

Habitat preferences of two sympatric lacertids in the Ebro Delta (NE Spain)

MIGUEL A. CARRETERO & GUSTAVO A. LLORENTE

Introduction

HEATWOLE (1977) defined habitat selection as "the interactive expression of responses which tend to maintain the association of an animal with a particular type of habitat". Saurians are not uniformly distributed in the space but preferably associated to some combinations of external factors, the fluctuations in which should be small enough to be recognized as environmental cues. Space has been considered as the main niche dimension in the segregation of many lizard communities (PIANKA 1966, 1973, BARBAULT & MAURI 1981, TOFT 1985, GONZÁLEZ-ROMERO et al. 1989, PÉREZ-MELLADO 1992) including those inhabiting the Mediterranean Basin (VALVERDE 1967, MELLADO 1980, MELLADO et al. 1975, PÉREZ-MELLADO 1982, ARNOLD 1987, STRIBOSCH et al. 1989). However, other studies seem to indicate the opposite idea (SEVA & ESCARRÉ 1980, SEVA 1984, POLLO & PÉREZ-MELLADO 1992). Scale changes may be important (MENGE & OLSON 1990). As to the spatial niche, the scale ranges between the boundaries of the biogeography and the ecology (ANTÚNEZ & MÁRQUEZ 1992). Consequently, some parameters which are important for the species in great areas may change when they are studied in smaller ones.

The dune ecosystems represent initial successional stages among the Mediterranean ecosystems (MARGALEF 1974), but they also show internal sea-land gradients. Thus, the plant cover and the vertical dimension of the vegetation are extremes when compared with other large scale studies. *Psammodromus algirus* (Large Psammodromus) and *Acanthodactylus erythrurus* (Fringe-toed Lizard) are two ground dwelling lacertids of medium-size. They live together in many open Mediterranean type biotopes of the Iberian Peninsula (BARBADILLO 1987) including the coastal sandy areas, where they are especially abundant (SEVA 1984). This study is a part of a wider survey on the ecology of these species conducted in one of these areas. Results of previous studies indicated that *A. erythrurus* followed a conservative strategy in comparison with *P. algirus* with regard to the trophic ecology (CARRETERO & LLORENTE 1993a), the thermal and temporal relations (CARRETERO & LLORENTE 1995b) and the life history traits (CARRETERO & LLORENTE 1995a). Some evidence of relaxation of trophic competition was detected (CARRETERO & LLORENTE 1993a) and that the ecological differences were mostly due to morphological and historical constraints (CARRETERO & LLORENTE 1993a, 1993/94). This study attempts to analyze the role of the spatial features in this species tandem and to determine the degree of inter- and intraspecific segregation.

Material and methods

The study was carried out in the delta of the Ebro river (NE Spain). The Riomar area (UTM 31TCF1810) is a mosaic of dunes and some saline depressions periodically covered by water which is sited at the north side of the river mouth. The vegetation consists of psammophile and halophile plant associations (see CAMARASA et. al. 1977 and CURCÓ 1990 for a complete phytosociological description). The climate is littoral Mediterranean, with a long dry season in summer (mean annual rainfall = 548 mm, mean temperature = 16.6°C; see PANAREDA & NUET 1973).

Psammodomus algirus and *Acanthodactylus erythrurus* are the only saurian species living in this area (abundance ratio: 2:1). Only two size classes (adult and immature) were distinguished for each species since both attained sexual maturity mostly in their first calendar year (see CARRETERO & LLORENTE 1993/94, 1995a, for the limit sizes of the classes). Only the immature *P. algirus*, the least thermophile species, remain active throughout the year while the rest of the classes show a winter diapause period (CARRETERO & LLORENTE 1995b).

Monthly sampling was carried out from March 1988 to February 1989 on 100 % sunny days without strong wind. An area of 0.35 Ha (35 x 100 m) containing a representative composition of the habitat was delimited. This rectangle was uniformly surveyed (CARRETERO & LLORENTE 1995b) for 30' each hour with walking at constant speed in search at active lizards throughout the period of daily and annual activity (from 6 to 18 hours GMT during all the year). Prospection effort was kept constant for hours and months (TELLERIA 1986). The species, the sex and the size class were determined when possible for each lizard observed during the transects. Several environmental variables (for whose semi-quantitative or qualitative states had been defined) were also registered in the exact place of the first sight of the animal. The variables and its corresponding states were the following:

BI = Associated biotope (moving dune / fixed dune / dune back / saline depression).

C20 = Lizard climbing higher than 20 cm over the ground level (yes/no).

SU = Substratum type (SU1 = loose sand / SU2 = compact sand and slime / SU3 = dead leaves and vegetation).

SL = Ground slope measured with a clinometer (SL1 = 0-10° / SL2 = 10-30° / SL3 = > 30°).

CO = Plant cover. Percentage of surface covered by vegetation within a radius of 3m from the observation point (CO1 = 0-25 % / CO2 = 25-50 % / CO3 = 50-75 % / CO4 = 75-100 %).

VH = Vegetation height. Mean height of the plants within a radius of 3 m from the observation (VH1 = 0-10cm / VH2 = 10-20cm / VH3 = 20-50cm / VH4 = > 50cm).

PS = The closest plant species to the observation point, which could provide shelter (PS1 = *Ammophila arenaria* / PS2 = *Teucrium polium* / PS3 = *Echinophora spinosa* / PS4 = *Thymelaea hirsuta* / PS5 = *Juncus* spp. / PS6 = *Eryngium maritimum* / PS7 = weedy vegetation / PS8 = *Thymus maritimus*).

PD = Distance from plant shelter (PD1 = 0-25 cm / PD2 = 25-50 cm / PD3 = 50-100 cm. / PD4 = > 100 cm).

Because of the limited time available, only C20 was registered at the same moment of the observation. The rest of variables were registered *a posteriori* since each observation point was marked by a small numbered flag.

The variables were analyzed at two different levels: macrohabitat, referred to BI, and microhabitat, which included the rest of the variables. Univariate comparisons were performed through chi-square tests and exposed when significant. When several tests were evaluated simultaneously the sequential Bonferroni adjustment was used (HOLM 1979, modified by RICE 1989). In the multivariate study, the Multiple Correspondences Factorial Analysis (MCFA, LEBART et al. 1984, 1985) was used to represent both, individuals (or populations) and categorical variables simultaneously (BISQUERRA 1989). The estimations of the variance explained by the factorial axes were calculated from the transformed eigenvectors by the Benzecri method (BENZECRI 1979). This method is more accurate than the standard one which often underestimate the variance explained (BISQUERRA 1989).

Macrohabitat overlap was calculated applying Schoener's index (SCHOENER 1968) following LINTON et al. 1981. Conversely, Maurer's index (MAURER 1982) for continuous variables was used to calculate the microhabitat overlaps:

$$S = \frac{2 s_1 s_2}{\sqrt{s_1^2 + s_2^2}} e^{-\frac{d^2}{2(s_1^2 + s_2^2)}}$$

... where s_1 and s_2 were the standard deviations of groups 1 and 2 and d was the difference between the means of both groups. This index was applied to the values of the projections on the factorial axes. Then, since the two axes are orthogonal, both results were multiplied to give the total microhabitat overlap (PIANKA 1974, CANO & CARRASCAL 1986). Finally, the summative and multiplicative matrices (MAY 1974, PIANKA 1974) were calculated from those of the two subdimensions in order to obtain the global habitat overlap.

Results

The number of individuals sighted by species and class considering the different variables and categories is shown in table 1. Since no intersexual differences were detected in any case (χ^2 tests, $p < 0.01$ Bonferroni corrected in all cases), adult males and females were grouped for the subsequent analyses. So, henceforth the comparisons were performed using the adult class, which included not only these two groups but also those adult individuals whose sex could not be determined.

Macrohabitat

Significant differences between the two species globally considered were found in the occupation of the four structural units ($\chi^2 = 55.7$, 3 d.f., $p = 4.48 \cdot 10^{-7}$). *A. erythrurus* was mainly observed in the dunes. Conversely, *P. algirus* was found more uniformly than the former in the four units, including the saline depression (when dry), where it was observed in great numbers. However, the moving dunes were avoided by this species. Considering the size classes, the differences between adult and immature *P. algirus* were scarce, only the latter occupied the dune backs more frequently. Conversely, strong differences were re-

gistered in *A. erythrurus* since immatures used the dunes more than the rest of classes and adults were observed in a high percentage in the saline depression (see tab. 1).

Var. state	<i>P. algirus</i>					<i>A. erythrurus</i>					Lacertidae
	♂♂	♀♀	ad. ¹	im.	total	♂♂	♀♀	ad. ¹	im.	total	
BI mov. dune	3	0	4	5	9	1	1	2	24	26	35
fixed dune	6	10	16	34	50	6	3	10	45	55	105
dune back	2	3	8	47	55	2	0	4	5	9	64
saline dep.	8	10	26	61	87	6	3	11	15	26	113
SU sand	9	11	22	54	76	9	4	16	72	88	164
compact	9	11	29	87	116	6	3	11	16	27	143
vegetation	1	1	3	6	9	0	0	0	1	1	10
SL 0 - 10°	15	14	39	108	147	11	5	20	44	64	211
10 - 30°	2	6	10	25	35	2	1	4	23	27	62
> 30°	2	3	5	14	19	2	1	3	22	25	44
CO 0 - 25 %	14	14	33	101	134	10	3	17	79	96	230
25 - 50 %	3	9	16	33	49	5	4	10	10	20	69
50 - 75 %	2	0	5	10	15	0	0	0	0	0	15
75 - 100 %	0	0	0	3	3	0	0	0	0	0	3
VH 0 - 10 cm	2	6	8	20	28	0	0	0	19	19	47
10 - 20 cm	4	5	11	39	50	5	1	8	49	57	107
20 - 50 cm	4	5	11	53	64	3	2	7	13	20	84
> 50 cm	9	7	24	35	59	7	4	12	8	20	79
PS <i>A.arenaria</i>	2	2	4	18	22	0	1	2	14	16	38
<i>T. polium</i>	2	1	3	6	9	0	0	0	5	5	14
<i>E. spinosa</i>	1	1	2	2	4	1	1	2	19	21	25
<i>T. hirsuta</i>	1	2	4	11	15	5	2	8	6	14	29
<i>Juncus</i> spp.	10	13	34	94	128	7	3	12	21	33	161
<i>E.maritimum</i>	0	0	0	1	1	0	0	0	3	3	4
weedy veg.	0	4	4	12	16	2	0	3	19	22	38
<i>T. maritimus</i>	3	0	3	3	6	0	0	0	2	2	8
PD 0 - 25 cm	14	18	42	141	183	11	5	19	80	99	282
25 - 50 cm	3	3	8	2	10	2	2	5	4	9	19
50 - 100 cm	0	0	0	2	2	0	0	1	2	3	5
> 100 cm	2	2	4	2	6	2	0	2	3	5	11
Total	19	23	54	147	201	15	8	28	89	117	318

Tab. 1. Number of lizards by species and classes seen associated with the macro- and microhabitat categories in the Ebro Delta. ¹ Also including those adult individuals whose sex could not be determined.

Microhabitat

Climbing capacity - Amongst the variables measured, C20 was deleted from the analysis because of its low discrimination. Thus, only four individuals (2 adults and 2 immatures), all belonging to the species *P. algirus*, were observed climbing.

Substratum type – As expected, sand was the main substratum used. However, significant differences between *P. algirus* and *A. erythrurus* were found ($\chi^2 = 47.22$, 2 d.f., $p = 4.68 \cdot 10^{-10}$). *P. algirus* was more frequently sighted on sandy soils whereas *A. erythrurus* often occupied compact sustrata. The former species was the only one that was significantly found on vegetation.

Ground slope – Both lizards were found on sligth gradients but some inter- and intraspecific differences were found. *P. algirus* used steeper slopes than *A. erythrurus* ($\chi^2 = 14.15$, 3 d.f., $p = 1.82 \cdot 10^{-3}$) and the immatures of the former species were found on lower slopes than those of the latter ($\chi^2 = 17.81$, 3 d.f., $p = 4.32 \cdot 10^{-4}$). No other significant differences were found.

Plant cover – The general cover was always low in all cases but significant differences between the two species were found ($\chi^2 = 12.05$, 3 d.f., $p = 2.05 \cdot 10^{-3}$). So, *P. algirus* occupied all the degrees of plant cover while *A. erythrurus* was limited to the most open areas. Furthermore, the immatures of the latter species were found in areas with less vegetation than any other class (χ^2 tests, 3 d.f., $p < 0.01$).

Vegetation height – The lizards were preferably found in association to vegetation between 10 and 50 cm. Interspecific differences were significant ($\chi^2 = 15.11$, 3 d.f., $p = 3.33 \cdot 10^{-5}$) since *A. erythrurus* was scarcer than *P. algirus* close to medium and large plants. Moreover, immature *A. erythrurus* were found in more significant association to lower plants than the rest (χ^2 tests, 3 d.f., $p < 0.01$).

Closest plant species – This variable was an important factor discriminating species and classes. So, *P. algirus* and *A. erythrurus* used different plant species ($\chi^2 = 64.32$, 7 d.f., $p = 4.47 \cdot 10^{-7}$). *P. algirus* was found in association to grasses (*Ammophila arenaria*) and, mainly, rushes (*Juncus* spp.). Conversely, *A. erythrurus* was associated to a wider range of plant species (tab. 1). At the intraspecific level, no differences were found in *P. algirus*. On the other hand, the adults of *A. erythrurus* were more concentrated in the bushes *Thymelaea hirsuta*. The immatures used the *Teucrium polium* and *Echinophora spinosa* shrubs as well as the weedy vegetation (χ^2 tests, 3 d.f., $p < 0.01$; see tab. 1).

Distance to plant shelter – No variation between the species considered as a whole was found. However, immature *P. algirus* were found to be closer to plants than adults of both species (χ^2 tests, 3 d.f., $p < 0.01$).

Global analysis of the variables – The representation of the habitat variables and the individuals by means of the Multiple Correspondences Factorial Analysis (MCFA) appears in fig. 1. It was decided to plot only the projections on the two first factorial axes since together they explained 89.55 % of total variance (tab. 2). The rest of the axes were considered "background noise". The relative contribution of each microhabitat variable to the inertia explained by both axes is also pointed out in table 2. Finally, the mean values and the dispersions of the projections on both exes are shown

	axis 1	axis 2
Variance explained	78.6	11.0
Variable		
SU	21.8	3.1
SL	16.4	5.6
CO	8.7	11.6
VH	24.4	29.4
PS	26.8	37.2
PD	1.9	13.2

Tab. 2. Percentages of the variance explained by the first two axes of the Multiple Correspondences Factorial Analysis (MCFA) and relative contribution of each microhabitat variable to the inertia explained by each axis.

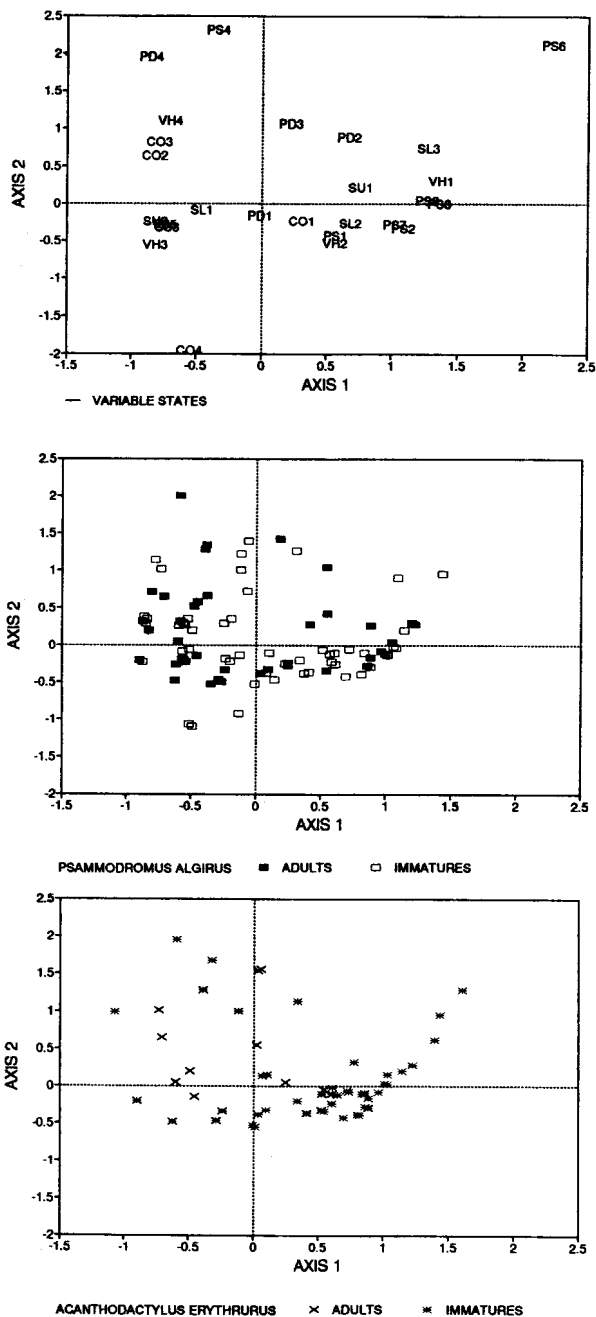


Fig. 1. Plot of the habitat variables (top) and individuals of *Psammodromus algirus* (middle) and *Acanthodactylus erythrus* (bottom) by means of the Multiple Correspondences Factorial Analysis (MCFA) using the first two axes. See material and methods for the meaning of the variable state abbreviations.

in table 3. The variables VH and PS were the most associated with both factorial axes. The variable SU is also included in the first axis. As a result, axis 1 was interpreted to depend on the general environmental conditions (salinity and sand fixation), and axis 2 on the local conditions (plant shelter).

In general, three tendencies in habitat occupation were observed: those areas with dense cover of *Juncus* (fig. 1, left bottom sector), those with sparse *Thymelaea* bushes (left top sector) and those with low cover of small plants and high slope (center and right half). The main difference between species considered as a whole was the absence of *A. erythrus* from the first areas, in contrast to the great number of *P. algirus* sighted in such places. Regarding the intra-specific variation, *P. algirus* immatures used habitats similar to the adults, with the exception of the great and dense accumulations of *Juncus*. However, the size divergence was more marked in *A. erythrus* because the immatures of this species were found in open, sloping areas with small plants, whereas the adults were more abundant in the open, flat spaces among *Thymelaea* bushes.

Finally, the habitat overlaps shown in table 4 provide a summary of the habitat relations. Values were always medium or high. Considering the species, macrohabitat overlap was higher than microhabitat. However, these differences were not evident at class level. No segregation was observed between sexes in any case but overlap bet-

ween immatures and adults was smaller. No significant differences were found between the inter- and intraspecific overlaps but the immatures of *A. erythrurus* appeared especially differentiated from the adults.

	N	axis 1			axis 2		
		\bar{x}	S	lim (95 %)	\bar{x}	S	lim (95 %)
<i>P. algirus</i>							
males	19	- 0.10	0.66	± 0.30	0.15	0.60	± 0.27
females	23	- 0.04	0.72	± 0.30	0.12	0.47	± 0.19
adults ¹	54	- 0.18	0.66	± 0.17	0.14	0.53	± 0.14
immatures	147	- 0.18	0.62	± 0.10	- 0.09	0.44	± 0.07
total	201	- 0.18	0.63	± 0.09	- 0.03	0.48	± 0.07
<i>A. erythrurus</i>							
males	15	- 0.14	0.52	± 0.26	0.38	0.73	± 0.37
females	7	- 0.20	0.42	± 0.31	0.42	0.76	± 0.56
adults ¹	28	- 0.14	0.50	± 0.19	0.33	0.73	± 0.27
immatures	89	0.46	0.64	± 0.13	- 0.03	0.52	± 0.11
total	117	0.32	0.66	± 0.12	0.05	0.60	± 0.11

Tab. 3. Projections of the values of each lizard category in the first two axes of the Multiple Correspondences Factorial Analysis (MCFA) performed with data on microhabitat. N = sample, \bar{x} = mean; S = standard deviation. lim (95 %) = confidence limits. ¹ Also including those adult individuals whose sex could not be determined.

Discussion and conclusions

The four types of the macrohabitat defined have proved to be useful in the study of habitat selection since differences between both species and their classes in the use of these units were detected in most cases. Nevertheless, this selection does not appear to be a direct consequence, but rather, an indirect result of the selection of microhabitat features correlated with the lizard morphology (CARRETERO & LLORENTE 1993b, 1993/94), which are commented next.

P. algirus has been reported to have climbing capacity and to be associated with plant cover, mainly bushes in all the Mediterranean ecosystems of the Iberian Peninsula (MELLADO et al. 1975, MELLADO 1980, PÉREZ-MELLADO 1982, SALVADOR 1985, BARBADILLO 1987, CARRASCAL et al. 1989, DÍAZ & CARRASCAL 1991, POLLO & PÉREZ-MELLADO 1991, PÉREZ-QUINTERO 1995). CARRASCAL et al. (1989) studying a successional forest gradient observed this lacertid avoiding sand substrata and open areas and keeping close to bushes in order to obtain food, shelter and shade. In fact, this climbing capacity has been interpreted to be due to the thermal relations (CARRASCAL & DÍAZ 1989, DÍAZ 1991, 1992). *P. algirus* may become highly abundant in areas densely covered by bushes (DELIBES AND SALVADOR 1986) but its populations suffer strong demographic decreases after the human destruction of the bushy stratum (SANTOS & TELLERÍA 1988). Conversely, *A. erythrurus* is thought to be associated with open, eroded areas with sandy soils and low plant cover with only some

	Macroh.	Axis 1	Axis 2	Microh.	S	M
<i>P.algirus</i> - <i>A.erythrurus</i>	64.40	85.96	98.25	84.46	71.49	13.04
♂♂ <i>P.algirus</i> - ♀♀ <i>P.algirus</i>	84.21	99.61	98.49	98.11	91.16	82.61
♂♂ <i>P.algirus</i> - im. <i>P.algirus</i>	78.55	99.46	92.78	92.28	85.41	72.49
♂♂ <i>P.algirus</i> - ♂♂ <i>A.erythrurus</i>	88.77	98.37	96.04	94.47	91.62	83.87
♂♂ <i>P.algirus</i> - ♀♀ <i>A.erythrurus</i>	87.97	94.48	94.76	89.53	88.75	78.76
♂♂ <i>P.algirus</i> - im. <i>A.erythrurus</i>	91.83	83.19	96.95	80.65	86.24	74.06
♀♀ <i>P.algirus</i> - im. <i>P.algirus</i>	77.67	98.25	94.71	93.05	85.36	72.27
♀♀ <i>P.algirus</i> - ♂♂ <i>A.erythrurus</i>	93.04	96.64	91.27	88.20	90.62	82.06
♀♀ <i>P.algirus</i> - ♀♀ <i>A.erythrurus</i>	85.71	91.68	89.45	82.01	83.86	70.29
♀♀ <i>P.algirus</i> - im. <i>A.erythrurus</i>	83.41	87.27	97.49	85.08	84.24	70.96
im. <i>P.algirus</i> - ♂♂ <i>A.erythrurus</i>	79.86	99.07	80.47	79.72	79.79	63.67
im. <i>P.algirus</i> - ♀♀ <i>A.erythrurus</i>	68.02	96.47	78.45	75.68	71.85	51.48
im. <i>P.algirus</i> - im. <i>A.erythrurus</i>	75.21	77.07	98.96	76.27	75.74	57.36
♂♂ <i>A.erythrurus</i> - ♀♀ <i>A.erythrurus</i>	86.66	98.64	99.88	98.52	92.59	85.38
♂♂ <i>A.erythrurus</i> - im. <i>A.erythrurus</i>	90.36	75.70	87.19	66.00	78.18	59.64
♀♀ <i>A.erythrurus</i> - im. <i>A.erythrurus</i>	84.65	66.43	85.36	56.70	70.68	48.00
Total mean	83.73	90.82	92.15	83.75	83.74	70.19
Interspecific mean	83.76	91.58	91.54	83.51	83.64	70.28
Intraspecific mean	83.68	89.68	93.07	84.11	83.90	70.07

Tab. 4. Habitat overlaps between the classes of the Lacertidae from the Ebro Delta for the subdivisions of macrohabitat and microhabitat. Matrices appear developed as columns. S = summative global overlap. M = multiplicative global overlap.

dispersed bushes (MELLADO 1980, BUSACK & JACKSIC 1982, SALVADOR 1985, BARBADILLO 1987, POLLO & PÉREZ-MELLADO 1991, GIL et al. 1993, PÉREZ-QUINTERO 1995). However, as a consequence of the constant "degradative" action of the sea, the coastal sandy areas are characterized by low general cover with scarce scrub patches and with bare, sandy soil being the main available substratum. So, it is plausible that the spatial relations in this kind of environments may shift from those mentioned above.

Thus, *P. algirus* hardly showed climbing behaviour. Two reasons not mutually exclusive may explain this fact: on one hand, the number of bushes and other plants on which to perch is lower than usual; on the other hand, both the low thermal variations in the coast and the sand as an additional heat source could prevent strict heliothermia in the bush branches to be the optimal tactic in this kind of ecosystems (see ADOLPH 1990 and CARRETERO & LLORENTE 1995b). Anyway, plants are used only as food sources and antipredator shelters. These roles are perfectly fulfilled by rushes and psammophile grasses. Both types of plant show a very dense base where this lizard often hunts, hides and has its burrow, without straying too far from them. This behaviour has been observed in other coastal areas of Mediterranean open forest (pers.obs.) and has incidentally been reported by SEVA (1984) in another coastal sandy area. Consequently, this species, which lacks psammophile or halophile specializations, is found in a wide variety of conditions from dunes sparsely covered by grasses to saline depressions with high density of rushes. In contrast to grasses, rushes have hard, thorny leaves which provide a safe shelter, even for adults. Since *Juncus* is a ha-

lophile plant, *P. algirus* is frequently found in saline, flat areas with compact substrata and low slopes (see also PÉREZ-QUINTERO 1989).

Nevertheless, *P. algirus* may occupy other areas with less cover and vertical development of vegetation often with higher slopes (dunes and dune backs). This is especially true for immatures. MELLADO (1980) considers this to be due to interspecific pressure (even predation) of adults which would force immatures to live in suboptimal areas, but this study does not support this hypothesis. Immatures are not absent from the most covered areas and it seems reasonable to hold that the cover requirements of small lizards are lower than those of adults and that, consequently, they can occupy more open areas. Only some adults were exceptionally found in extremely open areas, most of which were pregnant females which may have been looking for appropriate clutch sites (STRJIBOSCH 1987, pers.obs.).

Size spatial segregation is more evident in *A. erythrurus* (MELLADO 1980, BUSACK & JAKSIC 1982, PÉREZ-QUINTERO 1995) and could be related to the evident pattern and colour changes shown by lizards during growth (SEVA 1982). Similar phenomena have been reported in large lacertids (SALVADOR 1988, DOMÍNGUEZ & SALVADOR 1989). Adults are frequently seen close to *Thymelaea*, where they burrow. This behaviour seems to be thermal and not defensive (SEVA et al. 1982, SEVA 1984, CARRETERO & LLORENTE 1995b, PÉREZ-QUINTERO 1995) since the base of this bush is a bare trunk and lizards (and sometimes burrows) are perfectly accessible. The antipredator behaviour consist of a high vagility with large home ranges (POLLO & PÉREZ-MELLADO 1991, per.obs.) which is related to the limb length of this species (see CARRETERO & LLORENTE 1993b). A long run is sometimes followed by rapid borrowing. This tactic has been registered in many species of the genus *Acanthodactylus* (SEVA 1982, ARNOLD 1984, AL-JOHANY & SPELLERBERG 1989, obs.pers.) and it explains why many adults have been sighted in areas with low cover and far from any shelter. The *A. erythrurus* immatures used small scrubs which provide enough protection for small lizards. Nevertheless, in this case the avoidance of large *Thymelaea* bushes could be due to interactions with adults (MELLADO 1980, PÉREZ-QUINTERO 1995) thus producing intraspecific segregation (see tab. 4).

In conclusion, a clear spatial segregation between species appears when they are studied with reference to areas of great surface (MELLADO et al. 1975, PÉREZ-MELLADO 1982, ESCARRÉ & VERICAD 1983). However, when the same species are observed at a smaller scale (SEVA & ESCARRÉ 1980, BUSACK & JAKSIC 1982, SEVA 1984, POLLO AND PÉREZ-MELLADO 1991, PÉREZ-QUINTERO 1995, data of this study) both lacertids coexist and the spatial segregation between them is more diffuse and can be attributed to differences to microhabitat level. The vegetation structure and complexity are the main microhabitat factors implied. Others like substratum and slope depend on them. The overlap among the spatial niches is wide and neither the species nor the classes seem to be tightly "packed" as other lizard communities (see previous references). Nevertheless, the competition, especially within the species limits, may affect the microdistribution of these lacertids.

Acknowledgements

The field work was partially funded by a grant of the Spanish Ministerio de Educación y Ciencia (P.F.P.I.). The study permit (no. 2531) was provided by the Direcció General de Política Forestal, Departament d'Agricultura, Ramaderia i Pesca of the Generalitat de Catalunya.

References

- ADOLPH, S.C. (1990): Influence on behavioural thermoregulation on microhabitat use by two *Sceloporus* lizards. – *Ecology*, **71**(1): 315-327.
- ANTÚNEZ, A. & A.L. MÁRQUEZ (1992): Las escalas en Biogeografía. – In: VARGAS, J.M.; REAL, R. & A. ANTÚNEZ (eds.): *Objetivos y métodos biogeográficos. Aplicaciones en Herpetología*. – Monogr. Herpetol., **2**. pp. 31-38
- AL-JOHANY, A.M.H. & I.F. SPELLERBERG (1989): Home range and vagility of the lizards *Acanthodactylus schmidti* and *Acanthodactylus boskianus* in Saudi Arabia. – *J. Arid Environm.*, **16**: 79-86.
- ARNOLD, E.N. (1984): Ecology of lowland lizards in the eastern United Arab Emirates. – *J. Zool. Lond.*, **204**: 329-354.
- (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. – INCAFO Madrid. 694 pp.
- BARBAULT, R. & M.F. MAURY (1981): Ecological organization of a Chihuahuan desert lizard community. – *Oecologia (Berl)*, **51**: 335-342.
- BENZECRI, J.P. (1979): Sur le Calcul des Taux d'Inertie dans l'Analyse d'un Questionnaire. – *Les Cahiers de l'Analyse des Données*, **3**: 377.
- BISQUERRA, R. (1989): Introducción conceptual al análisis multivariable. Un enfoque informático con los paquetes SPSS-X, BMDP, LISREL y SPAD. Vols. 1 and 2. – PPU. Barcelona, 808 pp.
- BUSACK, S.D. & F.M. JAKSIC (1982): Autoecological observations in *Acanthodactylus erythrurus* (Sauria: Lacertidae) in Southern Spain. – *Amphibia-Reptilia*, **3**(2/3): 237-256.
- CAMARASA, J.M., FOLCH, R., MASALLES, R.M. & J.M. NINOT (1977): El paisatge vegetal del Delta de l'Ebre. – In: *Sistemes Naturals del Delta de l'Ebre*. – *Treb. Inst. Cat. Hist. Nat.*, **8**: 47-67 pp.
- CANO, C. & L.M. CARRASCAL (1986): Selección de hábitat en una comunidad de saurios del sur de la Península Ibérica. Análisis de la variación en la composición y diversidad de la herpetocenosis. – Original manuscript, 31 pp.
- CARRASCAL, L.M. & J.A. DÍAZ (1989): Thermal ecology and spatio-temporal distribution of the Mediterranean lizard *Psammodromus algirus*. – *Holarct. Ecol.*, **12**: 137-143.
- CARRASCAL, L.M., DÍAZ, J.A. & C. CANO (1989): Hábitat selection in Iberian *Psammodromus* species along a Mediterranean successional gradient. – *Amphibia-Reptilia*, **10**: 231-242.
- CARRETERO, M.A. & G.A. LLORENTE (1993a): Feeding of two sympatric lacertids in a sandy coastal area (Ebro Delta, Spain). – In: BÖHME, W., PÉREZ-MELLADO, V., VALAKOS, E. & P. MARAGOU (eds.): *Lacertids of the Mediterranean Region. A Biological approach*. – *Hellen. Zool. Soc.*, pp. 155-172.
- (1993b): Morfometría en una comunidad de lacértidos mediterráneos, y su relación con la ecología. – *Historia Animalium*, **2**: 77-79.
- Llorente (1993/94): Morfometría de *Psammodromus algirus* i *Acanthodactylus erythrurus* al Delta de l'Ebre. – *Bull. Parc Natural Delta de l'Ebre*, **8**: 19-26.
- (1995a): Reproduction of *Acanthodactylus erythrurus* in its Northern boundary. – *Russ. J. Herpetol.*, **2**(1): 10-17.
- (1995b): Thermal and temporal patterns of two Mediterranean Lacertidae. – In: LLORENTE, G.A., MONTORI, A., SANTOS, X. & M.A. CARRETERO (eds.): *Scientia Herpetologica*. – *Asoc. Herpetol. Españ.*, pp. 213-223.
- CURCÓ, T. (1990): La vegetació del Delta de l'Ebre (I): Les comunitats dunars (Classe Ammophiletea Br. Bl. & Tx. 1943). – *Bull. Parc. Nat. Delta de l'Ebre*, **5**: 9-18.
- DELIBES, A. & A. SALVADOR (1986): Censos de lacértidos en la Cordillera Cantábrica. – *Rev. Esp. Herp.*, **1**: 337-361.

- DÍAZ, J.A. (1991): Temporal patterns of basking behaviour in a Mediterranean lacertid lizard. – Behaviour, **118**(1-2): 1-14.
- (1992): Choice of compass directions around shrub patches by the heliothermic lizard *Psammodromus algirus*. – Herpetologica, **48**(3): 293-300.
- DÍAZ, J.A. & L.M. CARRASCAL (1991): Regional distribution of a Mediterranean lizard: influence of habitat cues and prey abundance. – J. Biogeography, **18**: 291-297.
- DOMÍNGUEZ, J.F. & A. SALVADOR (1989): Selección de microhábitat en *Lacerta schreiberi* BEDRIAGA, 1878 y *Podarcis bocagei* (SEOANE, 1884) en una localidad de la Cordillera Cantábrica, España (Reptilia; Lacertidae). – Bol. R. Soc. Esp. Hist. Nat. (Sec. Biol.), **84**(3-4): 273-286.
- GIL, M.J., GUERRERO, F. & V. PÉREZ-MELLADO (1993): Ecología térmica, uso del habitat y patrones de actividad en la lagartija colirroja *Acanthodactylus erythrurus* (SCHINZ, 1883) en España central. – Doñana, Acta Vertebr., **20**(1): 19-34.
- GONZÁLEZ-ROMERO, A., ORTEGA, A. & R. BARBAULT (1989): Habitat partitioning and spatial organization in a lizard community of the Sonoran desert, Mexico. – Amphibia-Reptilia, **10**: 1-11.
- HEATWOLE, H.T. (1977): Habitat selection in reptiles. – In: GANS, C. & D.W. TINKLE (eds.): Biology of the Reptilia. Vol. 7. Ecology and Behaviour A. – Academic Press. London. pp. 137-155.
- HOLM, S. (1979): A simple sequentially rejective multiple test procedure. – Scand. J. Stat., **6**: 65-70.
- LEBART, L., MORINEAU, A. & J.P. FENELON (1985): Tratamiento estadístico de datos. Métodos y programas. – Marcombo. Barcelona.
- LEBART, L., MORINEAU, A. & K.W. WARWICK (1984): Multivariate Description Statistical Analysis, Correspondence Analysis and Related Techniques for Large Matrices. – Dunod. Paris.
- LINTON, L.R., DAVIES, R.W. & F.J. WRONA (1981): Resource utilization indices: an assessment. – J. Animal Ecol., **50**: 283-292.
- MARGALEF, R. (1974): Ecología. – Ed. Omega. Barcelona. 951 pp.
- MAURER, R.A. (1982): Statistical inference for McArthur-Levins niche overlap. – Ecology, **63**(6): 1712-1719.
- MAY, R.M. (1974): On the theory of niche overlap. – Theoret. Pop. Biol., **5**: 297-332.
- MELLADO, J. (1980): Utilización del espacio en una comunidad de lacértidos del matorral mediterráneo en la Reserva Biológica de Doñana. – Doñana, Acta Vertebrata, **7**(1): 41-59.
- MELLADO, J., AMORES, F., PARREÑO, F.F. & F. HIRALDO (1975): The structure of a Mediterranean lizard community. – Doñana, Acta Vertebr., **2**(2): 145-160.
- MENGE, B.A. & A.M. OLSON (1990): Role of Scale and Environmental Factors in Regulation of Community Structure. – Tree, **5**(2): 52-57.
- PANAREDA, J.M. & J. NUET (1973): El clima i les aigües dels Països Catalans. – In: Geografia física dels Països Catalans. – Ed. Ketres, Barcelona. pp. 69-102,
- PÉREZ-MELLADO, V. (1982): Estructura de una taxocenosis de Lacertidae (Sauria, Reptilia) del Sistema Central. – Mediterránea Ser. Biol., **6**: 39-64.
- (1992): Ecology of lacertid lizards in a desert area of eastern Morocco. – J. Zool. Lond., **226**: 369-386.
- PEREZ-QUINTERO, J.C. (1989): Segregación espacial y trófica entre *Chalcides chalcides* y *Psammodromus algirus* en la Marisma del Río Tinto. – Communication presented to the IV Congreso Nacional de Herpetología. Madrid.
- (1995): Ecología de tres especies mediterráneas de Lacertidae (*Acanthodactylus erythrurus* (SCHINZ), *Psammodromus algirus* (L.) y *Psammodromus hispanicus* FITZINGER) en el litoral de la provincia de Huelva. – PhD dissertation. Universidad de Sevilla. 400 pp.
- PIANKA, E.R. (1966): Convexity, desert lizards and spatial heterogeneity. – Ecology, **47**: 1055-1059.
- (1973): The structure of lizard communities. – Ann. Rev. Ecol. Syst., **4**: 53-74.
- (1974): Niche overlap and diffuse competition. – Proc. Nat. Acad. Sci. USA, **71**: 2141-2145.
- POLLO, C.J. & V. PÉREZ-MELLADO (1991): An analysis of a Mediterranean assemblage of three small lacertid lizards in Central Spain. – Acta Oecologica, **12**(5): 655-671.

- RICE, W.C. (1989): Analyzing tables of statistical tests. – *Evolution*, 43(1): 223-225.
- SALVADOR, A. (1985): Guía de campo de los anfibios y reptiles de la Península Ibérica, islas Baleares y Canarias. – A. Salvador Ed. León. 212 pp.
- (1988): Selección de microhábitat del lagarto verdinegro (*Lacerta schreiberi*) (Sauria: Lacertidae). – *Amphibia-Reptilia*, 9: 265-276.
- SANTOS, T. & J.L. TELLERÍA (1988): Preferencias de hábitat y perspectivas de conservación en una comunidad de lacértidos en medios cerealistas del centro de España. – *Rev. Esp. Herp.*, 3(2): 259-272.
- SCHOENER, T.W. (1968): The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. – *Ecology*, 51: 408-418.
- SEVA, E. (1982). Taxocenosis de lacértidos en un arenal costero alicantino. – PhD dissertation, Universidad de Alicante. 317 pp.
- (1984): Reparto de recursos entre dos especies psammófilas de saurios, *Acanthodactylus erythrurus* y *Psammotromus algirus*. Arenal costero de Alicante. – *Mediterránea Ser. Biol.*, 7: 5-25.
- SEVA, E. & A. ESCARRÉ (1980): Distribución espacial y temporal de *Acanthodactylus erythrurus* (Sauria, Lacertidae) en un arenal costero alicantino. – *Mediterránea Ser. Biol.*, 4: 133-162.
- SEVA, E., FERRANDIS, E. & A. ESCARRÉ (1982): La selección del hábitat del arenal costero por *Acanthodactylus erythrurus* (Sauria: Lacertidae). Un proceso markoviano para la identificación de sus tendencias. – *Mediterránea Ser. Biol.* 6: 5-14.
- STRIJBOSCH, H. (1987): Nest site selection of *Lacerta agilis* in the Netherlands. – In: GELDER, J.J. VAN, STRIJBOSCH, H. & P.J.M. BERGERS (eds.): Proc. 4th O.G.M. of the S.E.H. – Nijmegen. pp. 143-146.
- STRIJBOSCH, H., BONNEMAYER, J.J.A.M. & P.J.M. DIETVORST (1980): The Northernmost Population of *Podarcis muralis* (Lacertilia, Lacertidae). – *Amphibia-Reptilia*, 1: 161-172.
- TELLERÍA, J.L. (1986): Manual para el censo de los vertebrados terrestres. – Ed. Raíces. Madrid. 278 pp.
- TOFT, C.A. (1985): Resource partitioning in amphibians and reptiles. – *Copeia*, 1985: 1-21.
- VALVERDE, J.A. (1967): Estructura de una comunidad de vertebrados terrestres. – C.S.I.C. Monografías de Ciencia Moderna. Madrid. 219 pp.

Authors' addresses: MIGUEL A. CARRETERO & GUSTAVO A. LLORENTE, Departament de Biologia Animal (Vertebrats), Facultat de Biologia, Universitat de Barcelona, Av. Diagonal, 645. E-08028 Barcelona (Spain) (e-mail: llorente@porthos.bio.ub.es).