwarf gecko *Lygodactylus capensis*, no differences were noted between the locomotor performance of the individuals with original or regenerated tails (Chapple and Swain 2002; Medger et al. 2008).

Fig. 2 Mean speed of lizards with freshly autotomised tails, regenerated tails and original tails. Means with standard errors are presented

Table 3 Statistical results from a general linear mixed model examining the effects of age, sex, tail autotomy (comparison of individuals with fresh caudal autotomy versus regenerated tails), tick load and cloaca temperature on mean speed of the sand lizard (*Lacerta agilis*)

Fixed effect tests

Source	DF numerator	DF denominator	F	P
Age sex	3	6.32	0.24	0.866
Autotomy (regenerated/fresh)	1	8.07	0.00	0.963
Tick load (Sqrt)	1	10.07	0.39	0.548
Temperature	1	10.7	0.00	0.945

Although predators do not actively select autotomised prey (Downes and Shine 2001; own data) and even avoid them due to their smaller body size (Padilla et al. 2007), the risk of predation of tailless lizards may be high (Downes and Shine 2001). Tailless lizards cannot use caudal autotomy during encounters with predators (Kelehear and Webb 2006). Increasing vulnerability of lizards to predation could be caused, at least in part, by the impairment of locomotor performance (Chapple and Swain 2002). Hence, autotomised lizards change their anti-predator behaviour (Downes and Shine 2001; Cooper 2007). In our study, most autotomised individuals had regenerated tails. It is presumed that lizards with regenerated tails have gained experience during the previous predator contact and modified their behaviour when encountering the potential predator (in this case a human) for the second time. Due to this experience, such individuals may run faster (Brown et al. 1995). Kelehear and Webb (2006) showed that lizards, both autotomised and with intact tails, made more pauses when chased on a racetrack after a week, which was probably due to re-encounter with the human "predator".

Some authors have shown that tail autotomy may reduce lizard running speed but only for a few weeks (Downes and Shine 2001; Chapple and Swain 2002). This suggests that tail autotomy may only temporarily affect locomotor ability. However, in the present study, there were no differences in running speed between lizards with regenerated tails and those with fresh caudal autotomy. This may suggest that in our study, lizards achieved faster speeds for longer, which may confirm a changing behaviour gained from experience. Alternatively, individuals that run faster, more often escape from predators and gain a better chance of survival. Hence, it is possible that the captured lizards with autotomy ran faster than those previously caught by predators.

Unexpectedly, we did not find any effect of tick presence and load on locomotor performance. Our results are in contrast with previous research, where lizards parasited by ticks ran slower than uninfected individuals of *T. rugosa* (Main and Bull 2000). It is known that lizards do not usually use their maximal locomotor ability (Hertz et al. 1988). Accordingly, both intact and autotomised sand lizards may not use their maximal locomotor ability, thus their physiological traits, even if changed by ticks or tick-borne pathogens, might not have influenced their mean speed. Moreover, *L. agilis* has longer legs in relation to body length than *T. rugosa*; hence, the effect of tick load on the mechanics of movements may be different. Ticks may influence traits other than average speed, which are related to locomotor performance. In a previous study, it was suggested that *Aponomma hydrosauri* and *Amblyomma limbatum* ticks decreased endurance in Australian sleepy lizard, *T. rugosa* (Main and Bull 2000).

Predation and parasites are regarded as major biological factors influencing survival of animals. In the present study, we have shown that caudal autotomy had a bigger influence on lizard speed than ticks. Some authors suggest that predation risk may be assessed by investigating tail losses (Clobert et al. 2000; Diego-Rasilla 2003). Autotomy of brown anoles (*Anolis sagrei*) influenced predator frequency, predator efficiency and prey behaviour (Bateman and Fleming 2011). Hence, our results suggest that predator pressure may cause changes in *L. agilis* behaviour, namely locomotor performance, and, consequently, modify their escape ability.

This is the first time when running speed has been assessed using wild caught lizards, almost immediately after catching them in the field. Moreover, to the best of our knowledge, this is the first time the influence of ticks and autotomy on running speed in *L. agilis* has been studied.

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