Some vaguely explored (but not trivial) costs of tail autotomy in lizards

Daniel E. Naya a,⁎, Claudio Veloso a,b, José L.P. Muñoz a, Francisco Bozinovic a

a Center for Advanced Studies in Ecology and Biodiversity, and Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago, CP 6513677, Chile
b Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile

Received 10 April 2006; received in revised form 3 October 2006; accepted 10 October 2006
Available online 14 October 2006

Abstract

Lizard tail autotomy is considered an efficient anti-predator strategy that allows animals to escape from a predator attack. However, since the tail also is involved in many alternative functions, tailless animals must cope with several costs following autotomy. Here we explicitly evaluate the consequences of tail autotomy for two costs that have been virtually unexplored: 1. we test whether the anatomical change that occurs after tail loss causes a reduction in the role of the tail as a distraction mechanism to predators; 2. we analyzed whether tail synthesis comprises an energetically costly process in itself, by directly comparing the cost of maintenance before and after autotomy. We found that original tails displace further and at greater velocity than regenerated tails, indicating that the anti-predation responses of a lizard probably changes according to whether its tail is original or regenerated. With regard to the energetic cost of tail synthesis, we observed a significant increase in the standard metabolic rate, which rose 36% in relation to the value recorded prior to tail loss. This result suggests that the energetic cost of tail synthesis itself could be enough to affect lizard fitness.

© 2006 Elsevier Inc. All rights reserved.

Keywords: Liolaemus belli; Lizard energetic; Predator–prey interaction; Standard metabolic rate; Tail function

1. Introduction

Autotomy consists in the self-induced separation of an expendable part of the body from the rest of the organism. This mechanism is present in many invertebrate and vertebrate species, and is considered an efficient anti-predator strategy. For the specific case of lizards, experimental studies have demonstrated that tail autotomy increases immediate survival by distracting the predator and/or increasing handling time (e.g., Congdon et al., 1974; Vitt et al., 1977; Dial and Fitzpatrick, 1983, 1984; Daniels, 1985; Medel et al., 1988). However, the lizard tail is involved in several alternative functions which go beyond the anti-predation mechanism. In this sense, tailless animals may save their lives through autotomy, but they may then suffer additional costs such as a reduction in social status (e.g., Vitt et al., 1977; Fox and Rostker, 1982), energy reserves (Congdon et al., 1974; Vitt et al., 1977; Lin et al., 2006) and locomotor ability (e.g., Formanowicz et al., 1990; Martin and Avery, 1998; Lin et al., 2006). Obviously, all of these handicaps could translate into reductions in the Darwinian fitness component — i.e., survivorship (e.g., Wilson, 1992; Fox and McCoy, 2000) and fecundity (e.g., Dial and Fitzpatrick, 1981; Doughty and Shine, 1998; Chapple et al., 2002).

On the other hand, autotomized animals can change their behavior to compensate, at least to some extent, the loss of their tail. Specifically, it is known that tailed and tailless animals differ in several behavioral variables, such as anti-predator response, foraging activity, home-range size, movement pattern, activity level, and micro-habitat use (e.g., Formanowicz et al., 1990; Martin and Salvador, 1992, 1993; Salvador et al., 1995; Martin and Avery, 1998; Downes and Shines, 2001; Cooper, 2003). All these adjustments – together with between species differences in the role of the tail and the inherent environmental variability of natural systems – may explain why a clear pattern of the effect of tail autotomy on fitness components has not yet emerged. For example, in some cases it was found that autotomy reduced growth rates but increased survivorship.
(Niewiarowski et al., 1997), in other cases it reduced survivorship, but did not affect growth rates and fecundity (Fox and McCoy, 2000), while in other cases it did not affect survivorship or growth rates (Althoff and Thompson, 1994). These puzzling results illustrate the fact that adjustments in an organism’s energy balance encompass myriad intercorrelated pathways, which make it difficult to predict the specific changes in fitness components due to variations in internal and external conditions.

In this study we evaluate two potential consequences of tail autotomy which have been practically unexplored. First, we test whether the anatomical change that occurs after autotomy causes a reduction in the role of the tail as a distraction mechanism to predators. Previous studies indicate that original and regenerated tails present several differences at skeletal, neural and muscular levels, which suggest that the functional role of the tail could differ according to whether a tail is original or regenerated (Bellairs and Bryant, 1985). Although this idea was proposed earlier (Clarke, 1971), to date very little effort has been devoted to testing it. Second, we test whether tail synthesis comprises an energetically costly process in itself by directly comparing the standard metabolic rate before and after autotomy. Standard metabolic rate (i.e., the metabolic rate of post-absorptive animals during resting) comprises a major component of daily energy expenditure and, thus, is taken as a good indicator of the energetic cost of maintenance (Ashby, 1998). Although tail synthesis has been suggested as an energetically costly process (e.g., Chapple et al., 2002; Merino et al., 2004), the effect of tail autotomy on maintenance costs has only been evaluated in three lizard species, with contrasting results.

2. Materials and methods

2.1. Animal husbandry and experimental design

Seventeen individuals of *Liolaemus belli* (8 with original tails and 9 with regenerated tails) were collected in the locality of La Parva (33° 21′ S, 70° 20′ W; 2800 m above sea level), in the Andes mountain range of central Chile, during March 2005. Specimens were transferred to the laboratory on the same day of capture. Then, they were housed in individual cages (15 × 30 × 20 cm), and kept in a room at an ambient temperature (Ta) of 26±4 °C (mean± range) and a photoperiod 12L:12D. The body mass (m_b) of each individual was measured using an electronic balance (Sartorius; ±0.1 g), while snout-to-vent length (SVL) was measured using a millimeter plastic ruler.

Individuals were fasted for two days, and then their standard metabolic rate (SMR) was measured (see below). Next, autotomy was induced by firmly grasping the base of the tail, approximately 2 cm from the vent, and allowing animals to break free. Blood loss during autotomy was minimal. Immediately after autotomy we conducted measurements of tail activity as described below. One week after autotomy animals were fasted again for two days, and their SMR was determined for a second time. Between fasting periods animals were fed mealworms (*Tenebrio molitor*) every day at 12:00. Water was always available *ad libitum* and was replaced every day.

2.2. Tail activity and energy content

Immediately following autotomy the base of the detached tail was placed in the center of a circular arena (2 m in diameter) and its position was marked every 5 s. We then reconstructed each tail’s trajectory by joining consecutive points with straight lines. Total tail movement was obtained by summing the length of each individual line, which was measured with a ruler to the nearest 1 mm. Because we were interested in tail movement as a predator distraction mechanism we stopped the chronometer when the detached tail remained at the same point for at least 10 s (and not when the tail became completely motionless). We measured the total length and maximum diameter of autotomized tails using a digital calliper (Mitutoyo; 0.01 mm), as well as tail wet and dry mass (after one week of drying in an oven at 60 °C) in an analytical balance (Chyo JK-180, ±0.0001 g). The energy content of each tail was determined in a Parr 1261 computerized calorimeter (Parr Instruments, Moline, IL, USA) on a dry basis.

2.3. Standard metabolic rate determinations

Carbon dioxide production (VCO2) was measured in a computerized open-flow respirometry system (Sable Systems, Henderson, NV), using an acrylic metabolic chamber of 250 mL, at Ta 30.0±0.5 °C. The metabolic chamber received dried air at a rate of 200 mL min−1 from mass flow controllers (Sable Systems, Henderson, NV). The air was passed through CO2 absorbent granules (Baralyme®) before entering the chamber and then through H2O absorbent granules (Drierite®) after passing the chamber. CO2 production was monitored four times per second during a 30 min period. Baseline measurements for each run were made using the same experimental chamber both at the beginning and at the end of each measurement period using certificated gas standards. Each record was automatically transformed by a macro program recorded in the Datacan software (Sable Systems), in order to: (1) correct for the 6 s lag introduced by the distance between the analyzer and the chamber and (2) transform the measurement from parts per million to mL CO2 per hour, taking into account the flow rate. We estimated SMR as the average of the 3–5 min steady state VCO2 consumption during periods of inactivity. Each animal was put inside the metabolic chamber 15 min before the beginning of the metabolic record. Before and after each measurement, m_b was recorded (±0.1 g), and an average of both body mass measurements was used in the statistical analysis. Individuals belonging to different groups were measured sequentially to avoid any temporal effect on our treatments.

2.4. Statistical analyses

Between group differences in initial m_b, SVL, and mass lost due to tail autotomy were compared separately by one-way ANOVAs. For animals with regenerated tails, the relative position where tail break occurred was estimated as follows: (a) we calculated the regression parameters of the relationship between tail length and SVL using only lizards with intact tails,
(b) we used this equation to estimate the original tail length of lizards with regenerated tails (ETL), (c) we calculated the ratio of TBL:ETL (where TBL is the length from the cloaca to the beginning of the regenerated portion), which indicates the relative position where the tail break occurred. Differences in tail mass, tail length and tail energy content between groups were compared separately by one-way ANOVAs, using $m_b$, SVL, and tail dry mass as covariates, respectively. With regard to tail activity, $m_b$ and SVL were investigated as possible covariates with tail movement measurements, but no significant relationships among them were found. Thus, we only report results from the one-way ANOVAs. Differences in SMR between groups (i.e., lizards with original and regenerated tails) and times (i.e., before and after autotomy) were evaluated by a two-way ANCOVA, with $m_b$ as the covariate. Prior to all statistical analyses data were examined for assumptions of normality and homogeneity of variance using Kolmogorov–Smirnov and Levene tests, respectively. We also tested for interactions between covariates and factors (parallelism test). Statistical significance was established at the 0.05 level. All analyses were performed using the statistical package, STATISTICA® (2001) version 6.0 for the Windows® operating system.

3. Results

We did not observe between group differences in $m_b$ or in SVL (Table 1). Mean loss of mass due to tail autotomy was $8.8\%\pm0.8$ (mean±SE), and this percentage did not differ between groups (Table 1). The breakage point of regenerated tails occurred between the first and second third of original tail length ($38.0\%\pm5.0$, mean±SE). Original tails were longer and thinner than regenerated ones, but did not differ in wet or dry mass (Table 1). Energy content (per gram of dry mass) was markedly higher in regenerated tails than in original tails (Fig.1A). Original tails tended to displace further, for longer time periods, and to reach greater maximum velocities than regenerated tails (Fig. 1B–D). In addition, movements were different between original and regenerated tails. Original tails showed a markedly higher degree of flexibility, whipping violently, jumping into the air, and continuously changing the direction of movement. In contrast, regenerated tails were less active, tending to move in circles and never jumping off the ground. Finally, standard metabolic rate did not differ between lizards with original and regenerated tails ($F_{1,31}=0.003$, $p=0.96$), but it was significantly

---

### Table 1

<table>
<thead>
<tr>
<th>Body size (absolute mean values±1SE) and tail morphometry (least adjusted means±1SE) for lizards with original and regenerated tails</th>
</tr>
</thead>
<tbody>
<tr>
<td>Original</td>
</tr>
<tr>
<td>$m_b$ (g)</td>
</tr>
<tr>
<td>SVL (cm)</td>
</tr>
<tr>
<td>Mass loss after autotomy (%)</td>
</tr>
<tr>
<td>Tail wet mass (mg)</td>
</tr>
<tr>
<td>Tail dry mass (mg)</td>
</tr>
<tr>
<td>Tail length (mm)</td>
</tr>
<tr>
<td>Tail diameter (mm)</td>
</tr>
</tbody>
</table>

---

Fig. 1. (A) Tail energy content (least squares adjusted value for a tail of 300 mg dry mass). (B) Total tail movement. (C) Tail movement duration (time elapsed between autotomy and the moment when the detached tail stayed at the same point for at least 10 s). (D) Maximum tail velocity (achieved during a 5 s period); this is likely the most meaningful variable regarding tail usefulness as a distraction for predators. In nearly all cases maximum velocity was achieved within the first 20 s following autotomy.
affected by tail autotomy; indeed, lizards of both groups increased their SMR after tail loss (Fig. 2).

4. Discussion

4.1. Tail activity and energy content

Dial and Fitzpatrick (1983) hypothesized that in those species in which autotomy is the principal tactic of escape from predation, post-autotomy tail thrashing should evolve to distract predator attention and/or increase predator handling time. In contrast, for species in which autotomy is a secondary line of defense, the detached tail does not thrash extensively, and thus tail breakage acts only as a mechanical release that facilitates escape from a predator’s grip. Here we demonstrate that tail thrashing activity and, thus, probably the anti-predation response of a lizard, change within the same individual according to whether its tail is original or regenerated. This result is in accordance with the theoretical prediction based on anatomical changes that follow autotomy i.e., the substitution of ossified vertebrae by a cartilaginous tube, and the lack of both segmental regularity and attachment to the skeleton of regenerated muscles (Bellairs and Bryant, 1985). In addition, our results also agree with other empirical evidence, such as the fact that original tails maintain muscular electrical activity for a longer time (Rumping and Jayne, 1996) and produce more lactate at exhaustion (Meyer et al., 2002) than regenerated tails.

Recently, some researchers have raised doubts regarding the relevance of laboratory results of the costs of energy storage loss due to tail autotomy (Chapple and Swain, 2002a, 2004; Doughty et al., 2003; Lin and Ji, 2005). This is because most laboratory studies provoke tail autotomy at a basal level (where the greatest proportion of lipids is stored), while tail breakage in the field usually occurs more distally. In our study, the breakage point of the regenerated tail occurred between the first and second third of the length of the original tail. This implies that, in contrast to the energy storage function, basal autotomy is not necessary to produce a substantial reduction in other tail roles, such as the anti-predation mechanism (this study) or the social status signal (Fox and Rostker, 1982).

Finally, our data also indicate that regenerated tails present higher energy content than original tails. Although this result could be due to differences in the energy content of tail tissue constituents (e.g., bone vs. cartilage), previous findings indicate that regenerated tails have a higher lipid content than original ones (e.g., Vitt et al., 1977). This suggests that after autotomy the role of the tail as an energy storage organ is increased. It may be that increasing the energy storage function helps to diminish the total impact of the reduction in the tail’s role as a distraction mechanism to predators.

4.2. Metabolic rate after autotomy

As mentioned earlier, tail autotomy entails several longer-term costs in addition to the loss of the anti-predator mechanism. Thus, in general terms tail regeneration is accepted as the most effective way to counteract the cost of tail loss (Chapple and Swain, 2002b). This means that, beyond behavioral changes to avoid predator encounters, phenotypic adjustments facilitating rapid tail regeneration (i.e., an increase in the rate of tissue synthesis) could be of relevance to lizard fitness.

To date, the effect of tail loss on lizard metabolic rate has only been evaluated in three species, with contrasting results. In Coleonyx variegates no differences were found in oxygen consumption between tailed and regenerating tail animals (Congdon et al., 1974), while in C. brevis and Liolaemus nitidus autotomized animals exhibited higher metabolic rates than tailed animals (Dial and Fitzpatrick, 1981; Naya and Bozinovic, 2006). The results obtained in our study are in agreement with those found for the latter species; specifically, the maintenance cost of L. belli specimens rose 36.4% in relation to the value recorded before autotomy. In addition, SMR data for a subgroup of the original lizards, taken during the first week of August (i.e., five months after autotomy was induced) indicate that the metabolic increase observed is maintained through the tail synthesis period (SMR=0.022 ± 0.003 mL CO₂ min⁻¹, least squared adjusted means ±1 SE, n=9). Thus, our results for SMR reinforce the idea that intensive cellular and physiological activity occurs during the tissue repair process (Bellairs and Bryant, 1985), and that tail regeneration itself is an energetically expensive process.

4.3. General conclusions and further directions

In summary, the present study shows that: 1. Tail thrashing activity, and thus probably the anti-predation response of a lizard, change according to whether its tail is original or regenerated. 2. The energetic cost of maintenance markedly increases following tail autotomy. There are at least three theoretical implications of these results, which we believe should be the focus of further investigation. 1. Behavioral adjustments, widely reported between tailed and tailless animals may also be found between lizards with original and regenerated tails. If this is the case, we further suspect that lizards with regenerated tails should behave similar to tailless lizards for traits related to predator avoidance (e.g., anti-predator behavior, home-range area), but different from lizards with original tails for traits related to energy storage (e.g., growth rate, clutch size). Some evidence for the home-range prediction currently exists.
(Salvador et al., 1996). 2. Lizards may more intensely avoid the autotomy of their original tail than the autotomy of a previously regenerated tail. To date, the only study that has analyzed differences in resistance to autotomy between original and regenerated tails, found that males of *Uta stansburiana* more easily autotomized their regenerated tail than their original tail (Fox et al., 1998). Although the authors discuss this finding in the context of the loss of social status (since no differences were found for females), a decrease in the tail’s anti-predation function could play an additional role. 3. Based on the relationship between SMR and field metabolic rate (McNab, 2002, p. 316), the reported increase in maintenance cost during tail synthesis corresponds to an increase in a lizard’s energy budget, ranging from 14.6% to 28%. This means that tail autotomy involves an important energetic cost that may affect lizard fitness components by itself.

**Acknowledgments**

We thank Raymond Huey, Fabian Jaksic, Carlos Martinez del Rio and Paula Neill for providing useful comments on an early version of the manuscript. This work was funded by FONDECYT (N° 3060046) to DEN, and FONDAP 1501-0001 (Program 1) to FB. All experiments were conducted according to current Chilean law.

**References**


