

Habitat selection in Iberian *Psammodromus* species along a Mediterranean successional gradient

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Abstract. Habitat selection of *Psammodromus algirus* and *P. hispanicus* was studied along a successional vegetation gradient in Southern Spain. The two species select areas with a high cover of herbs and bushes at ground level and at a height of 10 cm above ground. Whereas *P. algirus* avoids sandy substrates and selects wooded areas, *P. hispanicus*, which does not enter the forest, occupies areas with a denser cover of low shrubs and herbs. Therefore, and despite their coincidence in the centre of the habitat gradient and hence their high overlap in habitat use, both species appear to be segregated, with *P. hispanicus* having a narrower spatial niche than *P. algirus*. The observed differences in habitat selection are discussed in the light of differences in morphology, reproductive constraints and predator avoidance. We conclude that interspecific competition plays a negligible role in the habitat segregation of the two species.

Introduction

Members of the genus *Psammodromus* Fitzinger, 1826 are small-sized lacertid lizards with a Western Mediterranean distribution comprising NW Africa (Tunisia, Algeria and Morocco) and SW Europe (most of the Iberian Peninsula and Southern France). The two species inhabiting Europe (*P. algirus* and *P. hispanicus*) are fairly little known (though see reviews by Böhme, 1981; Salvador, 1981, 1985; Arnold, 1987 and Barbadillo, 1987), despite their broad distribution in the Iberian Peninsula and the abundance of *P. algirus* in many regions (Arnold and Burton, 1978).

Studies on lizard communities in which these two species occur sympatrically have been made by Pérez-Mellado (1982), Seva (1982) and Delibes and Salvador (1986); Mellado (1980) described the use of space by an assemblage of lizards which includes *P. algirus* but not *P. hispanicus*. Nevertheless, previous research does not focus on habitat selection mechanisms (the active choice of habitat rather than a passive presence in a habitat -Morse, 1980-; though see Seva, 1982 for a broad approach to habitat selection in a coastal sandy area). Delibes and Salvador (1986) discuss the habitats occupied by *P. algirus* and *P. hispanicus*, with very few observations, in an area



located near the Northern limits of their distributional ranges, where factors not related to habitat selection (environmental stress and considerable scarcity) can be important in determining the spatial distributional of the individuals. Pérez-Mellado (1982) describes their distribution in an enormous area of several thousand km²; this implies a large amount of climatic, floristic and geomorphological variability that generates a problem of scale, obscuring the expression of habitat preferences (see for instance Morris, 1984, 1987; Wiens, 1985 and Wiens et al., 1987). In addition, the above mentioned studies do not compare the use of habitats with their availability, an approach which is essential to reveal the variables responsible for a particular habitat selection pattern.

Considering the scarce and uncertain knowledge of the habitat preferences shown by *P. algirus* and *P. hispanicus* (see Arnold, 1987), the aim of this paper is to analyze the within-habitat distribution of both species, at a local scale, along a successional gradient in which they occur sympatrically. We compare the physical structure of the environment within the habitats chosen by both species with a random survey of the study area (habitat availability). This provides a pseudoexperimental approach (see James and McCulloch, 1985) to the analysis of habitat selection. We then examine interspecific differences in microhabitat use and morphology, and we discuss the biological traits that might provide a causal explanation for the observed patterns of habitat selection.

Material and methods

Study area.- Habitat selection was studied along a habitat gradient on the coast of Cádiz, Southwestern Spain (Chiclana de la Frontera; 30°26'N, 00°09'W). The study site occupied an area of sandy soil running 2 km parallel to the coast and 1 km towards the interior.

The vegetation gradient consisted of a well defined series of forest succession stages including a cleared mixed forest of *Pinus pinea* (84% of the trees) and *Quercus suber* (16%), a Mediterranean shrubland of intermediately sized bushes (*Cistus* spp, *Halimium* spp and *Genista* spp) expanding from the wood clearings towards the seashore, a xerophyte grassland with scattered low bushes (*Inula viscosa*, *Calluna vulgaris* and *Erica* spp), and a sand dune with bushes of *Juniperus phoenicia* (for more details on the physical structure of the study area, see the values of R in table 1).

Climate of the zone.- Mean annual temperatures are high (18°C; temperate winters and hot summers) and precipitation values reflect conditions of moderate summer drought (577 mm/year). During the month of April, in which the field work was carried out, mean temperature is 16.6°C, which a mean precipitation of 43 mm (data for 37 years taken from Elias and Ruiz, 1977).

Sampling methods.- Sampling was performed by walking in a randomly chosen direction for seven hours each morning and afternoon in April 1985. When a lizard

was first observed, two orthogonal 10 m transects were examined, intersecting at the point of initial sighting. The directions of the two survey lines were determined by the position of the sun upon the horizon in order to avoid sampling biases. A scored stick standing vertically on the ground was employed to note the presence or absence of herbs, shrubs and trees at different heights above the ground level. In this way, the presence of the habitat attributes listed in table 1 was noted at 1 m intervals along the transects. This provided an overall picture of the habitat, composed of 20 sample-points per lizard observations since the intersection point was not considered, that allowed the calculation of substrate and plant cover percentages. The same sampling design was employed at 113 randomly chosen spots that were used for comparison between availability and actual utilization of spatial resources. This survey method is similar to the point-centered method used in studies of bird habitat selection (see for instance James and Shugart, 1970; Noon, 1981 and Larson and Bock, 1986) and to those employed by Reagan (1974), Reinert (1984) and Scheibe (1987) with different reptilian taxa. Though this is a highly time-consuming technique (10-15 minutes per sample), it provides a detailed description of habitat structure based on the utilization of variables that can be universally considered (for instance vegetation cover). In addition, the sampling of surfaces rather than particular points (as it is the case in Pérez-Mellado, 1982) allows a better approach to the home range of the lizards (see Noon, 1981). Since there is a high probability of sampling a large proportion of the home ranges (see home range surface areas in Seva, 1982), biases due to the observation of basking individuals in exposed position, where they can easily be seen (Arnold, 1987), are expected to be minimal.

To avoid pseudoreplication (Hurlbert, 1984), which is expected if the same individual is repeatedly sampled in its own home range (not independent samples), all the considered observations are referred to a different individual lizard; the paths covered were separated by at least 50 m.

Although we considered initially 32 variables, we have employed only twelve for this study since many of the original variables were highly redundant (see Olóci, 1978). For instance, this is the case of the floristic composition of the scrubland, which is strongly associated with soil and plant structure attributes.

Morphology.- Morphological data were obtained from alcohol-preserved specimens deposited at the Museum of Vertebrate Zoology of the School of Biological Sciences at the Universidad Complutense of Madrid. The specimens, collected in different localities of Central and Southern Spain, belonged to the same subspecies inhabiting the study area. The variables considered were snout-vent length, hind limb length and tail length (the later was only measured on animals with unregenerated tails). To avoid body size effects, the two last mentioned biometrical variables were divided by snout-vent length (see Moermond, 1979 for a similar approach).

Data handling.- In the statistical handling of the data, the t-test for means was used to identify the habitat variables selected (either positively or negatively) by each species, and to find differences between the two species in the use of particular habitat

Table 1. Mean (\bar{x}) and standard deviation (sd) of twelve physical variables in the plots occupied by *Psammotromus hispanicus* (Ph) and *P. algirus* (Pa). R: random plots. p.c.: plant cover. ns: non-significant. +: $p < 0.1$. *: $p < 0.05$. **: $p < 0.01$. ***: $p < 0.001$.

	Ph		Pa		R		Ph-R	t-tests	
	\bar{x}	sd	\bar{x}	sd	\bar{x}	sd		Pa-R	Ph-Pa
cover of sand	49.4	29.7	33.8	33.5	50.2	40.2	ns	*	*
cover of litter	54.1	26.7	71.1	32.3	46.7	37.4	ns	***	ns
p.c. at the ground level	66.6	25.6	50.0	28.1	34.7	27.4	***	***	*
p.c. 10 cm in height	53.1	18.6	46.7	22.2	42.0	26.0	*	+	ns
p.c. 30 cm in height	20.6	14.9	23.2	17.4	22.6	17.7	ns	ns	ns
p.c. 50 cm in height	9.1	9.9	12.0	12.1	11.5	12.2	ns	ns	ns
p.c. 70 cm in height	5.6	7.7	6.3	8.0	5.5	7.8	ns	ns	ns
p.c. 90 cm in height	3.1	6.3	2.4	4.8	2.2	4.1	ns	ns	ns
p.c. 110 cm in height	1.6	4.0	1.2	2.9	0.5	1.7	ns	ns	ns
cover of trees	0	0	23.9	30.2	12.6	25.8	***	**	****
cover of herbs	70.6	22.9	62.2	25.7	53.6	30.5	**	*	ns
cover of bushes	50.3	23.8	39.4	24.3	32.8	32.5	**	*	+
sample size	16		71		113				

attributes. The original data were normalized by means of square root transformation (Sokal and Rohlf, 1969).

Patterns of covariation among the variables defining the microhabitats chosen by *P. algirus* and *P. hispanicus*, were revealed by a Principal Components Analysis (Cooley and Lohnes, 1971) run on the original matrix of habitat use. The resulting independent components offer a synthesis of the multidimensionality of the spatial niche (see Capen, 1981 and articles these presented; James et al., 1984 and Carrascal et al., 1987 for similar analyses) and allow an approach to the hutchinsonian spatial niche axes (Hutchinson, 1957). The initial factorial solutions were rotated by the Varimax procedure (Nie et al., 1975).

The extent of overlap in the situation of both species along the three components considered, was estimated using Maurer's index (Maurer, 1982) for continuous distributions.

Results

Habitat selection

Table 1 shows that both species select their position along the habitat gradient: eleven out of the 24 t-tests performed (five out of twelve for *P. hispanicus* and six out of twelve for *P. algirus*) reflect differences between availability and actual utilization of habitat variables at a significance level of 0.05.

P. algirus tends to avoid sandy substrates and selects available microhabitats with high percentages of litter cover, plant cover at the ground level, herbs, shrubs and

trees. There is also a marginally significant preference ($p = 0.065$) for the areas with highest plant cover 10 cm above the ground. Therefore, the areas selected by *P. algirus* are densely vegetated in the vicinity of the ground, have high percentages of litter cover and can be described as predominantly wooded (see table 1).

P. hispanicus strongly selects the microhabitats with the densest vegetation of herbs and shrubs at the ground level and 10 cm above the ground, avoiding the wooded areas.

In our study site, the cover of bushes higher than 10 cm has no effect on the habitat selection pattern of the two Iberian *Psammodromus* species. However, both species share a positive selection for the areas with high cover of plants lower than 10 cm.

Table 2 Principal components analysis with the physical variables describing the plots occupied by *P. algirus* and *P. hispanicus* (see table 1). Only correlations between variables and factors significant at $p < 0.001$ and with values of R^2 higher than 0.4 are shown.

	PC1	PC2	PC3
cover of sand			-0.75
cover of litter			0.65
p.c. at the ground level		0.85	
p.c. 10 cm in height		0.78	
p.c. 30 cm in height	0.73		
p.c. 50 cm in height	0.84		
p.c. 70 cm in height	0.88		
p.c. 90 cm in height	0.81		
p.c. 110 cm in height	0.65		
cover of trees			0.79
cover of herbs		0.78	
cover of bushes		0.75	
eigenvalue	3.40	3.16	2.02
% variance accounted for	28.32	26.60	16.84



Habitat axes and interspecific segregation

Although the two Iberian *Psammodromus* species are fairly similar in their habitat selection pattern, *P. algirus* and *P. hispanicus* are spatially segregated, since they differ significantly in the use of particular habitat variables. *P. algirus* is much more associated with trees than *P. hispanicus*, whereas the later species occupied sectors with higher sand cover and higher plant cover at the ground level than *P. algirus* (see table 1). The cover of bushes is higher in *P. hispanicus* at a marginal significance level ($p = 0.068$).

Since the variables employed to describe the habitat attributes show numerous significant intercorrelations (37 out of the 66 possible correlations among the twelve original variables are significant at $p < 0.05$), a Principal Components Analysis has been performed to obtain a few independent environmental components (table 2). We

have considered the three first factors, which account for 71.7% of the total variance.

The first factor (PC1) is a component of vegetation development at more than 30 cm above the ground, associated with an increase in the height and volume of the scrub canopy. PC2 reflects a gradient of increasing cover (density) of herbs and shrubs at, and up to 10 cm above, the ground level. PC3 separates the structurally simple sand dunes as opposed to the more complex wooded areas with soils covered by litter.

In the first factor, the situations of *P. algirus* and *P. hispanicus* do not differ significantly, being both species overlapping completely (see fig. 1). Although the overlap is still high along the second factor (gradient of increasing density of vegetation lower than 10 cm), this gradient is partially responsible for the segregation of the two species, since *P. hispanicus* is significantly more displaced than *P. algirus* ($p < 0.05$ in the t-test) towards the extreme with highest vegetation densities. The "forest gradient" (PC3; high sand cover *vs* high litter and tree cover -see table 2-) is the one that contributes the most to interspecific segregation ($p < 0.001$ in the t-test); despite the relatively high overlap value, it is made clear that *P. hispanicus* shows a tendency to occupy unwooded areas and to avoid entering the mixed forest.

The whole overlap in the habitat preferences between the two species, which has a value of 69%, has been estimated by the product of the particular overlaps in each of the three components, since these components are, by definition, independent (May, 1975, 1981).

Spatial niche breadth

The spatial niche breadth of each species has been measured by the product of the corresponding standard deviations along the three spatial axes considered; the spatial niche of *P. algirus* (1.08; see the values of SD in figure 1) appears to be broader than that of *P. hispanicus* (0.44). *P. hispanicus* has a more restricted distribution than *P. algirus* along the gradients in which interspecific segregation occurs (PC2 and PC3; $p < 0.05$ in both F-tests). In addition, whereas *P. algirus* exhibits a similar variance in the three axes ($p > 0.1$ in the three F-tests performed), *P. hispanicus* shows a smaller variance (and hence a greater selectivity; $p < 0.05$ in both F-tests) in PC2 and PC3 than in PC1; i.e. *P. hispanicus* carefully selects the sites with a dense low vegetation established on sandy substrates, thus decreasing its overall spatial niche breadth. These results conform the negligible role of shrub height in the habitat segregation of both of *Psammodromus*.

Morphological differences associated with habitat selection

In lizards, there is a consistent pattern of association between the relative length of the hind limbs and the degree of utilization of open spaces (Pianka, 1969, 1986; Moermond, 1979). Thus, long hind legs facilitate running, jumping and escape in structurally simple environments, whereas they make locomotion difficult within densely



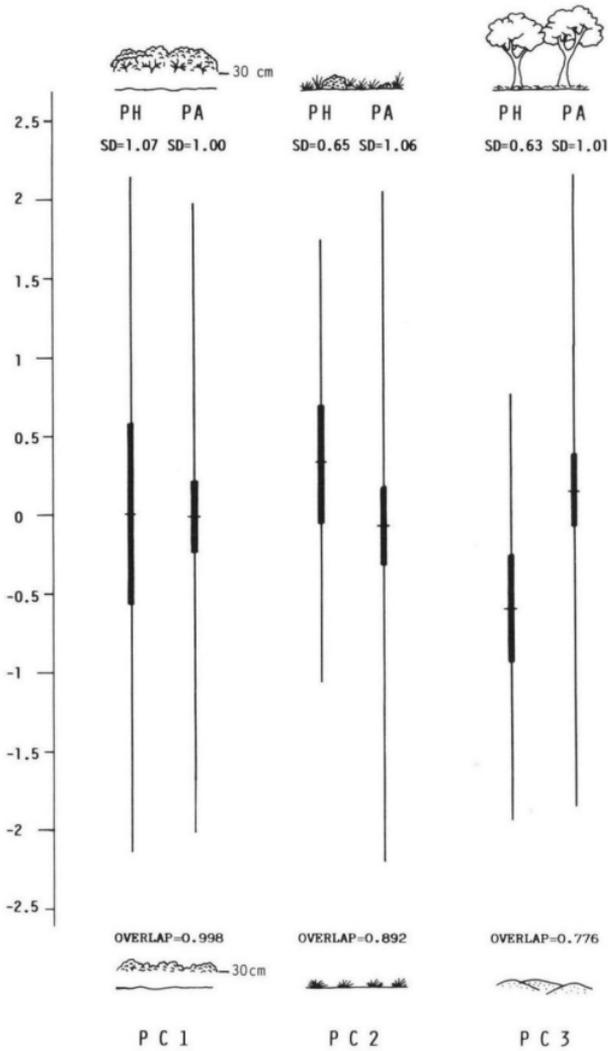


Figure 1. Locations of *P. algirus* and *P. hispanicus* along the three Principal Components (PC1, PC2 and PC3) described in table 2. Bars indicate the 95% CI around the sample means and thin lines indicate the intervals containing 95% of the individual observations. Standard deviations (SD) and overlap values are also shown.

vegetated areas. Therefore, it could be expected that *P. algirus*, which occupies forest and scrubland sectors with a lower density of vegetation at the ground level, should have longer hind limbs (relative to snout-vent length) than *P. hispanicus*. This should also be useful for jumping vertically (approximately 15% of the observed individuals were perching on branches when first sighted; see Díaz, 1988 for a similar result at a hom-oak forest). Similarly, a longer tail, which can be useful for balance during jumps, is expected in *P. algirus*. Figure 2 shows that *P. algirus* actually has relatively longer hind limbs and tail than *P. hispanicus* ($p < 0.001$ in both t-tests).

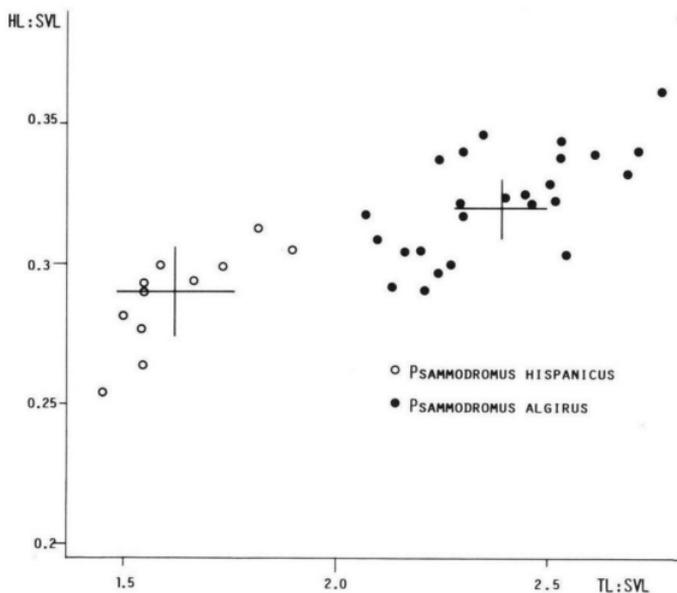


Figure 2. Mean and 99% CI for the relative values of hind limb length (HL) and tail length (TL) in *P. algirus* (dots) and *P. hispanicus* (circles). SVL: snout-vent length.

Discussion

Lacertids of the genus *Psammodromus*, which have a restricted Mediterranean distribution (Arnold, 1973), show a habitat selection pattern dominated by the tendency to occupy areas with a dense vegetation of herbs and shrubs in the vicinity of the ground (see also Arnold, 1987). Nevertheless, the two Iberian species (*P. algirus* and *P. hispanicus*) differ in their abundance and in the amplitude of their distribution range. Thus, the distribution range of *P. algirus* spans all the Mediterranean region of the Iberian Peninsula, where it can be found, within a wide range of altitudes, in holm-oak woods, oak woods, groves and a great variety of shrublands. On the other

hand, *P. hispanicus* is only locally abundant and reaches lower altitudes and latitudes than *P. algirus* (Salvador, 1985; Barbadillo, 1987; pers. obs.). These broad geographic trends are consistent with our results on the habitat selection patterns of both species along a successional gradient (local scale): *P. hispanicus* is about four times scarcer than *P. algirus* (16 vs 71 observed individuals) and has a considerably smaller habitat breadth. This difference in abundance and spatial niche breadth (both at local and geographic levels) should be related to the scarcity of the habitats potentially occupied by *P. hispanicus* (extensive sandy areas with a high cover of plants lower than 10 cm), since the probability to find loose soils suitable for the development of a dense vegetation of herbs and shrubs, is fairly small in Mediterranean environments.

The range of habitats occupied by *P. algirus* includes those occupied by *P. hispanicus* and others in which the later species does not occur (see fig. 1). It can be stated that the distribution of both species overlaps strongly; nevertheless, the two species differ in the extent to which they are constrained by particular habitat requirements (a majority of the areas inhabited by *P. hispanicus* are suitable for *P. algirus*, but not conversely). It is consistent with our results that *P. algirus* is the most common lizard in many regions of the Iberian Peninsula (Arnold and Burton, 1978) and seems to be expanding its distribution range in the Pyrenean mountains (Bauwens et al., 1986), whereas *P. hispanicus* appears to be much more scarce, with high population densities occurring only locally.

Cover of bushes higher than 10 cm above the ground has a negligible role on the habitat selection and segregation patterns of both species (though see Arnold, 1987 for an impression of the importance of bush cover above 10 cm in determining the habitats of the two species). This implies that the main habitat cues for the presence of either species are to be found at the ground level or its immediate surroundings. The association of *P. algirus* with wooded areas, for instance, should be considered as resulting from related edaphic attributes (consistently structured soils with a high cover of litter; see table 1) rather than emerging from attributes of the tree canopy itself.

Interspecific differences in habitat selection can be causally interpreted by considering ecomorphological associations, tactics of predator avoidance and reproductive constraints. Thus, the fact that *P. hispanicus* lays its eggs at a soil depth of about 40 cm (Salvador, 1981) might be responsible for its occupation of sandy, loose substrates and for its avoidance of Mediterranean wooded areas with compactly structured soils. Burrowing ability, developed by *P. hispanicus* but not by *P. algirus*, could also be important for predator avoidance in loose surfaces (Salvador, 1981 and personal observations). A peculiar feature of the morphology of *P. hispanicus* is the presence of double keeled subdigital lamellae (Arnold, 1973 and Salvador, 1981), these structures being absent in *P. algirus*. Double keeled subdigital lamellae can be considered adaptive for locomotion on/and within sand (though see Arnold, 1973 for an alternative explanation based on thermal requirements). In addition, densely vegetated areas with a complex structural arrangement could serve as predator refuges (Stamps, 1983) in otherwise open



spaces. In the study area, the raptors *Falco tinnunculus* and *Lanius excubitor*, which usually prey on small lizards (Valverde, 1967), were frequently seen. The low escape speed of *P. hispanicus* (pers. obs.), consistent with its small size (mean snout-vent length = 43 mm; see Avery et al., 1987) would favour its permanence within densely vegetated areas, in which short limbs facilitate locomotion (see for instance Pianka, 1986). On the other hand, *P. algirus*, which is a larger and more rapid species, has relatively longer hind limbs and tail. Besides being useful for jumping within the shrub canopy, this would allow faster (and safer) locomotion between adjacent vegetation patches, in sectors with a lower plant cover at the ground level.

Interspecific competition is considered as a factor which interacts with habitat preferences to produce natural distributions (Partridge, 1978; More, 1980 and review by Schoener, 1983; though see Connell, 1983). Nevertheless, competition does not seem to determine the within-habitat distribution of the species studied herein, since there is a high overlap of *P. algirus* and *P. hispanicus* along the habitat components considered. Both species consume similar prey items (see Pérez-Mellado, 1982; Seva, 1982; Pascual and Pérez-Mellado, 1987 and Díaz, 1988), do not present marked differences in times of activity during the day (Cano, 1984) and food is not limiting in their territories (Díaz, 1988). Therefore, it can be stated that competition seems to play a negligible role in the interspecific habitat segregation of these species. The observed differences in habitat preferences can be explained by considering species-specific habitat adaptations (locomotion, reproductive and defensive behaviour; see Vitt et al., 1981 for a similar conclusion). Nevertheless, more experimental effort is required in order to integrate the role played by interspecific competition between these two species with other ecological factors (see Haila, 1982; Pianka, 1986 and Tilman, 1987).



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