

Field Body Temperatures and Thermoregulatory Behavior of the High Altitude Lizard, *Lacerta bedriagae*

DIRK BAUWENS,^{1,3} AURORA M. CASTILLA,¹ RAOUL VAN DAMME,^{1,2} AND RUDOLF F. VERHEYEN/¹ *University of Antwerp (U.I.A), Field Biological Station, Verbindingsweg, B-2180 Kalnthout, Belgium, and, ²University of Antwerp (U.I.A), Department of Biology, Universiteitsplein 1, B-2610 Wilrijk, Belgium.*

Many species of lizards are known to maintain relatively high and constant body temperatures (Avery, 1982; Huey, 1982). Their abilities to do so depend largely on regulatory behaviors that alter heat exchange with the environment and on the thermal conditions within their habitats. Ectotherms living at high altitudes (and latitudes) offer unique opportunities to study thermoregulatory responses to the rather unfavorable and strongly variable thermal characteristics of these regions. High altitude lizards often exhibit lower and more variable activity body temperatures, and/or thermoregulate less precisely than conspecific or congeneric populations living at lower elevations (Brattstrom, 1965; Hertz and Nevo, 1981; Vial, 1984; Crowley, 1985).

We report here results of a short-term study on field body temperatures and aspects of thermoregulatory behavior of the lizard *Lacerta bedriagae*. This medium-sized lizard (adult male body size = 66-84 mm, mass = 7-14 g; adult female body size = 66-80 mm, mass = 7-11 g) is endemic to the Mediterranean islands Corsica and Sardinia, where its distribution is usually restricted to altitudes >1000 m (Schneider, 1984 reviews information on the habits of this poorly known species). We hypothesized that this lizard, living in an environment characterized by low and variable ambient temperatures, would be active over a relatively wide range of body temperatures. Our main aim therefore was to examine changes in body temperature and thermoregulatory behavior in relation to diel variations in the thermal environment.

Field work was carried out from 31 May to 3 June 1988 near Haut-Asco {42°25'N, 8°55'E; Département Haute-Corse, Corsica, France), where *L. bedriagae* seems to be restricted to altitudes >1650 m (pers. obs.). The study area was between 1750 and 1800 m elevation, on the steep east-facing slope of Mont Mufrella. The site was characterized by extensive areas with bare rock pavements, large boulders and screes, which alternate with grassy patches and shrubs (dominant species: *Funiperus nana*, *Genista labelli*, *Berberis actensis*).

We made random walks through the area and, upon each spotting of a lizard, we noted time of day, age

³Present Address: Institute of Nature Conservation, Kiewitdreef 3, B-3500 Hasselt, Belgium.

¹Present Address: Museo Nacional de Ciencias Naturales, c/ J. Gutierrez Abascal 2, E-28006 Madrid, Spain.

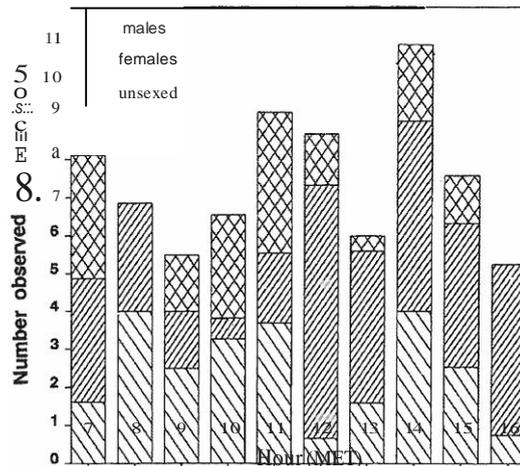


FIG. 1. Number of lizards observed per person hour at different times (Mean European Time) of day during periods of uninterrupted sunshine.

class (immature, adult), sex, exposure to sunlight {full sun, shade mosaic, shade, overcast}, behavior (basking, resting, walking, feeding, unknown) and weather conditions (sunny, cloudy/variable-either 5 or <5 min of continuous sunshine before observation). Most lizards were subsequently captured with a noose and we measured body temperature (cloacal = T_b), air temperature (shaded bulb, 3 cm above substrate = T_a) and substrate temperature (shaded bulb = T_s) to the nearest 0.1°C with a thermocouple connected to a quick-reading electronic thermometer (DGT Digital thermometer).

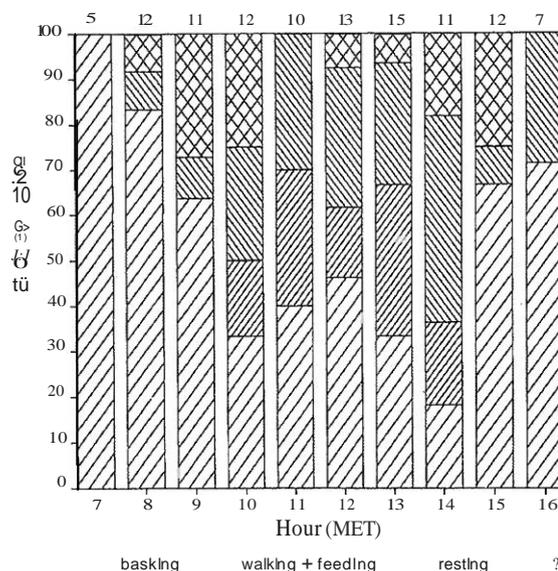


FIG. 2. Percentage of lizards observed during hourly intervals that were assigned to the behavioral categories of basking, resting, walking or feeding and unknown. Data for periods of uninterrupted sunshine only; sample sizes are above bars.

TABLE 1. Temperature means \pm 1SD and range (in parentheses) of body (Tb), air (T.) and substrate (T.) during sunny and cloudy weather. N = number of temperature measurements.

	T.	T.	T.	N
Sunny	32.79 \pm 2.30 (23.3-36.3)	15.28 \pm 2.89 (10.2-21.7)	26.07 \pm 4.90 (13.7-36.2)	73
Cloudy	28.35 \pm 1.80 (25.2-31.4)	13.71 \pm 2.79 (11.0-18.7)	24.18 \pm 2.31 (20.2-27.9)	17
Total	31.95 \pm 2.81 (23.3-36.3)	14.98 \pm 2.92 (10.2-21.7)	25.71 \pm 4.58 (13.7-36.2)	90

We used t-tests (two-tailed) or one-way analyses of variance (ANOVA) to evaluate differences among group means, G- and χ^2 -tests for contingency tests of independence (Sokal and Rohlf, 1981), analyses of covariance (ANCOVA) to test for differences between regression equations, and Spearman rank correlations (r_s). The standard criterion of statistical significance was $\alpha = 0.05$.

The number of lizards observed per person hour remained approximately constant during the course of sunny days (Fig. 1). The hourly number of observations was directly proportional to the amount of time spent searching ($\chi^2 = 5.373$, 9 df, $P > 0.80$). We observed the first individuals soon after our arrival at the study area at about 0700 h. Lizards retreated between 1600 and 1630 h (MET), when the sun gradually disappeared behind the mountain ridge. Our data suggest a sex-linked difference in diel activity ($G = 19.553$, 9 df, $P = 0.02$): adult males have a bimodal activity pattern and are relatively inactive at midday; activity in adult females peaks during midday and afternoon (Fig. 1).

All lizards were seen on rocky or stony substrates, and the majority (96% of $N = 108$) of those observed during sunny weather were in full sun when first sighted. The percentage of lizards that were basking varied with time of day (Fig. 2; $G = 24.478$, 9 df, $P < 0.005$). Between 1000 h and 1500 h basking incidence was lowest, but remained considerable (31% of $N =$

61). During this interval we observed all resting lizards and most of those that were walking or feeding (Fig. 2).

When weather conditions changed from sunny to cloudy during the midday or afternoon hours, lizards initially exposed themselves on stony substrates in a basking-like posture. Within one hour, most of them retreated to shelter.

We found no differences in mean body temperatures between immatures, adult males and adult females (ANOVA, $P > 0.60$). Therefore, our further analyses are based upon combined samples. Body temperatures recorded during sunny weather were higher than those observed under cloudy conditions (Table 1; $t = 7.429$, $P < 0.001$). Especially during sunny weather, differences between Tb and T. were large ($t = 17.5$, $s = 3.1$, range = 10.3-24.6, $N = 73$), and variation in Tb was remarkably low (CV = 7%; interquartile range = 3.1).

Relations between body, air and substrate temperatures are shown in Fig. 3. Slopes of the regression equations of Tb on T. are low, though significantly larger than zero, during both sunny ($b = 0.258$, $s = 0.089$, $P < 0.01$) and cloudy weather ($b = 0.336$, $s = 0.143$, $P < 0.05$), and are not mutually different (ANCOVA, $P > 0.70$). The intercept is highest for the regression line for sunny weather samples (ANCOVA, $P < 0.001$). We obtained comparable results for the relations between Tb and T. (sunny: $b = 0.205$,

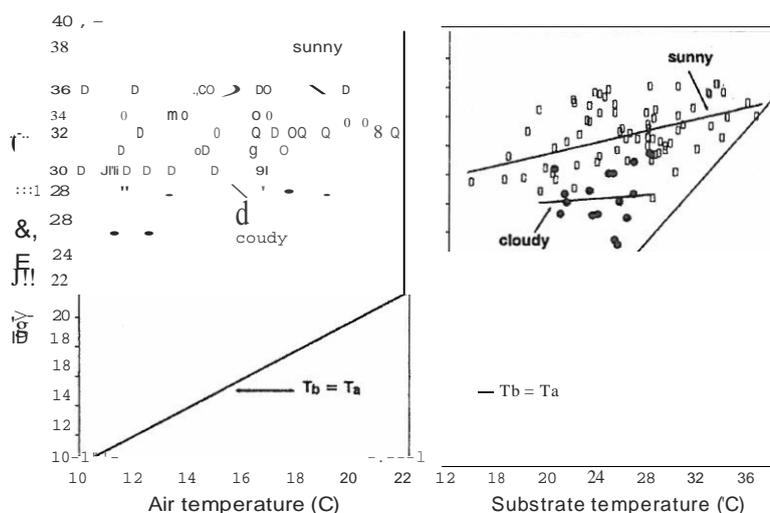


FIG. 3. Relations between body temperature and air and substrate temperature during sunny (squares) and cloudy weather (dots).

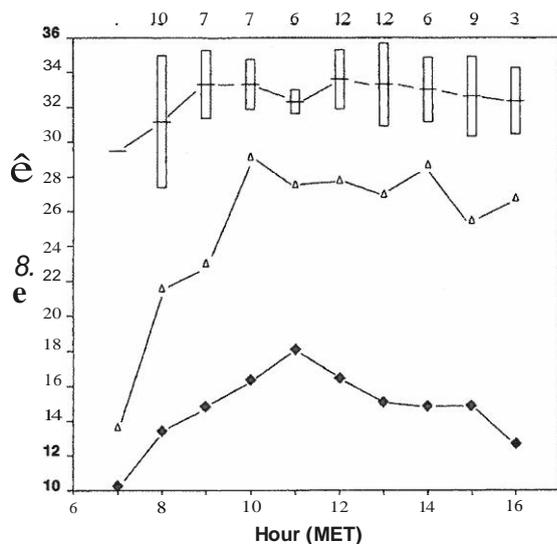


FIG. 4. Body, air and substrate temperatures at various times of day. Shown are hourly mean Tb (horizontal line) \pm 1SE (vertical bar), hourly mean T (diamonds) and Tsub (triangles), and sample sizes. Data for periods of uninterrupted sunshine only.

$s = 0.050$, $P < 0.001$; cloudy: $b = 0.060$, $s = 0.201$, $P > 0.70$; difference between slopes: $P > 0.50$; difference between intercepts: $P \ll 0.001$.

Mean body temperatures recorded during sunny weather at various times of day did not differ significantly (Fig. 4; ANOVA: $P > 0.50$), despite obvious variation in T and Tsub. (ANOVA: $P < 0.001$ in both cases). The percentage of lizards observed basking during hourly intervals (Fig. 2) is negatively rank correlated with hourly mean T, ($r = -0.738$, $P < 0.05$) and Tsub, ($r = -0.869$, $P < 0.001$). This percentage shows a positive rank correlation with the difference between hourly Tb and T, ($r = 0.742$, $P < 0.05$), but not with the difference between hourly \hat{T}_b and \hat{T} . ($r = 0.413$, $p > 0.20$).

The main finding of this study is that *L. bedriagae* regulates its Tb with a considerable degree of precision. This is shown by the low dispersion of the Tb-values, the low values of the regression slopes of Tb on both T and Tsub (Huey and Slatkin, 1976; Huey, 1982), and the constancy of Tb during the course of the day. This high degree of thermoregulatory precision is especially remarkable considering that Tbs are well elevated above ambient temperatures: on average, Tb-values exceeded T, by a factor greater than two.

Body temperatures of the montane *L. bedriagae* did not differ from those maintained by two closely related Corsican lizard species (*Podarcis tiliguerta*, *P. sicula campestris*) in an area at sea level with considerably higher ambient temperatures (R. Van Damme, D. Bauwens and A. M. Castilla, unpubl. data). Other lizards that are indigenous to higher altitudes, such as *Liolaemus multiformis* (Pearson, 1954; Pearson and Bradford, 1976), *Sceloporus jarrovi* (Burns, 1970) and *Lacerta monticola* (Pérez-Mellado, 1982), are known to maintain activity Tbs at rather high levels and within narrow ranges, although the latter two species seem

to experience higher and less variable air temperatures than *L. bedriagae*.

Several behavioral characteristics seem to enable this lizard to maintain high and constant Tbs. (1) Most lizards were seen on boulders, rocks and rock pavements that were exposed to full sun. Such sites were amply available in their habitat, where the only shade was provided by dwarf-scrubs. (2) When the sun became obscured by clouds, lizards rapidly retreated to shelter, thereby reducing the variation in environmental conditions to which they were exposed. The constancy of Tb at various times of the day suggests that lizards restricted their activity to times when external conditions enabled them to maintain Tbs within a narrow range. This needs to be confirmed by long-term observations and estimates of operative temperatures (Bakken and Gates, 1975; Beuchat, 1986; Peterson, 1987). (3) The percentage of lizards observed basking, which was highest at the onset and end of the diel activity period, remained considerable during the midday hours. These observations suggest that individual lizards basked frequently and/or for long periods of time. Comparable findings have been made for *Liolaemus multiformis*, that basks about 70% of the time spent above ground (Pearson and Bradford, 1976). (4) While basking or resting, lizards maintain close contact with sun-warmed rocks or boulders, seemingly to facilitate conductive heat gain. However, Tsub were lower during cloudy than during sunny weather, even after accounting for differences in air and substrate temperatures. Hence, Tbs seem to drop rapidly in the absence of direct sunshine, suggesting that thigmothermic heat gain is of but secondary importance to these lizards.

It should be noted that our results apply only to the spring period. Seasonal changes in thermoregulatory behavior and activity temperatures have been documented in other lizards (e.g., Huey and Pianka, 1977; Christian et al., 1983; Van Damme et al., 1987). At present, we can only speculate whether seasonal changes in the thermal biology of *L. bedriagae* would alter our conclusions.

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Site Attachment by the Red-backed Salamander, *Plethodon cinereus*

WILLIAM F. GERGITS, *Department of Biological Sciences, State University of New York at Albany, Albany, New York 12222, USA.*

ROBERT G. JAEGER, *Department of Biology, University of Southwestern Louisiana, Lafayette, Louisiana 70504, USA.*

Territoriality appears to be widespread within species of terrestrial (e.g., *Plethodon*) and stream-side (e.g., *Desmognathus*) plethodontid salamanders (see reviews in Jaeger, 1986; Hairston, 1987). Because territoriality is often defined as "a defended area" (Brown and Orians, 1970), it is necessary to determine to what extent conspecific salamanders are faithful to given sites and how tenaciously those sites are defended against competitive intruders. A considerable body of literature has accumulated for *Plethodon cinereus* concerning advertisement of sites (Jaeger and Gergits, 1979; Jaeger et al., 1986; Home and Jaeger, 1988), aggressive defense of sites (Jaeger, 1981, 1984), and exclusion of intruders from sites (Jaeger et al., 1982). However, the "sites" in the above experiments were enforced upon the salamanders under laboratory conditions. Thus, the description of *P. cinereus* as a territorial species rests upon insufficient documentation of site attachment in natural habitats.

The red-backed salamander is an inhabitant of the soil and leaf litter of moist forests throughout much of eastern North America. Taub (1961) studied the horizontal and vertical distribution of this species via a series of experiments in a forest. Her data showed restricted horizontal movements on the part of marked salamanders, leading her to conclude that individuals have a small home range. Kleeberger and Werner (1982) described the mean home range area (modified minimum) as ranging from 3.0-4.8 m². Using *P. cinereus* tagged with Co⁶⁰, they also displaced individuals from sites of capture for up to 30 m and found an average 90% (N = 39) return rate, with homing usually occurring within 24 h. Thus, there is evidence that red-backed salamanders remain in restricted areas and rapidly return to such areas once displaced.

We here examine the hypothesis that *P. cinereus* exhibits true site attachment: i.e., an individual confines most of its activities and time, while on the surface of the forest floor, in the limited area under or near a certain cover object (rock or log). Such behavior would be expected of a territorial animal.

The study was conducted during 1974 in Shenandoah National Park, Page County, Virginia. On 16 April, a 3 x 5 m quadrat was staked out on the north-west facing slope of Blackrock Mountain. The quadrat was searched during daylight hours for *P. cinereus* by turning all cover objects and leaf litter. All adult salamanders (>28 mm snout-vent length) were immediately marked using a variation of Wooley's (1973) technique. Using a hypodermic needle, a cut was made through the skin on the dorsal surface of the salamander, exposing the dermis. A drop of Liquitex Polymer Acrylic paint (blue, white, or yellow) was