

The role of ecological interactions on the physiological flexibility of lizards

D. E. NAYA† and F. BOŽINOVIĆ

Center for Advanced Studies in Ecology & Biodiversity, and Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, CP 6513677, Santiago, Chile

Summary

1. An organism's ability to adjust its physiological traits to changes in environmental conditions is central for its ecological success. However, the effect of ecological interactions on physiological flexibility has rarely been investigated. Here we carry out a factorial experiment to analyse how food limitation (a potential result of competition) and tail loss (a potential result of sub-lethal predation) affect anatomical and physiological traits of the South American lizard *Liolaemus nitidus*.

2. The size of several internal organs was affected by food availability. Small intestine mass increased with food consumption, allowing animals to keep constant digestibility at greater levels of digesta, which in turn permitted higher rates of food assimilation. Organs related to energy storage reached larger sizes in autotomized animals with high food availability, but tail regeneration rate after 3 weeks did not change with food availability.

3. Metabolic rate was affected by tail loss, and animals regenerating their tail showed higher metabolic rates than tailed ones. Because this increase in metabolic rate was independent of internal organ mass, a local effect of tail regeneration process (e.g. cell proliferation) on metabolic rate is suggested.

4. When anatomical and metabolic data are jointly considered it follows that lizards adopt different physiological strategies, changing both energetic inputs and expenditures. This fact illustrates the complex interplay between ecological factors and physiological flexibility, which ultimately determine an organism's fitness.

Key-words: Digestive flexibility, *Liolaemus nitidus*, phenotypic plasticity, tail autotomy

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Introduction

Phenotypic plasticity plays a central role in the ecological success of organisms (Pigliucci 2001). This 'fine-tuned' ability encompasses adjustments in the rates of energy acquisition and/or energy expenditure, and is thought to be the ultimately responsible for positive energy budgets in animals (Hammond & Wunder 1991; Piersma & Lindstrom 1997). In this way, phenotypic flexibility (*sensu* Piersma & Drent 2003) is closely associated with organism 'decisions' regarding energy allocation into maintenance, growth and reproduction. Wiener (1992) proposes the 'barrel model' to graphically represent this interplay among environmental variability, phenotypic plasticity and energy allocation. In Wiener's model, an organism is represented by a barrel, with input energy constraints – e.g. foraging, digestion and absorption – symbolized by funnels connected in tandem, and energy outputs – e.g. main-

tenance, growth, reproduction – symbolized by a series of spouts arranged in parallel. When environmental conditions change, organisms are able to respond, at least to some extent, by adjusting the size of the funnels, the output flow through the spouts, or the fluid stored inside the barrel (see also Bacigalupe & Bozinovic 2002).

From a physiological perspective, digestive and absorptive processes can be considered the classical 'funnels' in which phenotypic flexibility has been analysed. The close relationship between digestive system attributes and food processing capacity, suggests that adjustments in gut structure could be used to cope with changes in environmental temperature (Heroux & Gridgeman 1958), reproductive status (Mircha 1964) and diet quality (Moss 1972). Since these first observations, dozens of field and laboratory studies have investigated digestive flexibility in vertebrate species, and demonstrated that digestive flexibility is an important physiological mechanism to cope with environmental variability (reviews in Piersma & Lindstrom 1997; Starck 1999; McWilliams & Karasov

2001, Naya & Bozinovic 2004). On the other hand, concerning the adjustments in energy outputs, the classical 'spout' of physiological studies has been the metabolic cost of maintenance. In vertebrate ectotherms, the standard metabolic rate (SMR) has been chosen as a good indicator of the energetic cost of maintenance (Ashby 1998) and, thus, as an essential variable for determining whether ectothermic animals modulate their maintenance costs in response to different environmental conditions (Chown & Gaston 1999). It is known that SMR of vertebrate ectotherms change with diverse factors, such as food quantity (Anderson 1993) and quality (Simandle *et al.* 2001), seasonality (Christian, Bedford & Schultz 1999) and altitude (Sears 2005).

Regarding the causes of phenotypic flexibility, variation in the strength of ecological interactions has generated considerable interest among evolutionary ecologists (Agrawal 2001). However, most research evaluating the role of these interactions has focused on the analysis of external morphology, behaviour and life-history traits (e.g. Warkentin 1995; Van Buskirk & Schmidt 2000; Relyea 2002). By contrast, evolutionary physiological ecologists have mainly centred on the role of other biotic and abiotic factors, such as ambient temperature, reproductive status and diet quality (but see Relyea & Auld 2004).

Here, we analyse the physiological adjustments to changes in food availability and tail loss in the South American lizard *Liolaemus nitidus*. We used changes in food availability as an indicator of competition, because per capita resources should indicate the intensity of competition for resources both currently and in the immediate future (Relyea 2002). As a proxy of predation pressure we chose tail autotomy because voluntary tail loss is considered an antipredator mechanism that takes place only when a predator's attack occurs or is imminent (Vitt, Congdon & Dickson 1977). We tested two hypotheses:

1. Animals adjust their internal organs to meet their functional demands; thus, we predict that lizards reared with unrestricted food will have larger digestive tracts (and associated organs) than lizards reared with low food availability.
2. Animals compensate the energetic cost of tissue synthesis that occurs during tail regeneration process by diminish their maintenance cost; thus, we predict that lizards regenerating their tail should exhibit lower standard metabolic rates than tailed lizards.

Materials and methods

MODEL SPECIES AND ANIMAL HUSBANDRY

Thirty-nine individuals of *L. nitidus* (Liolaemidae) with intact tail were captured in Illapel, Chile (31°37'056"S, 71°08'769"W; 355 m above sea level), during the second week of November 2004. The climate in this area

is semiarid (mean annual rainfall *c.* 170 mm), and the vegetation is thorn scrub composed mainly of spiny dicots, bromeliads and cacti. *Liolaemus nitidus* is a medium-sized lizard that feeds primarily on insects, although adults can also consume plant material (Jaksic & Fuentes 1978). Oviposition occurs during October, corresponding to the beginning of the Austral spring (Donoso-Barros 1966).

Animals were housed in individual metallic cages (15 × 30 × 20 cm³); each cage was covered with a 2-cm layer of soil. All cages were held in a room at an ambient temperature (T_a) of 26 ± 4 °C (mean ± range) and a photoperiod 12:12 h light : dark. Every day T_a was elevated to 35 ± 2 °C, from 11.00 am to 16.00 pm, through 100-W infrared bulbs. Spotlights were fitted in a way that generate a thermal gradient inside each cage from *c.* 33 °C to *c.* 37 °C, which include the preferential body temperature of *L. nitidus* (Labra 1988). Ambient temperature was recorded using a tidbit data-logger (Onset, Pocasset, MA), placed on the floor of the cages. Individuals were fed mealworms (*Tenebrio molitor*) every day at 12.00. Water was available *ad libitum* and replaced every day.

EXPERIMENTAL DESIGN

A factorial experiment was designed, with food availability and tail loss as experimental factors. Lizards were randomly assigned to one of four groups: tailed lizards without food restriction (T⁺/F⁺, $n = 9$), tailed lizard with food restriction (T⁺/F⁻, $n = 10$), tailless lizard without food restriction (T⁻/F⁺, $n = 10$), and tailless lizard with food restriction (T⁻/F⁻, $n = 10$). To estimate daily food requirements we used the allometric equation for insectivorous lizards (Nagy 2001): fresh matter intake (FMI) (g day⁻¹) = 0.033 $m_b^{0.914}$ (with m_b = body mass = m_{b12} , see below). Unrestricted food treatment was considered as 100% of FMI and food restriction treatment was considered as 50% of FMI. Given that Nagy's equation refers to daily energy requirement in the field, we suppose that food-restricted animals are close to their maintenance requirements, while unrestricted lizards are far in excess (see McNab 2002, p. 316). To achieve tail autotomy we grasped the base of the tail (*c.* 2 cm from the vent) with forceps and allowed the animal to break free. Because tail autotomy is a neurologically controlled process, only shown by conscious animals, we did not anaesthetize lizards prior to provoking autotomy. Blood loss during autotomy was minimal.

DEPENDENT VARIABLES

Body size and tail regeneration

Initial body mass before and after caudal autotomy (m_{b11} and m_{b12} , respectively) and final body mass (m_{bF}) were recorded with an electronic balance (Sartorius GmbH (Göttingen, Germany); ±0.1 g). Mass balance was estimated as the difference between m_{bF} and m_{b12} .

Snout to vent length (SVL) at the first day of experimentation was measured with a ruler (± 0.1 mm). For lizards in the T groups, the length and dry mass of the regenerated tail were measured at the end of the experiment, when the animals were euthanized, with a digital callipers (Mitutoyo (Aurora, IL, USA); 0.01 mm) and an electronic balance (Chyo JK-180 (Kyoto, Japan), ± 0.0001 g), respectively.

Digestive variables

Two weeks after the beginning of the experiment, food intake (I) and faeces production (F) were measured for a period of 4 days (experimental days 14–18). Faeces and remaining food were collected every day, dried at 60 °C for 4 days and weighed (± 0.0001 g). Each faecal pellet was carefully cleaned with a paint brush before being weighed. In two cases, faeces disintegrated and mixed with the soil of the cage floor. These samples were not included in analyses. Dry-matter digestibility was calculated as $\text{DMD}(\%) = (I(\text{g day}^{-1}) - F(\text{g day}^{-1})) / I(\text{g day}^{-1})$, and digestible food intake as $\text{DFI}(\text{g day}^{-1}) = I(\text{g day}^{-1}) - F(\text{g day}^{-1})$. Dry-matter digestibility, also called apparent digestibility coefficient, has two important biases. First, it underestimates digestive efficiency because it takes into account the non-reabsorbed secretions of the digestive system. Second, energy true digestibility is additionally underestimated because faeces generally have lower energy densities than food. Here we assume that these biases are similar to all experimental groups, and thus, we used DMD to compare the digestive efficiency among them. Body mass of each lizard was measured before and after digestive determinations using an electronic balance (± 0.1 g).

Metabolic rates

The metabolic rate of each individual was measured 3 weeks after the experiment started. CO_2 production (V_{CO_2}) was measured in a computerized (Datacan V, Henderson, NE, USA) open-flow respirometry system (Sable Systems, Henderson, NE) in acrylic metabolic chamber of 0.25 l, at an ambient temperature of 30 °C. The metabolic chamber received dried air at a rate of 250 ml min^{-1} from mass flow controllers (Sierra Instruments, Monterey, CA). The air was passed through CO_2 absorbent granules (Baralyme®, St Louis, MO, USA) before entering the chamber and then through H_2O absorbent granules (Drierite®, Xenia, OH, USA) after passing the chamber. CO_2 production was monitored four times per second during 1 h. Each record was automatically transformed and recorded in the Datacan software (Sable Systems). Then, we estimated the standard metabolic rate (SMR) as the 3 min of minimum CO_2 production. Before and after each measurement, m_b was recorded in an electronic balance (± 0.1 g). Given the high protein content of the experimental diet, CO_2 production was converted into energetic units using the energy equivalent of 23.32 J ml^{-1} CO_2

(Hill & Wyse 1989). All metabolic records were obtained during three consecutive days (experimental days 21–23), and to avoid any temporal effect on our treatments, individuals belonging to different groups were measured sequentially. Lizards were fasted for 2 days before V_{CO_2} records.

Internal organs

During the morning (09.00–10.00) of the days after V_{CO_2} records (experimental days 22–24), lizards were cooled by decreasing ambient temperature (4 °C), and then killed by decapitation. After that, animals were dissected and internal organs (stomach, small intestine, large intestine, liver, heart, kidneys and abdominal fat bodies) were removed, washed with Ringer's solution, dried to a constant mass in an oven at 60 °C for 4 days, and weighed (± 0.0001 g). Finally, we cut the tail of the T⁺ animals (also *c.* 2 cm from the vent), dried the entire carcass (i.e. body free of viscera and tail) in an oven at 60 °C for 10 days, and weighed (± 0.0001 g).

STATISTICAL ANALYSES

Differences in body size (SVL, m_{bl} and m_b balance) among groups were evaluated separately by two-way ANOVA, with food availability and tail loss as the main factors. The effect of food availability on regenerated tail length and mass was analysed with a one-way ANCOVA, with food availability as the main factor and m_{bF} as covariate. Differences in dry-mass digestibility among groups were tested by a two-way ANCOVA, with food availability and tail loss as the main factors, faeces production as response variable and food intake as covariate (see Beaupre & Dunham 1995). Differences in all the remaining variables were also evaluated separately by two-way ANCOVA, with food availability and tail loss as the main factors. For these latter analyses, we used m_{bF} as covariate for digestible food intake and standard metabolic rate, and carcass dry mass as the covariate for internal organ mass. In all two-way ANOVAs and ANCOVAs, the interaction among main factors was tested. Prior to each statistical analysis, data were examined for assumptions of normality and homogeneity of variance, using Kolmogorov–Smirnov and Levene tests, respectively. Interactions between covariates and factors (parallelism test) were also tested. Differences among groups (post-hoc comparisons) were evaluated by Tukey HSD tests. Statistical significance was established at the 0.05 level. All the analyses were performed using the statistical package, Statistica® (2001) version 6.0 for the Windows® operating system.

Results

BODY SIZE AND TAIL REGENERATION

No significant differences between groups in m_{bl} or SVL were observed (Tables 1 and 2). Mean mass loss

Table 1. Initial body mass, snout to vent length and body mass balance (absolute mean values \pm SE), tail regeneration (least-square adjusted means \pm SE), and internal organs dry mass (least-square adjusted means \pm SE) for each experimental group. T⁺/F⁺, tailed lizards without food restriction; T⁺/F⁻, tailed lizard with food restriction; T⁻/F⁺, tailless lizard without food restriction; T⁻/F⁻, tailless lizard with food restriction

Attributes	T ⁺ /F ⁺	T ⁺ /F ⁻	T ⁻ /F ⁺	T ⁻ /F ⁻
Body size				
Initial body mass (g)	17.80 (3.30)	19.15 (2.87)	21.79 (2.16)	18.19 (1.74)
Body mass balance (g)	1.62 (0.41)	-0.06 (0.65)	1.57 (0.66)	0.02 (0.40)
Snout to vent length (mm)	80.3 (3.9)	80.2 (3.5)	86.7 (2.9)	81.5 (2.5)
Regenerated tail length (mm)	-	9.4 (1.8)	-	9.8 (1.8)
Regenerated tail dry mass (mg)	-	80.0 (31.6)	-	105.0 (21.6)
Internal organs				
Stomach dry mass (mg)	578.1 (56.0)	579.2 (24.6)	557.3 (25.3)	598.0 (24.6)
Large intestine dry mass (mg)	345.5 (26.4)	265.1 (24.9)	268.0 (25.7)	284.1 (25.0)
Heart dry mass (mg)	80.0 (4.7)	81.5 (4.2)	80.3 (4.4)	80.3 (4.2)
Lungs dry mass (mg)	195.2 (19.3)	212.7 (19.3)	197.8 (19.8)	215.2 (19.3)

caused by tail autotomy was $12.0 \pm 0.47\%$ (mean \pm SE) of m_{bi} . Body mass balance showed a significant effect of food availability, and, as expected, animals from F⁺ groups increased their m_b more than those from F⁻ groups (Tables 1 and 2). However, regenerated tail length and dry mass did not change with food availability (Tables 1 and 2), and a small cone of new tissue was apparent in all animals 2 weeks after autotomy.

DIGESTIVE VARIABLES AND METABOLIC RATES

DMD did not change with food availability or with tail loss treatments (Fig. 1a, faeces production analysis in Table 2). However, DFI showed a significant effect of food availability, and the *a posteriori* comparison indicated that animals from F⁺ groups showed larger values than lizards from F⁻ groups (Fig. 1b, Table 2).

On the other hand, SMR was significantly affected by tail loss, where T⁻ animals exhibited higher metabolic rates than T⁺ lizards (Fig. 2, Table 2).

INTERNAL ORGANS

Dry mass of stomach, large intestine, heart and lungs did not change with experimental factors (Tables 1 and 2). By contrast, a significant effect of food availability was found for small intestine, liver and kidneys, and a significant effect of both food availability and tail loss was found for fat bodies (Table 2). Post-hoc comparisons indicated that these four organs can be clustered in: (i) those for which T⁻F⁺ were larger than the two F⁻ groups, but not larger than the T⁺F⁺ group (small intestine and kidneys; Fig. 3a), and (ii) those for which T⁻F⁺ animals showed larger values than individuals from the other three groups (liver and fat bodies; Fig. 3b).

Table 2. Results of the ANOVA and ANCOVA tests. Significant probabilities are in bold

Attributes	Food availability	Tail loss	Interaction term	Covariate
Body size and tail regeneration				
Initial body mass	$F_{1,35} = 0.19; P = 0.66$	$F_{1,35} = 0.35; P = 0.56$	$F_{1,35} = 0.94; P = 0.34$	
Body mass balance	$F_{1,35} = \mathbf{8.42}; P < \mathbf{0.01}$	$F_{1,35} = 0.01; P = 0.97$	$F_{1,35} = 0.01; P = 0.91$	
Snout to vent length	$F_{1,35} = 0.67; P = 0.42$	$F_{1,35} = 1.40; P = 0.24$	$F_{1,35} = 0.60; P = 0.44$	
Regenerated tail length	$F_{1,18} = 0.16; P = 0.69$			
Regenerated tail dry mass	$F_{1,18} = 0.43; P = 0.52$			
Digestive and metabolic variables				
Faeces production	$F_{1,32} = 0.01; P = 0.92$	$F_{1,32} = 3.41; P = 0.07$	$F_{1,32} = 0.28; P = 0.60$	$F_{1,32} = 2.70; P = 0.11$
Digestible food intake	$F_{1,32} = \mathbf{27.8}; P < \mathbf{0.001}$	$F_{1,32} = 3.33; P = 0.08$	$F_{1,32} = 0.17; P = 0.68$	$F_{1,32} = \mathbf{80.0}; P < \mathbf{0.001}$
Standard metabolic rate	$F_{1,34} = 0.63; P = 0.43$	$F_{1,34} = \mathbf{6.79}; P = \mathbf{0.01}$	$F_{1,32} = 1.77; P = 0.19$	$F_{1,34} = \mathbf{14.0}; P < \mathbf{0.001}$
Internal organs				
Stomach dry mass	$F_{1,34} = 0.69; P = 0.41$	$F_{1,34} = 0.002; P = 0.97$	$F_{1,34} = 0.61; P = 0.44$	$F_{1,34} = \mathbf{251.5}; P < \mathbf{0.001}$
Small intestine dry mass	$F_{1,34} = \mathbf{9.10}; P < \mathbf{0.01}$	$F_{1,34} = 0.37; P = 0.55$	$F_{1,34} = 0.13; P = 0.72$	$F_{1,34} = \mathbf{97.1}; P < \mathbf{0.001}$
Large intestine dry mass	$F_{1,34} = 1.59; P = 0.22$	$F_{1,34} = 1.31; P = 0.26$	$F_{1,34} = 3.53; P = 0.07$	$F_{1,34} = \mathbf{99.9}; P < \mathbf{0.001}$
Kidneys dry mass	$F_{1,34} = \mathbf{6.47}; P = \mathbf{0.02}$	$F_{1,34} = 0.54; P = 0.47$	$F_{1,34} = 0.78; P = 0.38$	$F_{1,34} = \mathbf{35.3}; P < \mathbf{0.001}$
Liver dry mass	$F_{1,34} = \mathbf{16.8}; P < \mathbf{0.001}$	$F_{1,34} = 1.04; P = 0.32$	$F_{1,34} = 1.18; P = 0.28$	$F_{1,34} = \mathbf{144.0}; P < \mathbf{0.001}$
Fat bodies dry mass	$F_{1,34} = \mathbf{6.60}; P = \mathbf{0.01}$	$F_{1,34} = \mathbf{4.49}; P < \mathbf{0.04}$	$F_{1,34} = 1.26; P = 0.27$	$F_{1,34} = \mathbf{20.5}; P < \mathbf{0.001}$
Heart dry mass	$F_{1,34} = 0.03; P = 0.87$	$F_{1,34} = 0.01; P = 0.92$	$F_{1,34} = 0.03; P = 0.86$	$F_{1,34} = \mathbf{166.1}; P < \mathbf{0.001}$
Lungs dry mass	$F_{1,34} = 0.80; P = 0.38$	$F_{1,34} = 0.02; P = 0.90$	$F_{1,34} = 0.001; P = 0.99$	$F_{1,34} = \mathbf{70.7}; P < \mathbf{0.001}$

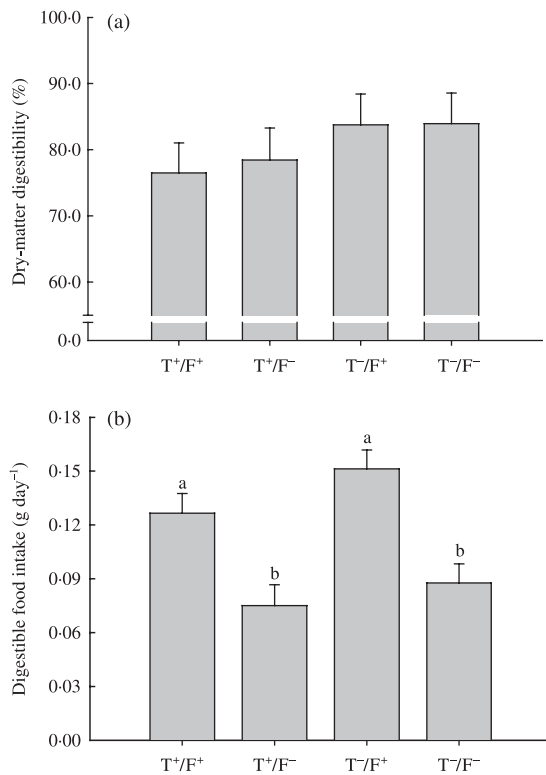


Fig. 1. Dry matter digestibility (a) and digestible food intake (b) for each experimental group. T⁺/F⁺, tailed lizards without food restriction; T⁺/F⁻, tailed lizard with food restriction; T⁻/F⁺, tailless lizard without food restriction; T⁻/F⁻, tailless lizard with food restriction. Values presented are least-squared adjusted means (bars = 1 SE). Covariate mean values: food intake = 0.52 g day⁻¹; final body mass = 18.99 g. Different letters indicate significant differences between groups.

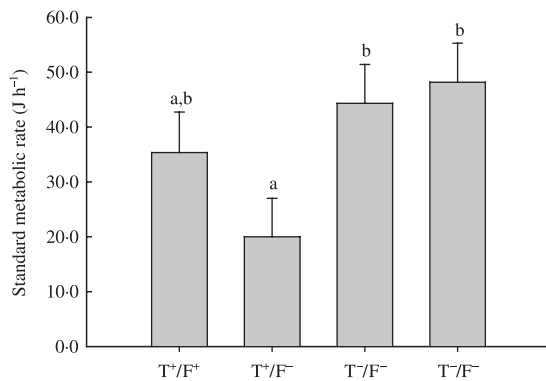


Fig. 2. Standard metabolic rate for each experimental group (abbreviations as in Fig. 1). Values presented are least-squared adjusted means (bars = 1 SE). Covariate mean values: final body mass = 18.99 g. Different letters indicate significant differences between groups.

Discussion

To understand lizard physiological responses to experimental factors, we first discuss how food availability affects digestive and anatomical variables, and then how tail loss affects metabolic rates. After that, we discuss phenotypic integration processes, and delineate

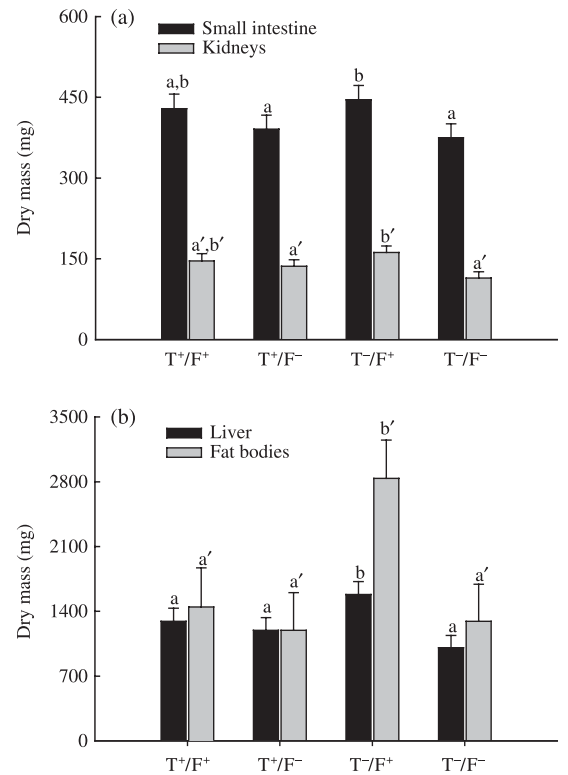


Fig. 3. Dry mass of small intestines and kidneys (a), and liver and fat bodies (b) for each experimental group (abbreviations as in Fig. 1). Values presented are least-squared adjusted means (bars = 1 SE). Covariate mean values: carcass dry mass = 4.45 g. Different letters indicate significant differences between groups.

different physiological strategies adopted by animals in different experimental groups.

FOOD AVAILABILITY AND ORGAN FLEXIBILITY

Although digestive flexibility has been investigated in dozens of vertebrate species, most of our knowledge on this topic came from two particular situations: (1) adjustments of small endotherms (e.g. rodent and birds) to cope with changes in ambient temperature, food quality and/or reproductive status and (2) adjustments of middle-size and large ectotherms (mainly snakes) after a meal ingestion. In recent years, an increasing number of studies about digestive flexibility in small ectotherm vertebrates have been published. These studies demonstrate that these organisms are able to adjust their digestive traits in response to changes in external conditions, such as food quantity (Relyea & Auld 2004; Naya et al. 2005) and quality (Sabat, Riveros & López-Pinto 2005), aestivation (Secor 2005) and hibernation (Tracy & Diamond 2005). Our study confirms that small ectotherm vertebrates are able to adjust their small intestine size to changes in the amount of food ingested. In addition, we found that the regulation of this digestive trait allows animals to maintain digestibility values at higher levels of digesta, which in turn results in higher rates of food assimilation.

Regarding energy storage, abdominal fat bodies and liver were also affected by food availability, but in this case only autotomized lizards with high food availability (F^+/T^- group) showed greater energy reserve organs than the other groups. There are two, not mutually exclusive, explanations for the fact that the two groups with high food availability differ in the mass of energy storage organs. First, because animals in the F^+/T^+ group retained their tail during the experiment, perhaps lizards in this group use this organ to store part of the gained energy. Second, the increase in energy demands due to tissue repair processes in autotomized animals may stimulate tailless lizards to process food more efficiently (e.g. increase enzymatic hydrolysis or brush-border nutrient transport activity) and, thus, store energy at higher rates than tailed lizards.

When the pattern of variation observed for energy storage organs is combined with results on tail regeneration, it follows that a peripheral limit (e.g. rate of tissue synthesis) to regeneration process probably occurs. This is because although F^+/T^- animals ingested and stored more energy than F^-/T^- lizard, both groups did not differ in the length or dry mass of their regenerated tail after a 3-week period.

TAIL LOSS AND METABOLIC RATE

Tail autotomy is a self-induced separation of the tail from the body, a mechanism that is considered an efficient antipredatory strategy (e.g. Congdon, Vitt & King 1974; Dial & Fitzpatrick 1983). However, lizard tails usually participate in other functions and, thus, autotomized animals may have to cope with several costs, in addition to the temporal loss of the antipredatory mechanism. In this sense, it is known that tail autotomy reduce lizards' survival (e.g. Congdon *et al.* 1974; Niewiarowski *et al.* 1997), reproduction (e.g. Dial & Fitzpatrick 1981; Salvador, Martin & López 1994), growth rates (e.g. Niewiarowski *et al.* 1997; Peterson, Walton & Bennett 1999), social status (e.g. Vitt *et al.* 1977; Fox & Rostker 1982), energy reserves (Congdon *et al.* 1974; Vitt *et al.* 1977), locomotion (e.g. Formanowicz, Brodie & Bradley 1990; Martin & Avery 1998) and foraging activity (Dial & Fitzpatrick 1981; Martin & Salvador 1993). Although some behavioural adjustments may mitigate these costs (Martin & Avery 1998, and references therein), it is accepted that tail regeneration is the most effective way to counteract the negative effects of tail loss (Chapple & Swain 2002). This suggests that physiological adjustments facilitating a rapid tail regeneration could be of relevance to lizards fitness.

To our knowledge, the effect of tail loss on lizard metabolism has been evaluated in only two other species, *Coleonyx variegatus* and *C. brevis*, with contrasting results. No differences in metabolic rate between tailed and regenerating tail animals were found in *Coleonyx variegatus* (Congdon *et al.* 1974). In contrast, autotomized *C. brevis* had higher metabolic rates than tailed

ones (Dial & Fitzpatrick 1981). In agreement with results for this latter species, and contrary to our original hypothesis, we found in *L. nitidus* that autotomized animals exhibit higher metabolic rates than tailed ones. This fact reinforces the idea that an intensive cellular and physiological activity occurs during tissue repair process (Bellairs & Bryant 1985), and that tail regeneration is an energetically expensive process by itself (Chapple, McCoull & Swain 2002). In addition, because lizards from both autotomized groups showed similar metabolic rates, we hypothesize that the increase of this variable in tailless animals is due to a local effect of regeneration process (e.g. cell proliferation), and not to differences in internal organ size (Secor & Diamond 2000) or to an increment in the specific metabolic activity of body tissues (Vézina & Williams 2005).

PHENOTYPIC INTEGRATION

Weiner's 'barrel model' had an influential role in physiological ecology research during the 1990s, mainly because of its conceptual simplicity. However, acquisition, storage and expenditure of energy embrace a myriad of intercorrelated venues that complicate the proximal understanding of how organisms adjust their energy balance to changing conditions. Here, we found that the physiological adjustments made by lizards depend on the interplay between external energy available and internal energy demands. Specifically, we observed that tail autotomy increased metabolic rate (both T^- groups), and that the size of several internal organ is up-regulated only when enough food is available (T^+/F^+). In contrast, when energy demands are low and food is scarce (T^+/F^- group), animals reduced both maintenance costs and internal organ size. A remaining question is, how can autotomized animals with low food availability (T^-/F^-) maintain higher metabolic rates without a substantial decrease in their energy reserves? We observed that lizards from this group spent more time at higher environmental temperature (i.e. in the back part on the cages) than individual from the other groups (data not shown). An increase in their preferential body temperature may explain the slightly higher values of digestibility and assimilation (see Bozinovic & Rosenmann 1988) in relation to the other food-restricted group and, thus, the maintenance of higher metabolic rates without depletion of energy reserves. In sum, lizards from different experimental groups appear to follow different physiological strategies, changing both energetic inputs and expenditures. Our work illustrates the complex interplay between physiological adjustments and ecological factors, which ultimately determine an organism's fitness.

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