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Reduced tail regeneration in the Common Lizard, *Lacerta vivipara*, parasitized by blood parasites

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Summary

1. Many lizards will lose their tail through autotomy as an antipredator device even though there must be significant costs during tail regeneration.

2. Parasites are energetically costly to the host, and may reduce the rate of cell regeneration. The relation between the presence of haemogregarines (phylum Sporozoa) and the rate of tail regeneration in the Common Lizard *Lacerta vivipara* (Jacquin) was examined.

3. Experimentally induced autotomy in parasitized lizards resulted in a significantly reduced rate of tail regeneration compared with non-parasitized lizards. On the other hand, tail loss was not associated with an abnormal increase of parasite load, suggesting that the physiological stress (induced by tail loss) did not cause a decrease in parasite defence.

Key-words: Cost of parasitism, haemogregarine, physiological stress, tail loss

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Introduction

Caudal autotomy to escape predators is widespread in lizards (Bellairs & Bryant 1985). The benefit of such a mechanism is immediate in terms of survival, but tailless lizards incur many costs. Indeed, it has been shown that tail loss may reduce social status (Ruby 1981; Fox & Rostker 1982; Tokarz 1985; Fox, Heger & Delay 1990), reduces escape from predators (Dial & Fitzpatrick 1984), reduces home range size and access to females (Martin & Salvador 1993a; Salvador, Martin & Lopez 1994), modifies foraging tactics (Martin & Salvador 1993b) and depresses reproductive output in females (Congdon, Vitt & King 1974; Smyth 1974; Maiorana 1977; Vitt & Cooper 1985).

In the Common Lizard, *Lacerta vivipara,* the tail is a major site of energy storage (Avery 1970) and represents a considerable portion of body mass. Moreover, caudal reserves may serve as an important source of energy for vitellogenesis (Greene 1969; Smyth 1974; Maiorana 1977). The importance of the presence of a complete tail is reflected by its rapid regeneration (Vitt & Ballinger 1981) and tail regeneration may require energy that would otherwise be used for other functions (e.g. growth, reproduction, immunological defence).

In a previous study (Oppliger, Célérier & Clobert 1996) we demonstrated that the presence of protozoan blood parasites of the genus *Haemogregarina* leads to important physiological costs in the Common Lizard. For example, parasitized lizards have a lower level of haemoglobin, an increase in the number of immature red cells, a decrease in resting oxygen consumption, and a reduced running speed. Another cost resulting from parasitism may involve the maintenance of the immunity system to keep the parasite load at a low level (Keymer & Read 1990). As both tail regeneration and parasitism can be costly, a parasitized tailless lizard may have less energy to allocate to tail regeneration than a non-parasitized tailless lizard. In this case, we would expect tailless parasitized lizards have a lower rate of tail regeneration. The aim of the present study is to test the effect of the haemogregarine on tail regeneration in the Common Lizard and to test the effect of tail loss on the level of parasite defence.

Materials and methods

SPECIES AND PARASITOLOGICAL STATUS

The Common Lizard is a small, live-bearing lacertid living in peatbogs and heathland. Snout–vent length (SVL) ranges from 50 to 70 mm for adults and 30 to 50 mm for yearlings. A more complete description of the species' biology can be found in Pilorge (1987). At the end of June 1995, 144 yearlings of both sexes were captured in southern France (Mont Lozère, 44°30'N, 3°45'E, altitude 1450 m). We chose yearlings to be sure that all individuals were of the same age, and to ensure that none of the lizards suffered debilitating effects of chronic, long-term parasitism, as might occur in older individuals. At the time of capture, each individual was toe-clipped and a small drop of blood was collected to make a smear. The smear was fixed in absolute methanol and coloured with May-Grünwald Giemsa stain (Colorap de Bioréac, Lausanne). The stained slides were examined by oil immersion microscopy (500×) for the parasite count. Haemogregarine parasites are naturally widespread in the Common Lizard: they have a complex life cycle that involves a blood-feeding invertebrate vector (Manwell 1977). The parasite prevalence is between 70 and 80% in adults and between 30 and 40% in yearlings. Parasites are usually intra-erythrocytic (Manwell 1977), but free forms can be observed in cases of very severe infection (A. Oppliger, personal observation). A quantitative estimation of parasite load was made by counting the number of parasites observed per 10 000 red cells. A slide was considered as negative when after 5 min (about 120 000 cells checked) of examination, no parasite was observed. Among the 144 checked lizards, 45 were parasitized with haemogregarines. For this present study 36 individuals were used, and the other lizards were used in another study.

REARING CONDITION AND AUTOTOMY EXPERIMENT

At the start of the experiment, body mass, tail length and SVL were measured on each lizard. Since body mass and structural size are often correlated, a higher body mass of lizards *per se* does not indicate that these lizards are in better nutritional state. To test the influence of body condition on the tail regeneration rate, regressions of log-transformed SVL *vs* weight were performed and the residuals from this common regression were used as an index of corpulence. Twelve parasitized and 12 parasite-free lizards with intact tail were randomly chosen for autotomy, which was induced at the most proximal caudal fracture plane. Twelve other parasitized lizards with intact tails constituted the control group to estimate the parasite multiplication rate. Lizards were individually housed in plastic terraria (15 cm × 20 cm × 15 cm) with damp soil, a shelter and a water dish. Lizards were fed *ad libitum* with moth larvae *Pyralis farinalis* and small crickets *Acheta domesticus*. Vitamins and minerals were also provided. A heat lamp was lit for 6 h per day to allow lizards to thermoregulate. After 45 days, the SVL and the size of the regenerated tail were measured, and a new blood sample was collected to estimate the change in parasite load. In another study (Oppliger, Célérier & Clobert 1996), we have shown that 45 days is an adequate period to observe an effect of temperature on the multiplication rate of parasites. The multiplication rate of parasites was estimated by comparing the percentage of infected red cells between the two dates. One parasitized tailless lizard died at the beginning of the experiment.

Statistical analyses were performed with the SYSTAT statistical package (Wilkinson 1989).

Table 1. Morphological characteristics of Common Lizard parasitized and non-parasitized by haemogregarines (mean ± SE)

	Parasitized $n = 11$	Non-parasitized $n = 12$	t-test
Body mass 1 (g)	1·68 ± 0·14	1·31 ± 0·13	1·880
SVL 1 (mm)	41·81 ± 1·32	38·58 ± 1·27	1·761
Tail length 1 (mm)	49·54 ± 5·45	49·66 ± 5·22	–0·016
Body mass 2 (g)	2·05 ± 0·14	1·84 ± 0·13	1·066
SVL 2 (mm)	44·81 ± 1·09	42·47 ± 1·05	1·580
Tail length 2 (mm)	17·18 ± 2·22	26·81 ± 2·22	–3·062*
Tail growth rate (mm/day)	0·29 ± 0·03	0·46 ± 0·03	–3·062*
SVL growth rate (mm/day)	0·067 ± 0·01	0·085 ± 0·01	–1·226

*P < 0·01.

Body mass 1, SVL 1 and tail length 1 are data at the start of the experiment (before autotomy). Body mass 2, SVL 2 and tail length 2 are data 45 days after the autotomy.

Results

TAIL REGENERATION WITH RESPECT TO PARASITE STATUS

At the start of the study, body mass, SVL and tail length did not differ between parasitized and non-parasitized lizards (Table 1). Forty-five days after the experimental autotomy, tail regeneration was about 1·5-fold higher in parasite-free than in parasitized lizards (Table 1). Analysis of covariance using an index of corpulence (= residuals from body mass/log-transformed SVL) as covariate, 'parasite' and sex as factor, revealed a strong significant effect of parasites but non-significant 'factors x covariate' interaction and non-significant effect of corpulence and sex on the size of the regenerated tail (parasite, $F_{1,19}$ = 9·279, P = 0·007; corpulence, $F_{1,19}$ = 0·060, P = 0·809; sex, $F_{1,19}$ = 0·933, P = 0·345; corpulence x parasite, $F_{1,19}$ = 0·340, P = 0·567). In 45 days, infected individuals had on average regenerated only 35% of their initial tail length, while non-parasitized ones regenerated 55% of their initial tail length. During this period, body mass and SVL did not differ between the two groups (Table 1).

PARASITE MULTIPLICATION RATE WITH RESPECT TO AUTOTOMY

At the start of the study, parasite load did not differ between lizards with and without autotomy (mean ± SE, 2·9 ± 1·1% *vs* 3·1 ± 1·1%; two-tailed t-test, log-transformed value, $t_{11,12}$ = 0·024, P = 0·981). Forty-five days after autotomy, we observed a significant increase in parasite load within the two experimental groups (paired t-test, log-transformed value; autotomy group: t_{11} = 2·866, P = 0·015; non-autotomy group: t_{12} = 3·938, P = 0·002). The final parasite load was not different between the two experimental groups (mean ± SE, 5·5 ± 1·5% *vs* 6·0 ± 1·5%; ANCOVA, factor = autotomy, $F_{1,20}$ = 0·163, P = 0·690; covariate = initial parasite load, $F_{1,20}$ = 21·901, P < 0·001).

Discussion

Our findings support the hypothesis that parasites affect the tail regeneration of their lizard hosts. However, as we were not able to infect the lizards experimentally (A. Oppliger, personal observation), our results are correlational. Thus, we may argue that naturally infected individuals are in bad condition and susceptible to parasitism and that they simply have less energy to invest in tail regeneration. For this reason, we cannot determine the causality of the results. However, since there was no difference in subadult quality (as measured by body mass, size and corpulence) between infected and uninfected lizards, it is unlikely that the correlation between tail regeneration and parasitism was caused by other, unidentified differences in phenotypic quality.

The consequences for tailless infected lizards of having a slower rate of tail regeneration may be important since we know that the period of regeneration is critical. This is a period when predation may increase (Dial & Fitzpatrick 1984). The longer the time required for regeneration, the greater the risk of increased predation and other costs associated with tail loss (cf. review in Introduction). This could explain the bell-shaped age-prevalence curve found in this population. Indeed, Sorci (1996) showed that parasite prevalence increased with the age of individuals to a threshold, before declining strongly, suggesting that old parasitized lizards suffer a higher mortality rate than non-parasitized ones. Since natural autotomy is common in this population (up to 30% of individuals with regenerated tail, unpublished data), the higher mortality rate of parasitized lizard could be due to an increased predation rate.

The reduction in the rate of tail regeneration may be due to the direct effect of parasites. In previous studies (Sorci, Clobert & Michalakis 1996; Oppliger, Célérier & Clobert 1996), we observed that the presence of haemogregarines in Common Lizards is associated with fitness and physiological costs, e.g. a decrease in haemoglobin level. This anaemic state could be responsible for the increased tail regeneration period. Another possibility to explain the effect of parasites on tail regeneration could be the existence of a physiological trade-off between parasite defence and cell regeneration. Studies have demonstrated that an increase in reproductive effort leads to a decrease in parasite defence and consequently an increase in the parasite load (Festa-Bianchet 1989; Gustafsson *et al.* 1994; Norris, Anwar & Read 1994; Richner, Christe & Oppliger 1995; Oppliger, Christe & Richner 1996; Oppliger, Christe & Richner 1997). As the maintenance of a strong immunity system is energetically costly (Keymer & Read 1990), a tailless lizard may face a trade-off between investing either in tail regeneration or in parasite defence. Depending on what is more beneficial to an individual's fitness, one of these investments may have priority over the other. Maiorana (1977) demonstrated in one species of salamander that tail regeneration has energetic priority over reproduction, but in a lizard species *Coleonyx brevis*, Dial & Fitzpatrick (1981) showed that tailless females prioritize energy allocation to reproduction at the expense of tail regeneration. This is also the case in the Common Lizard where pregnant females significantly reduce tail regeneration during gestation when compared with adult males ($P < 0{\cdot}05$; M. Massot & J. Clobert, unpublished data). The diversity of tail regeneration strategies reflects the capacity of lizards to 'choose' between investing or not investing energy into tissue repair. The decision to allocate energy in tail regeneration must depend on the importance of allocating energy to other processes.

Our results demonstrate that the rate of parasite multiplication did not differ between tailless and intact parasitized lizards, suggesting that the immunity level is not influenced by the stress of autotomy. Thus, the quantity of energy allocated to parasite defence did not seem to be reduced in favour of tail regeneration. This could mean that the negative effect of a heavy parasite load on the host's fitness will be greater than the negative effect of tail loss.

The difference between the cost of parasitism itself and the cost of parasite defence is difficult to demonstrate, because these two factors will always be confounded. Indeed, the presence of parasites always involves the host's immunity reaction. This emphasizes that parasites may sometimes have subtle but severe indirect effects on the host's fitness. The need for parasite load manipulative studies is crucial for a better understanding of host–parasite interactions. This will be the aim of our future research.

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