Multisensory system of orientation: An important feature of the orientation behaviour of amphibians is the integration of many potential cues into a redundant system which leads them safely to their goal even if the availability of cues changes during migration. The apparent contradiction to the principle of parsimony is probably consequence of (1) differences in the availability of potential cues among different biotopes inhabited by the same species, (2) the necessity to reach a breeding site at a fixed time (e.g. explosive breeders), and (3) the increased risk of losing life during a prolonged search for the goal. The natural migratory range, the diel activity period and the type of breeding site influence considerably the selection of normally-used cues for initial orientation. The ranking of the sensory input obtained from the potential cues into a specific hierarchy optimises the available information in every habitat. Thus, the interspecific differences in orientation behaviour are probably modifications of the same basic system.

PROSPECT

The concept of a multisensory orientation system in Amphibia (Ferguson, Ann. NY Acad. Sci. 188, 30, 1971) has stimulated research specifically with regard to the identification of directional cues and perceiving sensory systems. Presently, we know that amphibians usually prefer certain cues for initial orientation but also that they use every available source of information to back up their orientation system. A major future task will be the analysis of the neuronal base of ranking the sensory input to filter out reliable directional information. Moreover, the system of magnetoperception has still not been identified. Besides the neurophysiological approach, future field studies will contribute considerably to our understanding of orientation, if they consider the interactions of migratory range, habitat and preferred orientation cues during the complete life history of the studied species.

SUMMER ACTIVITY PATTERNS AND THERMOREGULATION IN THE WALL LIZARD, *PODARCIS MURALIS*

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ABSTRACT

Body temperature of active *Podarcis muralis* from Noreña (Asturias; Northern Spain) during summer averages 33.8°C (SD = 2.0, n = 116), and similar values were found in other close populations (grand mean: 33.8°C, SD = 2.3, n = 171). There were no significant differences neither in body temperatures between populations nor between sex/age groups within populations. Daily activity pattern is bimodal, with depressed activity during the warmer hours at the midday. This pattern of activity, as well as the significant negative correlation between the percentage of lizards at sun and the environmental temperatures, are indicative of behavioural thermoregulation. The standard deviations of the mean body temperature and the slopes of the regressions of body temperature on environment temperatures are indicative of a relatively imprecise thermoregulation. Populations from the highest altitudes show a higher variability in body temperature and a greater dependence on the thermal environment.

INTRODUCTION

Since the pioneer study by Cowles and Bogert (1944), finding that desert reptiles behaviourally regulate body temperature, many aspects of reptilian thermoregulation have been examined, so that thermal ecology represents currently a major topic in reptilian research. Many studies have shown that, under a variety of environmental conditions, most diurnal lizards are able to regulate their body temperature within relatively narrow limits during the active periods (see review in Avery, 1982).

The mean body temperature, calculated by averaging the temperatures recorded from active animals in the field, is commonly used as a measure of the thermal status of a species. However, field body

temperatures can vary widely in association with seasonal acclimation, habitat shift, size or sex (e.g. Patterson and Davies, 1978; Bowker *et al.*, 1986; Van Damme *et al.*, 1986), and therefore the mean body temperature may not be the only relevant trait for understanding thermoregulation. A better statement of the method and extent of temperature regulation also requires information about the thermal environment and the behaviour and activity patterns involved in thermoregulation (Huey, 1982).

The objective of this study was to examine the thermal biology and the behaviour and activity patterns associated with temperature regulation for a population of the wall lizard (*Podarcis muralis*) near the southern edge of its distribution range.

MATERIAL AND METHODS

This study was conducted at Noreña (Asturias; Northern Spain; 43° 23' N, 5° 40' W) from late June to early August in 1988. Thermal data were recorded from 116 lizards captured by noosing, taking care to minimise heat flow during handling and excluding data from animals that were chased or handled excessively. In addition, data from 55 lizards from other locations or years were considered for comparative purposes.

Body (cloacal) temperatures of lizards were measured to the nearest 0.2°C with a Schultheis mercury thermometer within 10 s of capture. Measurements of air temperature (10 cm above the ground) and substrate temperature were also taken at the time and point of capture of each lizard with the same instrument by shading the bulb. All temperature records concern active animals during the daylight hours.

Lizards were sexed and snout-to-vent length (SVL) measured, from which three age/sex groups were determined: subadults (born during the previous year; SVL from 35 to 45mm), adult males and adult females (SVL >50mm). Young of the year specimens appears from the second half of the study period, but were too small to accommodate the thermometer without

damage (SVL, 22 to 32mm), and therefore they will not be considered in this study.

In order to assess daily activity patterns, I performed a fixed transect along the study plot, repeated at hourly intervals throughout the daylight hours in two different days. Number of active lizards, environmental temperatures, and location in sun or shade (including here the sun-shade mosaic) for each lizard sighted without previous disturbance were recorded.
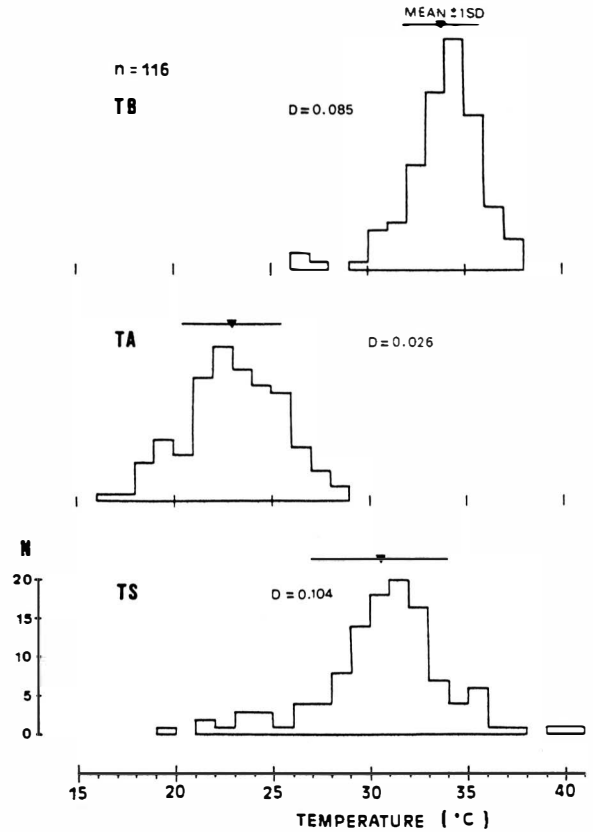

Fig. 1 Frequency distributions of temperatures of body (TB), air (TA), and substrate (TS) for *P. muralis* from Noreña-1988. At each histogram are indicated mean ± standard deviation and the statistic for the Kolmogorov-Smirnov test of normality (D, p<0.01 in all cases).

		Mean ± 1 SD	Minimum	Maximum	N
MALES	TB	33.65 ± 2.63	26.00	37.20	39
	TA	22.24 ± 2.25	16.60	26.60	39
	TS	29.75 ± 3.81	19.00	37.20	39
FEMALES	TB	33.87 ± 1.69	30.40	37.40	36
	TA	23.19 ± 2.72	17.80	28.40	36
	TS	30.16 ± 3.69	21.20	39.80	36
SUBADULTS	TB	33.93 ± 1.64	30.00	37.00	41
	TA	23.53 ± 2.25	19.00	28.40	41
	TS	31.42 ± 2.75	26.20	40.20	41
OVERALL	TB	33.82 ± 2.02	26.00	37.40	116
	TA	22.99 ± 2.45	16.60	28.40	116
	TS	30.47 ± 3.48	19.00	40.20	116

TABLE 1: Descriptive statistics of thermal variables for *P. muralis* from Noreña-1988. TB: Body Temperature; TA: Air Temperature; TS: Substrate Temperature. All temperatures in °C.
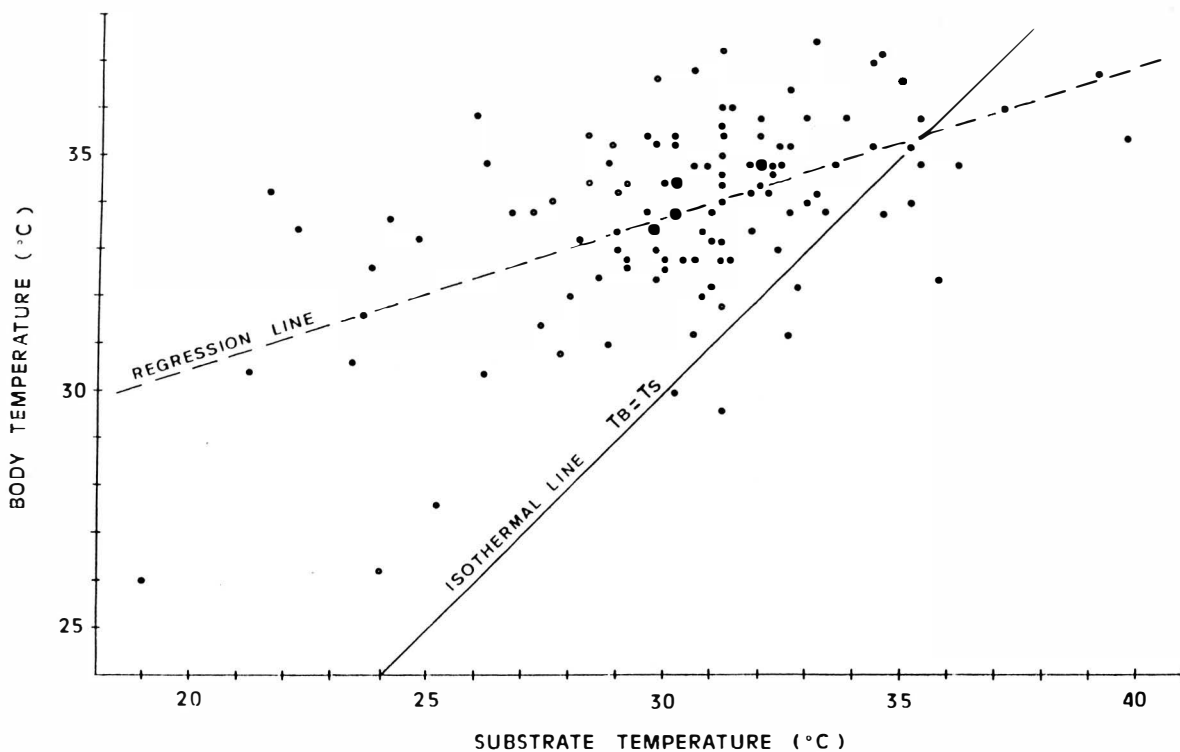
Fig. 2   Plot of body temperature against substrate temperature for lizards from Noreña-1988, showing the regression line and the isothermal line (body temperature equal to substrate temperature). Large points indicate more than one data.
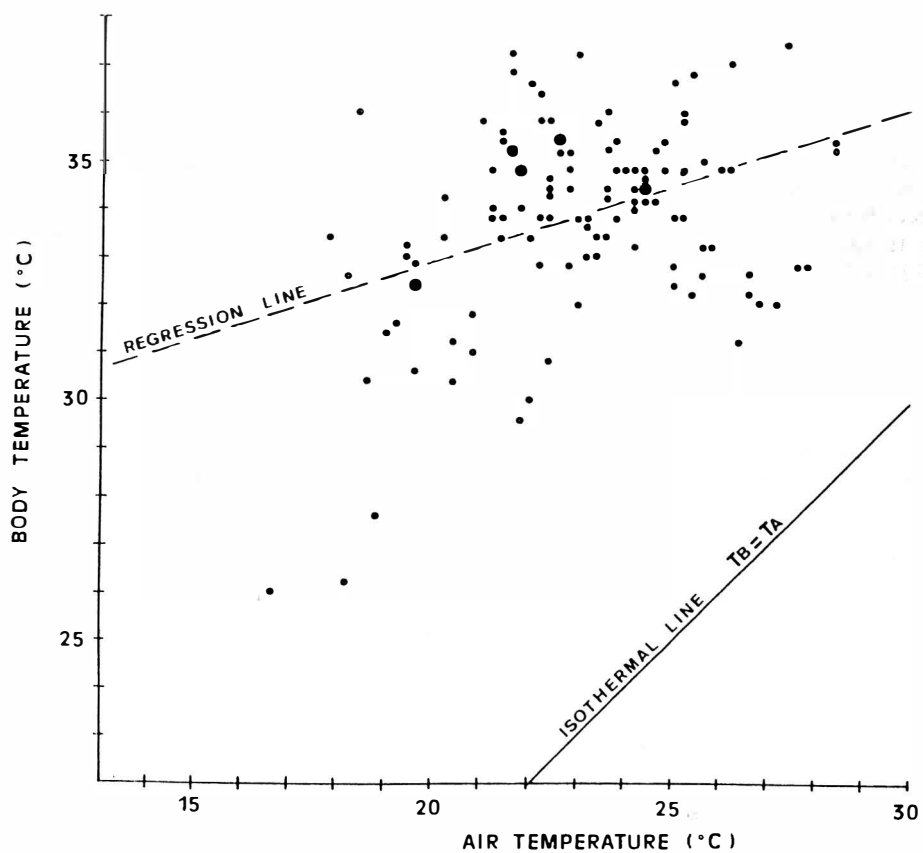

Fig. 3   Plot of body temperature versus air temperature. All considerations as in Fig. 2.

RESULTS

Body and environmental temperatures for 116 captured lizards, separated for subadults, adult males and adult females, are given in Table 1. Mean cloacal temperatures ($°C, \pm 1$ SD) were 33.93 ± 1.64 (N = 41) for subadults, 33.65 ± 2.63 (N = 39) for adult males, and 33.87 ± 1.69 (N = 36) for adult females. No significant differences were found in the mean body temperature for the three age and sex groups (one-way ANOVA, F = 0.207; d.f. 2,113; p = 0.813); thus, data were pooled for further analysis. Overall mean body temperature was 33.82 ± 2.02 (N $\pm$ 116). Maximum values were rather constant for all the age/sex groups, rarely surpassing 37°C. Differences in substrate temperature among groups were non-significant (ANOVA, F = 2.573; p = 0.081), whereas mean air temperature showed marginally significant differences (ANOVA, F = 3.064; p = 0.051), air temperature at point of capture for adult males being slightly lower than that for subadult specimens (Student-Newman-Keuls test; p <0.05). Pooled frequency distributions for the three thermal variables are normally distributed (Kolmogorov-Smirnov one-sample test, Siegel, 1956; p <0.01 in all cases; see Fig. 1), and show that lizard temperature was somewhat higher and fluctuates less than that of the physical environment (Fig. 1).

Plots of body temperature versus substrate and air temperature are given in Figs. 2 and 3. Body temperature exceeded that of the substrate under cold conditions (96.4 per cent of cases for substrate temperatures lower than 33.8°C, which corresponds to mean body temperature of lizards), whereas under warmer conditions most of the cases lie below the isothermal line (64.3% for substrate temperatures higher than 33.8°C; Fig. 2). In the plot of body temperature against air temperature all the points lie above the isothermal line (Fig. 3). There were no significant difference between the slopes of the regressions of body temperature on air (b = 0.316; Standard Error: 0.072) and substrate temperature (b = 0.320; SE: 0.046; ANCOVA, F = 0.056; d.f. 1,228; p>0.1).

Fig. 4 shows the daily activity pattern, as number of lizard active and percentage exposed to full sun at hourly intervals throughout the day. In the summer months, *P. muralis* shows a bimodal activity pattern, being more active in the morning (main interval from 0800h to 1000h a.m.) and in the afternoon (1500h to 1800h p.m.), and remaining relatively inactive at the midday (1100h to 1400h).
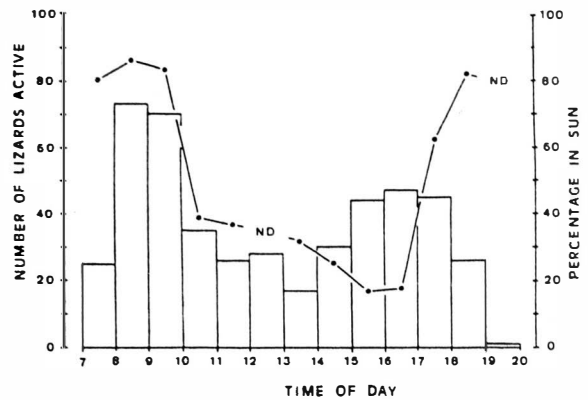

Fig. 4 Number of lizard active (histogram; two transect gathered) and percentage of animals observed in sun at different times of day. ND indicate fewer than 15 valid records for sun/shade location in that interval.
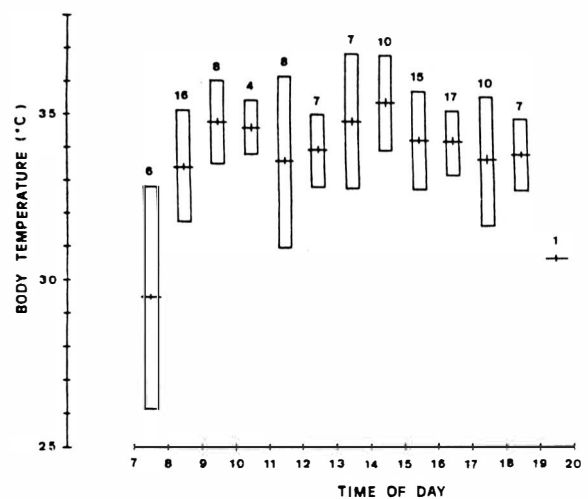

Fig. 5 Body temperatures (mean and standard deviation) of lizards active at different times of day. Sample size is indicated for each hourly interval.

The highest frequencies of lizards in full sun occurred early morning, when more than 80 per cent basked in open places, then decreased progressively until reaching a minimum between 1500h and 1700h (about 17 per cent in sun), and then increased to 80 per cent of active lizards in sun during late afternoon. There was a significant inverse correlation between per cent of lizards in open sun and both the air (r = -0.747; p<0.01) and the substrate temperature (r = -0.623; p<0.05).

Locality-Year	Body Temperature (Mean + 1 SD)	b	r^2	F ratio	N
Noreña - 1988	33.82 ± 2.02	0.320	0.302	49.34**	116
Noreña - 1989	34.41 ± 2.36	0.280	0.186	2.97 ns	16
Colunga - 1988	34.55 ± 1.25	0.198	0.264	3.22 ns	13
Caleao - 1989	33.26 ± 3.39	0.459	0.307	10.62*	26

TABLE 2: Mean field body temperature (°C), slope (b) and amount of variance explained by the regression on substrate temperature for different populations of *P. muralis*. ** — p<0.001; * — p<0.01; ns — p>0.05

Fig. 5 displays the mean body temperatures of lizards grouped at hourly intervals throughout the day. Body temperatures were remarkably constant between 0800-0900h and 1800-1900h (F = 1.245; d.f. = 10, 98; p = 0.272) but early morning (0700-0800) and late evening (1900-2000) temperatures were sustantially lower.

Field body temperatures of *P. muralis* from other localities or years (Table 2) showed no differences between groups (ANOVA; F = 1.229; d.f. 3,167; p = 0.301). However, both standard deviation of mean body temperature and slopes of the regressions of body temperature on substrate temperature were lower for a population from higher altitude (Caleao, 850m) than for a lowland population (Colunga, at sea level), showing the population from Noreña (300m) intermediate values.

DISCUSSION

Body temperature of active *Podarcis muralis* during the summer averages 33.82 ± 2.02°C in the main population studied, and similar values have been found in some close populations (overall average: 33.83 ± 2.28°C; n = 171). Our data agree with the figures presented by several authors reporting field body temperatures for *P. muralis* (Avery, 1978) and also for other more southerly *Podarcis* species (*P. sicula*, Avery, 1978; *P. hispanica*, Busack, 1978; Pérez Mellado, 1983; Bowker, 1986; *P. bocagei*, Pérez Mellado, 1983; *P. pityusensis*, Pérez Mellado and Salvador, 1981). The resemblance between *Podarcis* species is emphasised when their body temperatures are compared with those of other iberian lacertids, ranging from 29.3°C in *Lacerta monticola* (Argüello and Salvador, 1988) to 38.8°C in adult *Acanthodactylus erythrurus* (Pough and Busack, 1978). Thus, body temperature seems to be a conservative trait within the genus *Podarcis*, whose origin and radiation are quite recent (Arnold, 1973).

A distinct bimodal daily activity pattern, as shown by *P. muralis* seems to be a common pattern for diurnal lizards during the warm summer months (see, e.g. Pianka, 1977). This pattern, as well as the negative correlation between the proportion of lizards at sun and the environmental temperature, is indicative of behavioural thermoregulation (Huey *et al.*, 1977; Waldschmidt, 1980), and suggest that shuttling between sun and shade is a significant way to achieve an accurate control of body temperature. In fact, lizards maintain their body temperatures within relatively narrow limits and above that of the physical environment throughout the daylight hours, except for the first and latest one-hour intervals, as in this extremes the thermal environment likely precludes an accurate thermoregulation.

No differences were found in mean body temperatures of different populations (or years) of *P. muralis* examined in this study. Precision of thermoregulation, however, as indicated by standard deviation of the mean body temperatures did vary. The use of the slope of the linear regression of body temperature on ambient temperature has some

theoretical advantages (see Hertz and Huey, 1981; Huey, 1982) and provides similar results in this case, with lower slopes (implying less dependence of body temperature upon ambient temperature) in the lowland than in the highland populations. Contrary to the finding by Hertz and Huey (1981) in *Anolis*, slope was not inversely related to altitude, but the population from the highest location showed higher variability and dependence on thermal environment.

In general, according to the standards made by Bowker (1980, 1986) and Bowker and Johnson (1984), the studied populations of *P. muralis* exhibit low body temperatures and large standard deviations (coefficients of variation from 3.62 per cent to 10.19 per cent) and might be considered as thermophobic and relatively imprecise thermoregulators. Even during the times of day in which environmental temperatures would allow for a more precise thermoregulation, variability of body temperature was equally high (e.g. Noreña-1988: for 36 lizards caught from 10h to 15h, the time of depressed activity when mean substrate temperature was 32.31 ± 2.79°C, the standard deviation of mean body temperature was 1.82, very close to the overall figure). This agree with predictions driving from the cost-benefit models as developed by Huey (1974) and Huey and Slatkin (1976): although constant body temperature provide physiological advantages, increased precision of temperature regulation could increase costs in energy, time and risk of predation, among others (see review in Huey, 1982), so that excessive thermoregulation could lower fitness.

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THE DISTRIBUTION AND BREEDING SITE CHARACTERISTICS OF NEWTS IN CUMBRIA, ENGLAND

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ABSTRACT

The distribution and breeding site characteristics of the smooth newt, *Triturus vulgaris*, the palmate newt, *T. helveticus* and the warty newt, *T. cristatus* were investigated in Cumbria. *T. helveticus* was the commonest species on the acidic rocks in the Lake District, but was not found in limestone areas. *T. cristatus* was seldom found without the commoner *T. vulgaris*, and there was no evidence of the former preferring larger, deeper ponds than the latter.

T. vulgaris and *T. cristatus*, unlike *T. helveticus* were rarely found in water with pH<6. *T. vulgaris* was usually found in water relatively rich in metal ions, while the reverse was true for *T. helveticus*.

Newts were found in ponds in a wide variety of terrestrial habitats, but most often in rough pasture land.

INTRODUCTION

Three species of newt occur in Britain, the smooth newt (*Triturus vulgaris*) the palmate newt (*T. helveticus*) and warty newt (*T. cristatus*). Studies of newt breeding site characteristics have indicated certain differences in the ponds chosen by the different species. Cooke and Frazer (1976) found that the smooth newt tended to be found in water with relatively high concentrations of metals, while the reverse was true for the palmate newt.

Yalden (1986) noted that in the Peak district newts showed a distinct geographical separation between the species. *T. vulgaris* and *T. cristatus* occurred mainly on the carboniferous limestone in ponds of pH>7.0, while *T. helveticus* was mainly found on the millstone grit and shales in more acid ponds of pH<7.0. Other studies (Beebee, 1977, 1981, Green, 1984) have indicated the importance of certain terrestrial habitat types around newt ponds, notably the presence of dense vegetation.