

ANALYSIS OF THE STRUCTURE OF AN AMPHIBIAN COMMUNITY IN THE CENTRAL SYSTEM OF SPAIN

MIGUEL LIZANA, VALENTIN PÉREZ-MELLADO AND MARIA JOSÉ CIUDAD

Departamento de Biología Animal y Parasitología Universidad de Salamanca, 37071 Salamanca, Spain.

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ABSTRACT

This study examines the structure of an Amphibian community, composed of 10 species in the Central System of Spain. We studied resource partitioning in the main dimensions of the niche (food, space and time), the overlap in each dimension and the overall overlap. From a multidimensional scaling analysis (MDS) of the overlap matrices we inferred that the spatial dimension is the main factor responsible for species segregation. Overlap along the time and food dimensions was significantly correlated. The community is structured into three guilds formed, respectively, by the aquatic anurans, the terrestrial anurans together with a terrestrial salamander, and the newts.

INTRODUCTION

Studies on the structure of herpetological communities have mainly been based on lizards (see reviews in Schoener, 1974 and Toft, 1985). Amphibian communities have received less attention and have essentially been studied in frogs of tropical ecosystems (e.g. Inger, 1969; Inger and Colwell, 1977; Toft and

Duellman, 1979; Toft, 1980a and b; 1981; 1985) and in salamanders of the temperate regions of Europe (Avery, 1968; Griffiths, 1986) and North America, principally the studies of Jaeger and Hairston (see reviews in Toft, 1985 and Hairston, 1987).

Regarding the Iberian Peninsula, studies on herpetological communities have been restricted to the work of Valverde (1967), the recent studies of different

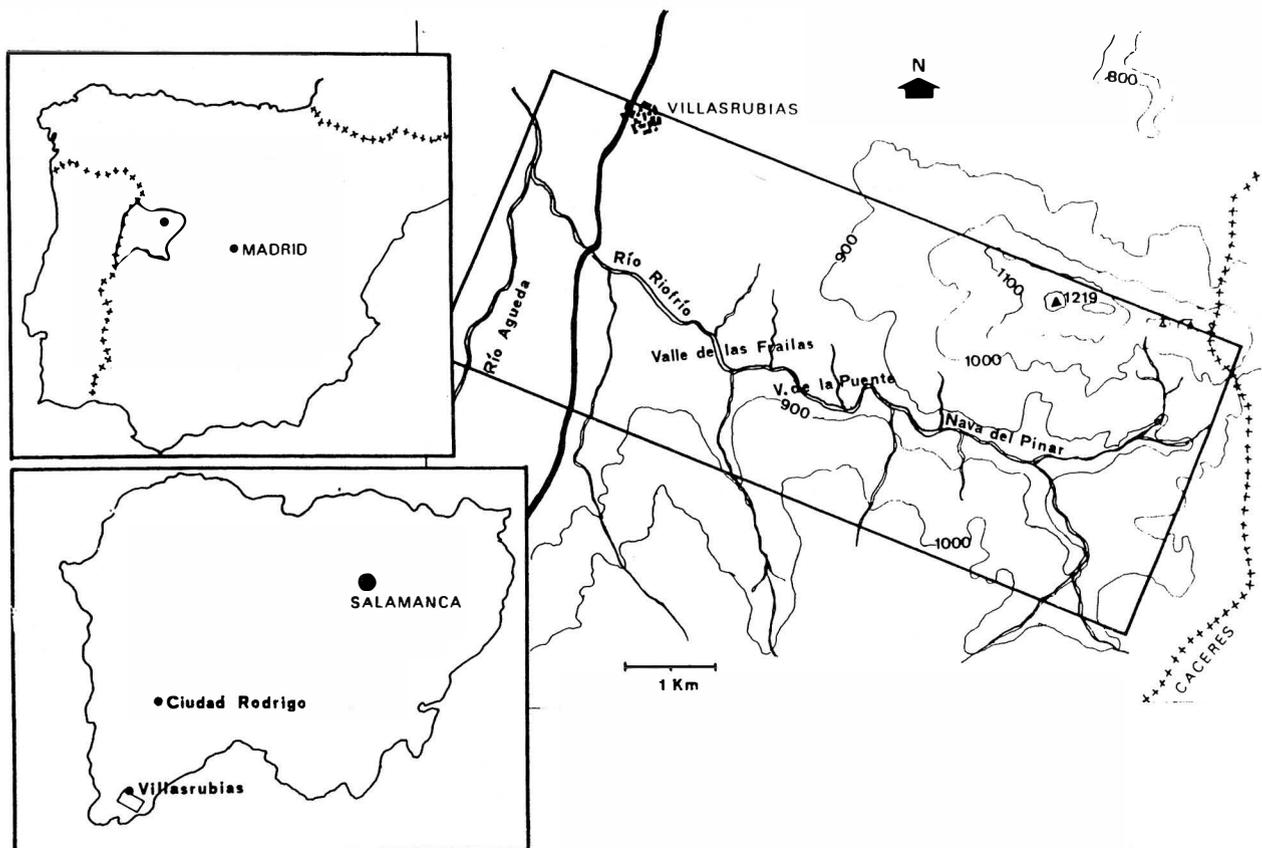


Fig. 1 Geographical location of the study area.

taxocenoses of Sauria, mainly the Lacertidae (Mellado, *et al.*, 1975; Pérez-Mellado, 1982; Seva, 1982 and Braña, 1984), and one study of a complete herpetological community (Bas, 1982). Finally, Díaz Paniagua (1979, 1982, 1983, 1988) studied the interactions within communities of larval amphibians.

The aim of the present study is to offer new data on the resource partitioning in an amphibian assemblage in a European temperate region. This will permit a comparison with other communities of salamanders and frogs that have been studied more extensively.

MATERIAL AND METHODS

STUDY AREA

The field work was carried out at Villasrubias (UTM 29TQE0366) located in the Southwest of the province of Salamanca on the northern slopes of the Spanish Central System (Fig. 1). Samples were taken over an area of approximately 8 x 3.5 km, at altitudes ranging between 800 and 1200 metres. All the aquatic habitats and the terrestrial habitats in their proximities were investigated.

The mean annual rainfall of the zone is 943.15 mm, and the area is subject to both Atlantic and Continental climatic influences. The dominant vegetation is the grade *Genista florida-Quercus pyrenaica*; characterised by oak forests and bushes of *Erica spp.* There are also plantations of *Pinus pinaster* and *P. sylvestris* (Bellot, 1966; Rico, 1978).

Periodic visits were made to the study area, usually twice a month, from November 1982 to February 1984. On each occasion all the habitats of the zone were sampled. For each animal observed, we noted species, habitat type and hour. We sampled terrestrial amphibians by searching in the vegetation, on the banks of aquatic environments, under stones, trunks, etc. Animals that were found inactive, were not taken into account in the analysis of daily and seasonal activity patterns, but were included in the analysis of habitat utilisation and diet composition.

We used netting methods to capture newts and other aquatic species in their aquatic environments. The number of terrestrial amphibians observed and the number of aquatic species observed, usually newts, were corrected in the same way for the time employed in searching. Observations were made and samples were taken during all hours of the day and night.

We calculated hourly and monthly activity indices (I_{ij}) by the formula (see also Lizana, *et al.*, in press):

$$I_{ij} = \frac{n_{ij}}{T_i \%}$$

where I_{ij} = corrected frequency of species j in time category i (months or hours); n_{ij} = number of observations of species j in time category i ; $T_i\%$ = percentage of the time spent sampling in time category i . This was then converted to a percentage using the formula:

$$I_{ij} \% = \frac{I_{ij}}{\sum I_{ij}} \times 100$$

Methods used in the analysis of diet composition and habitat use are detailed in Lizana *et al.*, 1986 and in press).

We studied resource partitioning along the three main niche dimensions: habitat, food and time (Pianka, 1973, 1986; Schoener, 1974), considering the subdimensions of seasonal and daily activity for time and the subdimensions of prey type and prey size for food. Niche overlap was calculated by the index of Pianka (1973):

$$S = \frac{\sum p_{ij} p_{ik}}{\sqrt{\sum (p_{ij})^2 (p_{ik})^2}}$$

where p_{ij} and p_{ik} are proportions of species j and k in the resource i . Overlap was calculated for each of the dimensions and subdimensions considered.

The resulting overlap matrices were analysed by the multidimensional scaling technique (MDS) using the Kruskal algorithm (Kruskal, 1964) with the Systat package. Plots were made on the plane defined by the first two dimensions since reasonably small stress (and high goodness-of-fit) were found on each (Schiffman, *et al.*, 1981).

This technique has several advantages that justify its use in the study of communities. First, it uses the distances or similarities between populations (in this case, species) as starting values, so that one can construct a similarity matrix with the overlap values found. Factor analysis and other multivariate techniques have several important premises in their application, among which perhaps the most important is the existence of linear relationships between the starting variables. The MDS does not feature this limitation. Finally the results obtained with the MDS technique are easier to interpret since they are based on the Euclidean distances between the points, while interpretation of the factor analysis must be based on results expressed as angular values between vectors (Schiffman, *et al.*, 1981).

We also analysed the correlation between the overlap values for each of the dimensions and subdimensions considered, using Spearman rank correlation coefficients (Siegel, 1956).

RESULTS AND DISCUSSION

The amphibian community in the study area considered of 10 species, in a zone of high herpetological diversity (Pérez-Mellado, 1983). Seven of them were anurans: *Rana iberica*, *Rana perezi*, *Discoglossus galganoi* (using the taxonomy proposed by Capula, *et al.*, 1985), *Alytes obstetricans*, *Hyla arborea*, *Bufo Bufo* and *Bufo calamita*. The latter species and *H. arborea* were very rare. The other three species encountered were urodeles: *Salamandra salamandra*, *Triturus boscai* and *Triturus marmoratus*.

Feeding Habits

The species are situated along a continuum that ranged from an exclusively terrestrial to an aquatic diet. At the latter end were *Triturus marmoratus* and *T. boscai*, that almost exclusively consumed aquatic

PREY ITEMS	SPECIES	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
BIVALVIA		—	—	—	—	—	—	—	—	2.06	—
GASTROPODA		0.08	—	—	0.19	—	—	—	—	0.19	—
CLADOCERA		—	—	—	—	—	—	—	—	1.27	0.82
OSTRACODA		—	—	—	—	—	—	—	—	25.39	82.66
COPEPODA		—	—	—	—	—	—	—	—	2.55	1.46
ISOPODA		0.45	0.05	0.27	—	—	—	—	—	—	—
OLIGOCHAETA		0.02	—	0.54	—	—	—	—	6.66	—	—
MYRIAPODA		0.99	0.50	2.19	0.38	—	0.45	—	8.88	—	—
PSEUDOESCORPIONES		0.24	0.05	—	—	—	—	—	—	0.29	—
SOLIFUGAE		—	—	—	0.38	—	—	—	—	—	—
OPILIONES		0.53	—	1.64	0.38	—	—	1.96	2.22	—	0.02
ARANEAE		10.49	5.35	7.39	6.58	4.99	0.91	5.88	2.22	0.19	0.05
ACARI		2.26	0.25	1.36	13.95	—	—	—	—	3.34	0.05
COLLEMBOLA		1.88	1.16	1.36	4.06	—	—	—	—	3.83	0.11
DIPLURA		0.13	—	—	—	—	—	—	—	—	—
ODONATA		0.08	0.75	—	—	—	—	—	—	0.19	0.32
EPHEMEROPTERA		0.80	0.45	0.27	0.19	—	0.09	—	—	9.44	2.46
PLECOPTERA		2.58	2.89	—	—	—	—	—	—	1.18	—
EMBIOPTERA		0.02	—	—	—	—	—	—	—	—	—
ORTHOPTERA		0.59	1.21	0.82	1.16	1.66	1.09	—	—	0.19	—
DERMAPTERA		0.32	0.65	0.54	—	—	—	3.92	8.88	—	—
BLATTODEA		0.13	0.15	1.36	—	—	—	—	—	—	—
PSOCOPTERA		0.16	—	—	—	—	—	—	—	0.09	—
HOMOPTERA		4.23	7.89	7.39	0.96	3.33	0.27	1.96	—	0.39	0.08
HETEROPTERA		3.10	3.03	0.54	3.87	—	0.27	—	—	0.09	0.11
UNID. HEMIPTERA		0.13	—	—	—	—	—	—	—	—	—
THYSANOPTERA		0.18	—	—	—	—	—	—	—	—	—
NEUROPTERA		0.08	0.05	—	—	—	—	—	—	0.19	—
COLEOPTERA		17.85	18.32	18.90	26.35	9.99	6.10	52.94	33.33	2.55	1.38
HYMENOPTERA		4.31	9.66	11.78	1.74	1.66	0.36	1.96	4.44	0.29	0.02
FORMICIDAE		4.47	11.77	16.98	33.72	75.00	88.50	25.49	15.55	—	—
TRICHOPTERA		3.82	1.87	—	0.38	—	0.09	—	—	3.34	0.11
LEPIDOPTERA		1.07	1.26	1.09	2.13	—	0.27	3.92	4.44	0.49	0.02
DIPTERA		36.16	31.00	24.10	2.13	1.66	0.36	1.96	6.66	40.25	9.66
UNID. HEXAPODA		1.29	0.55	0.54	0.38	1.66	—	—	2.22	0.98	0.26
UNID. HEXAPODA LARVAE		0.86	1.06	0.82	0.77	—	0.27	—	4.44	0.88	—
UNID. ARTHROPODA		0.67	0.05	—	0.19	—	—	—	—	—	—
VERTEBRATA		—	0.10	—	—	—	—	—	—	—	0.02
— NUMBER OF PREY		3708	1981	365	516	60	1098	51	45	1016	3403
— NUMBER OF INDIVIDUALS		424	199	43	39	8	8	2	4	60	58

TABLE 1: Percentage of prey groups predated by the species of the community. Abbreviations: R. ibe: *Rana iberica*, R.per: *Rana perezi*, D.gal: *Discoglossus galganoi*, A.obs: *Alytes obstetricans*, H.arb: *Hyla arborea*, B.buf: *Bufo Bufo*, B.cal: *Bufo calamita*, S.sal: *Salamandra salamandra*, T.bos: *Triturus boscai*, T.mar: *Triturus marmoratus*. ("unid." means unidentified prey).

SPECIES Size class/	% R.ibe	% R.per	% D.gal	% A.obs	% H.arb	% B.buf	% B.cal	% S.sal	% T.bos	% T.mar
0- 2mm	5.94	7.72	13.09	15.97	—	—	—	—	38.31	86.00
2- 4mm	42.98	34.55	47.35	43.58	10.00	46.58	—	2.32	23.99	2.33
4- 6mm	28.50	27.15	17.27	23.47	73.33	43.47	39.21	38.53	25.02	4.02
6- 8mm	12.45	14.58	9.74	13.21	13.33	4.50	39.21	18.60	9.78	5.25
8-10mm	5.46	5.48	5.57	1.77	—	1.24	15.68	18.60	2.16	0.96
10-12mm	2.74	3.24	2.50	0.98	1.66	0.46	3.92	16.27	0.51	0.52
12-14mm	1.35	3.30	0.83	0.59	1.66	0.46	1.96	4.65	0.10	0.40
14-16mm	0.39	1.22	0.83	—	—	1.24	—	—	—	0.52
16-18mm	0.17	0.85	1.67	0.19	—	0.77	—	—	0.10	0.02
18-20mm	0.07	0.37	—	—	—	0.15	—	—	—	—
20-22mm	0.07	0.31	—	0.19	—	0.46	—	—	—	—
22-24mm	—	0.26	—	—	—	0.15	—	—	—	0.02
24-26mm	0.03	0.15	—	—	—	0.46	—	—	—	—
26-28mm	—	0.05	—	—	—	—	—	—	—	—
28-30mm	—	0.05	—	—	—	—	—	—	—	—
30-32mm	0.07	0.37	1.11	—	—	—	—	—	—	—
32-34mm	—	0.05	—	—	—	—	—	—	—	—
34-36mm	—	—	—	—	—	—	—	—	—	—
36-38mm	—	—	—	—	—	—	—	—	—	—
38-40mm	—	—	—	—	—	—	—	—	—	—
40-50mm	—	0.15	—	—	—	—	—	—	—	—
>50mm	—	0.05	—	—	—	—	—	—	—	—
N. of Prey	2810	1861	359	507	60	644	51	43	971	3375
N. of Ind.	424	199	43	39	8	8	2	4	60	58

TABLE 2: Percentage of size classes of prey predated by the species of the community.

prey such as crustaceans (Ostracoda, Copepoda) and aquatic larvae of insects (Table 1). *Rana iberica*, *R. perezi* and *D. galganoi* occupied an intermediate position with preferential consumption of terrestrial prey, although they also consumed a large portion of aquatic items, such as larvae of insects (Lizana, *et al.*, 1986). *Alytes obstetricans* was the first species with a mainly terrestrial diet. The large number of Formicidae consumed by *Hyla arborea*, pointed to the importance of terrestrial prey in its diet. *Bufo bufo*, *Bufo calamita* and *Salamandra salamandra*, had an exclusively terrestrial diet.

In general, trophic generalists predominated in the community, although certain species such as *B. bufo* or *H. arborea* showed a pronounced preference for Formicidae, while *B. calamita* and *S. salamandra* seemed to prefer large, rather non-sclerotised preys (Table 1 and 2; see data on prey availability and electivity in Lizana, *et al.*, 1986).

The most euryphagous species were those, such as the ranids, that occupied aquatic environments and

their neighbourhoods. In some species there existed an important relationship between the degree of trophic specialisation and the use of terrestrial habitats (Lizana, *et al.*, in press).

Habitat Use

We considered sixteen habitat categories (see description in Table 3 and in Lizana, *et al.*, in press) that were used by at least one species, and described according to their proximity to the aquatic habitats. Three species of anurans were seen to be linked more tightly to the aquatic environments or their proximities. *Rana iberica* occupied a large variety of terrestrial biotopes, although the species was always present close to water. It was segregated from *R. perezi* through its use of habitats with a stronger water current and lesser depth, while *R. perezi* occupied sluggish water (Lizana, *et al.*, 1987 and in press). *Discoglossus galganoi* seemed to prefer more terrestrial environments than *R. perezi* and was usually found on the banks of streams or in flooded meadows (Table 3).

SPECIES	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar	
H A B I T A T S —AQUATIC— —TERRESTRIAL—	A	—	—	—	—	—	—	—	—	0.82	
	B	0.29	—	—	—	—	—	—	—	—	
	C	3.42	—	—	—	—	—	—	—	—	
	D	1.34	—	3.12	14.28	8.82	—	—	4.00	0.71	2.47
	E	0.59	1.78	10.41	16.07	8.82	41.66	40.00	36.00	2.14	4.95
	F	1.34	—	5.20	—	—	—	—	12.00	—	—
	G	—	—	—	3.57	—	—	—	—	—	—
	H	—	—	3.12	55.35	2.94	16.66	—	—	0.71	—
	I	2.38	—	2.08	—	—	—	—	8.00	2.85	2.47
	J	2.53	2.67	34.37	—	8.82	8.33	60.00	—	0.71	—
	K	14.45	20.77	7.29	5.35	58.82	—	—	—	35.71	37.19
	L	4.32	—	—	—	—	—	—	40.00	3.57	—
	M	28.76	15.43	21.87	—	8.82	33.33	—	—	19.28	2.47
	N	—	17.80	1.04	—	2.94	—	—	—	18.57	49.58
O	37.85	10.68	10.41	5.35	—	—	—	—	—	—	
P	2.68	30.86	1.04	—	—	—	—	—	15.71	—	
	%	%	%	%	%	%	%	%	%	%	
1	2.53	2.67	34.37	—	8.82	8.33	60.00	—	0.71	—	
2	33.97	64.68	15.62	5.35	20.58	8.33	—	12.00	91.42	87.60	
3	63.48	32.64	50.00	94.64	70.58	83.33	40.00	88.00	7.85	12.39	
N. of Obs.	671	337	96	56	34	12	5	25	140	121	

TABLE 3: Percentage of observations performed for each species in different habitats of the study area: A: Woodland, B: Sandy areas, C: Dry stream beds, D: Bushy meadows (with shrubs), E: Open meadows (grasslands), F: Litter floor (on dead leaves), G: Stony areas, H: Under large stones (stony areas used for refuge), I: Slopes next to streams, J: Flooded meadows, K: Temporal pools, L: Temporal streams, M: Permanent streams, N: Permanent pools, O: Zones of rivers and streams with rapid current, P: Zones of rivers and streams with slow current.

Class 1 represents the percentage of observations in flooded zones, Class 2 the percentage in water masses and Class 3 the percentage on solid ground, including those carried out in terrestrial habitats and those on the shores of aquatic habitats.

SPECIES	%	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
January	1.70	—	—	—	—	—	—	—	—	7.38	—
February	5.57	2.50	1.86	—	11.44	—	—	—	6.52	27.80	25.40
March	4.78	18.87	16.05	53.66	26.67	—	61.34	94.30	68.56	19.26	10.76
April	1.36	2.94	6.09	—	11.72	—	—	—	—	6.15	—
May	12.74	16.68	10.57	3.49	6.25	40.93	—	—	—	4.92	—
June	8.59	6.75	8.19	5.83	3.69	39.29	—	—	4.22	3.40	5.23
July	16.78	10.50	12.84	1.32	5.69	3.65	20.38	—	2.14	4.24	16.86
August	5.35	5.23	9.29	5.20	—	11.46	18.26	—	—	0.77	19.23
September	8.19	9.04	12.15	11.57	5.83	—	—	—	—	2.55	8.63
October	13.20	13.95	14.60	16.05	18.11	4.64	—	—	—	2.21	8.27
November	19.63	5.61	5.26	2.83	10.55	—	—	5.60	18.54	8.95	5.57
December	2.04	7.86	3.04	—	—	—	—	—	—	12.31	—
Total Sampling	%	%	%	%	%	%	%	%	%	%	%
Time (Minutes)	8785	561	468	137	58	34	15	5	22	163	142
NUMBER OF OBSERVATIONS											

TABLE 4: Percentage of corrected frequencies of the number of observations carried out in each month for each species. The first column details the percentage of minutes sampled each month with respect to the total of the study period.

The other anurans, together with *S. salamandra* has almost exclusively terrestrial habits, except during the reproductive season. They occupied habitats that were generally differentiated by the type and density of vegetation. *T. boscai* and *T. marmoratus* were almost always present in water masses, with no defined terrestrial phase (Lizana, *et al.*, in press), and were differentiated from one another by the presence or absence of aquatic vegetation, the depth of the water and the speed of the current (Table 3).

Activity

Rana iberica and *R. perezi* were active throughout the year except in January (Table 4). The same held for *Triturus boscai* and to a lesser extent for *T. marmoratus*. In these species there was a clear relationship between their use of aquatic habitats and their broad seasonal activity patterns (Lizana, *et al.*, in press). The other anurans and *S. salamandra* showed a more seasonal activity pattern, which was particularly limited by the occurrence of rainy periods in spring and autumn, coinciding in most species with the reproductive period.

Both ranids were active throughout all the hourly segments sampled (Table 5), although *R. iberica* showed the greatest nocturnal activity. *D. galganoi* showed its greatest activity after sunset. The terrestrial anurans and *S. salamandra* were almost exclusively crepuscular and nocturnal except during rainy periods. *T. boscai* and *T. marmoratus* seemed to exhibit a mainly diurnal activity, although our method of sampling the aquatic habitats may have biased their activity estimates (Lizana, *et al.*, in press).

Overlap

The overlap values for the three dimensions of the niche and for the overall overlap are shown in Appendices 1 to 9. As overlap values were highly correlated between subdimensions for food and time (see further), the arithmetic mean of these two subdimensions was also calculated. The highest overlap values were obtained for food and the smallest for habitat.

A fundamental aspect in studies dealing with communities is the degree of dependence between the niche dimensions considered (e.g. Pianka, 1986),

SPECIES HOUR	%	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
1- 2	0.56	—	—	—	—	—	—	—	—	29.70	—
2- 3	—	—	—	—	—	—	—	—	—	—	—
3- 4	0.68	13.33	4.90	—	—	16.69	—	—	—	—	—
4- 5	0.17	17.77	9.90	—	—	—	—	—	—	—	—
5- 6	—	—	—	—	—	—	—	—	—	—	—
6- 7	0.62	1.20	4.10	5.60	—	—	—	—	25.80	—	—
7- 8	0.68	4.40	11.20	10.29	—	—	—	—	—	—	—
8- 9	0.85	3.50	3.90	—	—	—	—	—	—	—	—
9-10	4.26	6.50	7.50	9.00	7.91	5.33	—	—	—	5.80	3.12
10-11	7.39	1.02	4.10	8.00	—	—	—	—	—	4.10	1.70
11-12	8.93	5.50	2.20	—	—	—	—	—	—	7.40	11.90
12-13	6.54	4.80	2.00	—	—	—	—	—	—	3.30	9.50
13-14	4.43	4.26	2.40	3.10	—	2.56	—	—	—	6.20	15.00
14-15	7.17	7.60	3.70	1.95	7.05	—	—	—	—	13.10	6.80
15-16	8.25	4.00	2.60	2.90	—	6.88	—	—	—	4.70	1.07
16-17	10.41	5.20	2.50	4.37	—	4.36	—	—	—	2.90	8.90
17-18	9.84	3.20	4.60	6.40	—	4.61	—	—	1.62	1.40	4.50
18-19	6.77	4.40	6.20	3.10	—	5.03	10.15	—	—	3.60	13.70
19-20	4.66	2.10	3.20	3.75	3.61	4.87	29.51	—	—	2.30	5.71
20-21	4.09	—	4.50	0.85	20.62	2.77	—	—	—	4.70	1.08
21-22	3.92	5.70	7.70	12.50	12.91	5.79	17.54	19.50	28.60	2.80	4.50
22-23	5.17	3.70	4.20	16.20	19.58	6.58	19.94	29.50	27.90	1.60	1.70
23-24	3.01	0.49	6.10	11.60	16.81	11.31	22.84	50.80	15.90	1.80	4.40
0- I	1.47	0.51	1.10	—	11.47	23.17	—	—	—	3.70	6.00
Total Sampling		%	%	%	%	%	%	%	%	%	%
Minutes: 8785		NUMBER OF OBSERVATIONS									
		561	468	137	58	34	15	5	22	163	142

TABLE 5: Percentage of corrected frequencies of the number of observations carried out in each hourly segment for each species. The first column details the percentage of minutes sampled in each hourly segment with respect to the total study period.

which is our case were analysed by correlations. In the first place, this analysis showed that there was no correlation between the degree of overlap in time (Appendix 6) and habitat (Appendix 7; $r_s = 0.29$, $P > 0.05$) or between habitat and food (Appendix 3) ($r_s = 0.23$, $P > 0.05$). However, there was a statistically significant correlation between the overlap in time and food ($r_s = 0.41$, $P < 0.05$), suggesting that the consumption of similar prey types was due to similar activity rhythms. A species diet composition would hence be related directly to its activity patterns and those of its prey (Lizana, *et al.*, 1986).

The correlation of the overlap values was highly significant between the trophic subdimensions of prey type (Appendix 1) and prey size (Appendix 2), ($r_s = 0.49$, $P < 0.001$), and also between the temporal subdimensions of annual (Appendix 4) and daily (Appendix 5) activity ($r_s = 0.48$, $P < 0.01$). This supports the hypothesis that in amphibian communities, owing to their strict ectothermy, differences in activity produce a pronounced segregation in diet composition (see also Schoener, 1974 and Toft, 1985).

Similar conclusions have been reached in studies on lizard communities, although the relationship between both dimensions has not proved to be as tight as would be expected for ectotherms with a greater thermoregulatory capacity (Pérez-Mellado, 1982). Only in the case of strongly stenophagous species such as *Bufo bufo*, food seems to be a sufficient segregating factor. It is striking that, in general, the food specialists in ectotherm communities eat ants (e.g. Mellado, *et al.*, 1975; Barbault, *et al.*, 1978; Toft, 1980 a and b; 1981; Pérez-Mellado, 1982, Pianka, 1986). As has been pointed out elsewhere, prey size seems to be of greater importance in intraspecific segregation than among the different species of the community (Lizana, *et al.*, 1986).

Multidimensional Scaling

MDS analysis shows that in the trophic dimension (Fig. 4) both newts were clearly separated from the other species, and were opposed to another group formed of *B. bufo* and *H. arborea*. The former consisted of quasi-specialists in aquatic prey and the

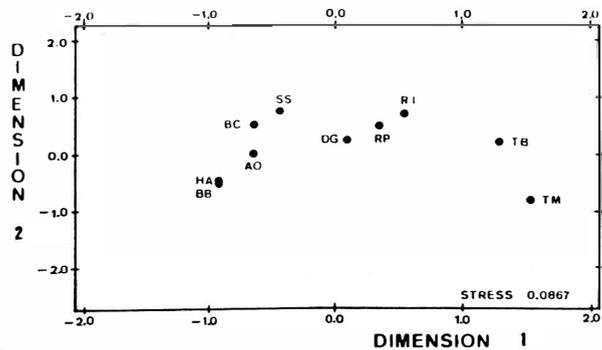


Fig. 2 Euclidean distances between the species according to an analysis of multidimensional scaling (MDS) for the overlap values in the trophic dimension, prey type subdimension. The value of stress for the final configuration is also given. Abbreviations: RI *Rana iberica*, RP *Rana perezi*, DG *Discoglossus galganoi*, AO *Alytes obstetricans*, HA *Hyla arborea*, BB *Bufo bufo*, BC *Bufo calamita*, SS *Salamandra salamandra*, TB *Triturus boscai*, TM *Triturus marmoratus*.

latter of myrmecophagous species. The analysis of prey type and prey size (Fig. 2 and Fig. 3 respectively) revealed a similar pattern, although it was possible to

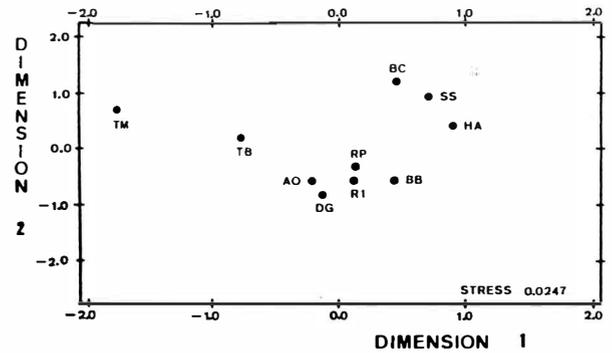


Fig. 3 MDS for the trophic dimension, prey size subdimension.

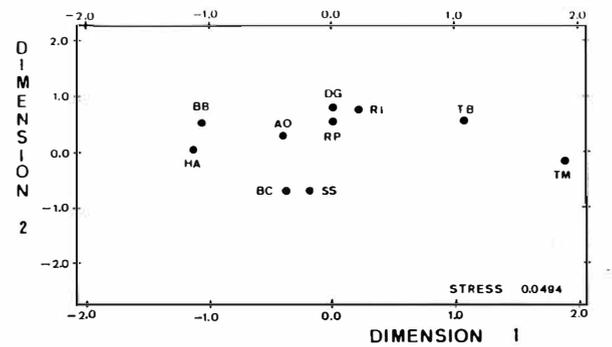


Fig. 4 MDS for the trophic dimension, arithmetic mean of the subdimensions.

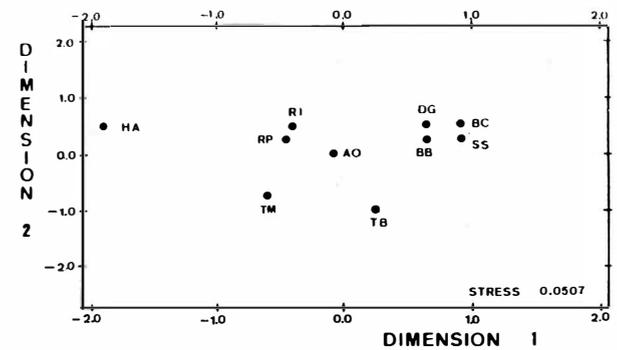


Fig. 5 MDS for the temporal dimension, annual activity subdimension.

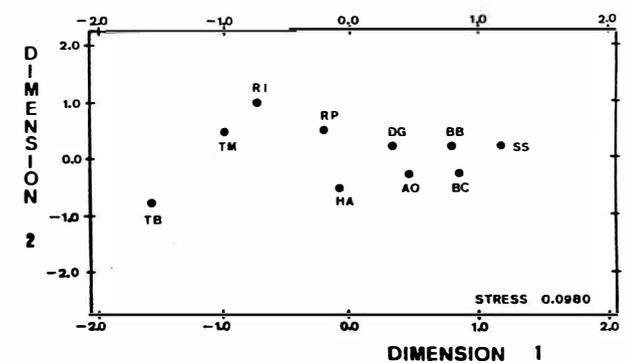


Fig. 6 MDS for the temporal dimension, daily activity subdimension.

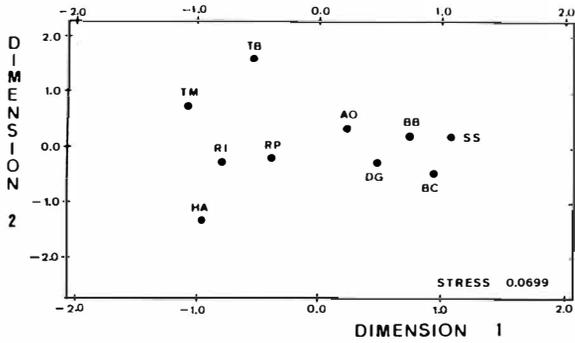


Fig. 7 MDS for the temporal dimension, arithmetic mean of the subdimensions.

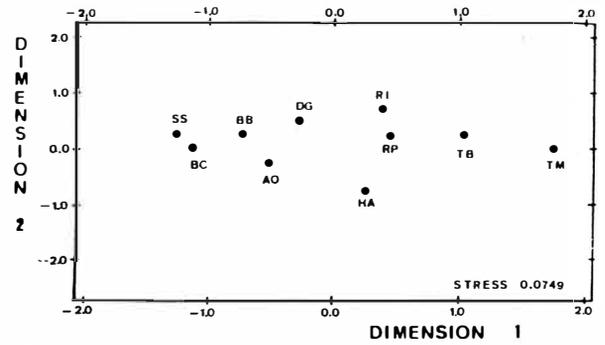


Fig. 9 MDS for the total overlap, arithmetic mean of the dimensions.

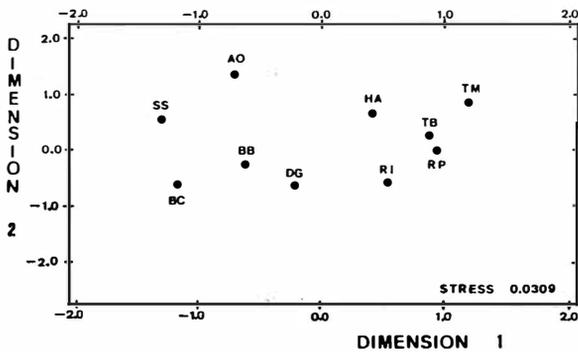


Fig. 8 MDS for the spatial dimension.

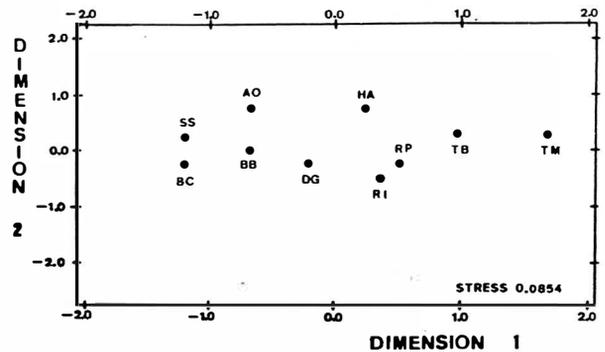


Fig. 10 MDS for the total overlap, multiplication of the dimensions.

appreciate the separation of *S. salamandra* and *B. calamita*, which consumed relatively large terrestrial prey.

Regarding the annual activity pattern (Fig. 5), the plane of the first two components divided the community in two groups: a central one with species, such as ranids and newts, that remained active throughout most of the year, and another to the right of the plane, which basically exhibited activity during autumn and spring. Regarding daily activity rhythms (Fig. 6), a central group of crepuscular species was observed, flanked to the right, by species that was increasingly nocturnal, and to the left by species with activity during almost all hourly segments.

The general plane of activity (Fig. 7) revealed relatively large Euclidean distances between species, indicating that this dimension, more than could be deduced from the overlap values alone (Appendix 6), contributed to a large extent to the interspecific segregation, specially by separating the nocturnal species that were situated to the right of the plane.

The plane corresponding to habitat (Fig. 8) revealed noteworthy large euclidean distances between virtually all species, with a clear trend towards terrestrial habits at the lower values of the first dimension. The planes corresponding to total overlap between the dimensions, calculated by arithmetic means (Appendix 8, Fig. 9) and multiplication (Appendix 9, Fig. 10) (see Pianka, 1974, 1986; May, 1975), again showed that habitat was the main dimension responsible for species segregation in the community studied. In this sense it is interesting to observe the strong correspondence of axis X in Fig. 8 with that in Figs. 9 and 10.

CONCLUSIONS

Habitat seems to be the main dimension responsible for species segregation in our community, with a strong correlation between activity rhythms and food composition of the species. Most species segregate due to the interaction of the three dimensions considered.

Our results agree reasonably well with those that have appeared in recent reviews on the mechanisms of resource partitioning in herpetological communities (Schoener, 1974; Heatwole, 1982; Toft, 1985) and point to the great importance of habitat in species segregation. In snake and larval amphibian communities, segregation seems mainly be due to food and activity rhythms, respectively (Heyer, 1976; Toft, 1985).

The structuring of the community studied seems to be a result of the interrelationship between the dimensions considered, in such a way that the more terrestrial species show basically nocturnal activity and are, in general, markedly seasonal, probably due to limiting factors such as environmental temperature and humidity. The more aquatic species show broader diel and seasonal activity patterns, probably as a result of the buffering effect of their aquatic environments (Brattstrom, 1970; Schoener, 1974; McFarland, *et al.*, 1979; Stevenson, 1985 a and b; Duellman and Trueb, 1986).

This conclusion was also held by Toft (1985) who indicates that 'in single communities, the resource partitioning patterns result from two or more factors that may operate independently, interactively, or both'.

Three main guilds can be distinguished in the community. The first is composed of terrestrial anurans and *S. salamandra*; their activity is overtly seasonal and nocturnal, and they have an exclusively terrestrial diet. The second group is formed by the anurans with aquatic or mixed habits, that are crepuscular or have a broad daily activity period, and that are generally euryphagous. A third guild contains *Triturus boscai* and *T. marmoratus*, which are aquatic and active over almost the whole year and in almost all the hourly segments. Note that for the total overlap, both species of *Triturus* appear separated from each other, to the same extent that *T. boscai* is separated from other the aquatic anurans.

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APPENDIX

	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal.	S.sal	T.bos	T.mar
R.ibe	—									
R.per	0.95	—								
D.gal	0.88	0.96	—							
A.obs	0.42	0.55	0.68	—						
H.arb	0.19	0.38	0.53	0.81	—					
B.buf	0.13	0.32	0.47	0.78	0.99	—				
B.cal	0.47	0.58	0.67	0.84	0.54	0.49	—			
S.sal	0.55	0.64	0.73	0.77	0.49	0.43	0.92	—		
T.bos	0.73	0.66	0.55	0.09	0.02	0.009	0.07	0.18	—	
T.mar	0.10	0.09	0.07	0.01	0.004	0.001	0.01	0.03	0.61	—

TABLE 1: Overlap matrix in the trophic dimension; prey-type subdimension.

	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
R.ibe	—									
R.per	0.98	—								
D.gal	0.96	0.94	—							
A.obs	0.97	0.96	0.98	—						
H.arb	0.66	0.71	0.46	0.57	—					
B.buf	0.96	0.94	0.88	0.90	0.77	—				
B.cal	0.54	0.63	0.37	0.47	0.78	0.51	—			
S.sal	0.59	0.66	0.41	0.48	0.84	0.60	0.90	—		
T.bos	0.74	0.70	0.77	0.84	0.55	0.66	0.46	0.48	—	
T.mar	0.17	0.22	0.29	0.35	0.06	0.05	0.07	0.06	0.77	—

TABLE 2: Overlap matrix in the trophic dimension; prey-size subdimension.

	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
R.ibe	—									
R.per	0.97	—								
D.gal	0.92	0.95	—							
A.obs	0.69	0.76	0.83	—						
H.arb	0.43	0.54	0.50	0.69	—					
B.buf	0.55	0.63	0.67	0.84	0.88	—				
B.cal	0.51	0.60	0.52	0.65	0.66	0.50	—			
S.sal	0.57	0.65	0.57	0.63	0.66	0.52	0.91	—		
T.bos	0.73	0.68	0.66	0.47	0.29	0.33	0.26	0.33	—	
T.mar	0.13	0.16	0.18	0.18	0.03	0.02	0.04	0.04	0.69	—

TABLE 3: Overlap matrix in the trophic dimension; arithmetic mean of the subdimensions.

	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
R.ibe	—									
R.per	0.95	—								
D.gal	0.74	0.72	—							
A.obs	0.82	0.82	0.82	—						
H.arb	0.54	0.49	0.15	0.21	—					
B.buf	0.63	0.62	0.87	0.66	0.07	—				
B.cal	0.55	0.48	0.92	0.69	0.001	0.91	—			
S.sal	0.59	0.53	0.90	0.75	0.04	0.88	0.97	—		
T.bos	0.59	0.52	0.51	0.72	0.16	0.48	0.50	0.60	—	
T.mar	0.57	0.67	0.41	0.60	0.22	0.50	0.27	0.36	0.70	—

TABLE 4: Overlap matrix in the temporal dimension: annual activity subdimension.

	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
R.ibe	—									
R.per	0.79	—								
D.gal	0.40	0.75	—							
A.obs	0.24	0.50	0.66	—						
H.arb	0.44	0.47	0.44	0.57	—					
B.buf	0.21	0.44	0.65	0.60	0.42	—				
B.cal	0.13	0.38	0.69	0.69	0.74	0.71	—			
S.sal	0.21	0.44	0.74	0.60	0.30	0.60	0.70	—		
T.bos	0.29	0.30	0.24	0.27	0.21	0.13	0.08	0.08	—	
T.mar	0.48	0.50	0.39	0.29	0.42	0.36	0.19	0.16	0.43	—

TABLE 5: Overlap matrix in the temporal dimension: daily activity subdimension.

	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
R.ibe	—									
R.per	0.87	—								
D.gal	0.57	0.74	—							
A.obs	0.53	0.66	0.74	—						
H.arb	0.49	0.48	0.29	0.39	—					
B.buf	0.42	0.53	0.76	0.63	0.24	—				
B.cal	0.34	0.43	0.80	0.69	0.37	0.85	—			
S.sal	0.40	0.48	0.82	0.68	0.17	0.74	0.83	—		
T.bos	0.44	0.41	0.37	0.49	0.18	0.31	0.29	0.34	—	
T.mar	0.53	0.58	0.40	0.44	0.32	0.43	0.23	0.26	0.56	—

TABLE 6: Overlap matrix in the temporal dimension; arithmetic mean of the subdimensions.

	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
R.ibe	—									
R.per	0.54	—								
D.gal	0.55	0.37	—							
A.obs	0.10	0.07	0.17	—						
H.arb	0.36	0.51	0.38	0.20	—					
B.buf	0.35	0.23	0.59	0.46	0.22	—				
B.cal	0.04	0.07	0.77	0.14	0.19	0.53	—			
S.sal	0.09	0.02	0.18	0.27	0.10	0.47	0.35	—		
T.bos	0.47	0.86	0.36	0.09	0.80	0.27	0.03	0.09	—	
T.mar	0.19	0.60	0.16	0.08	0.63	0.08	0.04	0.05	0.78	—

TABLE 7: Overlap matrix in the spatial dimension.

	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
R.ibe	—									
R.per	0.79	—								
D.gal	0.68	0.69	—							
A.obs	0.44	0.49	0.58	—						
H.arb	0.43	0.51	0.39	0.43	—					
B.buf	0.44	0.47	0.68	0.64	0.45	—				
B.cal	0.30	0.37	0.70	0.50	0.41	0.62	—			
S.sal	0.35	0.38	0.52	0.53	0.31	0.57	0.70	—		
T.bos	0.55	0.65	0.46	0.35	0.42	0.30	0.19	0.25	—	
T.mar	0.28	0.45	0.25	0.23	0.32	0.18	0.10	0.12	0.68	—

TABLE 8: Total overlap matrix calculated by arithmetic mean of the dimensions.

	R.ibe	R.per	D.gal	A.obs	H.arb	B.buf	B.cal	S.sal	T.bos	T.mar
R.ibe	—									
R.per	0.46	—								
D.gal	0.29	0.26	—							
A.obs	0.03	0.03	0.11	—						
H.arb	0.07	0.13	0.05	0.05	—					
B.buf	0.08	0.08	0.31	0.25	0.04	—				
B.cal	0.008	0.01	0.32	0.06	0.04	0.22	—			
S.sal	0.02	0.008	0.08	0.12	0.01	0.18	0.27	—		
T.bos	0.15	0.24	0.09	0.02	0.04	0.02	0.002	0.01	—	
T.mar	0.01	0.05	0.01	0.006	0.006	0.001	0.001	0.001	0.30	—

TABLE 9: Total overlap matrix calculated by multiplication of the dimensions.