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Basking and Antipredator Behaviour in a High Altitude Lizard: Implications of Heat-exchange Rate

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Abstract

This paper presents an observational and experimental study of the basking behaviour and heat exchange rate of the montane lizard *Lacerta monticola*. The results obtained by these procedures were coupled in order to understand behavioural mechanims promoting effective thermoregulation at high altitudes. Heating rate was higher when body size was smaller, and substrate temperature and sun rays incidence angle were higher. The lizards cooled faster when body size and substrate temperature were lower, and when the body temperature of the lizard going into shadow was higher. Time exposed to sun and mean duration of basking periods were longer early in the morning, while bask frequency increased through the morning. Our results suggest that time devoted to basking is mainly obtained by regulating bask duration. Lizards obtained the necessary time for heating by means of long basking periods. Mean travel distance per minute and distance to the nearest refuge increased from early morning to midday. These behavioural variables were tightly correlated with the expected heating rate of individuals. Body size affects thermoregulatory behaviour as well as locomotor activity. Juvenile lizards, with small body mass and high surface-to-volume ratios, were subjected to faster heating and cooling rates, basked more frequently than adults (but during shorter periods), and devoted more time to locomotion than adults. The thermoregulatory behaviour of *L. monticola* is the result of the combination of shuttling heliothermy by basking and the exploitation of thermal opportunities offered by patches in shade through thermal exchange with the substrate.

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Introduction

The body temperature of reptiles is dependent both on the magnitude of temperature variation in the environment and on the ability to regulate heat exchange with the environment. Body temperature of lizards is maintained behaviourally by modifying basking frequency, regulation of activity times and

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microhabitat use, with physiological control being less important than behavioural adjustments (HUEY 1974, 1982; CRISP et al. 1979; BARTHOLOMEW 1982). The maintenance of body temperature within a narrow range of preferred temperatures presumably benefits lizards by decreasing the risk of predation and enhancing growth and reproduction (HUEY & SLATKIN 1976; CHRISTIAN & TRACY 1981; AVERY 1982; HUEY 1982; STEVENSON et al. 1985).

Active thermoregulation by lizards is usually inferred from the relatively small variation in body temperature, in spite of larger spatial or temporal variation in environmental temperatures, and punctual observation of the spatial distribution of basking individuals. Nevertheless, these "static" methodological approaches do not cast light on the behavioural mechanisms responsible for the maintenance of body temperatures within the relatively narrow preferred range (BENNETT 1980; HUEY 1982). So, direct observation of thermoregulatory behaviour, combined with the determination of heat exchange rates under natural conditions, should provide evidence for the mechanisms of thermoregulation. Moreover, as thermoregulation may be linked with costs derived from predation risk (HOUSE et al. 1980; CHRISTIAN & TRACY 1981; HUEY 1982), basking should not be viewed as an independent behaviour. So, a dynamic analysis of thermoregulation behaviour should consider the specific characteristics of the individual (e.g. body size, sex, surface-to-volume ratio), and the trade-off between the maximization of heating rate and the minimization of predation risk, in order to cast light on escape strategies (changing behaviour between the passive defense near the refuge and the active flight tactic: BAUWENS & THOEN 1981; DOWDEY & BRODIE 1989).

In this paper we present an observational and experimental study of the thermoregulatory behaviour and heating and cooling rates of individuals of the Iberian rock-lizard (*Lacerta monticola*), an endemic species of the Iberian peninsula which inhabits high mountains (SALVADOR 1984). The results obtained by means of these two procedures are coupled in order to understand behavioural mechanisms promoting effective thermoregulation at high altitudes. Specific objectives were: (1) to assess the physical determinants of heat exchange (body size, radiation levels, environmental temperatures); (2) to determine the effects of behavioural adjustments on heat exchange rates; (3) the implication of body size on lizard behaviour considering the different surface/volume quotient of juveniles and adults, and the associated cooling and heating rates; and (4) to investigate the interaction between basking and anti-predator behaviour measured indirectly by the distance to the nearest refuge.

Material and Methods

1. Study Area

The study was carried out in Central Spain (Sierra de Guadarrama, 40°45′N, 4°W), at sites between 1500 and 1900 m a.s.l. The area is characterized by the presence of granite rocks, shrublands of *Cytisus oromediterraneus* and *Juniperus communis,* and pastures. Annual mean temperature in the area was 6.4 °C, and mean rainfall 1170 mm. During the study months mean temperature was 15 °C,

and the mean maximum temperature 21.9 °C (see RIVAS-MARTINEZ et al. 1987, and ELIAS & RUIZ 1977 for a more detailed description of botanical and climatological aspects of the area).

2. Thermoregulatory Behaviour Observations

Field studies were conducted from Jul. 15 to Aug. 15, 1989. Focal lizards were observed, during continuous exposition to the sun, from the time the animals came out from a refuge in the shadow until they returned into a refuge or protective cover in deep shadow. Activity of focal individuals was measured from a distance of 3—6 m with binoculars using continuous observations that were recorded on a portable tape recorder. Only lizards not reacting to observer's presence were monitored.

We recorded the duration of each exposition to the sun when an individual remained motion-less exposed to the sun rays with the body flattened on the substrate for a minimum of 10 s (bask duration), the number and distance of movements, and the distance to the nearest rock crevice or protective cover for each basking period.

For each individual observed we noted h of day, sex, and an estimate of its snout-vent length made by eye, and at the end of the observation period, the air and rock temperatures (measured with an electronic digital thermometer with the thermocouple in the shade), and an estimate of the angular height of the sun upon the horizon calculated from the h of day. To estimate available mean distances to the nearest refuge (rock crevice or protective cover), we chose 60 random points in the study area. Given the large size of the two areas surveyed (5 ha) and the relatively high density reached by this lizard species in mountain rocky areas (400—500 lizards/ha: PEREZ-MELLADO et al. 1988), we consider that the probability of repeated sampling of the same individual was very low. We made 69 timed observations of lizard behaviour while exposed to sun, totalling 560 min. Observations took place between the onset of the summer activity period (7.30 h GMT) and midday (13.00 h GMT), covering the morning activity of *Lacerta monticola* (ARGÜELLO & SALVADOR 1988). Behavioural rates were averaged for five 1-h intervals (scarce observations before 8.00 h and after 13.00 h were added to 8.00—9.00 and 12.00—13.00 h respectively).

3. Heating and Cooling Experiments

The experimental approach we try here analyzes the heating and cooling rates of lizards of different sizes placed in a variety of substrates considering the thermal state of the environment (see BECKMAN et al. 1973; PORTER et al. 1973; WYGODA 1989 for a similar approach). Heating and cooling rates were experimentally determined at three plots during Jul.—Aug. 1989 and 1990 in days without wind, following the procedure used by AVERY & MCARDLE (1973). The animals (n = 62) were captured at the sites where behavioural sequences were obtained and introduced into a portable refrigerated box until their cloacal temperatures reached about 16 °C (approx. the expected cloacal temperature of a lizard retreated into its refuge — rock crevice — exposed to deep shade). Each animal was measured (snout-vent length), weighed and sexed. The lizards were then exposed to direct sun radiation and fixed to the rock (granite) with two bands of transparent masking tape (around the base of the tail and on top of the forelimbs). A digital quick-reading cloacal thermometer was inserted into the lizard's cloaca and readings of body temperature were obtained at 15-s intervals (precision of 0.1 °C). Heating experiments were stopped when the cloacal temperature reached 36 °C (approx. 6 °C below the critical thermal maximum for medium sized lizards: BRADSHAW 1986; HEATWOLE & TAYLOR 1987). The time of day at which the heating experiment had begun, and air (1 cm above the rock surface) and substrate temperatures near the experimental animal were recorded.

After heating, the animals were moved to a deep shaded site. Cloacal temperature readings at 15-s intervals, and air and substrate temperature were again noted by the same procedure employed in the heating experiments. These trials provided the cooling rates of animals exposed to shade.

Both heating and cooling rates (in °C/min) were determined as the °C gained or lost in 2.5 min. After the animals had been used in the experimental trials they were released where captured. No lizards died during heating and cooling experiments.

4. Data Analysis

Statistical tests employed were one-way analysis of variance (ANOVA), t-test for means, stepwise multiple regression analysis, and simple and partial correlations. Where required (SOKAL &

Rohlf 1981) original data were transformed by means of logarithmic (log [x+1]), square root (sqrt [x+1]) or angular (arcsin $\sqrt{p_i}$) transformations prior to analysis.

Results

1. Heating and Cooling Rates

Heating rate was significantly correlated with body mass (range: 0.8—9.2 g), incidence angle of the sun rays over body surface (20—83°), and substrate temperature (16.9—33.5 °C; Table 1). The multiple regression model explained 70.3 % of the variance in heating rate. Heating rate was higher when body size was smaller, and substrate temperature and sun rays incidence angle were higher (the combination of sun angle upon the horizon and/or longitudinal body axis angle over the horizontal plane). Residuals of this model did not significantly differ between males and females (Anova, $F = 0.40$, df = 1, 46, $p = 0.534$).

Table 1: Regression models of body temperature rates (°C/min) in heating and cooling trials (sample size in brackets)

	Coefficient	p	$R^2 * 100$	p
Heating (62)			70.3	0.0000
Constant	−2.11	0.0000		
Weight (g)	−0.145	0.0002		
Incidence angle (°)	0.010	0.0073		
Substrate temperature (°C)	0.225	0.0000		
Cooling (58)			71.8	0.0000
Constant	1.45	0.0015		
Weight (g)	−0.080	0.0008		
Initial body temperature (°C)	0.157	0.0000		
Substrate temperature (°C)	−0.208	0.0000		

Cooling rate was significantly correlated with body weight, substrate temperature, and body temperature when lizards were transferred into shade (Table 1). The multiple regression model accounted for 71.8 % of the variance in cooling rate. The lizards cooled faster when body size and substrate temperature were lower, and when the body temperature of the lizard going into shadow was higher. There were no significant differences between male and female residuals of this regression model (Anova, $F = 0.003$, df = 1, 46, $p = 0.956$).

Both heating and cooling rates rise from 7.30 to 13.00 h, with the increase of heating rate more marked (Fig. 1). The difference between heating and cooling rate was always negative, with a slow decrease in difference between the onset of activity and midday (see Rismiller & Heldmaier 1985 and references therein for explanations on physiological control mechanisms).
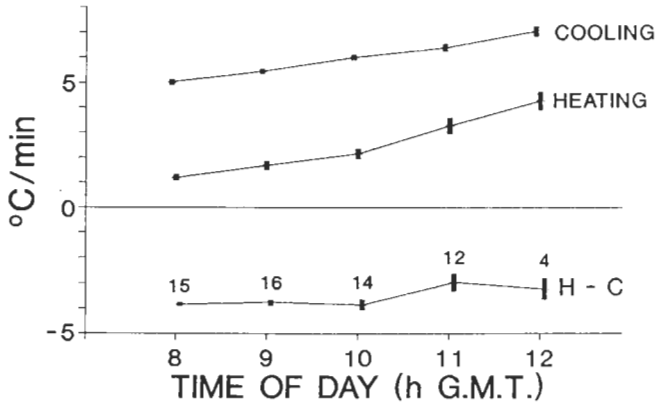
Fig. 1: Heating and cooling rates, and the difference between heating and cooling rates, through the morning (x̄ ± 1 SE). Sample sizes are shown for each morning period

2. Thermoregulatory Behaviour

Time exposed to sun differed significantly between the five morning periods (F = 8.59, df = 4, 64, p < 0.001 in the ANOVA comparing the five 1-h periods). The highest mean values were observed early in the morning, and values
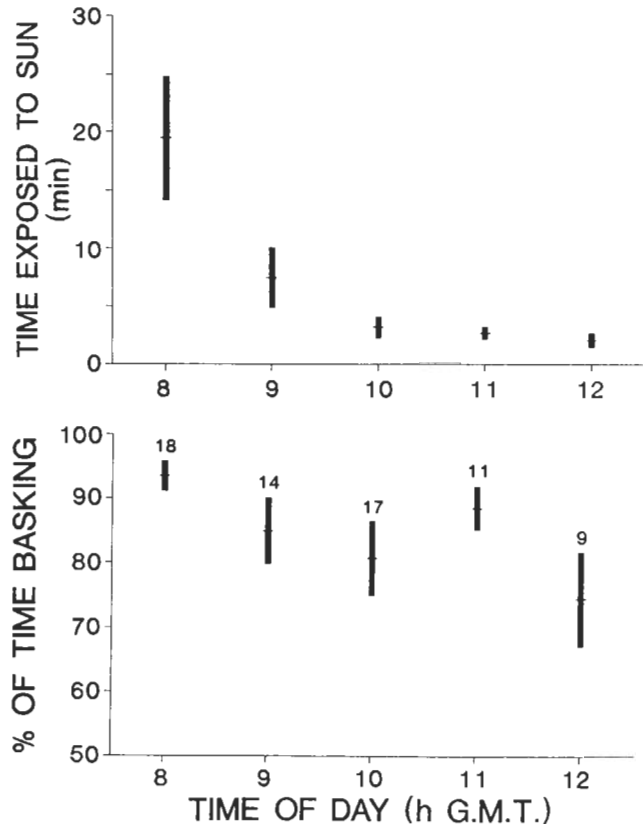
Fig. 2: Time that the lizards were exposed to the sun through the morning, and percentages of time spent basking during hourly morning periods (x̄ ± 1 SE). Sample sizes are shown for each morning period

decreased from the onset of activity until midday (Fig. 2). The percentage of time spent in basking behaviour by individuals was very high during all morning periods (higher than 75 %), but slightly decreased from early morning to midday (F = 2.74, df = 4, 64, p = 0.036; Fig. 2). Mean duration of the basking periods differed significantly between hours (F = 6.56, df = 4, 64, p < 0.001); bask duration was longer at early hours (Fig. 3). The basking rate (number of basking events per min) increased significantly through the morning (F = 4.75, df = 4, 64, p = 0.002; Fig. 3).
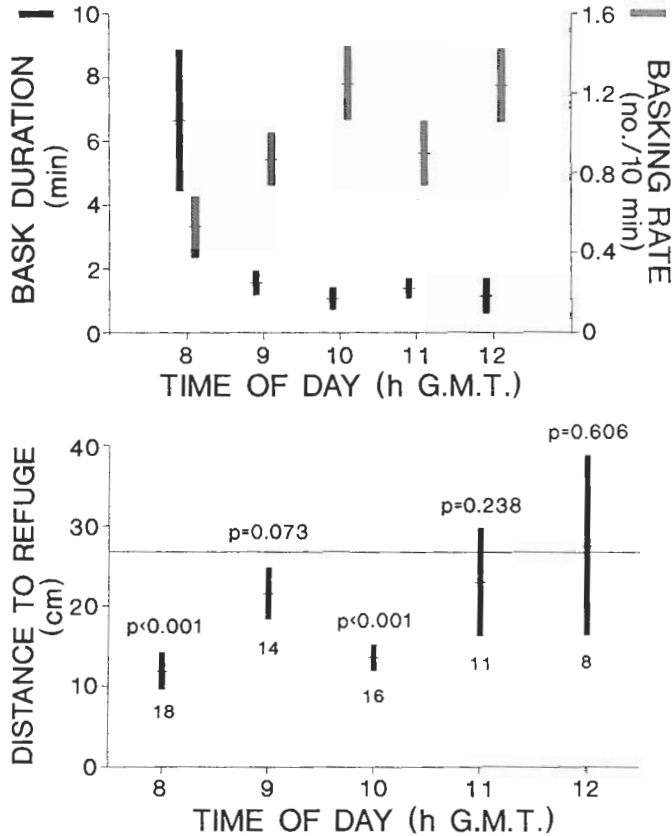

Fig. 3: Mean (± 1 SE) of average bask duration and basking rate in five 1-h morning periods, and distance to the nearest refuge during basking stops. The horizontal line indicates available mean distances to the refuge. Sample size (row numbers) and probabilities (t-tests for means) of the difference between lizard distances and random distance are shown

In order to test the role of lizard body size on basking behaviour, we compared the residuals of the Anovas performed above for small individuals (less than 45 mm of snout-vent length, n = 23), with those obtained for larger ones (snout-vent length > 65 mm, n = 27). Time exposed to sun (all other things being equal) was·shorter in small lizards (t = 4.131, p = 0.0001), as well as the

average bask duration (t = 2.626, p = 0.012). Nevertheless, basking frequency was marginally lower in large individuals (t = 1.947, p = 0.057). The percentage of time spent basking did not differ between the two size classes (t = 1.012, p = 0.317).

Basking frequency and bask duration were negatively correlated (r = −0.95, n = 69, p < 0.001 — power regression model —). However, a higher proportion of variance in the total duration of basking periods was explained by the duration of individual basking periods (partial correlations; bask duration: r = 0.52, p < 0.001, basking rate: r = 0.13, p = 0.288).

These variables related to basking behaviour were correlated with the expected heating rate of individuals, derived from the regression model for heating rate ($^{\circ}$C/min $= -2.12 + 0.16 \cdot Ts + 0.025 \cdot \alpha - 0.018 \cdot$ snout-vent length; $R^2 = 0.745$, p < 0.0001), and the figures of sun angle upon the horizon (α), substrate temperature (Ts), and size of focal lizards (this model is intrinsically similar to that obtained above, but snout-vent length was used instead of weight due to the impossibility of always capturing the focal lizard when it came into the refuge). Time exposed to sun and average bask duration were inversely correlated with expected heating rate, being the converse for basking rate (p < 0.001 for the three correlations).
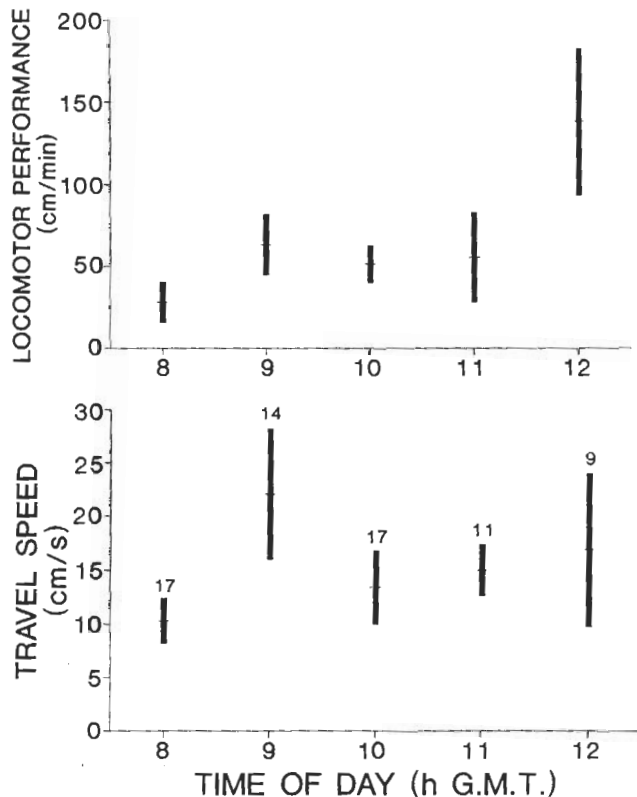

Fig. 4: Distance travelled per min during the total period of exposition to the sun (locomotor performance), and travel speed during movement ($\bar{x} \pm 1$ SE). Sample sizes are shown for each morning period

Average distance to the nearest refuge during basking stops was marginally different among the five 1-h morning periods (F = 2.17, df = 4, 62, p = 0.082). Average distance to refuge of basking lizards was not significantly different from random distances during late morning hours (11.00—13.00 h), and was significantly shorter earlier (7.30—11.00 h; Fig. 3). Mean travel distance per min during the total period of exposition to sun (locomotor performance) increased from 7.30 until 13.00 h (F = 2.85, df = 4, 64, p = 0.031; Fig. 4). Travelling speed, however, did not differ significantly among morning periods (F = 1.19, df = 4, 63, p = 0.323; Fig. 4). The t-tests for means, performed with the residuals of the ANOVAs, showed that small (snout-vent length < 45 mm) and large individuals (snout-vent length > 65 mm) did not differ either in the average distance to the nearest refuge while basking (t = 0.258, df = 49, p = 0.798) or in travelling speed (t = 1.170, p = 0.248). Nevertheless, the total distance moved per min exposed to sun (locomotor performance) was almost significant (t = 1.994, p = 0.052), being greater for small animals.

Average distance to the nearest refuge (p = 0.010) and locomotor performance (travel distance by min exposed to sun; p = 0.003) were positively correlated with heating rate. Travel speed was not significantly correlated with heating rate (p = 0.164), but was positively correlated with air temperature (r = 0.351, p = 0.003).

Discussion

Lacerta monticola showed a thermoregulation pattern that behaviourally exploits within-habitat patchiness through basking. The prominent role of heliothermy has been found considering the influence of incidence angle of solar radiation in heating experiments, and the regulation of frequency and duration of basking periods. The same thermoregulation pattern has been described for other small-, medium-sized lizards from arid to mountain areas (AVERY 1982; GRANT & DUNHAM 1988; CARRASCAL & DIAZ 1989; ADOLPH 1990; BAUWENS et al. 1990; but see TANAKA 1986). Nevertheless, thigmothermy (POUGH & GANS 1982) seems to play a significant role in the thermoregulation pattern of *L. monticola*, too. Substrate temperature affected both the heating and the cooling rate of individuals. However, thigmothermy is probably of secondary importance in the studied montane lizard population, as substrate temperatures, due to the sun-shade effect, are extremely variable. During their daily movements within their home-ranges *L. monticola* lizards could not spend in either cool or hot patches of the thermal mosaic the time necessary for body temperatures to equal substrate temperatures (BARTHOLOMEW 1982; CARRASCAL & DIAZ 1989). Moreover, the boundary layer effect and thermal radiation from the patch rather than conduction from the substrate, may be partly responsible for the thermal influence of rock-perch (BAKKEN 1989), the role of thigmothermy per se being negligible in this case.

Early morning emergence has been reported in other mountain lizards (VAN DAMME et al. 1989; BEUCHAT 1989). FOX (1978) has shown that individuals active early in the morning are subject to a higher mortality rate than individuals which

begin activity later in the morning. Lizards should emerge when the necessary heating rate for activity is fast enough to minimize exposure to predators under low performance levels (HOUSE et al. 1980). Early morning environmental temperatures are low, lizards cooled at a very high rate, and individuals show low locomotor performance and predator detection capabilities (Fig. 4; WERNER 1972; WALDSCHMIDT & TRACY 1983; AVERY et al. 1987; VAN DAMME et al. 1990a, b). Nevertheless, many *L. monticola* lizards were exposed motionless to the sun for long periods in the early morning (see Figs. 2, 3). Individuals exposed to solar radiation in early morning, with high levels of melatonin in blood, should desactivate pineal-melatonin synthesis (COWGELL & UNDERWOOD 1979; UNDERWOOD & CALABAN 1987). Therefore, being exposed motionless to the sun during long periods in early morning (basking), should contribute to decrease melatonin concentration and its inhibitory effect on activity in the next hours.

Some lizards alter their anti-predator behaviour by selection of the distance to the nearest refuge in response to body temperatures (e.g. RAND 1964; BENNET 1980; HERTZ et al. 1982; LOSOS 1988; CARRASCAL & DIAZ 1989; DIAZ 1991). In the early morning, rock iberian lizards face a high predation risk from homeothermic predators such as birds or weasels (escape reactions from *Corvus corax*, *Monticola saxatilis* and *Mustela nivalis* were observed; pers. obs.). *Lacerta monticola* escaped from these predators by simply moving a short distance back into a refuge (crevice or bush). Lizards carefully selected basking places near the entrance of a refuge during early morning, when their body temperatures (ARGÜELLO & SALVADOR 1988) and locomotor performance seemed to be lower than in midday (i.e., short escape distance; see Fig. 3). At higher body temperatures in the middle of the day (ARGÜELLO & SALVADOR 1988) lizards may attain greater speed and consequently could run longer distances to refuges (during midday lizards basked at similar distances to refuges as available in the habitat). Therefore, the distance to a refuge can be considered as a measure of predation risk perceived by these lizards, documenting a trade-off between escape distance and thermal state of the environment (LIMA & DILL 1990).

Body size influences heating and cooling rates, final equilibrium temperature and thermal inertia (PORTER & TRACY 1983; STEVENSON 1985; HEATWOLE & TAYLOR 1987). Our results suggest that body size affects thermoregulatory behaviour as well as locomotor activity in this montane lizard (but see GILLIS 1991). Juvenile lizards with small body mass and high surface-to-volume ratios were subjected to faster heating and cooling rates (see regression coefficient with weight in Table 1). They also basked more frequently and with basking periods of shorter duration than adults, and consequently could devote more time to locomotion and foraging (see SCHWARZKOPF & BROOKS 1985, for a similar result with the turtle *Chrysemys picta*).

Lizards can attain the basking time either by changing the rate at which they expose to solar radiation or the average duration of individual basking periods (SPELLERBERG 1972; AVERY 1976). Our results point out that time devoted to basking is mainly obtained by regulating bask duration. Lizards preferred to obtain the necessary time for heating by means of long basking periods. In this way, thermoregulation by heliothermy seemed to be a continuous process not

interrupted by frequent changes in activity switching between basking and other behaviours as foraging or patrolling behaviour. This behaviour allows lizards to be less conspicuous to predators than continuously changing from basking and locomotion behaviour. Therefore, thermoregulation seems to be linked to predator avoidance through the dynamic perception of predation risk and the internal state of the individual, and should not be viewed as an isolated behaviour.

Acknowledgments

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