Home range and habitat selection by *Podarcis hispanica* (Squamata, Lacertidae) in Western Spain

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A b s t r a c t . A population of the lacertid lizard *Podarcis hispanica* was studied in the Sistema Central Mountains in Salamanca Province, Spain. Lizards confined their activities to stable home ranges, but size range varied enormously between individuals. Home ranges generally contained 1) a high proportion of rocks > 100 cm in height and 2) a significantly higher abundance of crevices than expected. The overall abundance of lizards increased with decreasing amounts of shrubs and herbaceous plants cover and densities were highest in bare and rocky areas. Adult females selected particular habitat types according to the season, whereas habitat selection of males and juveniles did not differ between spring and summer. Non-resident adult lizards and juveniles occupied habitats of marginal quality in relation to crevice abundance.

Introduction

Animals are non-randomly distributed in space. In fact, heterogeneity in spatial resources determines habitat selection (L a w & B r a d l e y 1990). Animals respond to diversity in habitat resources by adopting selection strategies, which tend to increase their survivorship and opportunities for successful mating (W e r n e r et al. 1983, W e r n e r & H a l l 1988). Assuming equal availability (ratio of 1 to 1), disproportionate use of one resource over another is a demonstration of 'preference' for one over the other, with this preference exercised through the process of 'selection'. Therefore, it is necessary to identify the most significant features that are good habitat indicators, to determine which are used as cues by the animals, and to estimate their availabilities for the entire study habitat (K n i g h t & M o r r i s 1996).

Models of habitat selection commonly assume that higher quality source habitats will be occupied at higher densities than sink habitats (F r e t w e l l 1972, C l o b e r t et al. 1994). What are the cues on which squamates base habitat selection? Several have been identified: food abundance and its distribution (S i m o n 1975, W a l d s c h m i d t 1983, H e w s 1993), abundance of refuges for avoiding capture (S t a m p s 1983, C l a r k & G i l l i n g h a m 1990, P o u g h et al. 1998), and places with suitable conditions for thermoregulation (L a w & B r a d l e y 1990, C a s t i l l a & B a u w e n s 1991, D í a z et al. 1996, G r o v e r 1996).

Podarcis hispanica (Steindachner, 1870) (Squamata, Lacertidae) is a small (adult snout-vent length 37–70 mm) wall lizard whose distributional range is limited to the Iberian Peninsula, Southern France and North Africa. A complete description of this species and its geographical distribution can be found in P é r e z - M e l l a d o (1998) and B a r b a d i l l o et al. (1999). These lizards are able to regulate their body temperature (T_b) within relatively narrow limits during their active periods (D í a z et al. 1996). Behavioural

thermoregulation in *P. hispanica* is mainly characterised by the adoption of basking postures and shuttling between sun and shade (P é r e z - M e ll a d o 1983, D í a z et al. 1996). The preferred body temperature for our study species is 34.4 °C (B a u w e n s et al. 1995).

The aim of the present study was to assess the home range and habitat use of *P. hispanica*. We evaluated the habitat use of resident individuals in the study area as well as that of adult males introduced into the study area.

Material and Methods

The study was conducted at the western end of the Sistema Central of the Iberian Peninsula, at the Sierra de la Peña de Francia (1074 m a. s. l.), Salamanca, Spain (40° 31' 44" N, 06° 07' 10" W). This area comprised a granite afloration within an open mixed deciduous woodland dominated by oak *Quercus pyrenaica*. Vegetation in our study site was characterised by oak-bush and other scrub vegetation, like *Calluna vulgaris*, *Erica arborea*, *E. australis*, *E. umbellata*, *Lavandula stoechas*, and *Hallimium alyssoides. Agrostis castellana, Poa bulbosa*, and *Tuberaria guttata* dominate grassy areas.

The study was conducted during spring (25/05–30/05, 14/6–23/06) and summer (2/07–8/07, 4/09–13/09) 1991 in a 1500 m^2 plot within the study area, and divided into 25 m^2 quadrats. The National Institute of Meteorology (Territorial Meteorological Center of Castilla y León) provided climatic data from two weather stations up to 10 km from the study site. The maximum and minimum shade mean temperatures recorded in spring were 7.3 °C and 25.9 °C. Corresponding summer values were 12.2 °C and 30.1 °C, respectively.

Individual lizards were captured, marked, released and recaptured within the area. They were toe-clipped for permanent identification and painted with dorsal symbols to permit quick identification from a distance. Each specimen was determined for sex, measured for snout-vent-length (SVL, ± 1 mm), body mass (± 0.01 g), tail length and the presence of regenerated tail part was noted. Also, we measured body (cloacal = T_b), air (shaded bulb, 1 cm above substrate, = T_a) and substrate (shaded bulb, = T_s) temperatures to the nearest 0.1 °C with a thermocouple connected to an electronic thermometer (Digitron). Time and behaviour were also recorded for each sighting. We considered four behaviour categories: basking (dorsoventral flattening of the body and orientation perpendicular to the sun's rays), moving (locomotor activities), resting (voluntary inactivity periods in a protected and cool retreat) and other infrequent behaviours (prey capture, prey manipulation, and social behaviours), which were not included in the analyses (D i e g o - R a s i l l a & P é r e z - M e ll a d o 2000). Coordinates were determined to the nearest 0.1 m, using the point of initial sighting to the nearest grid marker. We established four categories of specimen: resident adult males, introduced adult males (see next paragraph), adult females, and juveniles (< 37 mm snout-vent-length).

At the beginning of summer 1991 (24/06) we introduced 29 adult males into the centre of the study plot, where the entire study was undertaken. The individuals had been captured from neighbouring areas approximately 6–7 km from the study site (D i e g o - R a s i l l a 1999).

Home range size was estimated as the area of the convex polygon that encloses all the capture locations for each individual (R o s e 1982). Polygonal home range area can only be calculated for lizards captured at least four times. The convex polygon method has a sample size bias when there is a low number of sightings (J e n n r i c h & T u r n e r 1969). In our study, polygonal home range estimates were based on an average of 7.5 sightings/individual during the spring and an average of 12.1 sightings/individual during the summer. Hence, we

corrected the estimates for sample size bias using the correction factors provided by J e n n r i c h & T u r n e r (1969). Fidelity to a home range, measured as the degree of area overlap between intervals (from spring to summer), was computed for all residents common to both periods. We computed the intersection of the two areas divided by the smaller of the areas (C o o p e r 1978):

Overlap = $[A_1 \cap A_2 / \min(A_1, A_2)]$ 100≥ K

A_1 = Home range area during the spring

A_2 = Home range area during the summer

K = Criterion to determine the presence of home range. We assumed fidelity to a home range when the degree of areal overlap between spring and summer was greater than or equal to K= 50 %.

Habitat use was characterised using one qualitative and one quantitative habitat variable: substrate type and height (bush, grass, sand, smooth rocks with no crevices, rock < 10 cm, rock 10–50 cm, rock 50–100 cm, rock > 100 cm), and number of crevices in every 25 m^2 square in which the plot was divided (0, 1–5, 6–10, 11–15, > 15 crevices). A map of the study area was constructed entering habitat shapes by keyboard in RANGES V software, an analysis system for biological location data (©K e n w a r d & H o d d e r 1996). The map was used to give estimates of habitat use/availability by those lizards to whom home range size were estimated. Thus, RANGES V gave us the opportunity to assess the entire map and estimate habitat type over the study area. Also, it assessed habitat in home ranges and at fixes during the same run. After the analysis was run, the display showed the preference or avoidance of habitat at fixes using J a c o b ' s (1974) improved version of Ivlev's electivity index, which ranges from -1 (avoidance) to +1 (preference): D = (r - p) / (r + p - 2rp), where D is the electivity value, r is the used proportion of that microhabitat category and p is the available proportion of that microhabitat category. However, this design does not address the critical question of why a home range was selected. J o h n s o n (1980) cautioned that comparing habitat use within home ranges may be misleading because in choosing a home range, the animal has already made an important selection. Thus, the researcher may be studying a higher order of selection than that intended and possibly not the most important one for management purposes (T h o m a s & T a y l o r 1990). Animals may select a home range because one resource is abundant. Use of this resource may appear low when compared to availability within the home range, but higher when compared to the general area from which the home range was selected. So, we examined available habitat within a radius of 0.5 m around every animal recapture point and we also estimated habitat availability in the entire study area in order to increase accuracy.

Food availability, absolute arthropod biomass, was measured using a 1 m^3 cubic frame, covered with a fine nylon mesh but with one open side (B r o w n & P é r e z - M e l l a d o 1994). During periods of lizard activity, the cube was placed at a randomly-selected point within each quadrat, which was selected pointing the finger in a random numbers table and counting 5 × 5 metre squares from 1 to the selected number from the table. This was repeated to provide a good coverage of the entire study area. An observer then inserted his head and upper body through a circular entry hole on one of the vertical sides of the cube and sealed the hole around the waist by means of an encircling cord. The nylon sides of the cube were trapped against the ground with sandbags to prevent arthropods from escaping. All arthropods trapped inside the cube were caught and frozen. Capture arthropods were later identified to order. Animals collected from each sample were dried to constant mass (at 65 °C) and weighed. Results are expressed as arthropod availability per m^2.

Statistical procedures

Pearson product-moment correlation, Spearman's rank correlation, ANOVA, Student-Newman-Keuls's *a posteriori* test, and the chi-square distribution were used to evaluate relationships, associations or differences among variables at 95 % statistical significance. Parametric statistics were used when the assumptions of the models could be reasonably met (S o k a l & R o h l f 1981). Test of homogeneity of variances (Levene test for homogeneity of variances) showed that in all cases variances were not significantly heterogeneous.

Bias-corrected estimates of home range areas were log-transformed (base 10) to achieve normality (S o k a l & R o h l f 1981). A two-way ANOVA on log-transformed estimates of residents home range areas was performed to test significant differences between seasons and between lizard categories. Differences in home range areas between lizard categories (residents and introduced) during the summer, were evaluated by means of analyses of variance (ANOVA).

We performed the analysis related to thermal properties of microhabitats used by lizards (T_s, T_a), T_b, and the types of behaviour lizards were engaged in, using just the first capture data of lizards, to avoid pseudoreplication.

A multivariate analysis of variance (MANOVA) was performed on air and substrate temperatures at the capture point. We previously tested the assumptions associated with this analysis: multivariate normality, homogeneity of covariance matrices and independence. We checked whether the thermal properties of sand substrate and rocks microhabitats differed. Therefore, we tested the null hypothesis that the thermal properties of the habitat (i.e., air and substrate temperatures) did not change across seasons or across microhabitat types used by lizards. Next we tested the null hypothesis that time intervals had no effect on different microhabitat thermal properties. We carried out multivariate tests of the hypothesis that season interacts with time intervals.

We used chi-square distribution to evaluate differences in microhabitat preferences of basking and moving lizards. The number of microhabitat categories was reduced (sand substrate, smooth rocks with no crevices, rocks < 50 cm, rocks > 50 cm) by pooling previous categories to achieve the assumptions associated with this analysis (S i e g e l 1956). Moreover, we used a chi-square distribution to assess microhabitat preferences of basking lizards. Only sand substrate and rocks microhabitats were included in this analysis because bush and grass microhabitats were too infrequent to be included.

We examined, through a 3-way ANOVA, whether T_b differed among resident lizards caught in different microhabitat categories, seasons and time intervals.

Microhabitat use may vary not only seasonally but also daily. Hence, we tested using a chi-square distribution, that the proportion of observed lizards at different time of day did not differ between spring and summer samples.

All statistical analyses were done with SPSS for Windows (Ver. 9.0.1).

Results

Home ranges

Bias-corrected estimates of home range areas were not significantly correlated with number of observations per lizard in either season (Pearson product-moment correlation; spring: $n = 23$, $r = -0.085$, $P = 0.698$; summer: $n = 78$, $r = -0.082$, $P = 0.473$). Observed home range area varied considerably among individuals in spring and summer (Table 1). Significant

differences in home range areas between seasons were found for resident animals, being greater during the summer ($F_{[1, 88]} = 4.260$, $P = 0.042$), but no significant differences were found between resident lizards categories ($F_{[2, 88]} = 0.210$, $P = 0.811$), nor interaction between these factors ($F_{[2, 88]} = 0.658$, $P = 0.521$). We did not find significant differences in home range size between lizards categories, including introduced adult males, during the summer (one-way ANOVA; $F_{[3, 74]} = 1.158$, $P = 0.332$).

Resident animals showed a high degree of area stability (Table 2). Thus, the degree of home range overlap between spring and summer was significantly higher than 50 % (chi-square distribution; $\chi^2 = 8.067$, $df = 1$, $P = 0.005$).

Table 1. Home range size (m^2) for *P. hispanica* in the Sistema Central Mountains, Spain, in 1991.

		Spring				Summer		
	n	$\bar{x} \pm SE$	Minimum	Maximum	n	$\bar{x} \pm SE$	Minimum	Maximum
Resident adult males	7	277.92 ± 50.87	113.45	467.88	25	482.08 ± 77.88	80.24	1819.06
Adult females	13	400.74 ± 78.77	53.13	1047.62	28	448.43 ± 61.09	112.96	1260.56
Juveniles	3	199.35 ± 38.22	122.93	239.25	18	495.11 ± 79.16	100.29	1321.76
Introduced adult males					7	891.09 ± 242.72	99.78	1807.61

Explanations: n, number of observations; $\bar{x}$, mean; SE, standard error

Table 2. Seasonal stability of area occupation by *P. hispanica* in the Sistema Central Mountains, Spain, in 1991. Percentage of home range overlap ≥ 50 was used as a criterion of fidelity to a home range.

Adult males		Adult females		Juveniles	
ID	% HRO	ID	% HRO	ID	% HRO
61316	100.0	61020	28.2	61516	95.7
61317	64.5	61318	52.1	70915	48.6
61820	76.2	61418	74.0		
60911	80.0	61419	56.7		
60917	91.9	61619	100.0		
70911	100.0	60918	68.6		
		71019	86.5		

Explanations: ID, identification number of the specimen; % HRO, percentage of home range overlap.

Thermal properties of microhabitats used by lizards

The thermal properties of habitat used did not differ between seasons (MANOVA; $F_{[2,193]} = 0.146$, $P = 0.865$) nor between microhabitat types (MANOVA; $F_{[10,386]} = 1.760$, $P = 0.066$). Thermal properties of microhabitat used by lizards varied significantly with respect to time of the day (MANOVA; $F_{[4, 386]} = 7.872$, $P < 0.001$). Differences between thermal properties of microhabitat used by lizards did not depend on microhabitat types in conjunction with season (MANOVA; $F_{[10, 386]} = 1.140$, $P = 0.331$) or time intervals (8:00–10:00 / 10:00–14:00 / 14:00–20:00) (MANOVA; $F_{[20, 386]} = 1.174$, $P = 0.273$). Thermal properties of microhabitat used by lizards across time intervals varied significantly according to season ($F_{[4, 386]} = 3.142$, $P = 0.015$). Moreover, we found that the thermal properties of sand substrate and rocks microhabitats used did not differ among resident lizards engaged in different behaviours

(MANOVA; $F_{[4, 432]} = 1.727$, $P = 0.143$). Lizard microhabitat use did not differ significantly when they were basking or moving (chi-square distribution; $\chi^2 = 1.678$, $df = 3$, $P = 0.642$). Moreover, lizards basked more frequently on some microhabitats (i.e., rocks > 10 cm in height having a higher number of crevices) than on others (chi-square distribution; $\chi^2 = 84.193$, $df = 5$, $P < 0.001$) (Table 3).

Table 3. Percentage of occurrence and frequency of resident lizards basking on different microhabitats of the Sistema Central Mountains, Spain, in 1991. Only the first capture data of lizards was used.

Microhabitat	Frequency	Percentage
Bush	2	1.1
Grass	1	0.6
Sand	20	11.5
Smooth rocks with no crevices	10	5.7
Rock < 10 cm	12	6.9
Rock 10-50 cm	68	39.1
Rock 50-100 cm	22	12.6
Rock > 100 cm	39	22.4

There was a significant difference between the animals' cloacal temperature (T_b) in different types of microhabitats ($F_{[5, 187]} = 4.315$, $P = 0.001$; Table 4). T_b was lowest on smooth rocks with no crevices and on rocks greater than 100 cm in height and highest on the other categories of rocky or sand substrates (Student-Newman-Keuls's *a posteriori* test, $P < 0.05$). The mean T_b of *P. hispanica* in spring was higher than the mean T_b in summer ($F_{[1, 187]} = 8.516$, $P = 0.004$; Table 4). There were also significant differences between time intervals ($F_{[2, 187]} = 8.313$, $P < 0.001$; Table 4), T_b was lowest at onset and middle of the day and highest during the rest of the day (Student-Newman-Keuls's *a posteriori* test, $P < 0.05$). Any differences between T_b do not reliably depend on microhabitat selected by lizards in conjunction with season ($F_{[5, 187]} = 0.346$, $P = 0.885$) or time intervals ($F_{[10, 187]} = 0.778$, $P = 0.650$), nor depend on season in conjunction with time intervals ($F_{[2, 187]} = 1.416$, $P = 0.245$). Finally, there was no interaction of microhabitat type with season and time interval ($F_{[7, 187]} = 1.058$, $P = 0.392$).

Also, we found that T_b did not differ among resident lizards engaged in different behaviours ($\bar{x}_{basking} = 30.11 \pm 0.20$ °C, $n = 174$; $\bar{x}_{moving} = 31.01 \pm 0.36$ °C, $n = 44$; $\bar{x}_{resting} = 31.66 \pm 0.63$ °C, $n = 5$), (one-way ANOVA, $F_{[2, 220]} = 2.755$, $P = 0.066$).

Habitat use and availability

The proportion of observed lizards at different time of day did not differ between spring and summer samples (adult females: $\chi^2 = 4.898$, $d.f. = 2$, $P = 0.086$; juveniles: $\chi^2 = 4.365$, $df = 2$, $P = 0.113$), except marginally significantly in resident males ($\chi^2 = 5.861$, $df = 2$, $P = 0.053$). Substrate height was positively correlated with abundance of crevices (Spearman's rank correlation; $r_s = 0.737$, $P < 0.001$).

Electivity values for spring revealed that lizards were highly selective (Fig. 1). Interestingly, no relationships were found between these electivities and the availability of habitat variables (resident adult males: $r_s = -0.531$, $P = 0.062$; adult females: $r_s = -0.358$, $P = 0.230$; juveniles: $r_s = -0.113$, $P = 0.713$). These data strongly suggest that the lizards were not selecting microhabitats because they were more abundant, but rather for some other reason.

Table 4. Summary statistics of lizard cloacal temperatures (T_b) (mean ± standard error; sample size in parentheses) in different microhabitat categories, seasons and time periods of the Sistema Central Mountains, Spain, in 1991.

Variables	T_b (°C)
Microhabitat	
Sand	31.20 ± 0.62 (24)
Smooth rocks with no crevices	28.88 ± 0.65 (12)
Rock < 10 cm	31.88 ± 0.49 (18)
Rock 10-50 cm	30.52 ± 0.25 (87)
Rock 50-100 cm	30.41 ± 0.43 (34)
Rock > 100 cm	29.03 ± 0.40 (45)
Season	
Spring	31.26 ± 0.25 (103)
Summer	29.45 ± 0.22 (117)
Time period	
8:00-10:00	29.81 ± 0.35 (30)
10:00-14:00	29.19 ± 0.28 (82)
14:00-20:00	31.27 ± 0.24 (108)

Resident adult males, adult females and juveniles preferentially occupied sites with rocks > 100 cm in height characterised by providing the highest number of crevices (>10 crevices per 25 m²). Also, rocks from 50 to 100 cm in height were avoided by adult females and juveniles, whereas this type of microhabitat was preferred by resident adult males (Fig. 1).

Electivity values for summer (Fig. 1) revealed that lizards were also highly selective. No relationship was found between electivities and availability of habitat variables, excepting adult females. Thus, resident adult males ($r_s = -0.534$, $P = 0.060$), juveniles ($r_s = -0.416$, $P = 0.157$), and introduced adult males ($r_s = -0.468$, $P = 0.107$) were not actively selecting habitat in relation to habitat variables abundance. Adult females ($r_s = -0.630$, $P = 0.021$) were actively selecting less abundant microhabitat variables.

During the summer, resident adult males and adult females used similarly habitat resources, differing from introduced adult males and juveniles (Fig. 1).

Mean arthropod density on the plot was 8.23 ind.m⁻² ($n = 73$, 95% confidence interval: 6.56 - 9.90 ind.m⁻²). Mean dry arthropod biomass was 29.17 mg m⁻² ($n = 73$, 95% confidence interval: 19.86 - 38.49 mg.m⁻²). Arthropods trapped ($n = 588$) were: Formicidae (22.62%), Homoptera (22.45%), Diptera (16.84%), Coleoptera (9.69%), Araneae (7.99%), Hymenoptera (6.46%), Heteroptera (5.78%), Orthoptera (5.10%), Lepidoptera (2.21%), Dyctioptera (0.85%).

Discussion

The overall abundance of lizards increased from areas with a dense cover of shrubs and herbaceous plants to bare and rocky areas in the Sistema Central mountains. Rocks were the most useful variable for distinguishing whether lizards were present or absent from a site. Rocks may be used as indicators of good basking conditions because they provide better thermal properties (thermally moderate and stable conditions) than grass or bush (B a u w e n s et al. 1996). However, only a narrow range of favourable basking sites was used, mainly rocks > 100 cm in height, which were more selected than smooth rocks with no crevices and rocks from 50 to 100 cm in height. Whereas other rocky microhabitats were not selected. The essential difference between these kinds of rocky substrata is the presence of crevices. Smooth rocks with no crevices and rocks from 50 to 100 cm in height provide fewer

refuges than rocks > 100 cm in height. Moreover, smooth rocks with no crevices could provide less refuge from predation since they lack shelters (G i l et al. 1988). This supports the habitat exploitation theory (T r a c y & C h r i s t i a n 1986), which predicts optimal patch selection when optimal and sub-optimal patches are equally accessible. Such a choice has a direct influence on an individual's fitness, therefore animals used sites having a higher number of crevices, possibly to reduce predation risk.

Structural features clearly play a major role in habitat selection of this species, as has been described in other reptile species (H e a t w o l e 1977, A d o l p h 1990, B a l t o s s e r & B e s t 1990, F r i e n d & C e l l i e r 1990, S h e n b r o t & K r a s n o v 1997), and are related to environmental characteristics. Thus, taller rocks, which have abundant crevices, were not only optimal sites for avoiding predation, but favourable basking sites (P é r e z - M e l l a d o 1983, G i l et al. 1988, D í a z et al. 1996). We found that T_b and thermal properties of sand substrate and rocks microhabitats used by lizards did not differ among residents engaged in different behaviours. Also, lizard microhabitat use did not differ significantly when they were basking or moving. However, available data do not allow us to assess thermal properties of particular microhabitats, since we obtained temperatures at capture points (i.e., microhabitats selected by lizards). Although the thermal properties of basking sites are important, presumably they choice basking places influenced by other factors too.

An animal basking to raise its body temperature, exposes itself to an increased risk of predation (H u e y 1974). Close access to a safe hiding place should be of great importance for survival (S c h a l l & P i a n k a 1980). Similarly, D o w n e s & S h i n e (1998) used habitat selection experiments with a rock-dwelling nocturnal gecko, *Oedura lesuerii*, to show that avoidance of predators was of greater priority than thermoregulation. Previous studies with *P. hispanica* from our study area revealed that the existence of rocky crevices appears to be the most important feature of its habitat (G i l et al. 1988). In fact, our population suffers from strong predation pressure (C a s t i l l a et al. 1999). Selecting the highest rocks, lizards can easily detect predators and rapidly seek cover, since these microhabitats offer the greatest number of crevices. Moreover, we frequently observed lizards basking a few centimetres from the entrance of the crevices, maintaining their bodies partially protected inside the hide. Also, crevices afford animals protection during inactive periods, when they may be vulnerable to predation (C l a r k & G i l l i n g h a m 1990). This resting behaviour is more frequent during the central hours of the day to compensate for the higher ambient temperatures (D i e g o - R a s i l l a & P é r e z - M e l l a d o 2000).

Some types of microhabitats were avoided, these electivities varying less than others, in particular zones covered by sand, bush or grass, that covered 43.3 % of the study site. Those areas with a dense cover of shrubs and herbaceous plants provided abundant trophic resources (D i e g o - R a s i l l a 1999), but food seems to be abundant throughout the site and would easily meet the low energetic needs of the lizards (P o u g h 1980, B r o w n et al. 1992, B r o w n & P é r e z - M e l l a d o 1994). Thus, their spatial distribution is not influenced by food resources as has been described in other saurian populations in which habitat selection was influenced by habitat structure but not by food abundance (R u b y 1986, E d s m a n 1990, M c C l o s k e y et al. 1990). Moreover, we have to consider the fact that sandy areas, and those with a dense vegetation cover are preferred by some lizard's predators, especially snakes (B e a & B r a ñ a 1998, G a l á n 1998, P l e g u e z u e l o s 1998).

The habitat preferences of adult female lizards varied according to season, but those of males did not. During spring, adult females preferred rocky areas (rocks > 100 cm), but
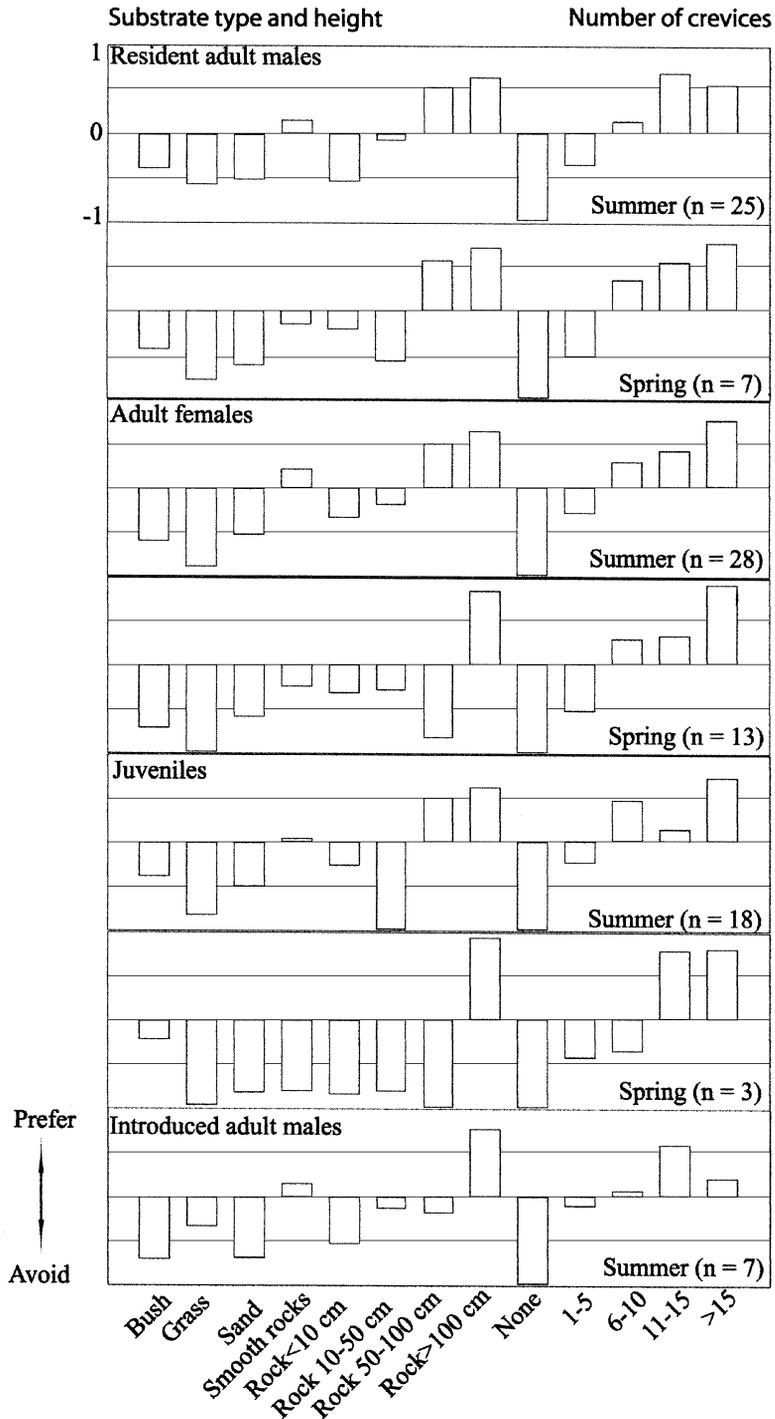
Fig. 1. Habitat preference of *P. hispanica* in the Sistema Central Mountains, Spain, in 1991. Electivity was calculated using J a c o b s ' (1974) version of Ivlev's index; values range from -1 (avoidance) to +1 (preference).

during summer their use of other rocky substrates increased. This shift may be explained by behavioural modifications related to reproduction. Pregnancy adversely affects locomotor performance and it is associated with changes in antipredator tactics, tending toward crypsis (S h i n e 1980, B a u w e n s & T h o e n 1981, B r o d i e 1989, C o o p e r et al. 1990, S c h w a r z k o p f & S h i n e 1992). Behaviours such as movement influence susceptibility to predators (B u r g h a r d t & D e n n y 1983). Hence, they avoid detection by a predator because they are cryptic, but rapid flight is the option of choice when they have been detected by a predator. Rapid flight is often toward crevices, which are abundant in rocks > 100 cm in height. So, they are optimal places for avoiding predation during gestation (spring).

Rocks > 100 cm in height were markedly selected by all lizard categories. Even those adult males brought into the plot from other areas preferred similar habitats to those of residents, as has been described in *Anolis* lizards (K i e s t e r et al. 1975). Levels of social interaction increased after introducing adult males (D i e g o - R a s i l l a & P é r e z - M e l l a d o 2000, 2001). High levels of social interaction might function to allow introduced adult males and juveniles to track resources by assessing the behaviour of neighbouring lizards (K i e s t e r & S l a t k i n 1974, S t a m p s 1987, 1988, G u y e r 1994). However, introduced adult males and juveniles occupied areas with fewer crevices than resident lizards and introduced adult males did not select rocks from 50 to 100 cm in height. They occupied habitats of marginal quality in relation to crevice abundance, perhaps because the best sites were already taken (C l o b e r t et al. 1994). Introduced adult males and juveniles were less competitive because they were not familiar with the habitat. Being familiar with the habitat, a lizard may also know the best places for basking, hiding and spending the night. Moreover, knowing the identity of other lizards in the area could save time, otherwise used in interactions, for activities such as feeding and basking (E d s m a n 1990, D i e g o - R a s i l l a & P é r e z - M e l l a d o 2000). Competitive ability may be a major determinant of success in settling into a new environment, because established residents usually have an advantage in competition for sites with new immigrants (L e i m a r & E n q u i s t 1984, C o o p e r & V i t t 1987, E d s m a n 1990).

L I T E R A T U R E

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