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### Influence of Behavioral Thermoregulation on the Use of Vertical Surfaces by Iberian Wall Lizards *Podarcis hispanica*

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Many lizard species show distinct preferences for particular substrates, perch heights, vegetation types

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and other aspects of habitat structure (Heatwole, 1977; Moermond, 1979; Adolph, 1990; Diaz and Carrascal, 1991), and they may be morphologically adapted to using their particular microhabitats (Pounds, 1988; Losos, 1990). On the other hand, microhabitat selection is an important component of behavioral thermoregulation by ectotherms (Christian et al., 1983; Grant and Dunham, 1988; Huey et al., 1989; Adolph, 1990; Huey, 1991), as it selectively translates the thermal properties of the environment into body temperatures. Thus, the consequences of habitat selection are of paramount importance for ectotherms (Huey et al., 1989; Huey, 1991).

The climbing habits of some wall lizards of the lacertid genus *Podarcis*, for instance, may be important for behavioral thermoregulation. Rock or stone walls, when available, are the favorite basking sites for *P. tiliguerta* and *P. sicula* (Van Damme et al., 1989, 1990). Similarly, Iberian wall lizards from a Mediterranean island (*P. hispanica atrata*) occupy rocky sites during the early morning and late afternoon, and shift to more vegetated microhabitats near midday (Castilla and Bauwens, 1991). Rocks and walls may offer opportunities to shuttle between shade patches within crevices and sun-warmed surfaces, and the variable orientations of sunlit rock and wall surfaces may facilitate regulation of net radiation intake (Van Damme et al., 1990; Castilla and Bauwens 1991).

However, the thermal consequences of choosing a particular type of substrate cannot be evaluated without measuring operative temperatures (Christian et al., 1983; Grant and Dunham, 1988; Adolph, 1990; Huey, 1991; Hertz et al., 1993). Operative temperatures ( $T_o$ 's) are the predicted equilibrium temperatures of inanimate objects experiencing the same interactions between morphological and biophysical factors as the study animal (Bakken and Gates, 1975; Bakken, 1992). In this study, we use  $T_o$ 's to analyze the relationships between behavioral thermoregulation and the occupation of vertical surfaces in a population of *P. hispanica hispanica* inhabiting a structurally simple human-made wall. The Iberian wall lizard *Podarcis hispanica* is a small (snout-vent length up to 70 mm), saxicolous, insectivorous, diurnal, lacertid lizard (Salvador, 1974). It is a common species across most of its range (Iberian Peninsula, Mediterranean coastal region of France, and north-west Africa; Arnold, 1973), and is apparently more abundant in man-made environments such as walls than in its original, natural rock habitats (Salvador, 1974). *Podarcis hispanica* is probably the most rock-dwelling species within its genus. Its depressed body shape and flattened skull facilitate entrance into narrow, irregular crevices (Arnold, 1973). Here we address the question of whether Iberian wall lizards exhibit behaviors that exploit the thermoregulatory opportunities offered by wall surfaces. Specifically, we consider the thermal consequences, in early summer and during the first part of the lizards' daily activity period, of shuttling between sun and shade, switching position between vertical and horizontal surfaces, and perching at different heights above the ground. We also evaluate the overall accuracy and effectiveness of lizard thermoregulation using the procedures developed by Hertz et al. (1993).

Our study site was located in Madrid, central Spain (40° 35' N, 03° 34' W). Field work was carried out along a 700 m transect along the outer side of the 'El Pardo'

wall, which separates an evergreen woodlot of *Quercus rotundifolia* from an open landscape. The wall was made out of red brick and concrete, with a mean height of 185 cm and a N-S orientation. The top of the wall was covered by roof tiles. Patches of shadow were scarce; they were either located in crevices, or provided by roof tiles on top of the wall or by plants at the base of the wall. Data on thermoregulatory behavior were collected from 14 to 27 June 1993. The wall was patrolled hourly between 0600 and 1000 h (Mean European Time) because few animals were active on the wall after 1000 h. Field work took place on the side of the wall facing the open habitat, which received direct sunlight during the morning. For each lizard seen on the wall we recorded: (1) position in sun or shade; (2) location on a horizontal or vertical surface (independently of the orientation of the long axis of the lizard); and (3) height in cm above ground level. Due to the structure of the wall, vertical surfaces were much more abundant than horizontal ones; the only horizontal surfaces available were on top of exposed bricks or on top of roof tiles. In addition, we captured 14 active lizards during the period of field work, and measured their cloacal temperatures ( $T_b$ ) with a Miller-Weber mercury thermometer. All  $T_b$  measurements were taken after 0700 h, to allow lizards the opportunity to raise their body temperature during the earlier warm-up period. Data on target temperatures (range of selected or preferred  $T_b$ s; Licht et al., 1966; see Hertz et al., 1993) were taken from Bauwens et al. (1995).

We characterized the thermal environment by measuring the  $T_e$  of copper models that were either exposed to direct sunlight or in full shade. Models were five cm long by one cm diameter copper cylinders, closed at both ends except for a small hole allowing insertion of the sensing tip of a thermometer. To simulate the absorbance of real lizards, each model was covered with the skin of a *P. hispanica hispanica* specimen obtained from the collections of the Departamento de Biología Animal I, Universidad Complutense de Madrid (Spain). The similarity of the thermal responses of models and lizards was checked by comparing the temperatures at equilibrium of two models and two restrained live lizards, under the same conditions of radiant heat load (100 W incandescent bulb at different heights above experimental subjects; range of  $T_b$ 's = 28.8–39.6 °C). The equilibrium temperatures for lizards and models were highly correlated ( $r^2 = 0.977$ ), and we used the resulting regression equation ( $T_e = 6.85 + 0.79 T_{\text{model}}$ ,  $n = 10$ ,  $P < 0.001$ ) to correct  $T_e$ 's measured in the field. To measure  $T_e$  in the sun, we placed models at different heights above the ground, always in close contact with the wall surface. Measurements were taken simultaneously with observations of lizard behavior, on at least three different sampling days during each hourly period (five models in horizontal and five in vertical position). We also measured  $T_e$  in the shade at different hours using models placed at arbitrary spots in crevices, plant shadows, or beneath roof tiles. We recorded the height above the ground level of all models (mean = 120 cm, SD = 54.6, range = 8–210).

We used chi-square tests to analyze whether the sun-shade distribution of lizards and the orientation of their perching surface when in full sun were independent of time of day. We also used chi-square tests to analyze the hourly deviations from random

TABLE 1. Variation of the mean height (cm) of lizard perching sites with time of day. Common superscripts indicate means that do not differ significantly according to Duncan's test.

Time of day	$\bar{x} \pm \text{SE}$	N
0600–0700	45.8 $\pm$ 4.70 <sup>a</sup>	69
0700–0800	72.7 $\pm$ 7.02 <sup>b</sup>	65
0800–0900	90.0 $\pm$ 9.68 <sup>b</sup>	38
0900–1000	115.0 $\pm$ 9.32 <sup>c</sup>	38

of the height distributions of perching lizards, by comparing observed distributions with the null expectation that equal numbers of lizards occupied the lower, middle, and upper thirds of the average wall height. The effects of time of day, orientation, and type of shade on  $T_e$  were tested using two-way ANOVAs. We employed the square root transformation to normalize the height of lizards and make data homoscedastic. Assumptions of statistical tests were met in every case.

The mean height of lizards perched on the wall increased almost continuously between 0600 and 1000 h (Table 1;  $F_{3,206} = 14.43$ ,  $P < 0.001$ ). Lizards selected perch heights lower than expected at random between 0600 and 0700 h ( $\chi^2 = 71.6$ ,  $df = 2$ ,  $P < 0.001$ ) and between 0700 and 0800 h ( $\chi^2 = 14.4$ ,  $df = 2$ ,  $P < 0.001$ ). Between 0800 and 0900 h lizards were not selective in their choice of wall heights ( $\chi^2 = 0.68$ ,  $df = 2$ ,  $P > 0.7$ ). Finally, between 0900 and 1000 h lizards selected perches higher than expected at random ( $\chi^2 = 8.6$ ,  $df = 2$ ,  $P < 0.02$ ) and closer to the deep shade beneath roof tiles on top of the wall.

The distribution of lizards in sunny and shaded areas on the wall surface (Fig. 1) varied markedly with time of day ( $\chi^2 = 58.6$ ,  $df = 3$ ,  $P < 0.001$ ). For lizards perched in the shade, the proportion beneath roof tiles tended to increase, though not significantly, with time of day (1 of 4, 2 of 9, 6 of 20, and 12 of 22 at hourly intervals; chi-square test pooling together the two first hours:  $\chi^2 = 4.3$ ,  $df = 2$ ,  $P = 0.11$ ). The occupation of vertical and horizontal surfaces by lizards in full sun also varied with time of day (Fig. 1;  $\chi^2 = 9.40$ ,  $df = 3$ ,  $P < 0.05$ ).

Operative temperatures increased with time of day in both sunny and shaded locations (Table 2; two-way ANOVAs with time of day and orientation or type of shade as factors:  $F_{3,32} = 22.1$  and  $F_{3,35} = 85.0$ , respectively;  $P < 0.001$  in both cases). The orientation with respect to the sun also influenced model temperatures ( $F_{1,32} = 9.6$ ,  $P < 0.005$ ): horizontal models reached higher  $T_e$ 's than vertical ones. The difference in mean  $T_e$ 's between the two orientations tended to increase throughout the morning (Table 2). Operative temperatures in the shade were lower beneath roof tiles than in crevices or plant shadows ( $F_{1,35} = 23.7$ ,  $P < 0.001$ ), especially after 0800 h; the interaction between the effects of time of day and type of shade on  $T_e$  was significant ( $F_{3,32} = 3.1$ ,  $P < 0.05$ ). Operative temperatures in the shade were negatively correlated with height above the ground after 0800 h ( $r = -0.638$ ,  $n = 26$ ,  $P < 0.001$ ), due to the lower temperatures experienced by models beneath roof tiles.

The  $T_b$  of lizards captured between 0700 and 1000 h averaged 33.7 °C (SD = 1.7, range 31.0–35.8, N = 14). A majority of the lizards captured after 0700 h

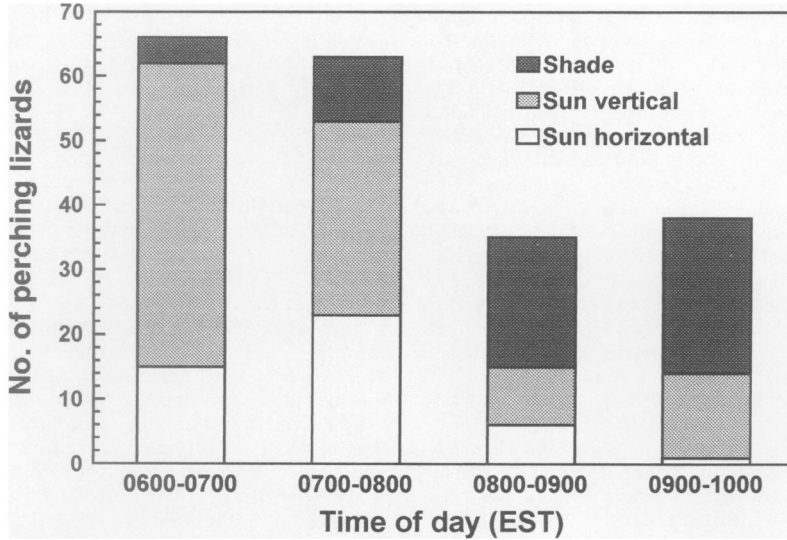


FIG. 1. Frequency of observations of lizards perching vertically or horizontally in full sun, and of lizards perching in the shade, according to time of day.

(12 of 14, or 86%) had  $T_b$ 's within the species' preferred range, which is 31.93–36.30 C (Bauwens et al., 1995; central 80% of all  $T_b$ 's selected in a laboratory photothermal gradient). The deviations of body temperatures from the preferred range were fairly small (mean  $\pm$  SD = 0.10  $\pm$  0.27 C), suggesting a high degree of thermoregulatory accuracy (Hertz et al., 1993). However, a high accuracy does not necessarily imply active thermoregulation, because most  $T_b$ 's may also fall within the preferred range. Nevertheless, the proportion of temperature readings that fell within the preferred range was larger for lizards than for models in the sun (43%; two-tailed Fisher exact  $P = 0.01$ ) and in the shade (39%; two-tailed Fisher exact  $P < 0.005$ ). In addition, the deviations from preferred

range measured after 0700 h were smaller for lizards than either for models in the sun ( $1.89 \pm 2.54$  C;  $t = 2.59$ ,  $df = 42$ ,  $P < 0.02$ ) or in the shade ( $1.80 \pm 1.92$  C;  $t = 3.29$ ,  $df = 47$ ,  $P < 0.002$ ). These observations, together with the behaviors described above, provide strong evidence that lizards were actively and successfully regulating their  $T_b$ . Indeed, the effectiveness of thermoregulation, as defined by Hertz et al. (1993), was high in the population examined ( $E = 1 - [0.10/1.12] = 0.91$ ). The value of  $E$  will generally range between zero, when lizards do not thermoregulate and their deviations from preferred range are similar to those of models, and one, when lizards thermoregulate carefully and their deviations from preferred range are much smaller than those of models (Hertz

TABLE 2. Variation with time of day (mean  $\pm$  1 SE and sample size) of operative temperatures ( $T_e$ ) and absolute values of deviations from 80% preferred range ( $d_e$ ) for both vertically and horizontally positioned sunlit models, and the same for models in the shade of crevices or plants or within the shadow beneath roof tiles. The percentage of  $T_e$  readings within preferred range (PTR) is also shown in each case.

Time of day	Models in the sun							
	Vertical				Horizontal			
	$T_e$ (C)	$d_e$ (C)	N	% in PTR	$T_e$ (C)	$d_e$ (C)	N	% in PTR
0600-0700	30.4 $\pm$ 0.9	1.70 $\pm$ 0.8	5	20	31.0 $\pm$ 1.1	1.55 $\pm$ 0.8	5	40
0700-0800	32.4 $\pm$ 0.7	0.46 $\pm$ 0.5	5	80	35.3 $\pm$ 1.6	1.13 $\pm$ 0.6	5	40
0800-0900	35.3 $\pm$ 0.8	0.32 $\pm$ 0.3	5	80	38.2 $\pm$ 1.6	2.07 $\pm$ 1.4	5	20
0900-1000	37.8 $\pm$ 1.2	1.89 $\pm$ 1.0	5	40	41.7 $\pm$ 1.1	5.39 $\pm$ 1.1	5	0
Time of day	Models in the shade							
	Beneath roof tiles				Crevices or plants			
	$T_e$ (C)	$d_e$ (C)	N	% in PTR	$T_e$ (C)	$d_e$ (C)	N	% in PTR
0600-0700	21.9 $\pm$ 0.2	9.98 $\pm$ 0.2	4	0	22.9 $\pm$ 0.2	9.02 $\pm$ 0.1	4	0
0700-0800	27.3 $\pm$ 0.4	4.64 $\pm$ 0.4	5	0	27.9 $\pm$ 1.1	4.00 $\pm$ 1.1	4	0
0800-0900	30.9 $\pm$ 0.5	1.21 $\pm$ 0.4	9	33	34.5 $\pm$ 0.4	0.00 $\pm$ 0.0	3	100
0900-1000	30.7 $\pm$ 0.6	1.54 $\pm$ 0.5	5	20	35.1 $\pm$ 0.8	0.59 $\pm$ 0.3	9	56

et al., 1993). To calculate  $E$ , we estimate average proportions of vertical and horizontal sunlit surfaces, shade beneath roof tiles, and other types of shade, of 0.84, 0.06, 0.08, and 0.02, respectively. We then use these figures and the  $d_e$  values shown in Table 2 to obtain the 1.12 value of the denominator, which is a weighted average of the deviations from preferred range available in the habitat for a hypothetical non-thermoregulating lizard. Our procedure to estimate  $E$  is therefore somewhat indirect, compared to the method of Hertz et al. (1993).

Our data show that lizards were able to regulate their  $T_b$  within a relatively narrow range by means of the rather limited behavioral options offered by the wall. Lizards chose shaded or sunlit perches, and used sunlit vertical and horizontal surfaces, such that they could maintain their  $T_b$  within, or close to, their preferred temperature range. Between 0600 and 0700 h, when the sun was still low, nearly all lizards were perching in the sun and most of them used vertical surfaces, which receive more solar radiation because they are perpendicular to the sun's rays. Between 0700 and 0800 most lizards were still in full sun, but a high proportion were perching on horizontal surfaces. Given the relative scarcity of horizontal substrates on the wall, this probably indicates a strong selectivity. This is consistent with the higher temperatures reached by horizontal models, whose  $T_e$ 's were in fact somewhat higher than the preferred range (Table 2). After 0800 h, activity apparently decreased, and most individuals were either in the shade of crevices or plants or perching vertically in the sun (i.e. in those perch categories with a majority of  $T_e$ 's within the range of selected  $T_b$ 's; see Table 2). The low number of lizards seen after 0800 h could also reflect an increased number of animals devoted to non-thermoregulatory activities on the shaded side of the wall, which was not scanned during this study. From 0900 h onwards,  $T_e$ 's in the sun were above the lizards' preferred range, and the orientation of models had an important effect on temperature, with horizontal models reaching temperatures close to the critical thermal maximum for *P. hispanica* (44.5 C; Bauwens et al., 1996). Consequently, many lizards were in the shade beneath roof tiles on top of the wall, where  $T_e$ 's were slightly lower than the preferred temperature range (Table 2). Our data also suggest that lizards were using thermal patches either as heat sources (e.g., sunlit horizontal surfaces between 0700 and 0800 h) or heat sinks (e.g., shade beneath roof tiles between 0900 and 1000 h), rather than letting their  $T_b$  equilibrate to the  $T_e$  of any particular patch. The relatively low mass-specific heating rates of *P. hispanica* (JAD, unpubl. data) support this interpretation, as they lengthen the time required to reach thermal equilibrium with the environment.

Thus, the pattern of surface usage by lizards was clearly interpretable in terms of thermoregulatory mechanisms. A similar result was obtained by Adolph (1990) in a study where *Sceloporus* lizards had predominantly vertical orientations at a desert site, whereas their orientation was mainly horizontal at cooler sites. This variation parallels differences in  $T_e$  between horizontal and vertical surfaces ranging between 3.9 C in this study (0900–1000 h), and up to 10–15 C at Adolph's (1990) desert site. Such differ-

ences follow directly from biophysical principles, because objects oriented perpendicular to incoming solar radiation receive increased heat loads that raise their equilibrium temperature (Porter and Gates, 1969; but see Muth, 1977).

Similarly, the continuous increase in perch height observed throughout the morning is, at least in part, consistent with thermal considerations. The rise of  $T_e$  with time of day, for instance, was less pronounced within the shade beneath roof tiles on top of the wall (Table 2), and this could explain the tendency of lizards to perch higher at later times of day. Lizards were also selective in their choice of wall heights before 0800 h, when they perched lower than expected by random; lower perches may have higher temperatures early in the morning (Stevenson, 1985) because air temperature increases, and wind speed decreases, near the ground (Geiger, 1965; Muth, 1977; Stevenson, 1985; Bakken, 1989). For similar reasons, convective cooling may increase with height above ground at later times of day (0900–1000 h).

To what extent are the temperatures measured in this study relevant to the physiology of *P. hispanica*? The optimal temperature for sprinting in *P. h. hispanica* is 35.5 C, with lizards running at 80% or more of their maximal capacity when their  $T_b$  is within the range 31.1–39.5 C (Bauwens et al., 1995). Most  $T_b$ 's measured in this study (93%) were within this range of high performance levels. Hence, the temperatures achieved are likely to be adaptive as long as sprint speed is an ecologically relevant trait (Huey and Stevenson, 1979; Bauwens et al., 1995). This is probably the case in wall lizards, which rely on burst speed to capture prey and escape from predators (Van Damme et al., 1989).

In summary, the ability of lizards to thermoregulate behaviorally was not constrained by the scarcity of options on the wall surface. If anything, the dominant vertical orientation facilitates heat gains in the early morning and avoidance of overheating at midday. We have shown that subtle hourly changes in the location, surface use, and height of lizards, were fully consistent with expectations based on  $T_e$  measurements (Christian et al., 1983; Grant and Dunham, 1988; Adolph, 1990; Díaz, 1994) combined with the information available on the thermal preferences of *P. hispanica* (Bauwens et al., 1996). Thus, both ecomorphological and thermal relations (Arnold, 1973, and results of this study) may have favored the expansion of Iberian wall lizards into highly modified human environments, ranging from stone walls in the countryside to buildings in the center of large towns (García-Paris and Martín-Albadalejo, 1987).

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### Tail Loss in the Striped Plateau Lizard, *Sceloporus virgatus*

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Tail loss in lizards can incur several costs, including those on growth, reproduction, locomotion, and social status (e.g., Ballinger and Tinkle, 1979; Dial and Fitzpatrick, 1981; Fox et al., 1990; Brown et al., 1995). Recently, Martín and Salvador (1992, 1993a, b, c) demonstrated experimentally that tail loss in *Lacerta monticola* reduced male and female reproductive success and influenced microhabitat use, prey size selection (e.g., tailless lizards take smaller prey items than tailed lizards), and thermoregulatory behavior. Thus, tail loss can have important ramifications for lizard life histories and individual performance.

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