

Adjustment of basking postures in the high-altitude Iberian rock lizard (*Lacerta monticola*)

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Abstract: We studied the relationships between thermoregulatory basking postures and heating rates in the Iberian rock lizard (*Lacerta monticola*). Heating rates were high when body size was small, the substrate temperature was high, and the angle of incidence of the sun's rays was high (i.e., the rays were perpendicular to the lizard's body). However, heating rates were not related to the compass orientation of lizard's body axis to the sun (perpendicular versus in line with the sun). In the field, the slopes of the body axis of basking individuals were higher during the early morning. However, neither the cardinal orientation of a lizard's body axis to the sun nor the frequency of flattening varied during the morning. Postural adjustments to select an adequate angle of incidence of the sun's rays on the dorsal part of the body suggest that this behaviour might enhance absorption of solar radiation.

Résumé : Nous avons étudié les relations entre les postures thermorégulatrices au soleil et les taux de réchauffement chez le lézard ibérien *Lacerta monticola*. Les taux de réchauffement étaient élevés chez les petits lézards lorsque la température du substrat était élevée et lorsque l'angle d'incidence de la lumière solaire était élevé (i.e., lorsque les rayons frappaient perpendiculairement le corps du lézard). Cependant, il n'y avait pas de corrélation entre les taux de réchauffement et l'orientation de l'axe du corps par rapport au soleil (perpendiculaire par rapport au soleil versus en ligne avec le soleil). En nature, la pente de l'axe du corps chez les individus exposés au soleil était plus élevée au petit matin. Cependant, ni l'orientation cardinale de l'axe du corps par rapport au soleil, ni la fréquence des aplatissements ne variaient au cours de la matinée. L'ajustement de la posture, à savoir le choix d'un angle d'incidence des rayons solaires sur les parties dorsales, semble indiquer que les lézards cherchent à absorber le plus de radiations solaires possible.

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Introduction

The body temperature of reptiles is dependent on both the magnitude of temperature variation in the environment and their ability to regulate heat exchange with the environment. The body temperature of lizards may be adjusted behaviourally by modification of basking frequency, regulation of activity times, and microhabitat use (Huey 1982), and also by selection of the body's orientation and exposure to the sun (e.g., flattening, and selecting the angle at which the body axis is held above the ground; Axtell 1960; Muth 1977; Waldschmidt 1980). Careful thermoregulation by means of microsubstrate and posture selection may increase the time during which lizards can be active at physiologically favourable body temperatures (Avery 1982; Huey 1982; Grant and Dunham 1988). However, not every postural change has a thermoregulatory function. Heat-transfer models establish

that the parameter of interest in lizard thermoregulation is the shadow area projected on a plane normal to the sun's rays (e.g., Muth 1977; see also Tracy 1982; Bakken 1989; O'Connor and Spotila 1992). So it should be possible to predict when a postural change will affect thermoregulation.

Montane lizards are subjected to variable radiation levels and low environmental temperatures that constrain their activity times to a larger extent than those of lizards at lower altitudes (Sinervo and Adolph 1994). Therefore, montane lizards should invest a high proportion of time in thermoregulatory activities, and should adopt precise postures to maximize heat gain (Hertz and Huey 1981; Van Damme et al. 1989, 1990; Adolph 1990).

In this paper we present an observational and experimental study of the thermoregulatory postures and heating rates of the Iberian rock lizard *Lacerta monticola*, a lizard endemic to the Iberian peninsula that inhabits high-altitude areas (Salvador 1984). We aimed to test whether behavioural mechanisms promote effective thermoregulation at high altitudes through studying basking postures (flattening, orientation to the sun and the slope of rock) and heating rates.

Methods

Field study

Behavioural observations were conducted from 15 July to 15 August 1989 in central Spain (Sierra de Guadarrama,

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Table 1. Average postures (mean \pm SE) of focal lizards while basking (when basking lasted longer than 30 s) during three morning periods.

	07:30–09:00 (<i>N</i> = 15)	09:00–11:00 (<i>N</i> = 22)	11:00–13:00 (<i>N</i> = 12)
Slope over the horizontal plane (deg.)	36.9 \pm 7.4	18.5 \pm 3.8	20.6 \pm 3.7
Cardinal orientation (% time perpendicular to the sun)	43.1 \pm 8.0	54.8 \pm 6.7	35.7 \pm 8.0
Degree of flattening (% of time)			
Complete flattening	27.4 \pm 9.5	24.0 \pm 8.0	12.1 \pm 6.8
Half the belly flattened	30.8 \pm 11.2	29.2 \pm 8.5	50.0 \pm 10.3

40°45'N, 4°W) at sites between 1500 and 1900 m above sea level. The area is characterized by the presence of granite rocks, shrublands (*Cytisus oromediterraneus* and *Juniperus communis*), and grasslands (Rivas-Martínez et al. 1987).

Focal lizards were observed during continuous exposure to the sun from the time of their emergence from shadow (rock crevices or bush cover) until they returned to a refuge or protective cover in shadow. Observations took place between the onset of the summer daily activity period (07:30 GMT) and midday (13:00 GMT), covering the morning activity period of *L. monticola* (Argüello and Salvador 1988). The mean (\pm SE) field body temperature of active individuals in the same area was 29.4 \pm 0.2°C, while the mean associated air temperature was 18.3 \pm 0.3°C (Martín and Salvador 1993). Individuals were observed without disturbance from a distance of 3–6 m with binoculars and their behaviour was recorded on a portable tape recorder.

The following behavioural variables were measured while the lizards were basking: the slope of the longitudinal body axis with respect to the horizontal plane, the compass orientation of the body axis, and the degree of body flattening on the rock surface. We considered a lizard to be basking when it remained motionless during a prolonged stop (>30 s) in a patch of open sun. We arbitrarily selected periods longer than 30 s in order to choose stable postures reflecting intentional behaviours. For each individual the average angle of the longitudinal body axis with respect to the horizontal plane was calculated as the weighted average of slopes adopted in each basking event (the slope measured in sexagesimal degrees multiplied by the duration of basking). Slopes were measured at the end of each observation period in the places where the lizards were basking. The orientation of the longitudinal body axis of lizards while basking was determined by means of a compass. The percentage of time during which the body axis was approximately perpendicular (\pm 25°) to the sun's rays was calculated for each individual. We differentiated between two flattening postures: all underparts in close contact with the rock, and approximately half of the ventral surface flattened to the substrate. Behavioural rates were averaged for each of three time intervals (07:30–09:00, 09:00–11:00, 11:00–13:00).

Heating rates

We determined experimentally the heating rate of lizards by manipulating their posture on the rock surface (cardinal orientation to the sun and slope over the horizontal plane of body axis) and measuring the air and substrate temperatures. Lizards were captured at the study site and held in a portable

refrigerated box until their cloacal temperature reached about 16–18°C (approximately the predicted cloacal temperature of a lizard that had retreated into its refuge, usually a rock crevice in deep shade; see above). Each animal was sexed, measured, and weighed (snout–vent length 68.4 \pm 2.3 mm; mass 5.4 \pm 0.3 g; *N* = 62), fixed to a rock (granite, approximately 40 \times 60 \times 10 cm) with two bands of transparent masking tape, and then exposed to direct solar radiation. Cardinal orientation to the sun was manipulated, placing the body axis of the lizard in line with (0°) or perpendicular to (90°) the sun's rays. The slope of the body axis in the horizontal plane was manipulated by modifying the inclination of the stone to which the lizard was fixed; thus, the angle of incidence of the sun on the lizard's dorsal surface was 45° or 90° (the sun's angle above the horizon and the angle of the longitudinal body axis with respect to the horizontal plane). The probe of a digital thermometer was inserted into the lizard's cloaca, and the body temperature (\pm 0.1°C) was measured at 15-s intervals (Avery and McArdle 1973; Wygoda 1989). Heating experiments were stopped when the cloacal temperature reached 36°C to avoid potentially dangerous high body temperatures (Bradshaw 1986). We recorded the time and the air (1 cm above the rock surface) and substrate temperatures near the experimental animal.

Heating rates (°C/min) were calculated over time intervals ranging from 2.5 to 7.5 min (10–30 units consisting of 15-s intervals, depending on the cloacal temperature reached by experimental individuals). This was an appropriate procedure, as body temperature increased linearly with time in the interval from 18 to 36°C (the coefficient of determination of a linear regression model for heating trials 2.5–7.5 min long was 0.98). As neither males nor females differed significantly in heating rates (Carrascal et al. 1992), data were pooled. Experimental treatments for each factor (cardinal orientation and slope with respect to the horizontal plane) were distributed randomly among morning hours.

We applied stepwise multiple regression analysis to analyze heating rates and one-way analysis of variance (ANOVA) using logarithmic or angular transformations (percentages of variables) to behavioural data (Sokal and Rohlf 1981).

Results

In the field, the average slope of the body axis of basking individuals differed significantly between periods of the day ($F_{[2,46]} = 3.81$, $P = 0.03$; Table 1), being higher during the early morning and remaining similar after 11:00. However, the frequency of perpendicular cardinal orientation of a lizard's body axis to the sun did not differ significantly

between the three morning periods ($F_{[2,46]} = 0.64$, $P = 0.53$; Table 1). The flattening frequency did not differ significantly among the periods, either for complete flattening ($F_{[2,46]} = 1.34$, $P = 0.27$) or for half the belly flattened to the substrate ($F_{[2,46]} = 2.46$, $P = 0.18$; Table 1).

Heating rates averaged $2.2 \pm 1.2^\circ\text{C}/\text{min}$ and were significantly correlated with body mass (mass), angle of incidence of the sun's rays over the body surface (α), and substrate temperature (T_s) (stepwise multiple regression analysis: $^\circ\text{C}/\text{min} = -2.11 - 0.14\text{mass} + 0.01\alpha + 0.22T_s$; $R^2 = 0.70$ (mass is in grams and α in sexagesimal degrees)). Thus, heating rates were higher when body size was small and when the substrate temperature and angle of incidence of the sun's rays were high. The heating rate was higher when the angle of incidence of the sun's rays was 90° ($2.6 \pm 1.3^\circ\text{C}/\text{min}$) than when it was 45° ($1.9 \pm 1.1^\circ\text{C}/\text{min}$). The cardinal orientation of a lizard's body axis to the sun did not affect its heating rate during the morning hours (in line: $2.4 \pm 1.3^\circ\text{C}/\text{min}$; perpendicular: $2.1 \pm 1.2^\circ\text{C}/\text{min}$; ANOVA on residuals from the regression model: $F_{[1,53]} = 0.05$, $P = 0.83$).

Discussion

Lacerta monticola shows a pattern of thermoregulation that exploits microclimate variation through basking (Carrascal et al. 1992). The prominent role of heliothermy is shown by the importance of the angle of incidence of solar radiation in heating experiments and by the selection of basking-site slope on rock perches. The same thermoregulation pattern has been described for other small and medium-sized lizards (Avery 1982; Grant and Dunham 1988; Adolph 1990; Bauwens et al. 1990).

Heliothermic lizards can regulate their heat absorption by changing the angle of incidence of solar radiation on their dorsal surface. Maximum heating rate and operative environmental temperatures are obtained when the body axis is at a right angle to solar radiation (Muth 1977; Pearson 1977; Grant and Dunham 1988). Therefore, the steeper slope of rock perches selected by *L. monticola* in cold mountain areas during the morning could indicate intentional behaviour to maximize the heating rate at low environmental temperatures and lower sun angles.

In some animals (e.g., insects), changes in the compass orientation of their longitudinal body axis with respect to the sun result in significant changes in body temperature and serve to maximize heat gain (Whitman 1987; O'Neil et al. 1990). In lizards, however, compass orientation to the sun does not greatly contribute to changes in body temperature (see Table 1 and Results section) (Muth 1977; Waldschmidt 1980). The flatter body shape of lizards indicates that compass orientation of the body axis with respect to the sun should contribute little to heating, owing to the small changes in body surface area exposed to direct solar radiation (i.e., the flanks are a small proportion of the total dorsal body surface). Therefore, body shape differences and their effects on the proportion of the body surface that can be oriented to the sun could explain the different mechanisms of behavioural thermoregulation in different taxa (for example, compare the conclusions of Muth (1977) and O'Neil et al. (1990) concerning lizards and dipterans, respectively).

Flattening behaviour has been interpreted as evidence of the importance of conduction in heat exchange (Waldschmidt

and Tracy 1983), but it also might be a way of increasing the absorption of solar radiation on the dorsal surface. Nevertheless, although flattening behaviour increases the body surface area exposed to solar radiation and in close contact with the rock, for *L. monticola* it does not seem to be related to changing environmental conditions. This result is in agreement with the heat-transfer model of Muth (1977), which indicates that conduction via substrate contact should be unimportant for small lizards under most conditions. The low importance of flattening in *L. monticola* may also be explained by their low body mass and the rough surface of the granite rock, which would reduce the amount of contact between the lizard's body and the rock and therefore reduce the efficiency of conduction (Bakken 1989). The boundary-layer effect and thermal radiation from the surrounding rock, rather than conduction from the substrate, may be partly responsible for the thermal influence of the rock perch (Bakken 1989).

In conclusion, the careful selection of basking perches and postural adjustments to select an adequate angle of incidence of the sun's rays on the dorsal part of the body suggest that these behaviours might enhance absorption of solar radiation in this cool montane environment.

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