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TEMPORAL PATTERNS OF BASKING BEHAVIOUR IN A MEDITERRANEAN LACERTID LIZARD

by

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(With 2 Figures)
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Introduction

Since the pioneer demonstration that desert lizards behaviourally regulate body temperature (COWLES & BOGERT, 1944), thermoregulation has come to be seen as a major facet of reptilian ecology. It is now clear that in reptiles behaviour is the principal agent of temperature regulation and that the role of physiological control is at best one of potential modulation (BARTHOLOMEW, 1982). This is specially so in small and medium-sized diurnal baskers whose body temperature changes so rapidly that physiological control is negligible in comparison with behavioural adjustments (CRISP *et al.*, 1979). Behaviour, in turn, should respond to the environmental variables that determine the value of heating and cooling rates. However, and though previous work has considered the modification of heat exchange rates by other variables (*e.g.* GRIGG *et al.*, 1979; CLAUSSEN & ART, 1981; FRASER, 1985), most of this work has been carried out in laboratory conditions that bear little ressemblance to the ecological context of temperature regulation, and has focused on physiological processes that pay little attention, if any, to the behavioural component (HUEY, 1982).

On the other hand, an ever growing number of field studies on lizard thermoregulation have emphasized that the thermal environment can be

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viewed as an ecological resource through which selection, competition and partition can take place (MAGNUSON *et al.*, 1979; ROUGHGARDEN *et al.*, 1981; CHRISTIAN *et al.*, 1983; GRANT & DUNHAM, 1988; ADOLPH, 1990 and many others). But behavioural mechanisms *per se* have received much less attention than their ecological consequences. For instance, it is clear that shuttling heliotherms could regulate their body temperature in two ways. They could either change the rate at which they expose themselves to radiant heating or the average duration of individual basking periods (SPELLERBERG, 1972; AVERY, 1976). However, the environmental cues (characteristics of the physical environment that determine the choice of a particular strategy) and ecological implications (association with other relevant traits such as time allocated to foraging or predator escape) of these behavioural alternatives remain largely unexplored.

The goal of this study was to investigate how the thermal environment determines, through its effects on heating and cooling rates, the daily patterns of thermoregulatory behaviour in a typical diurnal basker. The organism of choice was *Psammodromus algirus* (L.) 1758, a medium sized lacertid lizard (adult body size: 18-30 cm, out of which *ca.* 2/3 are contrived by the extremely long tail) that inhabits thermally patched habitats in the western Mediterranean. It is a ground-dwelling shuttling heliotherm (CARRASCAL & DÍAZ, 1989) being commonest in broad-leaved (both deciduous and perennial) degraded forests with a well developed undergrowth of shrubs (ARNOLD, 1987; DÍAZ & CARRASCAL, 1990a).

Material and methods

Field observations.

Field observations were conducted in Soto de Viñuelas, Madrid, central Spain (40°35′N, 03°34′W). The study plot (1 ha) is located within a larger Mediterranean evergreen forest in which holm-oaks (*Quercus rotundifolia*) are the dominant species in the tree and shrub layers. The latter also includes interspersed patches of *Cistus ladanifer*, *Halimium viscosum* and *Thymus vulgaris*. The ground is covered mainly by leaf litter, with areas of bare ground at the more steep slopes.

Individual adult lizards (N = 15) were noosed, sexed, paint marked and released at the spot of capture one week before the beginning of behavioural observations. These took place over 11 different clear days (less than 15% cloud cover) scattered between 6 June and 6 July 1990. Samples were taken between 0600 h Mean European Time (onset of the activity period) and 1200 h (sun zenith).

In order to avoid biases attributable to my own presence, I only considered the behaviour of animals that did not show a flushing reaction or, alternatively, waited a few minutes until a "normal" activity pattern (low moving speeds, long and/or frequent pauses and little attention to my own movements) was again exhibited.

Behavioural sequences were dictated without interruption to a portable tape recorder. I considered the alternation of locomotion and pauses and specified each time the focal animal shuttled between sun and shade or *vice versa*. I registered as independent variables the time at which recording had started and the temperatures of air (15 cm above ground) and substrate both in the shade and in full sun. Temperatures were measured with an electronic digital thermometer (bulb in the shade; precision of 0.1°C), immediately after the end of the behavioural record, at the sun and shade spots where the lizard had spent most time; or, in case the animal had not shuttled during the observation period, both at the observed lizard's location and at the nearest sun or shade patch. The sun angle was calculated as a function of the exact time of the beginning of each observation relative to daylength and time of local sunrise. Later I measured the total time spent watching each animal and defined as basking periods those of at least 10 s staying motionless in full sun, so that I could exclude temporary expositions to sun during foraging, home range patrolling or other activities. I then counted the number of basking periods within each sequence and calculated the basking rate (number per minue). I also measured the duration of individual basking periods and calculated their average. The average bask duration was log-transformed prior to analysis before being employed in parametric tests. The proportion of time spent basking (hereafter ''basking time'') was determined by dividing the total duration of basking (sum of individual basking periods) by the total observation time. The same procedure was employed to estimate the proportion of time spent moving. All time measurements were taken with a precision of 1 s, and no sequence of less than 5 min was included in the analyses.

A series of ANOVAs with the observations of lizards registered more than four times ($N = 5$) showed no clear-cut interindividual differences in any of the behavioural thermoregulation traits examined ($P > 0.35$ in all cases). This reduces the probability of an additional, uncontrolled source of variation obscuring my data set.

The body temperatures of free-ranging lizards, needed for the prediction of cooling rates (see below), were estimated by the regression equation $Tb = 14.46 + 0.69 \cdot Ta$, obtained in a previous study of summer thermoregulation at the same forest (CARRASCAL & DÍAZ, 1989). The Ta values introduced in the equation (independent variable) were the means of sun and shade measurements weighted by the percent of time the focal lizard had spent in each type of location.

Experimental measurement of rates of heat exchange.

Heating and cooling rates were experimentally determined at the Estación Biogeológica El Ventorrillo (Navacerrada) during July 1990. Experimental animals ($N = 15$) were captured in the same forest where field observations took place and were kept in open enclosures for a couple of days before the beginning of experiments. Each animal was employed twice (always in different days and hours) in the heating and cooling processes, thus providing a sample size of 30 for the heating rate and 29 for the cooling rate (one of the cooling series of data had to be interrupted due to logistical impediments).

In order to measure heating rates, the animals were introduced into a refrigerated camera where they were kept until their body (cloacal) temperature (Tb) fell to about 21°C (mean ± SE: 21.2 ± 0.78), the expected temperature of a lizard retreated into the deep shade of its refuge. The experimental subject was then fixed with two bands of transparent masking tape, around the base of the tail and on top of the forelimbs, to a 12 x 25 cm wooden table on which a single layer of holm-oak litter (the usual substrate at the study area) had previously been glued. A Miller-Weber quick-reading cloacal thermometer (precision of 0.1°C) was inserted into the lizard's cloaca to allow continuous readings of Tb. The table was then exposed to sun radiation always with the lizard's head pointing to the sun position. Air and substrate temperatures (quick-reading digital thermometer with bulb in the shade) were measured near the end of each trial, and the time

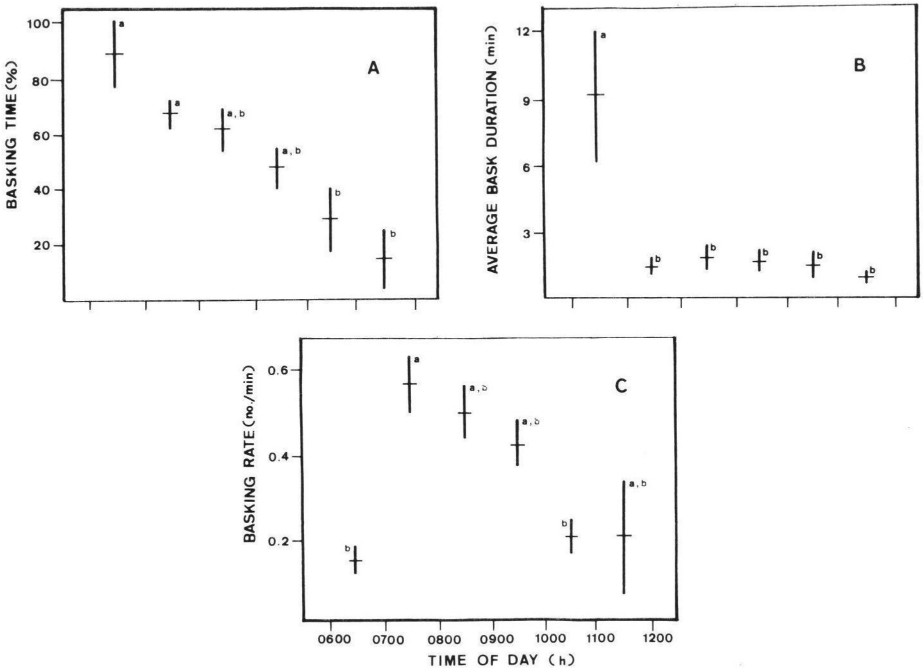

Fig. 1. Temporal patterns of basking behaviour: hourly means (± one standard error) between 0600 and 1200 h (Mean European Time) for: A) The percent of the total observation time spent basking; B) The average duration of basking periods; C) The number of basking periods per minute. Within each box, equal letters indicate not significantly different means according to Tukey's test.

at which basking had begun was noted to allow the calculation of the sun angle. Tb was registered every 15 s in order to determine the rate of heliothermic heating until an average time of *ca.* 8 min had elapsed (Table 1).

The table was then moved to a full shade position to allow the measurement of radiative and convective cooling rates. Tb readings every 15 s were again registered from the moment Tb began to fall. I measured air and substrate temperatures by the same procedure employed in the basking trials. Both heating and cooling rates (in °C $\cdot$ min^{-1}) were determined as the slopes of the linear regressions relating Tb and time elapsed.

Results

I obtained 48 records of lizard behaviour with an average duration of 7 min 33 s (sd = 5 min 9 s). A first, quite obvious result was that the average percent of time spent basking (*i.e.*, the basking time) correlated well with the average duration of basking periods and with the basking rate (partial correlations: r = 0.923 and r = 0.776 respectively, P = 0.001 in both cases, N = 43 since 5 of the recorded animals did not bask at all during the corresponding observation periods). The basking rate, however, did not affect the basking time *per se* (simple correlation: r = -0.007, $P > 0.96$), but rather appeared to modulate the relationship between basking time and average bask duration. The full meaning of this a priori evident pattern of association is clarified by examining the hourly variations of the three behavioural parameters (Fig. 1). The average basking times corresponding to 1 hour periods (Fig. 1a) decreased monotonically from the onset of the activity period (0600-0700 h) until midday (ANOVA: $F_{5,42} = 5.21$, $P < 0.001$). This trend was paralleled by a decrease in the average duration of basking periods ($F_{5,37} = 3.5$, P = 0.011), but the shape of this later decrease was not linear (Fig. 1b). The average duration was about 4.5 times longer before 0700 h, and then fell abruptly to remain more or less constant throughout the rest of the morning. In turn, basking rates also showed a significant temporal variation ($F_{5,42} = 5.08$, P = 0.001). They were minimal before 0700 h (Fig. 1c), consistently with the extremely long duration of an average early-morning basking period, but reached a peak betwen 0700 and 0800 h followed by a progressive fall that continued until noon; these rise and fall compensated for the maintained low values of average bask duration.

In order to obtain a causal explanation for the observed clear-cut pattern of basking behaviour, I investigated the environmental correlates of heating and cooling rates. It should be noted that all the series of data fitted almost perfectly into linear functions of the time elapsed (see the ranges of coefficients of determination in Table 1), so that the regression

TABLE 1. Evolution of lizard Tb as a function of the time elapsed in full sun (heating) or in full shade (cooling)

	Heating (N = 30)		Cooling (N = 29)	
	Mean ± SD	Range	Mean ± SD	Range
D	7.9 ± 2.17	4.3 - 12.5	7.9 ± 1.15	5.8 - 10.0
Tb_0	21.2 ± 1.56	18.0 - 24.2	31.9 ± 4.22	23.7 - 37.2
b	1.56 ± 0.97	0.13 - 3.52	-0.10 ± 0.05	-0.2 - -0.02
R^2	99.0 ± 0.90	96.3 - 100	98.3 ± 1.86	94.1 - 99.8

Mean ± SD and range for the duration (D) of measurements (Tb was determined every 0.25 min), the initial value of Tb (Tb_0: intercept, in °C), the rate of change in Tb (b: slope, in $°C \cdot min^{-1}$), and the percent of variance explained by the time elapsed (R^2, the coefficient of determination).

slopes obtained provided accurate measurements of the rates of heat exchange. I then introduced the heating rates (Hb) as the dependent variable of a stepwise regression analysis with the temperatures of air and substrate (Ta_{sun} and Ts_{sun} respectively, both in °C) and the solar angle (α, in degrees) as the independent variables. The final model obtained, which had a very high predictive power ($R^2 = 91.5\%$, $P \ll 0.001$), was:

$$Hb\ (°C \cdot min^{-1}) = -2.603 + 0.125\ Ta_{sun} + 0.019\ \alpha. \qquad (1)$$

Therefore, the velocity at which lizards warmed up increased with ambient temperature and solar angle. Similarly, the cooling rate (Cb) was a function of body temperature (Tb_o — the higher the temperature reached, the more it could fall before equalling the thermal environment — and substrate temperature (Ts_{shade}), according to the equation ($R^2 = 81.7\%$, $P \ll 0.001$):

$$Cb\ (°C \cdot min^{-1}) = 0.402 - 0.075\ Tb_o + 0.063\ Ts_{shade}. \qquad (2)$$

After verifying that the values of independent variables, obtained in the field as indicated in the Materials and methods section, were within the ranges employed for the building of the predictive models, I used equations 1 and 2 to estimate the expected heating and cooling rates of the observed free-ranging animals. The results obtained were subsequently examined for the detection of temporal patterns, together with the original measurements of heating and cooling rates (Table 2). Whereas both heating rates (estimated and measured) increased linearly throughout the morning, thereby showing a significant hourly variation (estimates: $F_{5,42} = 19.82$, $P < 0.001$; measurements: $F_{5,24} = 27.6$, $P < 0.001$), the cooling rate showed a less clear-cut pattern (estimates: $F_{5,42} = 2.28$, $P = 0.064$; measurements: $F_{5,23} = 1.6$, $P = 0.2$), consistent with the fact that both Tb_o and Ts_{shade} (independent variables in equation 2) tend to increase throughout the morning but have opposite effects on the cooling rate (equation 2).

The next step was to calculate the quotient between the estimated cooling and heating rates and to analyze its temporal variation (Fig. 2). Estimates were employed rather than measurements because my goal was to interpret the behavioural sequences observed in the field and because the different altitudes of the study plot (800 m a.s.l.) and the field station where measurements were conducted (1500 m a.s.l.) could originate differences in the thermal regime at the same time of day. The quotient Cb/Hb was actually a negative potential function of the sun angle ($r = -0{,}812$, $n = 48$, $P \ll 0.001$) whose shape coincided with the

TABLE 2. Hourly variation of the heating and cooling rates

Hour	Measurements		N	Estimates		N
	Heating	Cooling		Heating	Cooling	
6-7	0.36 ± 0.10	-0.30 ± 0.07	5	0.26 ± 0.12	-0.49 ± 0.05	3
7-8	0.88 ± 0.20	-0.30 ± 0.04	6	1.02 ± 0.13	-0.51 ± 0.03	9
8-9	1.31 ± 0.20	-0.45 ± 0.06	6	1.21 ± 0.08	-0.47 ± 0.01	10
9-10	1.82 ± 0.22	-0.45 ± 0.15	3	1.68 ± 0.11	-0.55 ± 0.03	13
10-11	2.41 ± 0.12	-0.52 ± 0.12	6-5[1])	2.07 ± 0.17	-0.49 ± 0.02	10
11-12	3.01 ± 0.25	-0.50 ± 0.06	4	2.70 ± 0.18	-0.37 ± 0.05	3

[1]) One of the cooling series of measurements had to be interrupted due to logistical impediments.

Hourly variation as mean ± standard error and sample size, in °C $\cdot \mathrm{min}^{-1}$, measured under controlled conditions (see Material and methods) and estimated for focal lizards according to equations 1 and 2 in text.

observed evolution of average bask durations (Fig. 1b), so that the hourly means of bask duration and cooling *vs* heating ratio were almost perfectly correlated ($r = 0.993$, $n = 6$, $P < 0.0001$). Interestingly enough, the moment at which both rates of heat exchange are expected to become equal ($\alpha = 24°$ and hour = 0650 h) appeared to set off the behavioural shift depicted in Fig. 1: lizards shortened the duration of basking periods but shuttled from shade to sun at a substantially higher rate; this effect was most marked between 0700 and 0800 h, with expected cooling rates ranging between 0.9 and 0.5 times the value of expected heating rates (Fig. 2).

In turn (Table 3), basking behaviour conditioned to some extent the time available for locomotion. Though basking and moving were by definition alternative behaviours, increased basking times could be achieved either with little or no movement (high duration of basking periods) or, duration being equal, with frequent movements between sun and shade patches (high basking rate). These two trends seemed to compensate each other thus producing a low level of association between basking time and time spent moving. The time-budgets of males and females (Table 4) illustrated these relationships between locomotion and basking behaviour. Although males spent more time moving than females did, basking times were similar in the two sexes. One could therefore expect males to bask more often but during shorter periods, and these were the trends observed although at a marginal significance level.

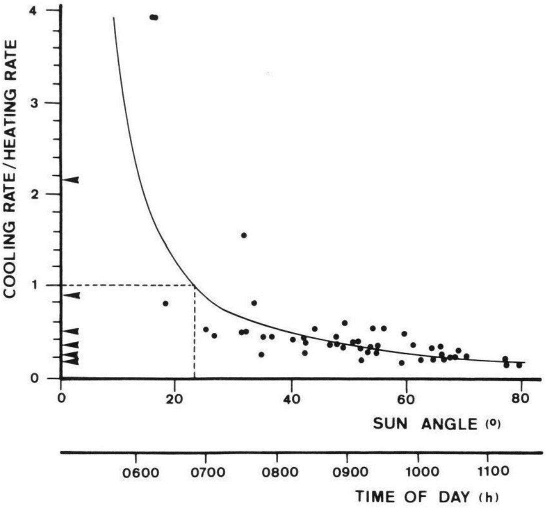

Fig. 2. Inverse potential relationship between the quotient of estimated heat exchange rates (cooling/heating) and the sun angle. The dashed line indicates the coordinates of the point at which both rates are expected to become equal (at 0650 h) and the arrows at the Y-axis show, from top to bottom, the cooling/heating ratios predicted at one-hour intervals between 0600 and 1100 h (bottom line).

Discussion

The observed temporal patterns of shuttling behaviour and basking intensity demonstrate that *P. algirus* has achieved a high extent of temperature regulation by behavioural means. Since the proportion of ground that is in full sun increases with time of day, the morning evolution of basking times could not be explained by considering basking opportunities (Heath, 1964; Huey *et al.*, 1977), but rather should be regarded as the result of active behavioural adjustments. Such adjustments were primarily mediated by the effects of the thermal environment on the rates of heat exchange. Correlations between estimates of external heat loads and heating and cooling rates were as high as one would expect from biophysical, complex but mechanistic processes (Tracy, 1982; Porter & Tracy, 1983) such as solar radiation absorbed, long-wave thermal radiation emitted or heat conduction-convection between the animal and its environment. It is clear that these processes must be in the basis of the observed relationships. Thus, the solar angle is an index of radiant intensity, low ambient temperatures reduce heat

TABLE 3. Correlations between the percentage of time spent moving and the parameters that describe basking behaviour

	r	N	P
Basking time	-0.258	48	0.077
Bask duration[1])	-0.537	43	0.000
Basking rate	0.311	48	0.031

[1]) Log-transformed.
Parameters of basking behaviour: basking time (% total time), average duration of basking periods and basking rate.

TABLE 4. Differences between the sexes

	Males	N	Females	N	t	P
Tmov (%)	22.5 ± 2.4	35	7.7 ± 2.4	13	3.56	0.001
Tbask (%)	49.8 ± 4.6	35	51.4 ± 11.0	13	0.16	0.874
Db (min)[1])	1.69 ± 0.36	33	3.29 ± 1.14	10	1.82	0.076
Rb (No·min^{-1})	0.41 ± 0.04	35	0.26 ± 0.06	13	1.91	0.063

[1]) Log-transformed prior to analysis.
Differences in the percentage of time spent moving (Tmov), the percentage of time spent basking (Tbask), the basking rate (Rb) and the average duration of basking periods (Db): mean, standard error, sample size, t-test and significance level.

gains by conduction-convection, radiative heat losses increase with body temperature, and conductive cooling is favoured by sharp differences between body and substrate temperatures. However, I did not intend to explore the underlying mechanisms (see Introduction), but rather employed the observed relationships (equations 1 and 2) to interpret the interactions between behaviour, time of day and thermal environment.

On the other hand it should be noted that temperature regulation is not an end in itself, but a behavioural device that helps animals gather and digest food, reproduce and avoid predation by directly affecting physiological performance (DAWSON, 1975; HUEY & STEVENSON, 1979; HUEY, 1982). Therefore, basking behaviour should not be isolated from other ecologically relevant processes. For instance, the fact that males showed a marginal tendency towards basking more often but during shorter periods, could be due to the demands posed by their enhanced activity at the end of the reproductive season (mate searching, home range patrolling, *etc.*; ROSE, 1981). Thus, males not only spent more time moving but also were observed more frequently than females (73% of male observations *vs* 27% of female observations; $\chi_1^2 = 4.4$, $P < 0.05$).

Similarly, the extent of compatibility between basking and other behaviours should also be considered. As long as *P. algirus* is an active forager (DÍAZ & CARRASCAL, 1990b), it needs to allocate time to food-gathering movements (HUEY & PIANKA, 1981), but once an average-sized prey (DÍAZ & CARRASCAL, 1990b) has been captured, its handling, which is by far the largest time-consuming part of the foraging process (POUGH & ANDREWS, 1985), can be performed while the lizard is basking. In several occasions, I observed basking animals handling recently captured prey items for more than 3 min, and shuttles between sun and shade were also observed without interrupting the handling process. These observations suggest that the costs of thermoregulation in terms of foraging time are unimportant for this species (but see HILLMAN, 1969). Concerning risk of predation (HUEY & SLATKIN, 1976; CHRISTIAN & TRACY, 1981), both high basking rates and high duration of basking periods may have complex relationships. Shuttling very often involves movements that may reveal the presence of lizards to their potential predators, whereas staying motionless in the sun seems less hazardous only if sunlight patches are either sheltered or not so scarce as to produce a too predictable distribution (HUEY, 1982). Conversely, thermoregulation should facilitate lizards to escape their predators (BENNETT, 1980). The longer bask durations were observed in the early morning, *i.e.* when sun availability was at its lowest so that predators could learn to locate lizards easily, but the orientations faced by lizards were subject to a careful selection that allowed animals to choose basking sites within short reach from the safety of shrubs. In any case, the fact that some lizards still basked for long periods instead of delaying the onset of activity, suggests that long periods of exposition to sun could be needed for some physiological reason other than increasing temperature, thus favouring lenghtened basking when the risk of overheating was absent.

Within this context of complex interactions, a first inspection of the results depicted in Fig. 1 leads to the conclusion that there were operative limits to behavioural flexibility (COWLES & BOGERT, 1944; MCFARLAND, 1976; PORTER & TRACY, 1983; GRANT & DUNHAM, 1988; CARRASCAL & DÍAZ, 1989) at both sides of the sampling period (early morning and midday). The expected balance between heating and cooling rates (Fig. 2) provides an insight into the performance of such thermal constraints. Interestingly, the high duration (and hence low rate) of early basking periods seemed to respond not so much to the convenience of heating as to the disadvantages of cooling, since the expected rate of heat exchange was higher in the shade (heat loss) than in full sun (heat gain). Conversely, at midday both the low duration and the low rate of basking budgets were presumably aimed to avoid overheating more than to favour cooling. It is within these limits that the effectiveness and flexibility of behavioural thermoregulation appeared to be maximal. In this sense, the frequency of movement between shade and sun, as a direct measurement of shuttling behaviour (Heath, 1965; Grenot, 1967; Spellerberg, 1972), correlated well with the general patterns of lizard activity. In June-July, activity peaked between 0700 and 1000 h, but was much more restricted before and after these set points (Carrascal & Díaz, 1989), so that thermal constraints seemed to restrict lizard activity (Grant & Dunham, 1988; Beuchat, 1989) previous to conditioning the thermoregulatory behaviour of active animals. On the other hand, the moment at which heating and cooling rates were expected to become equal should coincidence with a random use of sun and shade patches (Grant & Dunham, 1988; Carrascal & Díaz, 1989) only under the assumptions that body temperatures were close to the range optimal for performance (Huey & Stevenson, 1979) and that lizards shuttled frequently between sun and shade. Whereas the first assumption is reasonable but remains untested, the second one — frequent yet short basking periods — was among the most clear-cut results of this study. An interesting consequence of this argument is that random movement of heliotherms with respect to sun and shade does not necessarily imply lack of thermoregulation (though see Huey *et al.*, 1977), as long as movement could still be required in order to maintain preferred body temperatures. Hence, the inverse relationship between behavioural complexity and latitude among European lacertid lizards (Avery, 1976, 1979) could reflect the fact that thermoregulation might not only allow (in the sense of occupying a smaller fraction of the time budgets), but also be improved by, a more diversified behaviour.

Summary

1. I studied the thermoregulatory behaviour of the diurnal basker *Psammodromus algirus* (Reptilia, Lacertidae) in the mosaic of sunshade patches of a Mediterranean evergreen forest. 48 behavioural sequences associated with measurements of the thermal environment provided data on the percentages of time spent basking by focal animals, the duration of individual basking periods and the frequency of basking.

2. The percentage of time basking decreased linearly from the onset of the activity period until midday. The average duration of basking periods had a pronounced decrease after 0700 h and remained constant throughout the rest of the morning, whereas the bask-

ing rates, that were minimal before 0700 h, reached a peak between 0700 and 0800 h followed by a progressive fall that continued until noon.

3. In order to explain these behavioural patterns, I experimentally determined the effects of environmental variables (air and ground temperature and solar angle) on the heating and cooling rates of captive lizards. The resulting regression models were then used to predict the heat exchange rates of the observed free-ranging animals.

4. The moment at which heating rates should equal and then exceed cooling rates, appeared to set off the behavioural shift towards a larger frequency of shorter basking periods. Under these circumstances, the apparently random movement of a shuttling heliotherm with respect to sun and shade might still be of thermoregulatory significance.

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Resumen

1. Se ha estudiado el comportamiento termorregulador de *Psammodromus algirus* (Reptilia, Lacertidae) en el mosaico de manchas sol-sombra de un encinar mediterráneo. Se utilizaron 48 secuencias comportamentales, asociadas a registros del ambiente térmico, para obtener datos acerca del porcentaje de tiempo invertido en solearse, la duración media de los períodos de exposición al sol y la tasa de soleamiento.

2. El porcentaje de tiempo dedicado al soleamiento disminuye linealmente desde el comienzo de la actividad hasta el mediodía. La duración media de los soleamienos disminuye bruscamente a partir de las 0700 h para luego estabilizarse, mientras que la tasa de soleamiento, que es mínima antes de las 0700 h, se hace máxima entre las 0700 h y las 0800 h para luego disminuir progresivamente hasta el mediodía.

3. Para explicar el modelo de comportamiento observado se determinaron los efectos del ambiente térmico (temperaturas del aire y del suelo y ángulo solar) sobre las tasas de calentamiento y enfriamiento de animales cautivos. Las ecuaciones de regresión resultantes se utilizaron para predecir las tasas de transferencia de calor de los animales observados en el campo.

4. La igualación de las tasas predichas de enfriamiento y calentamiento parece desencadenar el cambio de conducta observado hacia una mayor frecuencia de períodos de soleamiento más cortos. Bajo estas circunstancias, el movimiento al azar de un reptil heliotermo respecto de los parches sol-sombra de su entorno, puede ser contemplado como una estrategia de termorregulación.