THERMOREGULATORY BEHAVIOUR OF ROCK LIZARDS IN RESPONSE TO TAIL LOSS

by

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Summary

The consequences of tail loss on the thermal biology of high-altitude rock lizards (Lacerta monticola) were studied by comparing field body temperatures, selected body temperatures in a gradient, and behavioural patterns of thermoregulation of tailed and tailless lizards in the field. Neither field nor selected body temperatures differed significantly between these groups. Time spent basking, mean duration of basking, and basking frequency did not differ between tailed and tailless lizards. Tailless lizards seemingly adjusted for running impairment by using rocks to a greater extent than did tailed lizards, and low morning body temperatures by increasing maximal duration of basking periods and keeping shorter distances to the nearest refuge. Tailless lizards modify thermoregulatory behaviour, but obtain the same thermoregulatory precision as tailed lizards, possibly allowing maximization of physiological processes linked to tail regeneration.

Introduction

Numerous lizards autotomize their tail to escape when grasped by a predator (BELLAIRS & BRYANT, 1985). Autotomy can produce an immediate benefit to survival, but its associated costs may reduce individual fitness (ARNOLD, 1988). Among these costs have been identified lack of agility (ARNOLD, 1984), lower running speed (BALLINGER *et al.*, 1979; PUNZO, 1982; ARNOLD, 1984), and reduced social status (Fox & ROTSKER, 1982; Fox *et al.*, 1990). Tail regeneration is also a costly process that may require increased food intake or diversion of energy away from other functions, such as somatic growth (BALLINGER & TINKLE, 1979; but see VITT & COOPER, 1986) or reproduction (DIAL & FITZPATRICK, 1981).

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Tailless lizards are relatively vulnerable to predation (CONGDON et al., 1974; DIAL & FITZPATRICK, 1984), but some tailless lizards are able to compensate for the costs of autotomy by modifying their defensive behaviour, for example, by becoming more cryptic or wary (FORMANOWICZ et al., 1990). Such behavioural modifications (e.g. in activity levels, basking frequency, movement rate, or microhabitat use) could, however, affect thermoregulatory behaviour because thermal microclimates vary spatially and temporally (GRANT & DUNHAM, 1988). If these changes would occur,tailless lizards might not be able to achieve preferred body temperatures (BENNETT & DAWSON, 1976; HUEY, 1982; WALDSCHSMIDT & TRACY, 1983), and the efficiency of various physiological functions, included tail regeneration, would decrease at lower temperatures (MADERSON & LICHT, 1968; DAWSON, 1975; HUEY, 1982).

Thermoregulation in cool climates as in the high mountains is particularly costly. Lizards inhabiting such habitats must devote a high proportion of their activity time to thermoregulation (PEARSON & BRADFORD, 1976; BEUCHAT, 1989; VAN DAMME et al., 1989). Montane lizards are sometimes unable to achieve optimal body temperatures, and thus can experience reduced running abilities (HERTZ et al., 1983; VAN DAMME et al., 1989, 1990). As tail loss also reduces running speed (BALLINGER et al., 1979; PUNZO, 1982; ARNOLD, 1984), tail autotomy in the high mountains could be especially disadvantageous with respect to thermoregulation and to defense. Consequently, behavioural shifts associated with autotomy could have a major effect on thermoregulation.

This report addresses two questions:

Do tailed and tailless lizards differ in body temperatures or in thermoregualatory precision?;

Do tailless lizards change their thermoregulatory behaviour to compensate for the costs of tail loss?

We hypothesize that tailless lizards are able to compensate for impaired running performance by shifting their thermoregulatory behaviour, so they can obtain the same thermoregulatory precision as tailed lizards.

The effects of tail-loss on thermoregulatory behaviour and on responses to hourly variation in the thermal environment were experimentally studied in the Iberian rock lizard *Lacerta monticola* at a montane site in central Spain. The effects of tail condition are examined in relation to: 1) field body temperatures and thermoregulatory precision; 2) selected body temperatures in a laboratory thermal gradient; 3) percent time, frequency, mean and maximal duration of basking periods; 4) distance to the nearest refuge during basking as a measure of perceived predation risk; 5) habitat use and its relationship to environmental temperatures; and 6) time devoted to resting and to other activities unrelated to thermoregulation. We discuss the relevance of tail condition and associated behaviour for the balance between costs and benefits of thermoregulation (HUEV & SLATKIN, 1976).

Methods

Species.

Lacerta monticola is a small insectivorous lacertid lizard principally found in montane areas of the north and central Iberian peninsula. In the Sierra de Guadarrama (central Spain), it is found between 1750 and 2350 m elevation, and the smallest reproductive size is 67 mm snout-vent length (SVL) for females, and 61 mm for males. In this region, *L. monticola* is active from May to October, mating in May-June, and producing a single clutch in July (SALVADOR, 1984; ELVIRA & VIGAL, 1985). Tail autotomy is a frequent event in this *L. monticola* population as shown by relatively high (60%) proportion of individuals with regenerated tail at first capture (unpublished data).

Study site and experimental plots.

The study was carried out in the Sierra de Guadarrama, on the western slope of Cerro de Valdemartín, 2.5 km from Puerto de Cotos (40° 49' N, 3° 58' W), Madrid Prov., Spain, at 1900 m elevation. Average minimum (January) - maximum (July) temperatures are -4.1° C, and 21.9° C respectively. Average annual precipitation is 1170 mm, and snow cover occurs from December to April (MONTERO & GONZALEZ, 1984). Granite rocks interspersed with shrubs (*Cytisus oromediterraneus* and *Juniperus communis*) predominated at the study site with meadows of *Festuca* sp. and other grasses (RIVAS-MARTINEZ *et al.*, 1987).

The experiment was conducted from 9 May to 30 June 1990 on four 50×50 m plots, being the distance between adjacent plots 75 m. The site was chosen to obtain plots with similar microhabitat availabilities. We divided each plot into a grid with markers set at 5-m. Two plots were randomly assigned to the experimental treatment and the other two plots as the controls. Only adult individuals were included in the analyses.

Field body temperatures.

We searched for lizards by walking over the plots between 0700 and 1400 h (G.M.T.). Sampling effort was similar on the four plots, and each plot was visited once per week. We noosed lizards and immediately measured their body (=cloacal, Tb), air (shaded bulb, 3 cm above the sighting point, Ta), and substrate temperatures at the sighting point (Ts), with a digital thermometer to the nearest 0.1° C. To meet independence of data we took only one measurement from each individual captured in the plots. To increase sample size, we have added temperature measurements from other tailed individuals captured around the plots. We also recorded the SVL and tail length to the nearest mm, mass with a Pesola spring scale, sex, and tail condition. Lizards were individually marked by toe-clipping and with paint on the dorsum for temporary identification. On experimental plots we removed at first capture each lizard's tail approximately 17 mm away from the cloaca. Tailless lizard body temperatures were taken after a minimum period of one week after tail removal.

Selected body temperatures.

The selected body temperature of tailless and tailed lizards was determined in phototemperature gradients during June, 1991. We captured lizards (9 tailed, 7 tailless) in the study plots and immediately transferred them to "E1 Ventorrillo" field station laboratory (distant 5 km by air) where they were measured the next day. The selection chamber (100×75 cm) was filled with sand and stones. A 200-W light was suspended above one end of the chamber, producing a gradient of air temperatures from 18 to 50° C. We measured selected body temperatures (Tsel) of active lizards in the chamber, with a time interval of two hours between measurements, using the same thermometer as in the field. The selected body temperature range was defined as the central 50% ($\times\pm0.674$ s) of all Tsel measured (VAN DAMME *et al.*, 1990).

Thermoregulatory behaviour.

Every plot was visited once each week for behaviour observations. Using binoculars we observed individual (focal) lizards at a distance of 5-7 m, and recorded on a pocket tape recorder the time spent in each behaviour. Only time budgets of 20 min or longer were used (Mean individual time (\pm 1SE) was 26.4 \pm 0.8 min, resulting in about 36 h of observation). Only one observation period per marked individual was analyzed.

We classified the behaviour of focal animals according to the following definitions. "Basking": lizard remains motionless during a prolonged stop (more than 15 s) in a patch of open sun, with the body flattened on the substrate. "Resting": lizard remains in a shaded site such as a crevice or under a bush for a prolonged period. "Moving": lizard runs for more than two seconds and moves further than 10 cm (when the lizard moved less than this time and distance, we considered it comfort movements). : "Other activities": include behaviour not directly related to thermoregulation, such as "alert" (when the lizard stands motionless with head elevated. This behavior is frequently followed by short chases after prey), "hunting" (this refers to captures of prey), "agonistic" and "sexual" behaviors. Comfort movements (when the lizard moves less than two seconds and shorter than 10 cm) were included here.

During basking periods we recorded the time of basking between two movements. Basking frequency was measured as the number of basking episodes per minute of observation. We also recorded the substratum (rock, grass or bush) used by the lizards during baskings. At the same time one of us measured the temperature of rock exposed to the sun (shaded bulb, Trock), and grassy ground exposed to the sun (shaded bulb, Tgrass).

Lacerta monticola escape from predators by moving a short distance into a crevice or to the protective cover of a bush. The distance to such a refuge may be considered as a measure of predation risk perceived by the lizard (CARRASCAL et al., 1992). So, for each focal observation period, we recorded the distance to the nearest refuge, averaged among basking periods. To estimate available mean distance to the nearest refuge (null hyphotesis), we measured 120 random points (30 points per plot, preliminary analyses did not show significant differences between plots), each point being an average of twenty random measurements around the random point (MARTIN & SALVADOR, 1992).

Data analysis.

Lizard behaviour may differ in relation to time elapsed since tail loss. Our results are based on temperatures and observations recorded between one and five weeks after tail removal. We could not analyze the same time interval between tail break and the observations for every individual because of difficulties of gathering data in the field.

We used one-way and two-way analysis of variance (ANOVA) to evaluate mean differences between hourly periods and between tailed and tailless lizards groups, Pearson correlation for analysis of relationships between body and air temperatures, and Fmax tests for comparing homogeneity of variances of Tb (SOKAL & ROHLF, 1981).

Results

Field body temperatures.

We found no differences in field Tb between males and females of tailed ($F_{1,206}=2.82$, p>0.05) and tailless lizards ($F_{1,58}=1.80$, p>0.05), therefore subsequent analyses are based upon samples pooled by sex. Tailed and tailless groups did not differ significantly in mean body or environmental temperatures (Table 1). Moreover, the groups did not differ significantly in variance of Tb (tailed, $\sigma^2=9.0$; tailless, $\sigma^2=8.8$; Fmax=1.02, p>0.05), suggesting that thermoregulatory precision was similar. Tb of tailed and tailless lizards were weakly correlated with the corresponding Ta (Tailed: r=0.30; Tailless: r=0.26; p<0.0001 in both cases) (Fig. 1). Mean Tb varied among hourly periods but not between tailed and tailless lizards (Two way ANOVA; hour effect: $F_{7,252}=3.63$, p<0.001; tail effect: $F_{1,252}=0.85$, p>0.40; factors interaction; $F_{7,252}=0.43$, p>0.80) (Fig. 2).

Selected body temperatures.

>0.70

p

Selected body temperatures did not differ significantly between tailed and tailless lizards (Table 1). Also, the sexes did not differ significantly in Tsel ($F_{1,54}$ =1.80, p>0.15; data pooled). Many lizards in the field maintained

Lacerta monticola lizards						
	Tb	Та	Ts	Tsel		
Tailed	$\begin{array}{c} 29.4 \pm \ 0.2 \\ (18.4 \text{-} 35.2) \end{array}$	$18.3 \pm 0.3 \\ (5.2 - 29.0)$	$\begin{array}{c} 22.7 \pm \ 0.3 \\ (8.8 - 34.3) \end{array}$	32.2 ± 0.3 (29.8-33.9)		
Tailless	$\begin{array}{r} 208 \\ 29.5 \pm 0.4 \\ (17.5 - 34.4) \end{array}$	$\begin{array}{r} 208 \\ 18.4 \pm \ 0.5 \\ 9.2 \text{-} 28.0 \end{array}$	$208 \\ 23.3 \pm 0.6 \\ (13.0-34.2)$	$\begin{array}{r} 31\\ 31.9\pm \ 0.3\\ (28.5-33.4)\end{array}$		
	60	60	60	25		
F	0.13	0.003	0.33	0.48		

TABLE 1. Mean (\pm 1 SE, range in parentheses, and sample size) of body (Tb), air (Ta), and substrate (Ts) temperatures in the field, and selected body temperatures (Tsel) in a laboratory gradient of tailed and tailless *Lacerta monticola* lizards

F and p values from univariate ANOVA on tailed and tailless lizard temperatures are given.

>0.50

>0.50

>0.90



Fig. 1. Relations between body (Tb) and air (Ta) temperatures in tailed (open circles) and tailless (solid circles) *L. monticola.* Regression lines for tailed (continuous) and tailless lizards (dotted) are shown.



Fig. 2. Hourly variation in air (Ta) and body (Tb) temperatures in tailed (open boxes) and tailless (solid boxes) *L. monticola.* Hourly means (± 1 SE) and sample sizes (row numbers) are shown.

activity below their Tsel range, 66.8% of all field Tb of tailed lizards, and 63.3% of field Tb of tailless lizards being below this range.

Thermoregulatory behaviour.

Time devoted to basking significantly varied between hourly periods decreasing from early morning to evening, but did not differ between tailed and tailless lizards (Two way ANOVA: hour effect: $F_{6,68}=4.61$, p<0.001; tail effect: $F_{1,68}=2.38$, p>0.10; factors interaction: $F_{6,68}=0.71$, p>0.60). Basking time decreased in tailless lizards along the morning (one way ANOVA; $F_{6,40}=4.68$, p<0.001), but remained similar in tailed lizards ($F_{6,28}=0.75$, p>0.60).

Mean duration of an individual basking period and basking frequency were not significantly different between lizard groups, or between hourly periods (Table 2). maximal duration of a basking period in an individual observation was, however, significantly greater during the morning in tailless lizards (Two way ANOVA; hour effect: $F_{6,68}=2.56$, p<0.03; tail effect: $F_{1,68}=4.20$, p<0.04; factors interaction; $F_{6,68}=0.65$, p>0.60) (Fig. 3).

Distance of lizards to the nearest refuge during basking periods (pooled data, $\bar{x}\pm SE=11.8\pm0.7$ cm) was significantly shorter ($F_{1,200}=77.81$, p<0.0001) than the distance available in the habitat (27.2±1.3 cm) (Fig. 4). There were no significant differences in daily average distance to the refuge between tailed and tailless groups ($F_{1,80}=0.27$, p>0.60). In tailed lizards average distances remained similar both in the morning (8-12)

Hours	Mean duration		Basking rate	
	Tailed (N)	Tailless (N)	Tailed	Tailless
8-9	88.4± 20.3(2)	397.8±107.7(7)	0.43±0.2	0.25±0.1
9-10	75.6± 13.9(7)	$240.4 \pm 106.1(9)$	0.54 ± 0.1	0.38 ± 0.1
10-11	257.4±180.2(19)	$115.5\pm$ 76.2(6)	0.48 ± 0.1	0.63 ± 0.1
11-12	$47.3 \pm 9.4(5)$	$176.6 \pm 91.9(7)$	0.69 ± 0.1	0.41 ± 0.1
12-13	$51.2 \pm 11.9(3)$	$97.2\pm 53.4(3)$	0.53 ± 0.3	0.41 ± 0.2
13-14	$132.5 \pm 93.1(5)$	$81.5\pm 32.3(6)$	0.32 ± 0.2	0.52 ± 0.1
14-15	29.6± 7.8(3)	54.4± 19.7(9)	0.81 ± 0.1	0.60 ± 8.1
Hour effect:		F=1.21, p>0.30		F=1.34, p>0.20
Tail effect:		F=0.67, p>0.40		F=0.91, p>0.30
Interaction:		F=0.77, p>0.50		F=1.05, p>0.40

TABLE 2. Mean (± 1 SE, sample size in parentheses) of average basking time (sec) and basking rates (number/min) in hourly (G.M.T.) periods

F and p values from two-way ANOVA on hourly periods and tail condition are given.



Fig. 3. Hourly variation in maximal duration of an individual basking period in tailed (open boxes) and tailless (solid boxes) *L. monticola.* Hourly means (± 1 SE) and sample sizes (row numbers) are shown.



Fig. 4. Hourly variation in average distance to the nearest refuge during basking periods in tailed (open boxes) and tailless (solid boxes) L. monticola. Hourly means (± 1 SE) and sample sizes (row numbers) are shown. The horizontal line is the available distance to the refuge in the environment.



Fig. 5. a) Hourly variation in percent time that tailed (open boxes) and tailless (solid boxes) L. monticola use rocks as substrate. Hourly means (± 1 SE) and sample sizes (row numbers) are shown. b) Hourly variation in temperature of rocks exposed to the sun (Trock) and grassy ground exposed to the sun (Tgrass) registred during the focal observations. Hourly means (± 1 SE) and sample size (row numbers) are shown.

hours: $F_{3,20}=0.43$, p>0.70) and in the afternoon periods (12-15 hours: $F_{2,8}=0.34$, p>0.70). In tailless lizards average distances increased significantly through the morning (8-12 hours: $F_{3,25}=3.68$, p<0.02) but remained similar after the midday (12-15 hours: $F_{2,15}=0.74$, p>0.40).

Rocks were the substrate that lizards used most often (Tailed: $\bar{x}\pm SE=62.2\pm5.1\%$ time; Tailless: 74.5 \pm 4.4%). Rock use was not significantly different between hourly periods, but tailless lizards used rocks more frequently than did tailed ones (Two way ANOVA: hour effect: $F_{6.68}$ =1.38, p>0.20; tail effect: $F_{1.68}$ =4.81, p<0.03; factors interaction: $F_{6.68}$ =1.88, p>0.05) (Fig. 5a). Grass use was not significantly different between hourly periods, but tailless lizards (10.2±3.3%) used grass less frequently than did tailed ones (21.0±3.3%) (Two way ANOVA; hour effect: F_{6.68}=1.33, p>0.20; tail effect: F_{1.68}=5.73, p<0.02; factors interaction: $F_{6.68}$ =1.78, p>0.05). During the morning (8-12 h) tailless lizards used more time on the rocks (one-way ANOVA; $F_{1,51}$ =4.83, p<0.03) and less time on grass ($F_{1.51}=5.72$, p<0.02) than tailed ones, but in the afternoon (12-15 h) rock use ($F_{1,27}=0.03$, p>0.90) and grass use $(F_{1,27}=0.13, p>0.70)$ were similar in both groups. On the other hand, rock substrate temperatures (21.6±0.5° C) were significantly lower (F_{1.162}=17.72, p<0.0001) than those of grassy ground substrate (24.9±0.6° C) (Fig. 5b).

Time devoted to resting was not significantly different either between lizard groups or between hourly periods (Table 3), while time devoted to moving and other activities was marginally lower in tailless lizards (Table 3).

	Resting activities		Moving and other	
Hours	Tailed	Tailless	Tailed	Tailless
8-9	24.3±13.5	2.3± 1.6	18.8± 0.8	4.9± 3.5
9-10	9.3 ± 5.2	17.2 ± 8.2	34.6± 5.0	13.4± 5.5
10-11	10.8± 3.8	14.6± 6.9	36.0± 8.8	34.9±12.6
11-12	17.5 ± 6.2	19.3 ± 11.4	37.0± 4.9	36.9 ± 11.4
12-13	11.3±11.3	35.9±19.0	53.2±22.0	22.3 ± 14.6
13-14	47.6±19.7	16.1 ± 6.4	18.0 ± 10.6	31.3±11.6
14-15	7.0± 7.0	33.7± 9.7	55.7±11.6	26.3± 5.9
Hour effect:		F=1.54, p>0.10		F=1.94, p>0.08
Tail effect:		F=0.08, p>0.70		F=3.57, p>0.06
Interaction:		F=2.01, p>0.50		F=1.32, p>0.20

 TABLE 3. Mean (± 1 SE) of percent time devoted to resting, and to moving and other activities in hourly (G.M.T.) periods

F and p values from two-way ANOVA on hourly periods and tail condition are given.

Discussion

Tail loss in *L. monticola* did not alter its capacity for thermoregulatory precision. Tailless lizards were able to maintain their body temperature within a range similar to that of tailed lizards. The similarity of selected body temperatures also indicates that, in absence of physical and biotic restrictions, lizards regulated their body temperature within the same range independently of tail condition. The maintenance of body temperatures within a narrow range may maximize the efficiency of various physiological functions (DAWSON, 1975; HUEY, 1982). Some of these are also relevant to tailless lizards, for example sprint speed, and tail regeneration (MADERSON & LICHT, 1968).

Selected body temperatures were higher than body temperatures achieved in the field. This might be a consequence of the difficulty of attaining elevated body temperatures in the mountains (HERTZ & HUEY, 1981). Alternatively, lizards may at high altitude thermoregulate at lower temperatures to maximize the daily period at which they can maintain a constant body temperature (CHRISTIAN *et al.*, 1983; VAN DAMME *et al.*, 1989).

Tailless lizards bask at closer distances to refuge than tailed ones during the early morning, but in the course of the day this distance becomes larger and similar to that of tailed ones. This could be a consequence of low locomotor performance due to low body temperatures (HERTz et al., 1983; VAN DAMME et al., 1989, 1990), increased by tail loss constraints (BALLINGER et al., 1979; PUNZO, 1982; ARNOLD, 1988). The effect of low temperatures on anti-predator behaviour may be of critical importance for lizards (GREENE, 1988), and some lizards modify their anti-predator behaviour in response to body temperature (RAND, 1964; BUSTARD, 1968; HERTZ et al., 1982; Losos, 1988).

Maximal duration of a single basking period was different between lizards groups. Both tailed and tailless lizards spend the amount of time in basking which leads to the same body temperature range. Tailless lizards, however, obtain heating by means of longer single basking periods than tailed lizards. This behaviour diminishes the chance that the lizard must switch continuously between basking and evasive behaviour, thereby interrupting continuous thermoregulation. Lower movement rates of tailless lizards may difficult their detection by predators (RAND, 1964; BAU-WENS & THOEN, 1981; AVERY et al., 1987).

Microhabitat structure and the availability of patches with different thermal characteristics affect the time and energy spent in thermoregulatory behaviours (HUEY & SLATKIN, 1976; ADOLPH, 1990). The opportunity for undisturbed thermoregulation depends, however on predation risk (CARRASCAL et al., 1992). Tailless L. monticola lizards make more use of rocks (MARTIN & SALVADOR, 1992), especially early in the morning (this paper). By doing so they increase survival chances, because crevices are abundant; while in grassy areas their running speed and moving ability are reduced and refuges are scarce and far apart. Lizards exposed in such places may be easier for predators to see and capture. On grassy ground tailed lizards, having relatively better locomotor performance, may minimize conductive heat loss to a cold substrate (PEARSON & BRADFORD, 1976; PEARSON, 1977) and benefit from a warm surface boundary layer (BAKKEN 1989).

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Resumen

Se han estudiado las consecuencias de la pérdida de la cola sobre la biología térmica de la lagartija serrana (*Lacerta monticola*) comparando temperaturas corporales medidas en el campo, temperaturas seleccionadas en un gradiente de laboratorio y patrones de comportamiento termorregulador de individuos con y sin cola en el campo. No se han encontrado diferencias en las temperaturas corporales en el campo ni en las seleccionadas en gradiente. Tampoco fue diferente el tiempo dedicado a soleamiento, ni la duración media y frecuencia de soleamientos. Las lagartijas sin cola hicieron un mayor uso de las rocas, y a primeras horas de la mañana aumentaron la duración máxima de los periodos de soleamiento y se mantuvieron a distancias más cortas a los refugios. Los datos aportados demuestran que las algartijas sin cola usan la flexibilidad de comportamiento para termorregular con la misma precisión que las lagartijas con cola, lo que probablemente sea favorable para maximizar algunos procesos fisiológicos como la misma regeneración de la cola.