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SHORT COMMUNICATION

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Tail loss and thermoregulation in the common lizard *Zootoca vivipara*

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Abstract Tail autotomy in lizards is an adaptive strategy that has evolved to reduce the risk of predation. Since tail loss reduces body mass and moving ability—which in turn are expected to influence thermal balance—there is potential for a trade-off between tail autotomy and thermoregulation. To test this hypothesis, we studied a common lizard (*Zootoca vivipara*) population at high latitude, inhabiting a high-cost thermal environment. *Z. vivipara* is a small, non-territorial lizard known as a very accurate thermoregulator. We made two predictions: (1) the reduced body weight due to tail loss results in faster heating rate (a benefit), and (2) the reduction in locomotor ability after tail loss induces a shift to the use of thermally poorer microhabitats (a cost), thus decreasing the field body temperatures of active lizards. We did not find any effect of tail loss on heating rate in laboratory experiments conducted under different thermal conditions. Likewise, no significant relationship between tail condition and field body temperatures, or between tail condition and thermal microhabitat use, were detected. Thus, our results suggest that tail autotomy does not influence the accuracy of thermoregulation in small-bodied lizards

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Introduction

Trade-offs between different traits that affect fitness are widespread (Roff 1992; Stearns 1992), and occur not only among classical life-history traits, but also among traits such as physiological performance and activity time (Grant 1990), and predation risk and feeding (Cooper 2000). In lizards, there is a potential for a trade-off between tail autotomy and capacity for accurate thermoregulation. Tail autotomy in lizards is an adaptive strategy to increase the chances of survival under predator attacks (Congdon et al 1974; Dial and Fitzpatrick 1983). However, the immediate benefit of tail loss appears to come with many costs. These include losing social status, decreased home range size, decreased running speed, decreased diet diversity, increased later life mortality, and decreased reproductive output (Dial and Fitzpatrick 1981; Fox and Rostker 1982; Punzo 1982; Martín and Salvador 1993a; Salvador et al. 1996; Fox and McCoy 2000). However, the potential trade-off between tail loss and thermoregulation has rarely been investigated.

For lizards, the maintenance of body temperature (T_B) in an optimal range is important as it maximizes their physiological performance (Stevenson 1985), and thereby also affects feeding, locomotor, and reproductive performance (Van Damme et al. 1990, 1991; Shine and Harlow 1993). It is known that escape tactics depend on T_B (see, e.g., Braña 1993), and that the frequency of tail autotomy, as well as the size of the automized tail portion, is temperature-dependent (Bustard 1968). Martín and Salvador (1993b) showed that tail loss did not affect field or preferred T_B (measured in a zero-cost laboratory environment) of *Lacerta monticola*, while it influenced the lizards' microhabitat use and basking behavior. However, as *L. monticola* is an inaccurate thermoregulator irrespective of tail status (Martín and Salvador 1993b), it is not surprising that tail loss did not influence its thermoregulatory precision.

In this paper, we investigate how tail loss influences thermoregulation of the common lizard, *Zootoca vivipara*. This species is one of the most accurate thermoregulators among the reptiles (Gvoždík 2002), providing an excellent model to study the relationship between tail loss and thermoregulation. We tested two explicit predictions in a high-latitude population inhabiting a thermally challenging environment, where accurate thermoregulation is likely to be important for individuals' fitness. First, since heating rates are strongly and inversely size-dependent (Carrascal et al. 1992), we predicted that tail loss should lead to faster heating. Second, as tail loss has shown to influence microhabitat selection (Martín and Salvador 1992), we predicted that lizards should reduce their use of thermally optimal microhabitats following tail loss, and, consequently, lower their field T_B.

Materials and methods

Study organism and site

Zootoca vivipara is a small (approx. 4–5 g), diurnal, heliothermic and non-territorial lizard. Its distribution extends from northwestern Spain to Sakhalin in the east, and well beyond the Arctic Circle in the north. Our investigation was conducted in the Oulanka region (66°22′N), northern Finland, in early summer of 2003. The study site included meadows and backyards of local farms, surrounded by forest with scrublands at the edges.

Heating rate measurements

Heating rates of 18 *Z. vivipara* individuals of varying sizes [snout–vent length (SVL): 24 – 70 mm] were measured, first with intact tails and then with induced broken tails. Tail breaks were induced by a few gentle taps on the tail base with forceps. Measurements were taken at two operative temperatures (T_e; T_e actually gives an estimate of T_B for an object that does not thermoregulate and is at thermal equilibrium; Bakken 1992), at 35°C (warm) and at 50°C (hot). During the measurements, lizards were fixed with transparent adhesive tape onto a white plastic board (25×45 cm) on stands (15 cm high) to reduce conductance with the substrate. A 100W reflector bulb was suspended above the centre of the board, placed at a height to produce the right T_e. Before the trials, each lizard was measured for SVL, body weight (BW), tail length (TL), and after the tail breaks we measured the weight (TW_{BR}) and length (TL_{BR}) of the broken tail portion. During the experiment, a K-type thermocouple connected to a digital thermometer (Testo 925; Testo, Lenzkirch, Germany) was inserted into the lizard's cloaca. Lizards were cooled to 10°C before being placed under the light bulb. Once T_B had reached 15°C, it was recorded at 15-s intervals until it reached 30°C. T_e of the experimental area was measured with physical lizard models (Hertz et al. 1993). Hollow copper pipes (65 mm long, 12 mm diameter, 1 mm wall thickness) sealed with plastic caps and painted brown were used and fitted with the same thermocouple that was used to measure the T_B of the lizards. Heating rates of the lizards were estimated as the slopes of the T_B–time regressions (Belliure et al. 1996).

Field study

Lizards (n=73) were captured by hand on sunny days from 28 May to 29 June 2003. Cloacal T_B of the lizards and near-ground air temperature (T_{A1}; recorded at ground level) and air temperature (T_{A2}; recorded 1 m above the ground) of the sites where they were first seen were measured immediately after capture. We measured T_{A1} instead of surface temperature, as most lizards were encountered on a herbal substrate, such as grass or moss, and measuring temperature of these substrates is problematic compared with rock or wooden surfaces, for example. We used the same thermometer that was used in the laboratory experiment. Before releasing animals back into the wild, SVL and TL of the lizards were recorded. For analyzing tail data, we calculated the TL–SVL ratio (and squared it for normality) as a variable describing the tail condition of free-ranging lizards.

Results

Autotomizing the total tail caused a large [19% (SD= 3.5%, n=18)] decrease in BW. Despite this, repeated measures ANCOVA [where thermal treatment (warm or hot) and tail status (intact or broken) were considered as repeated measures and SVL as the covariate] revealed that only the different thermal conditions significantly influenced the heating rates; whereas tail status or their interaction did not (Table 1). As expected, SVL had a significant effect on heating rates in all cases; further, it influenced the effects of the thermal treatments as well (Table 1; for the heating rates see Appendix 1 in the Electronic Supplementary Material).

Solar radiation was the main heat source, as T_{A1} (x=25.3±5.7°C) and T_{A2} (x=17.7±4.2°C) of the sites where lizards were captured were significantly lower than the lower limit of the preferred body temperature of *Z. vivipara* [27°C; calculated as the mean of the four populations studied by Gvoždík (2002); one sample t-tests: n=73; both P<0.02]. In the second repeated measures ANCOVA with lizard group as factor (male, female, juvenile; as the autotomy-induced shift in microhabitat use could possibly differ between them), T_B, T_{A1} and T_{A2} as repeated measures, and tail condition as the covariate, we found no difference between lizard groups, while T_B, T_{A1} and T_{A2} differed significantly from each other (Table 2). None of the temperatures correlated with tail condition and this

Table 1 Results of a repeated measures ANCOVA. Model was built with heating rates measured under different thermal conditions (warm and hot) and tail status (intact or broken) as repeated-measures factors, and snout–vent length (SVL) as the covariate; * denotes significance at P<0.05, and ** at P<0.001

Source	MS effect	MS error	F(1,16)
Thermal condition	18.39	0.15	119.72**
Tail status	0.005	0.07	0.07
Snout–vent length (SVL)	63.04	0.44	142.99**
Thermal condition×SVL	0.83	0.15	5.41*
Tail status×SVL	0.006	0.07	0.08
Thermal condition×Tail status	0.04	0.05	0.88
Thermal condition×Tail status×SVL	0.01	0.05	0.26

Table 2 Results of a repeated-measures ANCOVA. Model was built with lizard group (male, female, juvenile) as factor (Group), field temperature type (body, air temperature at 1 cm and at 1 m above the ground) as repeated-measures factors (Temptype) and tail condition (Tailcond) as covariate; ** denotes significance at $P<0.001$

Source	*df* effect	MS effect	*df* error	MS error	*F*
Group	2	20.82	67	40.05	0.52
Temptype	2	786.89	134	9.53	82.54**
Tailcond	1	7.30	67	40.05	0.18
Group×Tailcond	2	7.86	67	40.05	0.20
Temptype×Tailcond	2	9.21	134	9.53	0.97
Group×Temptype	4	4.72	134	9.53	0.49
Group×Temptype×Tailcond	4	8.86	134	9.53	0.93

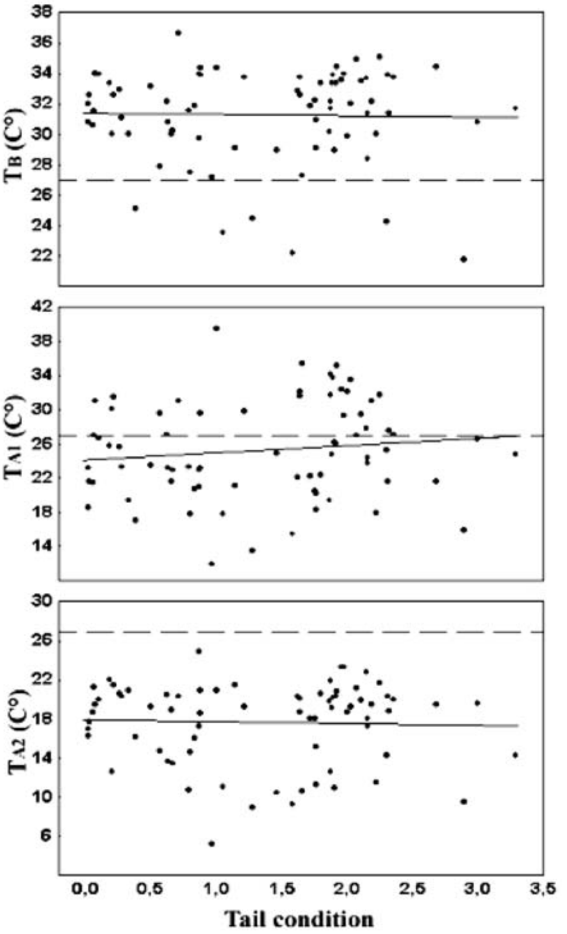

Fig. 1 Body temperatures (T_B) and air temperatures measured 1 cm (T_{A1}) and 1 m (T_{A2}) above the ground where the individuals with different tail condition were first seen. Tail condition is the squared ratio of tail length and snout–vent length. The *dashed lines* represent the lower limit of the preferred body temperature of *Z. vivipara* (after Gvoždík 2002)

pattern did not differ among the lizard groups (see Fig. 1, Table 2).

Discussion

Total tail autotomy caused a considerable (19%) decrease in the experimental lizards' BW. In spite of this, we found that heating rate was independent of tail status irrespective of body size in both thermal conditions tested. Even in the warm thermal condition, modeling an environment where *Z. vivipara* can only reach its preferred T_B slowly, we found no sign of a tail effect. This result suggests that the role of the tail in heat exchange is negligible for lizards the size of *Z. vivipara*. A possible explanation is that although tail loss implies weight reduction, it is also accompanied by body surface reduction, so surface-to-volume ratios would not be very different between lizards with intact and broken tails; and therefore heating rates would also remain unaffected. We note that this result cannot be generalized to all lizards, as both heating rate and its physiological control are strictly size-dependent (O'Connor 1999; Dzialowsky and O'Connor 1999). In theory, the tail can act as either a heating or cooling organ in large lizard species, due to their ability to shunt blood flow between their torso and appendages (Dzialowsky and O'Connor 1999).

One could still predict differences in field T_B of active lizards with different tail conditions, as changes in microhabitat use (resulting either from a decreased moving ability or the interactions with conspecifics after losing social status) could lead to a different exploitation of the thermal resources (Tracy and Christian 1986). Previous studies have indicated that tail loss affects microhabitat use (Martín and Salvador 1992, 1993b). Therefore, tailless lizards could be constrained to use microhabitats with lower thermal quality (in theory, more precise thermoregulation as compensation for tail loss could also be predicted). However, our results revealed no difference in field T_B of lizards with different tail condition, or in the thermal characteristics of the sites where they were encountered (Fig. 1). We conducted our field surveys under favorable conditions from the lizards' viewpoint (i.e., on sunny days in early summer). Under less favorable thermal conditions, when the costs of thermoregulation are higher (Huey and Slatkin 1976), some effect of tail loss could be hypothesized, but as *Z. vivipara* is known to decrease its activity dramatically and rapidly when radiant heat is not available (Van Damme et al. 1987), even this possibility can be discounted. Maintenance of an optimal T_B in fact seems to be the main priority of this species in order to maximize physiological functions, including tail regeneration. We suggest that the possible constraints originating from tail loss (e.g., increased vulnerability to predation) are not able to override this priority.

Taken together, our results suggest that tail loss does not affect heating rates. Likewise, tail loss does not seem to inflict any thermal cost by forcing individuals to shift their thermal microhabitat use. Whether these results can be generalized to larger lizard species is not known, and studies with large species are needed to establish conclusively the link between tail autotomy and thermoregulation.

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