HABITAT SELECTION AND THERMAL ECOLOGY OF THE SYMPATRIC LIZARDS *PODARCIS MURALIS* AND *PODARCIS HISPANICA* IN A MOUNTAIN REGION OF CENTRAL SPAIN

JAVIER MARTÍN-VALLEJO[1], JAVIER GARCÍA-FERNÁNDEZ[2], VALENTÍN PÉREZ-MELLADO[2,3] & JOSÉ LUIS VICENTE-VILLARDÓN[1]

[1] *Departamento de Estadística y Matemática Aplicadas, Universidad de Salamanca, C/ Espejo 2, E-37007 Salamanca, Spain*

[2] *Departamento de Biología Animal, Universidad de Salamanca, E-37071 Salamanca, Spain*

[3] *Present address: Departamento de Ciencias Ambientales y Recursos Naturales, Universidad de Alicante, Spain*

We studied habitat selection, field body temperatures (TB) and activity cycles in sympatric populations of the lacertid lizards *Podarcis muralis* and *Podarcis hispanica* in a mountain area in Central Spain. Different patterns of habitat selection for the two species were found: *P. muralis* occupies N and NW facing talus sites, while *P. hispanica* shows a less habitat-specific distribution at the study site. Inter- and intraspecific differences in TBs were found, while thermoregulatory precision analyses showed differences between adult male and female *P. muralis*. Hypotheses based on activity cycles, habitat selection and basking behaviour are discussed to explain such results in two closely related species.

INTRODUCTION

Thermoregulatory behaviour and habitat selection are intimately related and strongly influence life history traits and fitness of lizards (Ouboter, 1981; Huey, 1982; van Berkum, Huey & Adams, 1986; Adolph, 1990). Many authors have approached the study of interactions between the conditions of the habitat occupied by a given species and its thermal behaviour (Hillman, 1969; Moermond, 1979; Roughgarden, Porter & Heckel, 1981; Hertz & Huey, 1981; Tracy & Christian, 1986; van Damme, Bauwens, Castilla & Verheyen, 1989; Marquet, Ortíz, Bozinovic & Jaksic, 1989), as well as focusing on the connection between thermoregulation and activity time (Porter & Tracy, 1983; Grant & Dunham, 1988).

We here report a study of body temperatures, activity cycles and features of habitat selection in the lizards *Podarcis muralis* and *Podarcis hispanica,* that are sympatric in some areas of the Iberian Peninsula, including the Sierra de Guadarrama (Central System, Spain), where this study was undertaken. The analysis of thermoregulatory precision, activity cycles and basking behaviour have been developed through field observations, and the conclusions extracted are therefore mainly directed towards suggesting working hypotheses for future studies.

Our main objectives were to: (1) quantify habitat occupation by the two species in the area, and identify any intra- and interspecific differences between them; (2) determine some aspects of their thermal ecology, and relate these to the habitat selection features; and (3) inspect whether differences in thermal ecology could be found between the two species.

MATERIAL AND METHODS

ANIMALS

Lizards of the lacertid genus *Podarcis* from the Iberian Peninsula seem to be very similar in basic ecological characteristics such as diet composition, foraging behaviour, activity cycles and thermoregulatory behaviour (Arnold & Burton, 1978; Pérez-Mellado, 1983a,b; Arnold, 1987; Gosá, 1987). These similarities are especially strong between *P. muralis* and *P. hispanica*, two species so closely related that there are some problems for their systematic distinction over a wide part of their distribution range (e.g. Martínez-Rica & Laplaza, 1989). These two small lizards are similar in size (adult snout-vent length 49.7-67.6 mm and 46.7-66.8 mm respectively, personal data), morphology (Pérez-Mellado & Galindo, 1986) and habitat requirements (Arnold, 1987). *Podarcis muralis* occupies a wide range of latitudes in Europe -the southwestern extreme of which is the Sierra de Guadarrama-, while *P. hispanica* is limited to the Iberian Peninsula, southern France and northern Africa.

STUDY AREA

The study area is located in the westernmost part of the Sierra de Guadarrama, Spain, a mountain range reaching a maximum altitude of 1902 m. The altitudinal range surveyed extended from 1450 to 1902

m. The dominant vegetation consists of *Pinus sylvestris* forest, widely spread throughout the whole mountain range. In the high mountain areas, the forest was gradually replaced by small shrubs, with *Juniperus communis* subsp. *nana* being the dominant species. Below 1550 m, the forest becomes very open, and *Quercus ilex* subsp. *ballota* is the predominant tree species. Important habitat differences occurred resulting from the topography: the southern slopes of the mountains present a greater number of open habitats with Mediterranean shrubs such as *Cistus laurifolius*, *Halymium viscosum*, *Erica arborea* and *Thymus bracteatus*. The northern slopes exhibit closed *Pinus* forests with a few accompanying scrubs (mainly *Arctostaphyllos uva-ursi*) and have much higher humidity.

METHODS

Observations were made at monthly intervals from May 1988 to September 1989. We captured lizards by hand or noose, and recorded the following data upon each capture: species, date, time, age, sex, reproductive condition of females, behaviour (basking or active), orientation of slope (N, NW, W, SW, S, SE, E, NE), altitude, body temperature (cloacal = TB), air temperature (shaded bulb, 10 cm above substrate = TA), and substrate temperature (shaded bulb = TS). Temperatures were measured with a Schultheis thermometer to the nearest 0.1°C.

Three age classes were considered: juveniles, the individuals born in the year of capture; subadults, one-year-old individuals, which have not yet reached sexual maturity; and adults, sexually mature individuals.

Activity rhythms were determined from the frequencies of lizard observations made in the different months and time intervals (data from 1988 and 1989 were pooled since no differences were detected). Correction indices (Tellería, 1986) were used to avoid possible biases caused by an irregular survey intensity.

The microhabitat selection field study was developed between April and August 1989, at monthly intervals. A 5 x 5 m square was used as the survey unit, the centre of which was a lizard previously observed (these observations were made randomly, using two hour intervals and considering the first lizard seen after each of these periods of time). Within each square we estimated 28 variables: (1-5) percentage cover at ground level of gravel, grass, fallen leaves, rock and soil; (6-10) percentage cover of vegetation layers with heights <25 cm, 25-50 cm, 50-100 cm, 1-2 m, >2 m; (11-15) percentage cover of walls, and rocks with heights <25 cm, 25-50 cm, 50-100 cm, >100 cm; (16) percentage cover of talus structures; (17-18) percentage cover of dead tree trunks and branches; (19-20) percentage cover of 0-20° and 20-40° slopes; (21-28) SW, S, SE, E, NE, N, NW or W dominant orientations. Percentages were calculated as means of estimates made by eye by two independent observers. Similarly

we estimated the availability of microhabitats in the environment by measuring the same variables in squares for which the centres were the points occupied by us after stopping every two minutes during random directed walks.

STATISTICAL ANALYSIS

We used one-way analysis of variance (ANOVA) and Bonferroni's multiple comparison test (see Keppel, 1991) on arcsin x^{-1} transformed data to examine differences between samples (*P. muralis*, *P. hispanica* and availability) for each microhabitat variable. When variances were heterogeneous across samples (Bartlett's test) we used the non-parametric Kruskal-Wallis test, followed by Dunn's multiple comparison test (Dunn, 1964; see Hollander & Wolfe, 1973).

Thermoregulatory precision was estimated by the slope of the least square regressions of TB on TA or TS. Differences between lizard species and age/sex groups were assessed by analyses of covariance (ANCOVA). As another indicator of thermoregulatory precision we employed the interquartile range. To analyse differences between two means we used the two-tailed Student *t*-test, with the Welch approximation (t_w) in case of heterogeneity of variances, or a Z-test for *n*>50. Frequency distributions of distinct behavioural categories were compared with χ^2 tests. The significance level used was α= 0.05.

RESULTS

HABITAT SELECTION

Podarcis muralis occupied a narrower altitudinal range in the study area (1490-1725 m; Fig. 1), while *P. hispanica* was present along the whole surveyed range (1450-1900 m).
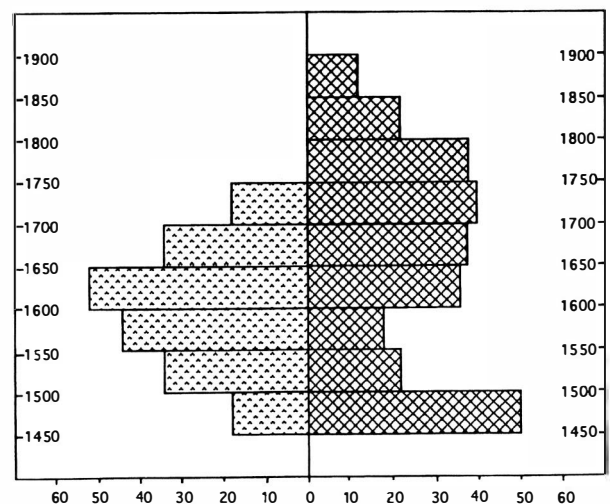

FIG. 1. Absolute frequencies (on horizontal axis) of *Podarcis muralis* (left hand) and *Podarcis hispanica* (right hand) lizards seen at the different altitude intervals (on vertical axis).

TABLE 1. Average percentages and standard deviations for the three groups considered: Availability, *P. muralis* and *P. hispanica.*

	Availability (n=45)		P. hispanica (n=24)		P. muralis (n=22)	
	mean	SD	mean	SD	mean	SD
Gravel	2.2	14.7	16.7	37.3	15.5	34.6
Grass	72.6	41.4	41.7	49.3	13.2	30.3
Withered leaves	8.8	28.5	0.0	0.0	0.0	0.0
Slab	4.1	16.8	9.4	18.1	3.4	11.4
Soil	12.2	30.3	24.0	38.1	67.9	43.2
Trees:						
>2m	20.0	27.1	3.1	13.5	6.2	18.4
< 2m	1.2	5.3	6.7	10.1	8.6	13.9
Shrubs:						
< 25cm	8.0	15.2	2.5	5.9	2.8	9.8
25-50cm	15.3	20.6	6.8	9.1	9.7	12.9
> 50cm	3.8	10.3	4.0	8.3	2.5	10.9
Wall	0.0	0.0	2.3	5.2	0.0	0.0
Rocks:						
< 25cm	9.1	10.3	17.3	12.6	19.2	12.3
25-50cm	2.6	4.9	15.0	14.6	2.7	5.0
50-100cm	2.2	11.2	2.4	5.7	0.5	1.7
> 100cm	0.7	3.3	2.7	7.2	0.0	0.0
Talus	0.0	0.0	7.8	21.1	34.8	30.2
Slope:						
0-20°	80.0	40.0	77.2	37.2	46.5	31.3
>20°	20.0	41.5	22.8	37.2	53.4	31.3

In the analyses of variance and Bonferroni tests, made with the percentages obtained in the microhabitat selection study (Table 1), *P. muralis* exhibited significantly higher percentages for the variables soil, talus and 20-40° slope, and lower ones for grass and the 0-20° slope. Both *P. muralis* and *P. hispanica* showed significantly higher percentages than available for rocks under 25 cm (Table 2).

In the group of variables analysed through non-parametric tests, significant results were found for the following variables: trees (>2 m high vegetation cover) and <25 cm scrubs were more available than utilized. Regarding interspecific comparisons, *P. hispanica* selected rocks of heights between 25 and 50 cm.

BODY TEMPERATURES AND THERMOREGULATORY PRECISION

Body temperatures for all age/sex classes are shown in Table 3. TBs are significantly higher in *P. muralis* than in *P. hispanica*, regarding the whole species (Z=4.07, P<0.001), and for adult males (t=2.54, df=79, P<0.05) and subadults (t_w=5.05, df=47, P<0.001).

TABLE 2. Results obtained in the habitat selection study. (* P<0.05; ** P<0.01. The last three variables were analysed using non-parametric tests).

Variables	Availability/ P. hispanica	Availability/ P. muralis	P. muralis/ P. hispanica
Grass	-	*	*
Soil	-	*	*
Rocks < 25cm	*	*	-
Talus	-	*	*
Slope 0-20°	-	*	*
Slope >20°	-	*	*
Trees >2m	*	*	-
Shrubs < 25cm	*	*	-
Rocks 25-50cm	*	-	*

Both in *P. muralis* and in *P. hispanica*, the juveniles exhibited lower mean TBs than the other age groups, which did not differ significantly (ANOVA, F=5.64, df=2-81, and 3.24, df=2-116 respectively, P<0.05; Bonferroni test, P<0.05).

The interquartile range of TB was lower in males of *P. muralis*, followed by the adult females of both species. Regression slopes of TB on TA and TS (Fig. 2) are similar for adults of the two species; but considering the two sexes separately, we notice that in adult male *P.muralis*, the slopes are not statistically different from 0 (b=0.22 and 0.08; t=1.62; df=25 and 1.45; df=22 for TA and TS respectively), whereas adult females have high slope values (b=0.60 and 0.50). *P. hispanica* shows, instead, more similar values for males and females (b=0.47 and 0.41 respectively for TA; b=0.38 and 0.50 for TS). The results of the analyses of covariance show no differences between *P. hispanica* males and females, while differences were detected in the slopes of males and females in *P. muralis* (F=6.31, df=1-54 P<0.05 for TA; F=9.05, df=1-47 P<0.01 for TS).

The regression slopes of gravid and non-gravid females were analysed, and differences have not been detected between the two groups for either of the two species.

ACTIVITY CYCLES AND BASKING BEHAVIOUR

Annual and daily activity periods of adult males and females, and subadults, of both species are shown in Fig. 3. Activity cycles differed between sex/age groups considered.

Frequencies of basking individuals for adults of both species show low differences among groups, as follows: *P. muralis* males, 57.1% and females, 60.7%; *P. hispanica* males, 64.7% and females, 66.7%. There are no intraspecific differences in the proportions of

TABLE 3. Statistics (mean ± SE, range in parentheses, interquartile range, and sample size) of body (TB), air (TA), and substrate (TS) temperatures for *P. muralis* and *P. hispanica.*

P. muralis				*P. hispanica*			
sex/age group:	TB	TA	TS	sex/age group:	TB	TA	TS
adult males	32.60 ± 0.69 (24.0 - 38.0) 3.2 28	19.22 ± 0.96 (12.5 - 31.1) 6.0 27	26.37 ± 1.45 (13.6 - 39.0) 11.4 24	adult males	30.16 ± 0.59 (21.4 - 36.0) 5.7 53	16.97 ± 0.69 (9.6 - 26.0) 8.7 48	25.13 ± 0.78 (14.0 - 34.0) 6.0 41
adult females	31.08 ± 0.72 (23.3 -36.8) 5.3 30	18.80 ± 0.98 (8.8 - 31.1) 8.4 30	25.78 ± 1.24 (13.6 - 37.0) 11.7 26	adult females	30.20 ± 0.55 (21.4 - 36.6) 4.5 45	19.07 ± 0.82 (10.9 - 28.5) 8.8 40	26.03 ± 0.77 (15.6 - 34.0) 6.7 34
subadults	34.10 ± 0.44 (30.3 - 37.8) 1.9 17	22.58 ± 0.85 (17.8 - 28.1) 6.1 17	28.75 ± 1.24 (17.0 - 27.0) 10.0 15	subadults	29.99 ± 0.68 (22.0 - 36.0) 5.9 31	19.10 ± 0.90 (11.0 - 26.9) 5.6 24	25.49 ± 1.39 (14.0 - 40.0) 9.6 21
juveniles	29.02 ± 0.94 (26.2 - 32.6) 2.8 6	17.50 ± 0.78 (15.6 - 20.0) 4.0 6	20.0 ± 1.58 (17.0 - 27.0) 4.8 6	juveniles	26.07 ± 1.89 (22.0 - 34.5) 9.0 7	14.04 ± 2.01 (9.6 - 23.0) 9.9 7	18.77 ± 2.72 (14.2 - 29.0) 11.2 6
total	31.99 ± 0.40 (23.3 - 38.0) 4.2 81	19.32 ± 0.51 (8.8 - 31.1) 7.0 80	25.12 ± 0.70 (13.6 - 39.0) 12.0 71	total	29.79 ± 0.36 (21.4 - 36.6) 6.5 136	17.42 ± 0.44 (9.6 - 28.5) 8.6 119	23.67 ± 0.54 (14.0 - 40.0) 9 102

basking or active individuals in either of the two species (χ^2=0.07, df=1 for *P. muralis*; χ^2=0.042, df=1 for *P. hispanica*). After pooling the data, we found no interspecific differences (χ^2=0.69, df=1).

DISCUSSION

HABITAT SELECTION

Probably, the genus *Podarcis* was present in the Iberian Peninsula from the Upper Miocene (Vives-Balmaña, 1982, 1984). There is no agreement about the ancestral species inhabiting this area (Busack, 1977; Blasco, 1980; Vives-Balmaña, 1980). In any case, the available data indicate an almost general distribution of *P. hispanica* throughout the area, occupying several Mediterranean habitats (Salvador, 1985; Barbadillo, 1987), while *P. muralis* is restricted to mountain areas of the northern half of the Iberian Peninsula. Usually, the species show there a parapatric microdistribution, lacking altitudinal overlap in their ranges; for instance, in the Pyrenees mountains, *P. hispanica* reaches a maximum altitude of 1600 m, co-

inciding with the lowest of *P. muralis* (Vives-Balmaña, 1982; Martínez-Rica & Laplaza, 1989). For this reason, the situation in the Sierra del Guadarrama seems to be especially suitable to investigate factors segregating both species.

Our results show that *P. hispanica* has a less microhabitat-specific distribution at the study site, although it is partially dependent on rocky habitats. *Podarcis muralis* exhibits a greater habitat-specificity, occupying ground talus in humid slants. This picture is the inverse of the situation in other northern populations of the Iberian Peninsula, where *P. muralis* occupies a greater number of habitats and *P. hispanica* is limited to a narrow spatial distribution (Braña, 1984; Gosá, 1987).

FACTORS INFLUENCING THE LOCALIZED DISTRIBUTION OF *P. MURALIS*

We could argue that microhabitat differences between these species are due to their different physiological and historical constraints, i.e., a greater adaptation of *P. muralis* to its originally more mesic
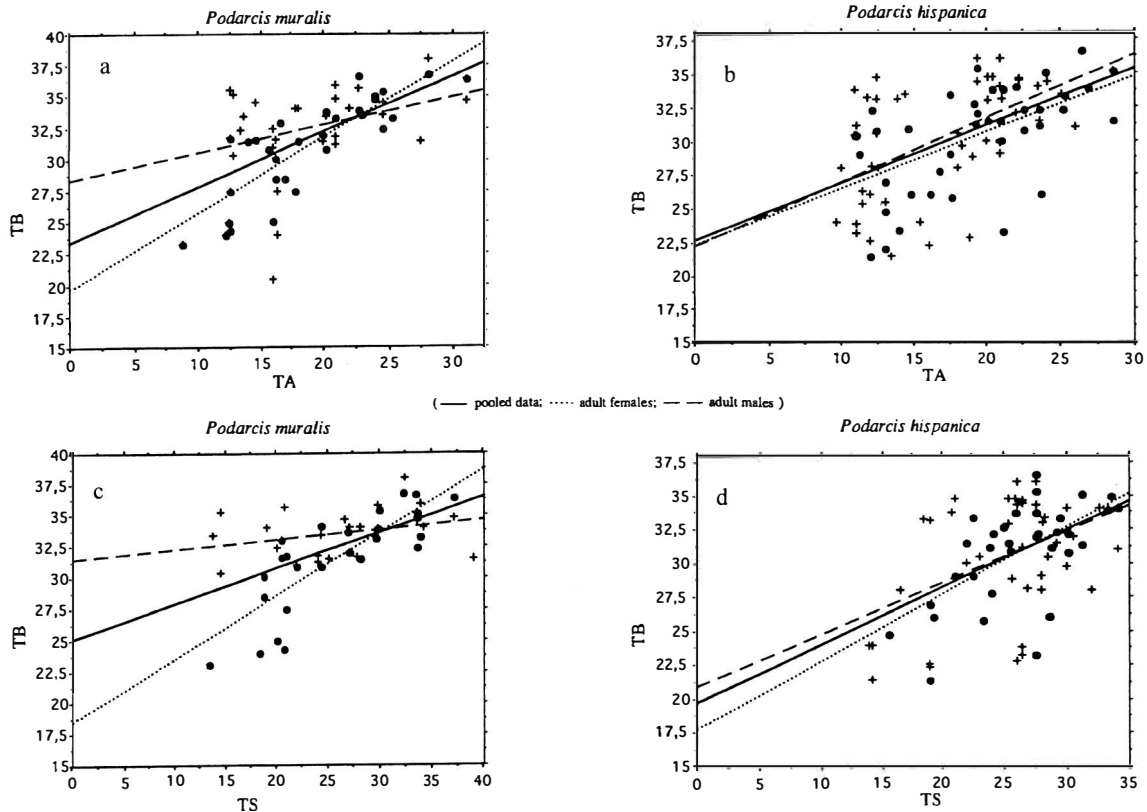
FIG. 2. Regression scatterplots of body temperatures (TB) on air (TA) and substrate (TS) temperatures. Dashes and crosses represent adult males, points and solid circles represent females, while solid lines show regressions after pooling the data of both sexes. Correlation coefficients and equations of regression lines are:

(a) TB/TA *P. muralis*: Males (r=0.30, TB=28.30 + 0.22 TA); females (r=0.83, TB=19.73 + 0.60 TA); pooled data (r=0.59, TB=23.47 + 0.44 TA).

(b) TB/TA *P. hispanica*: Males (r=0.52, TB=22.24 + 0.47 TA); females (r=0.55, TB=22.35 + 0.41 TA); pooled data (r=0.52, TB=22.65 + 0.42 TA).

(c) TB/TS *P. muralis*: Males (r=0.30, TB=31.55 + 0.08 TS); females (r=0.82, TB=18.50 + 0.50 TS); pooled data (r=0.58, TB=25.18 + 0.28 TS).

(d) TB/TS *P. hispanica*: Males (r=0.43, TB=20.92 + 0.38 TS); females (r=0.62, TB=17.79 + 0.50 TS); pooled data (r=0.50, TB=19.72 + 0.43 TS).

microhabitats of Central Europe and the xeric adaptation of *P. hispanica* in Mediterranean habitats (Arnold, 1987). Roughgarden, Porter & Heckel (1981) mention the importance of humidity as a variable favouring the thermoregulatory processes in some species. The presence of more mesophytic plant species in the talus indicates greater soil moisture, probably favouring *P. muralis*.

An alternative hypothesis could be that competition with *P. hispanica* is the primary determinant of the distribution of *P. muralis*, since the former species should exploit the rocky microhabitats, showing several ecomorphological traits specially adapted to crevice occupation (Arnold, 1987), i.e., a flattened head morphology (Pérez-Mellado & Galindo, 1986; García-Fernández, Martín-Vallejo & Pérez-Mellado, in prep.), which is thought to favour access to narrow shelters and crevices, as well as greater climbing abilities (Arnold & Burton, 1978; Arnold, 1987). A similar situation has been recorded in other areas of southern

Europe, where *P. muralis* occurs sympatrically with other lacertid species, e.g., in Greece, with *Podarcis erhardii* (Strijbosch, Helmer & Scohlte, 1989; and pers. obs.), and in the Balkans area with *Lacerta horvathi* (Arnold, 1987). In both cases, *P. muralis* restricts its microhabitat to soil dwellings in shaded zones, while the other species occupies sunny and rocky microhabitats.

Hence, our results would support the two hypotheses mentioned above, the second of which needs to be verified with an experimental design consisting of displacements of one species from the area (see, for instance, Nevo, Gorman, Soule, Yung Yang, Clover & Jovanovic, 1972). However, the restricted mountainous distribution of *P. muralis* in the Iberian Peninsula mentioned above could favour the acceptance of the first hypothesis of physiological constraints, indicating a residual situation of this rock lizard population at the very edge of the species' geographical range (Pérez-Mellado & Galindo, 1986).
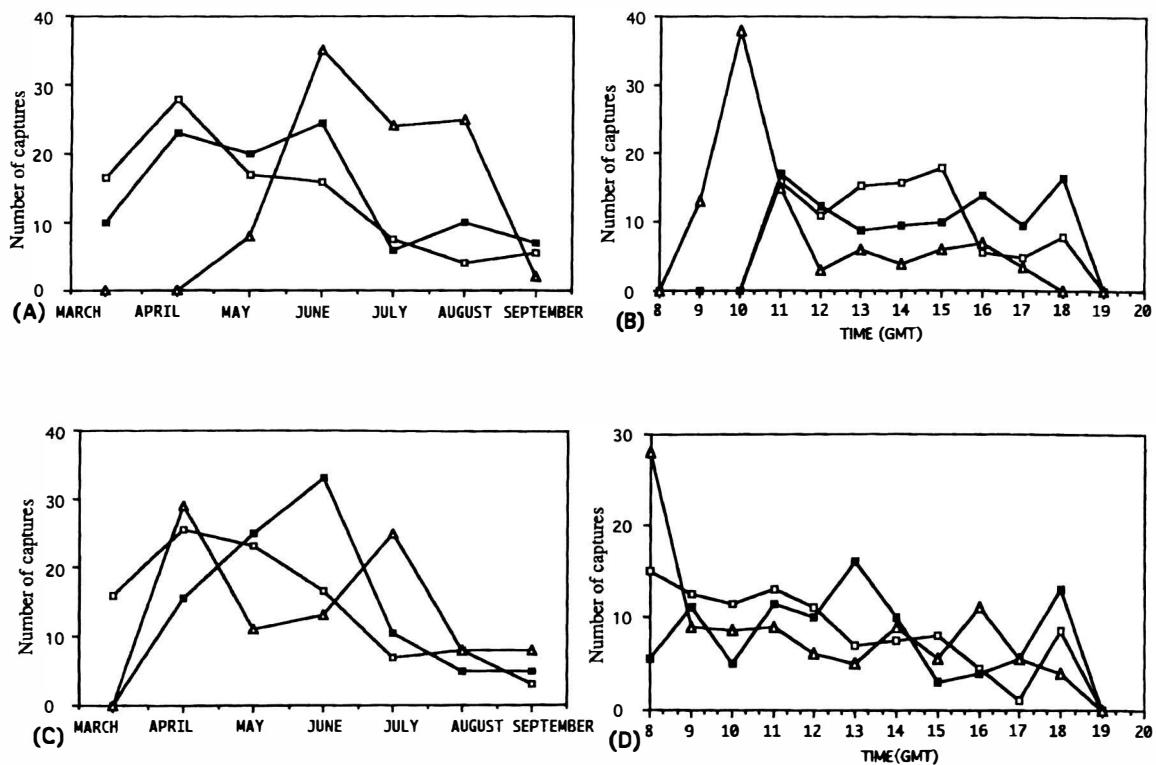
FIG. 3. Annual and daily activity rhythms of *P. muralis* (A and B) and *P. hispanica* (C and D). White squares represent adult males and black squares adult females, triangles stand for subadults.

THERMAL ECOLOGY AND ACTIVITY

The average TBs reported here for *P. hispanica* are somewhat lower than those recorded at lower altitudes (Pérez-Mellado, 1983*b*). These differences are not likely to be due to physiological changes, but rather to a slightly less effective thermoregulation; or to physical limitations derived from the higher altitudes, that would not let them achieve the TBs they exhibit at lower sites (van Damme, Bauwens & Verheyen, 1990).

FACTORS INFLUENCING THERMOREGULATORY PRECISION IN MALE *PODARCIS MURALIS*

Differences in TBs between two species could be due to differences in their thermal preferences or thermal physiology. In this particular situation, intraspecific differences in selected body or optimal temperatures have not been detected (Bauwens, pers. com.). Therefore, differences in TBs should not be due to physiological differences. Hertz & Huey (1981), van Damme *et al.* (1989, 1990) point out three possible behavioural causes to explain a greater independence from the environmental conditions in some reptiles: habitat shifts; increases in basking intensity; and changes in activity times.

However, the hypotheses concerning habitat shifts would be valid only for *Podarcis muralis* adult males, since females achieve a thermoregulation pattern similar to *Podarcis hispanica,* i.e., greater dependence on

environmental temperatures. If we still would consider a differential microhabitat use as a hypothesis to explain the interspecific variations we ought to verify whether males and females use space differently. We have not detected intraspecific differences in microhabitat selection in either of the two species (see results).

The second of the possible factors mentioned by van Damme *et al.* (1990) is an increase in basking intensity. Significant intra- or interspecific significant differences in the frequencies of various types of behaviour have not been detected, therefore this hypothesis would not be valid either to explain the thermoregulatory differences.

The third hypothesis explains the differences with changes in activity periods. *P. muralis* exhibits shorter activity periods than *P. hispanica,* which appears to be because the talus is less exposed to the sun (most talus areas are in shade during the first morning hours, from 8-11 hr). This could also explain the thermoregulatory imprecision of *P. hispanica,* i.e., it may sacrifice a higher thermal control for longer activity times (Bowker, 1986).

Another hypothesis is linked to food availability. Huey & Slatkin (1976) predict that increased habitat productivity should cause increased thermoregulatory benefits; in this sense, Lee (1980) affirms that in an environment with abundant trophic resources, lizards are expected to thermoregulate more precisely, since

the time inversion in feeding behaviours decreases. The mean number of available prey items per day (García-Fernández, Martín-Vallejo & Pérez- Mellado, in prep.), an estimate of the relative abundance of prey in the environment, is lowest in habitats occupied by *P. muralis*, which contradicts this hypothesis.

Finally, intraspecific differences in TBs found in *Podarcis muralis* could be due to differences in reproductive condition. More cryptic behaviour in females, related to the survivorship of themselves and their offspring could explain these differences, since they would invest less time in thermoregulation. The high reproductive effort made by females of this species, with very high clutch sizes (mode=8; unpub. data) could support this hypothesis. However, we found no differences in TB-TA regression slopes between gravid and non-gravid females of *P. muralis*. We therefore conclude that sexual differences in thermoregulatory precision in *P. muralis* are unlikely to be the result of possible behavioural modifications induced by the females reproductive condition.

The third hypothesis mentioned above (changes in activity periods) could likewise explain intraspecific differences in *Podarcis muralis*: adult males have greater frequencies of activity at midday (Fig. 3), while females exhibit more bimodalism with a greater presence at less thermally favourable hours. However, if we inspect the regression scatterplots, we notice that the points concerning these particular hours (with lower TA and TS), show higher TBs again in males. This, together with some occasional observations in the field, suggested a new hypothesis: adult males *Podarcis muralis*, because of their more aggressive and territorial behaviour (Boag, 1973; Mou, 1987; Edsman, 1990), would exploit small sunny patches at early times, when the talus is almost completely in shade, so that in the moment of capture, they could have already achieved high TBs. Magnuson, Crower & Medvick (1979) and Edsman (1990) report the influence of territoriality on the thermal ecology of lizard species, in the sense that dominant animals occupy the best basking sites to achieve high temperatures as soon as possible. In our study area, subadults begin their annual cycle in May, with the highest frequency occurring in June, possibly to avoid interactions with adult males that would exhibit intense territorial behaviour in the months dedicated to reproductive behaviour.

In summary, both species showed at the study site a similar thermal biology with only apparently slight interspecific differences linked to their different microhabitat selection and changes in activity periods. Microhabitat selection arises as a major factor in species segregation, but the observed pattern could be explained by several alternative hypotheses only testable within an experimental framework.

REFERENCES

Adolph, S. C. (1990). Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology* **71**, 315-327.

Arnold, E. N. & Burton, J.A. (1978). *A field guide to the Reptiles and Amphibians of Britian and Europe.* Collins, London.

Arnold, E. N. (1987). Resource partition among lacertid lizards in southern Europe. *J. Zool. Lond. (B)* **1**, 739-782.

Barbadillo, L.J. (1987). *La Guía de Incafo de los anfibios y reptiles de la Península Ibérica, Islas Baleares y Canarias.* Madrid, Incafo SA.

Blasco, M. (1980). Contribución al conocimiento de los lacértidos de Andalucía. *Monografías y trabajos del Dept. Zool. Univ. Málaga* 1- 81.

Boag, D. A. (1973). Spatial relationship among members of a population of wall lizard. *Oecologia* **12**, 1-13

Bowker, R. G. (1986). Patterns of thermoregulation in *Podarcis hispanica* (Lacertilia: Lacertidae). *Studies in Herpetology*, 621-626. Rocek, Z. (Ed.). Prague: Charles University.

Braña, F. (1984). *Biogeografía, biología y estructura de nichos de la taxocenosis de saurios de Asturias.* Tesis Doct Univ Oviedo.

Busack, S. D. (1977). Zoogeography of Amphibians and Reptiles in Cádiz Province, Spain. *Ann. Carnegie Mus. Nat. Hist.* 46 (17), 285-316.

Dunn, O. J. (1964). Multiple comparisons using range sums. *Technometrics* **6**, 241-252.

Edsman, L. (1990). *Territoriality and competition in wall lizards.* PhD Thesis, Department of Zoology, University of Stockholm.

Gosá, A. (1987). Las lagartijas del género *Podarcis* en la costa del País Vasco (Vizcaya, Guipúzcoaz y Lapurdi). *Cuad. Secc. Cienc. Nat. (Aranzadi)* **3**, 333-346.

Grant, B. W. & Dunham, A. E. (1988). Thermally imposed time constrains on the activity of the desert lizard *Sceloporus merriami. Ecology* **69**, 167-176.

Hertz, P. E. & Huey, R. B. (1981). Compensation for altitudinal changes in the thermal environment by some *Anolis* lizards on Hispaniola. *Ecology* **62**, 515-521.

Hillman, P. E. (1969). Habitat specificity in three sympatric species of Ameiva (Reptilia: Teiidae). *Ecology* **50(3)**, 470-481.

Hollander, M. & Wolfe, D. A. (1973). *Nonparametric statistical methods*. John Wiley & Sons, New York.

Huey, R. B. (1982). Temperature, physiology, and the ecology of reptiles. *Biology of the reptilia, vol 12*, pp 25-91. Gans C., Pough F. H. (Eds). London, New York: Academic Press.

Huey, R. B. & Slatkin, M. (1976). Costs and benefits of lizard thermoregulation. *Quart. Rev. Biol.* **51**, 363-384.

Lee, J. C. (1980). Comparative thermal ecology of two lizards. *Oecologia* **44**, 171-176.

Keppel, G. (1991). *Design and analysis: A researcher's handbook*. Prentice Hall.

Magnuson, J. J. Crower, L. B. & Medvick, P. A. (1979). Temperature as an ecological resource. *Amer. Zool.* **19**, 331-343.

Marquet, P. A. Ortíz J. C. Bozinovic F & Jaksic F. M. (1989). Ecological aspects of thermoregulation at high altitudes: the case of the Andean *Liolaemus* lizards in northern Chile. *Oecologia* **81**, 16-20.

Martinez-Rica, J. P. & Laplaza, E. (1989). Variaciones morfométricas y de folidosis en poblaciones vecinas de *Podarcis hispanica* y *Podarcis muralis* (Reptilia, Sauria), y su relación con la altitud. *Rev. Esp. Herp.* **3**, 159-172.

Moermond, T. C. (1979). Habitat constraints on the behavior, morphology and community structure of *Anolis* lizards. *Ecology* **60**, 152-164.

Mou, Y. P. (1987). *Ecologie comparée de deux populations de lezard des murailles,* Podarcis muralis *(Laurenti, 1978), en France* .- Thése de Doctorat de l'Univ. de Paris VI.

Nevo, E. Gorman, G. Soule, M. Yung Yang, S. Clover, R. & Jovanovic, V. (1972). Competitive exclusion between insular *Lacerta* species (Sauria: Lacertidae). Notes on experimental introductions. *Oecologia* **10**, 183-190.

Ouboter, P. E. (1981). The ecology of the island lizard *Podarcis sicula salfii*: Correlation of microdistribution with vegetation coverage, thermal environment and food-size. *Amphibia-Reptilia* **2**, 243-257.

Pérez-Mellado, V. (1983*a*). Alimentación de dos especies simpátridas de saurios en el Sistema Central. -*Studia Oecologica* **4**, 89-114.

Pérez-Mellado, V. (1983*b*). Activity and thermoregulation patterns in two species of Lacertidae: *Podarcis hispanica* (Steindachner, 1870) and *Podarcis bocagei* (Seoane, 1884).- *Cienc. Ecol. Syst. (Portugal)* **5**, 5-12.

Pérez-Mellado, V. & Galindo, M. P. (1986). *Sistematica de* Podarcis *(Sauria Lacertidae) ibéricas y norteafricanas mediante técnicas multivariantes.* Edic. Univ. Salamanca. 1-163.

Porter, W. P. & Tracy, C. R. (1983). Biophysical analyses of energetics, time-space utilization, and distributional limits. In *Lizard ecology. Studies on a model organism,* pp. 55-83. Huey R. B. , Pianka E. R., Schoener T. W. (Eds). Cambridge: Harvard Univ. Press.

Roughgarden, J. Porter, W. & Heckel, D. (1981). Resource partitioning of space and its relationship to body temperature in *Anolis* lizard populations. *Oecologia* **50**, 256-264.

Salvador, A. (1985). *Guía de campo de los anfibios y reptiles de la Península Ibérica, Islas Baleares y Canarias.* Santiago García - editor. León.

Strijbosch, H. Helmer, W. & Scohlte, P. T. (1989). Distribution and ecology of lizards in the Greek province of Evros. *Amphibia-Reptilia* **10**, 151-174.

Tellería, J. L. (1986). *Manual para el censo de los vertebrados terrestres.* Ed. Raíces, Santander.

Tracy, C. R. & Christian, K. A. (1986). Ecological relations among space, time, and thermal niche axes. *Ecology* **67**, 609-615.

van Berkum, F. H. Huey, R. B. & Adams, B. A. (1986). Physiological consecuences of the thermoregulation in a tropical lizard (*Ameiva festiva*). *Physiol. Zool.* **59**, 464-472.

van Damme, R. Bauwens, D. Castilla, A. M. & Verheyen, R. F. (1989). Altitudinal variation of the thermal biology and running performance in the lizard *Podarcis tiliguerta. Oecologia* **80**, 516-524.

van Damme, R. Bauwens, D & Verheyen, R. F. (1990). Evolutionary rigidity of thermal physiology: the case of the cool temperate lizard *Lacerta vivipara. Oikos* **57**, 61-67.

Vives-Balmaña, M. V. (1980). *Podarcis* Wagler, 1830 en Iberie Orientale et l'évolution du groupe en Méditérranée occidentale. *Journées Etud. System. et Biogegr. Médit. Cagliari* , 187-188.

Vives-Balmaña, M. V. (1982). El género *Podarcis* Wagler 1830 en el NE ibérico: diferenciación específica y distribución geográfica. *P. Cent. Pir. Biol. Exp.* **13**, 77-82.

Vives-Balmaña, M. V. (1984) *Els amfibis i els réptils de Catalunya.* Ketres, Barcelona.