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Lacertids of the Mediterranean region

A Biological Approach

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Chapter 10

Feeding of two sympatric lacertids in a sandy coastal area (Ebro Delta, Spain)

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Introduction

Psammodromus algirus (Large *Psammodromus*) and *Acanthodactylus erythrurus* (Fringe-toed Lizard) are two medium sized Mediterranean lacertids. Both range the Iberian Peninsula, (excepting the north and the Pyrenean Mountains, Barbadillo, 1987), and the Mediterranean regions of NE Africa. *Ps. algirus* also reaches the SE of France (Fretey, 1987) and it is more north-spread than the other species. The two species live together in many Mediterranean open areas. This study was carried out in a zone of coastal dunes where they are especially abundant.

The basic diet of each species, its interspecific and seasonal variation and the segregation factors were studied in order to caracterize the trophic niche of them.

The study area

The Ebro Delta is an alluvial plain extending over about 350 km^2 in north east Spain. 75% of its surface is occupied by farmland (mostly rice fields) and the remaining 25% is mainly composed of littoral lagoons. Sandy ground and dunes (9%) are found in the coast and they often mix with moist zones producing a mosaic habitat. This is the case of Riomar area (UTM 31TCF1810) at the north side of the river mouth, where psammophile and halophile vegetation mix in a patchy structure (see Camarasa *et. al.*, 1977 and Curcó, 1990 for a complete phytosociological description). Climate can be defined as littoral Mediterranean, with an long dry season in summer. Mean annual rainfall and temperature are 548 mm and 16.6°C respectively (Panareda and Nuet, 1973).

The lizard populations

Psammodromus algirus and *Acanthodactylus erythrurus* are the only saurian species living in this area. Their abundances are in a ratio of 2:1, respectively. *A. erythrurus* is close to its northern distributional limits and it is endangered in this area at present. Referring to other reptiles, only the snakes *Malpolon monspessulanus* and *Natrix maura* are present. The former is a probable predator of these lizards.

Both lizard species reach their sexual maturity mostly at the first year of age (unpublished data). We distinguish only two classes (Arnold, 1987): adult and immature. Minimum adult sizes (SVL) were 52.15 mm (males), 53.20 mm (females) for *Ps. algirus* and 56.60 mm (males), 56.40 mm (females) for *A. erythrurus.* The latter species is the most thermophilous one and it undergoes a winter diapause period. However, immatures *Psammodromus* can be seen even in the middle of winter, on sunny days.

Material and Methods

133 *Psammodromus algirus* and 87 *Acanthodactylus erythrurus* were captured during 1986 and 1987 in monthly campaigns during the period of maximum activity. At the laboratory, their snout-vent length (SVL) was measured using a calliper (0.05 mm precision). Animals were injected with 70% ethanol and stored in that liquid. This material was used not only in this study but also for biometry and reproduction analysis.

The stomach was the only segment of the digestive tract that was used considering it is a more accurate and more uniform representation of diet (Seva, 1982). Stomach contents were analyzed under a binocular lens. The minimum numbers criterion was used in the prey counting of every stomach content (Vericad and Escarré, 1976). Preys were identified using determination keys. The Order level was used as operational taxonomic unit (OTU, Sneath and

Sokal, 1973) with some exceptions (Figures and Tables). Prey lengths were measured using a milimetric scale or a calliper (0.05 mm precision) and grouped into classes of 1 mm of interval (see Figures and Tables).

Jover's method (1989) was used in the statistical analysis of diet description and trophic diversity.

Four diet descriptors were calculated: the abundance (%P), the occurrence (%N), the probabilistic index (IP) or lambda "λ" (Ruiz and Jover, 1981) and the intensity of resource use (IUR, Jover, 1989; Jover and Ruiz, in press). This last descriptor combines in one number (standardized as a percentage) the three diet components:

a. The proportion of a prey in the total diet of the population.

b. The proportion of individuals belonging to the population which consume that prey.

c. The homogeneity in the comsumption of that prey.

This last component has not usually been considered in feeding studies. So, IUR is obtanined from combination of two independently calculated criterions: a (quantity, N%) and b-c (distribution). This last one is estimated calculating the diversity, as a measure of variance of the individuals consuming a resource. The more individuals consume a resource (b) and/or the more homogeneusly they consumed this (c), the higher will be the diversity. See González-Solis and Ruiz (1991) for an example of application of this index.

Margalef's diversity index (Brillouin's index for diet) was used according to Pielou (1966; 1975) and Hurtubia (1973). Mean individual diversity (Hi), populational diversity (Hp) estimated by the Jack-knife technique (Jover, 1989) and total accumulated diversity (Hz) were calculated.

Populational diversities were compared by t tests, (considering the Bonferroni test) instead of using the analysis of variance, because of their non-additivity.

Diet overlap was calculated using Schoener's index (Schoener, 1968). This index has proved to be more accurate than others for estimating intermediate real overlaps (Linton *et al.*, 1981). Dendrograms were generated from the overlapping matrices by calculating the euclidean distances.

Results

7 *Psammodromus* and 7 *Acanthodactylus* stomachs were empty. So, the available contents were 123 for *Ps. algirus* (31 males, 30 females and 65 immatures) and 80 for *A. erythrurus* (24 males, 19 females and 37 immatures). Considering the seasonal distribution, there were 24 winter, 25 spring, 32

summer and 45 autumn contents for *Ps. algirus* and 14 spring, 24 summer and 42 autumn-winter contents for *A. erythrurus* (only 3 contents were from winter).

729 and 538 prey items were determined for each species respectively. The number of preys per stomach was significantly higher in *A. erythrurus* (6.72) than in *Ps. algirus* (5.61) (Mann-Whitney U test, $Z = -1.779$, p 0.05). No intraspecific differences were found.

Taxonomical analysis. Resource use

The diet of both species was of animal origin, except for some vegetal fibres. Sand grains (0.15-1.60 mm), eaten probably with the prey, were found in many contents. Arthropods were the main diet of both lizads, excluding 4 snails found in *P. algirus* stomachs (Fig. 1). Table 1 shows the comparative values of the descriptors.

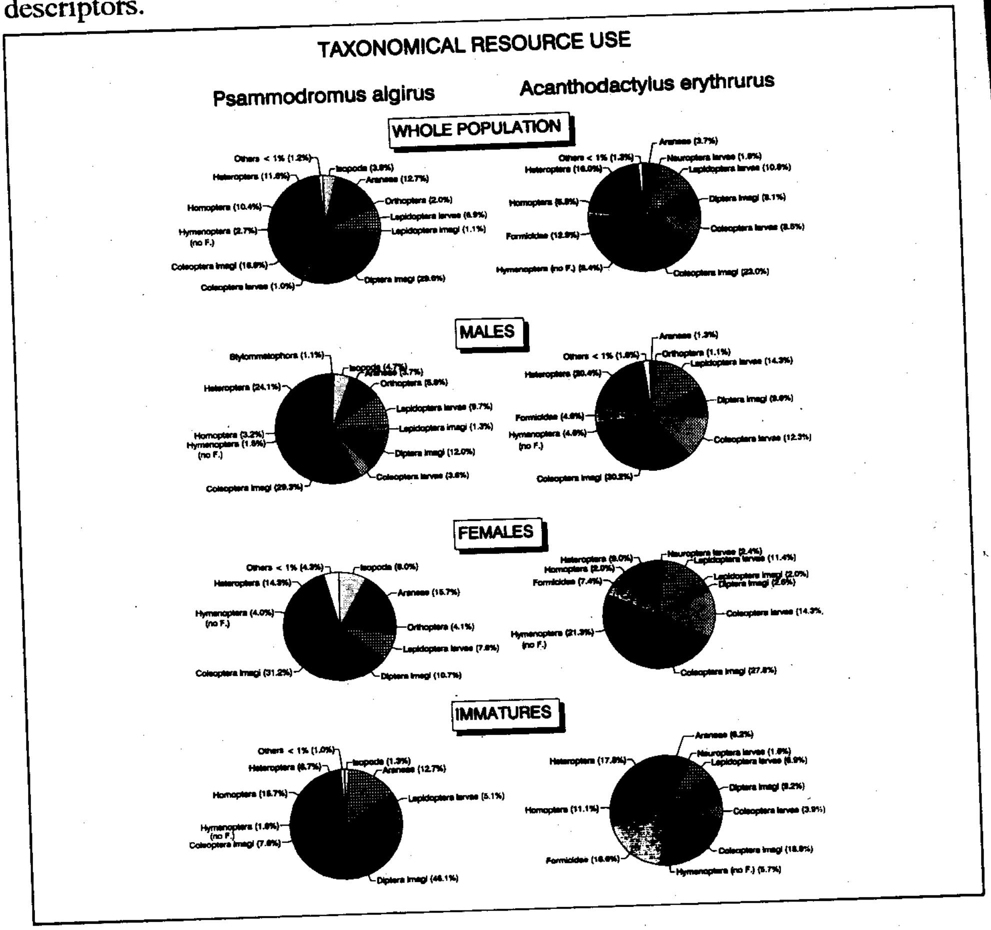


Fig. 1. Percentage of resource use considering the taxonomical categories consumed by the whole population and the classes of *Psammodromus algirus* and *Acanthodactylus erythrurus*.

Table 1. Compared descriptors of the taxonomical categories in the diet of *Psammodromus algirus* and *Acanthodactylus erythrurus*.
%P = Percentage of occurrence.
%N = Percentage of abundance.
IP = Probabilistic index (lambda "λ" of Ruiz and Jover, 1983).
IU = Resource use index (Jover, 1989; Ruiz and Jover, in press).

OTU	*Ps. algirus*				*A. erythrurus*			
	% P	% N	IP	IU	% P	% N	IP	IU
Stylommatophora	3.17	0.81	1.00	0.36	0.00	0.00	0.00	0.00
Isopoda	15.08	5.41	3.76	3.78	3.75	0.55	0.36	0.22
Araneae	38.10	10.27	10.81	12.75	18.75	4.19	2.67	3.71
Acari	0.00	0.00	0.00	0.00	1.25	0.18	0.02	0.00
Dictyoptera	3.17	0.54	0.35	0.26	3.75	0.55	0.07	0.22
Orthoptera	11.90	2.16	2.20	2.01	3.75	0.55	0.16	0.22
Dermaptera	0.79	0.14	0.41	0.00	2.50	0.36	0.11	0.09
Neuroptera larvae	3.97	0.68	0.68	0.38	12.50	2.19	3.47	1.76
Lepidoptera larvae	26.98	6.08	8.11	6.92	33.75	10.93	13.26	10.80
Lepidoptera imagi	7.94	1.35	1.95	1.09	6.25	0.91	0.48	0.54
Diptera larvae	0.00	0.00	0.00	0.00	1.25	0.18	0.02	0.00
Diptera imagi	54.76	26.89	31.60	29.65	31.25	9.65	9.99	8.16
Coleoptera larvae	7.14	1.35	1.45	1.01	35.00	7.47	7.98	8.50
Coleoptera imagi	40.48	13.38	11.12	16.88	56.25	17.49	17.44	22.99
Hymenoptera (no F.)	12.70	2.97	2.60	2.71	32.50	7.83	11.77	8.39
Formicidae	1.59	0.68	0.56	0.09	27.50	15.48	11.54	12.89
Homoptera	24.60	17.16	9.94	10.37	20.00	8.74	7.51	5.46
Heteroptera	39.68	9.60	13.35	11.64	52.50	12.75	13.18	16.03
Ova insecta	1.59	0.54	0.11	0.09	0.00	0.00	0.00	0.00

In general, none of the OTU categories was excessively high. However, there was an exception: *Psammodromus* showed 29.6% of Diptera consumption, corresponding mainly to mosquitoes. Other important preys were Coleoptera (16.9%), Araneae (12.7%), Heteroptera (11.6%) and Homoptera (10.4%). *Acanthodactylus* appeared to be a more ecclectic predator than *Psammodromus*. Their most consumed preys were Coleoptera (23%) and Heteroptera (16%), Formicidae (12.9%) and Lepidoptera larvae (10.8%). The comsumption of Diptera was low (8.1%).

The intraspecific differences were poorly marked between sexes in both species (Fig. 1). *Psammodromus* females ate more spiders and less heteropters than did males. The diet of *Acanthodactylus* was richer in flying hymenopters for males than for females. However, the clearest differences were those between adults and immatures. *Psammodromus* immatures ate many more mosquitoes (46.1%) than adults, producing a stenophagous diet (see diversities). On the other hand, *Acanthodactylus* immatures ate more ants than did adults (18.6%).

The seasonal variation in the taxonomical composition of the diet was important in both species (Figs. 2 and 3). Two kinds of prey were observed:

1. Seasonal preys: Prey appearing only during a part of the year. This was the case of Formicidae and Coleoptera larvae for *A. erythrurus* and Isopoda for *P. algirus*.

2. 'Warranty' preys (Carretero, 1989): important in all seasons. For instance, Araneae, Diptera and Heteroptera for *P. algirus* or Coleoptera imagi and Heteroptera *A. erythrurus*.

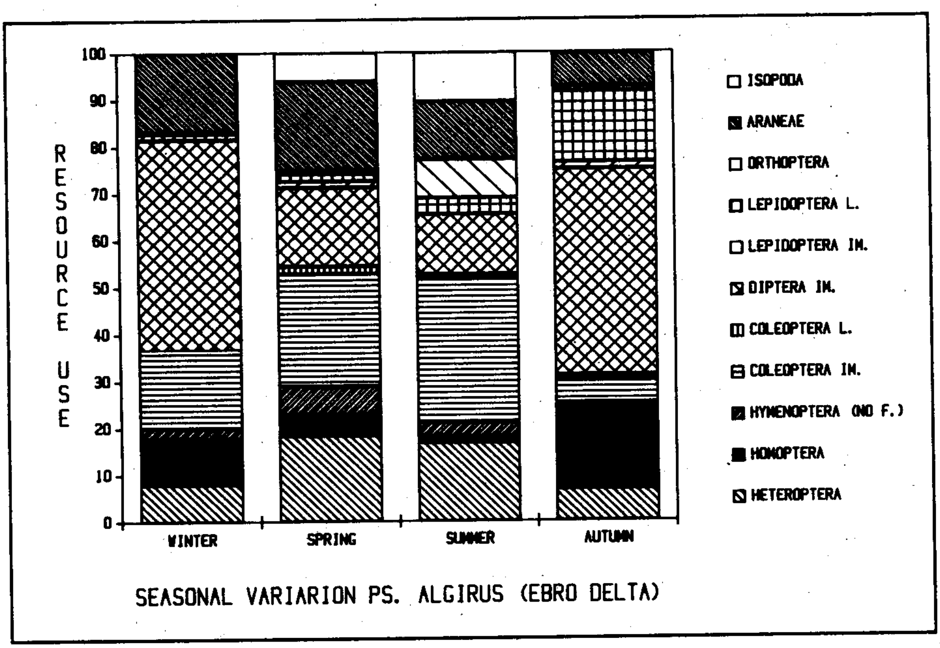


Fig. 2. Seasonal variation of the taxonomical diet composition in *Psammodromus algirus*.

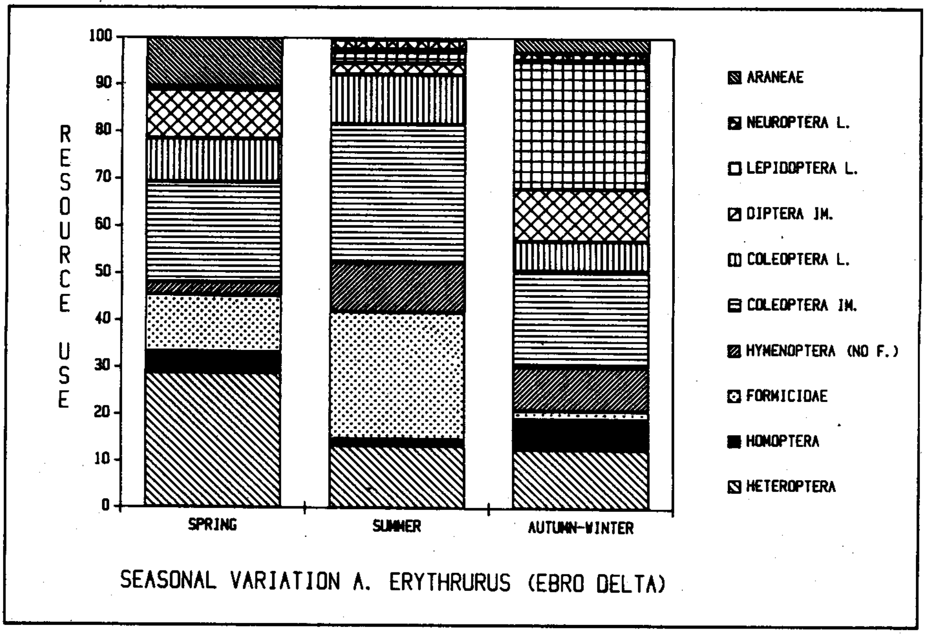


Fig. 3. Seasonal variation of the taxonomical diet composition in *Acanthodactylus erythrurus*.

Taxonomical analysis. Diversity.

Diversities were calculated for the whole population and the classes (Table 2). The *Psammodromus* contents were more diverse individually than the *Acanthodactylus* ones (test, t = 2.12, 204 d.f., $p < 0.05$). This did not happened to the populational diversity. Considering the size classes of *Psammodromus,* the stomachs of immatures showed lower individual diversities than adults, but there were no intersexual differences (one way ANOVA, F = 3.32, $p < 0.05$; Duncan's a posteriori test, $p < 0.05$ for the mentioned differences). The only significant difference in the populational diversity was found between females and immatures (t tests, $p < 0.05$, using the Bonferroni test). No intraspecific differences were found in *Acanthodactylus,* either in individual diversities or in populational diversities.

Table 2. Individual, populational and total accumulated (Hn) diversities of the taxonomical categories in the diet of the lacertids of Ebro Delta. N = number of stomachs.

		Individual Diversity			Populational Diversity		
Species	Class	N	Mean	Var.	Estim.	St. er.	Hn
Lacertidae	total	206	0.8494	0.2437	3.4324	0.0592	3.36
Ps. algirus	total	126	0.7916	0.1934	3.1881	0.0886	3.08
Ps. algirus	males	31	0.7582	0.1944	3.3867	0.1241	3.05
Ps. algirus	females	30	0.9676	0.1368	3.3143	0.1029	3.05
Ps. algirus	immatures	65	0.7263	0.2053	2.7155	0.1366	2.56
A. erythrurus	total	80	0.9406	0.3125	3.3726	0.0508	3.25
A. erythrurus	males	24	0.9895	0.3221	3.2465	0.0891	2.97
A. erythrurus	females	19	0.8836	0.3019	3.2583	0.1003	2.93
A. erythrurus	immatures	37	0.9380	0.3257	3.2730	0.0802	3.08

Seasonal variation in trophic diversity was low. It was registered only in the populational diversities of *Psammodromus algirus* (Fig. 4): winter diversity was lower than summer and autumn diversity was lower than spring (t tests, $p < 0.05$, using the Bonferroni test). *Acanthodactylus erythrurus* did not show any seasonal change.

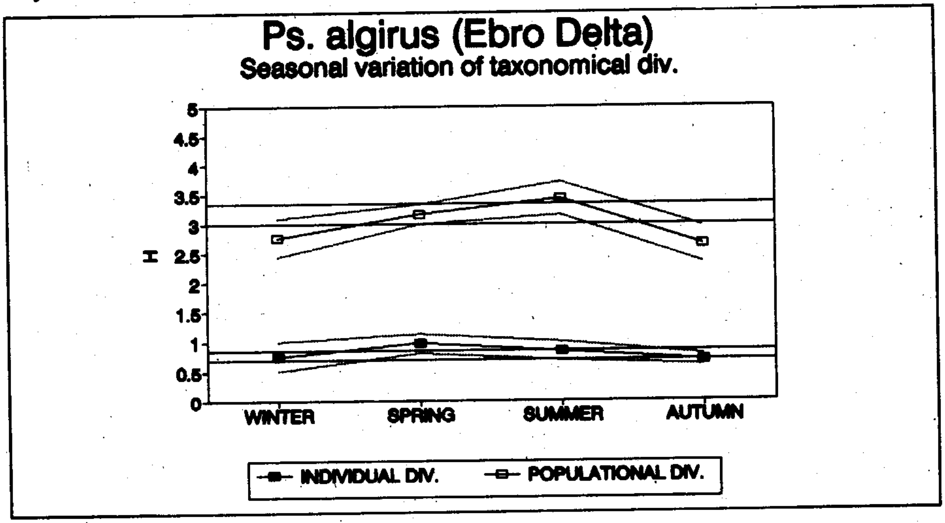


Fig. 4. Seasonal variation of trophic diversities (H) in *Psammodromus algirus*. Dotted lines: confidence limits (95%) of the mean seasonal diversities. Horizontal continue lines: confidence limits (95%) of the mean annual diversities.

Prey size analysis. Resource use.

The prey size spectrum was wide in both lacertids (from 0.5 mm to more than 30 mm). In every analyses, the modal prey size consumed was displaced to lower sizes and the distribution of resource use followed a logarithmic curve (Fig. 5). Table 3 shows the comparative values of the descriptors.

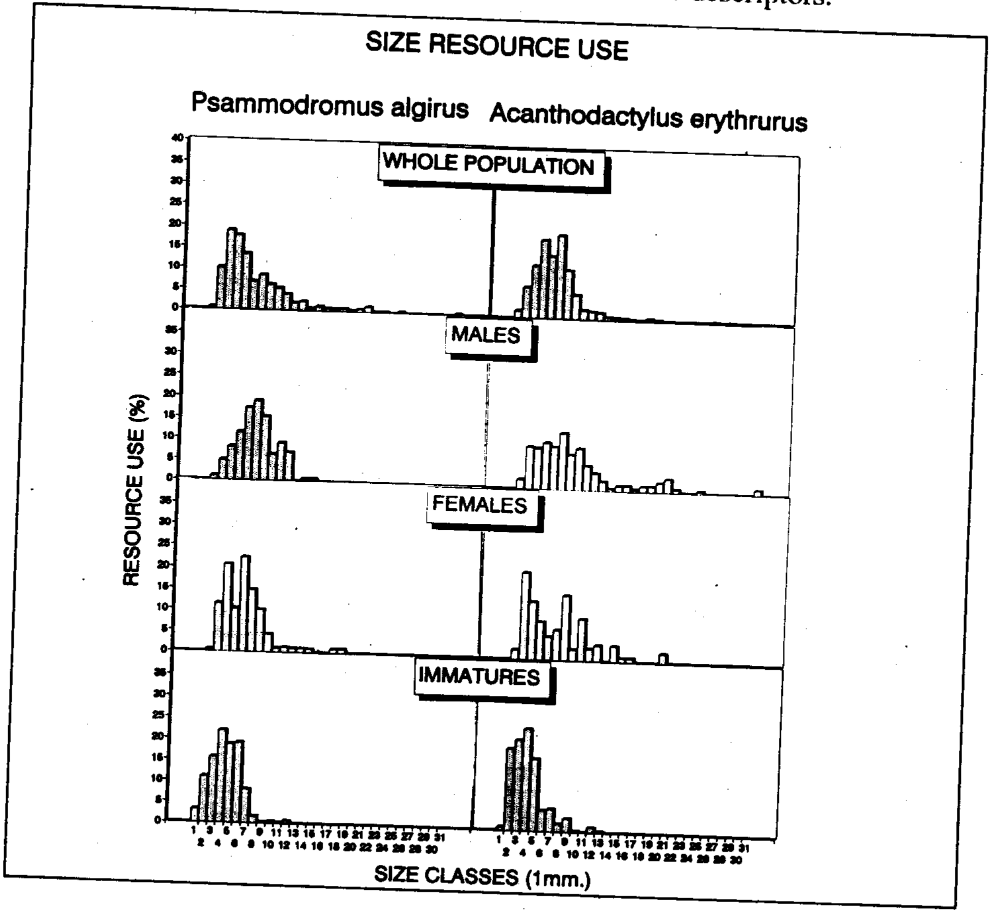


Fig. 5. Percentage of resource use considering the prey size categories consumed by the whole population and the classes of *Psammodromus algirus* and *Acanthodactylus erythrurus.*

Acanthodactylus ate larger preys than *Psammodromus* (Mann-Whintney U test, Z = -1.98, $p < 0.05$). There were intraspecific differences in the sizes consumed in both species. There were no differences between sexes, but immatures ate smaller preys than adults in *Psammodromus* (Kruskal-Wallis test, H = 102.40, 2 g.d.l., $p < 0.01$; Dunn's a posteriori test $p < 0.05$) and *Accanthodactylous* (Kruskal-Wallis test, H = 102.24, 2 g.d.l., $p < 0.01$; Dunn's a posteriori test $p < 0.05$).

Table 3. Compared descriptors of the prey size categories in the diet of *Psamodromus algirus* and *Acanthodactylous erythrurus*. %P = Percentage of occurence. %N = Percentage of abundance. IP = Probabilistic index (lambda "λ" of Ruiz and Jover, 1983). IU = Resource use index (Jover, 1989; Ruiz and Jover, in press).

		Psammodromus algirus				*Acanthodactylous erythrurus*			
	SIZE CLASS	%P	%N	IP	IU	%P	%N	IP	IU
1	(0-1mm)	5.56	5.27	2.78	1.63	3.75	1.86	0.52	0.30
2	(1-2mm)	20.63	10.68	4.54	7.28	33.75	9.67	14.92	10.05
3	(2-3mm)	37.30	9.87	8.00	12.46	46.25	17.66	14.41	18.70
4	(3-4mm)	46.83	13.78	20.12	18.64	51.25	13.94	15.70	17.61
5	(4-5mm)	40.48	14.87	14.54	14.89	38.75	14.13	11.35	13.35
6	(5-6mm)	43.65	19.32	18.82	19.73	31.25	5.76	9.60	6.77
7	(6-7mm)	36.51	9.19	8.41	11.54	32.50	6.88	3.11	8.21
8	(7-8mm)	23.81	5.14	5.07	5.77	27.50	5.76	13.54	6.10
9	(8-9mm)	12.70	2.30	3.17	2.21	25.00	4.83	1.40	5.24
10	(9-10mm)	11.90	2.03	2.21	1.94	20.00	4.46	1.78	3.87
11	(10-11mm)	9.52	1.89	4.22	1.60	12.50	2.23	0.66	1.78
12	(11-12mm)	5.56	0.95	1.75	0.65	15.00	2.42	1.03	2.25
13	(12-13mm)	3.97	0.68	0.45	0.38	6.25	0.93	3.39	0.57
14	(13-14mm)	3.17	0.81	0.72	0.37	8.75	1.30	0.82	0.97
15	(14-15mm)	1.59	0.27	0.04	0.07	6.25	0.93	0.62	0.57
16	(15-16mm)	1.59	0.27	0.28	0.07	5.00	0.74	0.68	0.40
17	(16-17mm)	3.97	0.68	0.46	0.38	6.25	0.93	0.59	0.57
18	(17-18mm)	3.17	0.54	0.65	0.26	3.75	0.56	0.22	0.24
19	(18-19mm)	0.79	0.14	0.46	0.00	6.25	0.93	0.25	0.57
20	(19-20mm)	0.79	0.14	0.04	0.00	10.00	1.49	3.74	1.19
21	(20-21mm)	0.00	0.00	0.00	0.00	2.50	0.56	0.15	0.13
22	(21-22mm)	0.79	0.14	0.20	0.00	2.50	0.37	0.08	0.10
23	(22-23mm)	0.79	0.14	0.11	0.00	0.00	0.00	0.00	0.00
24	(23-24mm)	0.79	0.14	0.11	0.00	3.75	0.56	0.41	0.24
25	(24-25mm)	1.59	0.27	2.03	0.07	1.25	0.19	0.03	0.00
26	(25-26mm)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
27	(26-27mm)	1.59	0.27	0.28	0.07	1.25	0.19	0.12	0.00
28	(27-28mm)	0.00	0.00	0.00	0.00	1.25	0.19	0.19	0.00
29	(28-29mm)	0.79	0.14	0.46	0.00	0.00	0.00	0.00	0.00
30	(29-30mm)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
31	(>30mm)	0.79	0.14	0.07	0.00	3.75	0.56	0.70	0.24

If only the largest prey from every stomach was considered, the results were similar in *Psammodromus* (Kruskal-Wallis test, $H = 45.65$, 2 g.d.l., $p < 0.01$;

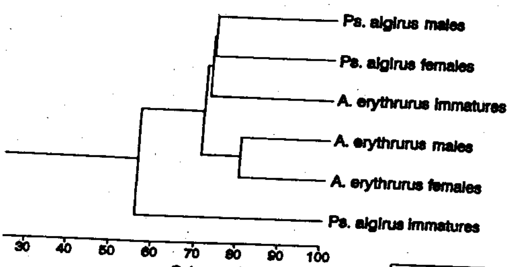
Dunn's a posteriori test, $p < 0.05$;) and *Acanthodactylus* (Kruskal-Wallis test, $H = 102.24$, 2 g.d.l., $p < 0.01$; Dunn's a posteriori test, $p < 0.05$).

Significant correlations between lizard (SVL) and prey sizes, considering all the preys, were found in *Psammodromus* ($R_{Spearman} = 0.37$, 726 d.f., $p < 0.01$) and *Acanthodactylus* ($R_S = 0.48$, 536 d.f., $p < 0.01$). The same results were obtained with the largest prey from each stomach ($R_S = 0.53$, 124 d.f., $p < 0.01$ and $R_S = 0.53$, 78 d.f., $p < 0.01$, respectively).

Finally, the trophic overlaps between species and among classes were calculated using the percentages of resource use for OTUs and size classes. For the species, they were 60.00% (OTUs) and 78.54% (size classes). The overlaps among classes have been represented with their corresponding dendrograms in Fig. 6.

a.- Taxonomical overlaps

		Ps. algirus males	Ps. algirus females	Ps. algirus immatur.	A. erythrurus males	A. erythrurus females	A. erythrurus immatur.
Ps. algirus	males	---					
" "	females	72.00	---				
" "	immatures	56.14	52.12	---			
A. erythrurus	males	66.71	65.70	36.05	---		
" "	females	57.38	58.41	34.53	80.12	---	
	immatures	71.89	60.35	56.08	71.11	58.47	---



b.- Size overlaps

		Ps. algirus males	Ps. algirus females	Ps. algirus immatur.	A. erythrurus males	A. erythrurus females	A. erythrurus immatur.
Ps. algirus	males	---					
" "	females	69.17	---				
" "	immatures	58.43	67.99	---			
A. erythrurus	males	70.75	70.86	50.46	---		
" "	females	70.14	65.51	50.16	78.68	---	
	immatures	53.73	57.34	77.03	55.94	55.28	---

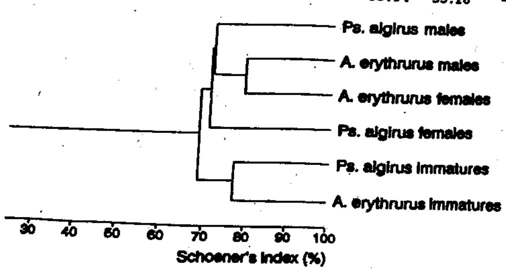


Fig. 6. Trophic overlapping matrices and dendrograms for the subdimensions of taxonomical categories (a) and size classes (b) of the preys consumed by the Lacertidae from Ebro Delta.

Discussion and conclusions

The feeding habits of *Psammodromus algirus* and *Acanthodactylus erythrurus* has been the object of several studies (Table 4). Similarities and divergences have been observed and they will now be discussed with a view to elucidating the trophic niche of these two species.

Table 4. Some parameters corresponding to other populations of *Psammodromus algirus* (PSA) and *Acanthodactylus erythrurus* (AE) previously studied. %V = Percentage of volume. P = present. * Animals captured in June and July.

Locality	Reference	sample PSA	sample AE	digestive segment	diet descriptors
Punta Sabinal (Almeria prov.)	Valverde (1967)	41	49	stomach	%N
W. Siera Morena (Huelva prov.)	Mellado *et al.* (1975)	141	-	stomach	%N
Alicante prov.	Escarre and Vericad (1981)	60	55	total	%N
El Saladar (Alicante prov.)	Seva (1982-1984)	0/8	72/41	fecal stomach	%N
La Algaida (Cadiz prov.)	Busack and Jaksic (1982)	P	529	total	%N
W. Sistema Central	Pérez-Mellado (1982)	116	19	total	%P, %N
Isola dei Conigli (Lamperdusa)	Di Palma (1984) Sorci (1990)	119	-	fecal	%N
Espeja (Salamanca prov.)	Pollo & Pérez-Mellado (1988)	233	151	total	%P, %N, IP
Torredembarra (Tarragona prov.)	Carretero (1989)	144	64	stomach	%P, %N, IP
N of Madrid prov.	Diaz and Carrascal (1990)	*53	-	total	%P, %N, %V
Ebro Delta (Tarragona prov.)	Present study	126	80	stomach	%P, %N, IP, IU

First, *A. erythrurus* consumes a greater number of prey items than the other species. Some authors have even found intraspecific differences in both species (Pollo and Pérez-Mellado, 1988), but not others (Busack and Jaksic, 1982; Pérez-Mellado, 1982; Carretero, 1989; present work).

The vegetal component is almost absent here, but the results of Seva (1984); Busack and Jaksic (1982) and Di Palma (1984) demonstrate that both lacertids are able to eat a certain amount of vegetal food. In small lizard species, this may be associated with situations of low arthropod availability (Pough, 1973), mainly in insular ecosystems (Di Palma, 1984; Mayol, 1985 and Pérez-Mellado, 1989).

As to diet composition, this depends on three factors: the available trophic resources (Arnold, 1987) and their limitation, the "internal preferences" of the species (Díaz and Carrascal, 1990; Pérez-Mellado *et al.*, 1991; Pollo and Pérez-Mellado, 1991) and the competition with other species, not only lizards (Pianka, 1974). Trophic availability has not been evaluated in this work, but it can be assumed that the same species combination in the same type of habitat can be directly compared. Then, diet coincidences will demonstrate some of the species preferences and the great diet divergences will be due to differences on food availability, if there are no different energy demands among populations.

So, our results show some important differences with those registered by Seva (1984) and Carretero (1989) in two similar ecosystems. *Psammodromus algirus* diet differs substantially from that of other populations (which Colepotera is the main OTU) because of its high consumption of Diptera, whereas other taxa, frequently registered in other areas, are poorly consumed in Ebro Delta. Mosquitoes are abundant in delta ecosystems (González *et al.*, 1983) and they can be considered as a dominant prey (sensu Ruiz, 1984). When the air temperature is high, they accumulate on humid grounds in shade, close to bushes and other plants (personal observations). There, they can be easily captured by *Psammodromus* which is asociated to coverted microhabitats (Mellado *et al.* 1975). The preys are captured by both widely foraging and 'sit and wait' hunting strategies (Pianka, 1978; Pérez-Mellado, 1981).

On the other hand, *Acanthodactylus erythrurus*, an active forager, shows a more balanced diet than the other species. The incidence of ants in the diet is low enough (12.9%) for them not to be considered myrmecophagous lizards. Consequently, diet is displaced to other more widely consumed taxa like Coleoptera and Heteroptera. This situation also occurs in a nearby area of the Mediterranean coast (Carretero, 1989) but not in the other localities studied. So, the phylogenetic constraint proposed for this species by some authors (Pérez-Mellado, 1982; Pollo and Pérez-Mellado, 1988; Pollo and Pérez-Mellado, 1991) should perhaps consider this new facts. Moreover, there is no evidence of prey aggregation for the other main taxa of *A. erythrurus* in Ebro Delta (see Pollo and Pérez-Mellado, 1991). Curiously, *Psammodromus algirus* is the species which tends to myrmecophagy in one population studied *(Di Palma, 1984; Sorci, 1990)*.

The intraspecific differences in the eaten taxa agree with previous studies, since sexual segregation is lower than size segregation. The latter is higher in *Psammodromus* than in *Acanthodactylus*. There is no evidence of differential food requirements in the immatures. Hence, only the smaller size of the immatures or a spatio-temporal difference may produce this segregation indirectly (see previous studies and also Mellado, 1980; Seva and Escarré, 1980; Pollo and Pérez-Mellado, 1989).

Seasonal variation has been studied by many authors in many lacertid species. The subsequent differences have often been interpreted as a consequence of variations in trophic availability, taking into account the activity period (Darevskii, 1967; Avery, 1966; Arnold, 1987) or as a result of the optimization of nutrient input (Pérez-Mellado *et al.*, 1991). Considering the species *Psammodromus algirus*, there are some coincidences with other studies (Carretero, 1989). Spiders seems to be constant in the diet, probably because they remain active even in winter (Jones, 1985). The same result has been found for heteropters. However, the high dominance of Diptera has no equivalent in other studies in lizards, but it has been reported for the amphibian *Rana perezi* in the study area (Jover, 1989), depending on the rice field cycle. *Acanthodactylus* shows the same regularity of heteropters in the diet (Carretero, 1989; present study) but this does not occur in other populations (Busack, 1982; Pollo and Pérez-Mellado, 1988). Generally, there is a tendency to increase the proportion of formicids in the diet from winter to autumn (see references). The present results are the exception to this rule, because of the low consumption of ants in autumn by the fringe-toed lizard.

The results of the diversity analysis agree with the previous remarks. As most of the species of the Lacertidae, the diet is characterized by a wide trophic niche, manifested in high trophic diversities. There is a great heterogeneity among individuals. So, the populational diversity is nearly twice the individual diversity in every group analized.

The dominance of Diptera in *Psammodromus* and the low frequencies of Formicidae in *Acanthodactylus* produce higher values of populational diversity in the latter, in contrast to other populations analyzed (see references of Table 1). This does not happen with individual diversity. So, there are more interindividual differences in *Psammodromus* than in *Acanthodactylus*. This is reflected in the adult-immature comparison. *Psammodromus* immatures have lower trophic diversity than adults because they eat more Diptera. This pattern is repeated, but to a lesser extent, by *Acanthodactylus* with regard to the Formicidae.

The low annual variation of diversity may be explained by the concept of diversity itself (Carretero and Llorente, 1991). If the same diet equitability and number of taxa eaten remain, the diversity can be the same under abundance (spring and autumn) or scarcity (summer and winter) conditions (Ruiz and Jover, 1981). The differences found in *Psammodromus* are due to a decrease in taxa number in winter (arthropod diapause) and autumn (dominance of Diptera) compared with summer and spring, respectively.

Prey size is considered by some authors as the most important factor implied in the selection of preys (Diaz and Carrascal, 1990). The ranges of sizes predated by both species are the usual in the medium-sized Lacertidae (see previous references and the studies reported therein). The logarithmic distribution of prey sizes in both species should be interpreted as an absence of prey size selection within each species outside the body/mouth size limits of the predator (Pianka, 1986). As a consequence, prey-predator size correlations have been found and adults eat larger preys than immatures. This correlation is not necessarily associated with low trophic availability (Nouira and Mou, 1983) or "sit and wait" strategies (Valakos, 1990), but they also depend on the sample size and the SVL ranges (Carretero and Llorente, 1991).

Consequently, no intersexual differences were found since the SVL of males and females are equivalent. Immatures cannot consume larger preys, and thus show lower mean prey sizes than the adults.

Size correlation extends outside the species limits: *Acanthodactylus* eats larger prey than the smaller lizard *Psammodromus*. There is again an inverse tendency in relation to those observed in other populations (see references in Table 1), all with them associated with higher predation of ants. Then, this item can explain most of the variance of prey-size associated with the fringe-toed lizard.

The general relations can be summarized observing the trophic overlaps (Fig. 6). Values are intermediate in most cases, a common situation in trophic opportunist species from temperate regions (Pianka, 1974). Considering the species level, the prey size overlap is higher than taxonomical (see results and also Seva, 1984). Interspecific segregation is based mainly on prey taxa. However, looking at the overlaps among classes (Fig. 6), prey size plays an important role whithin each species. So, considering prey size overlap, two groups can be distinguish (immatures and adults). However, considering taxonomical overlap, adults and immatures mix, but adults of both species are separated. *Acanthodactylus* immatures are grouped with *Psammodromus* adults and *Psammodromus* immatures are clearly separated from the rest. The results found by Pollo and Pérez-Mellado (1991) are similar in prey size relations but not in the taxonomical analysis.

To sum up, it can be concluded that some of the classic trophic features corresponding to this species tandem may be altered by a probably unrestricted resource (Diptera). This prey is highly consumed by *Psammodromus algirus*, thus optimizing its energy input (Stephens and Krebs, 1986). Consequently, this species (potentially the most euryphagous one) restricts its real niche (Heatwole and Taylor, 1987) by consuming this abundant resource. The other species, *Acanthodactylus erythrurus*, close to its northern limit of distribution (Barbadillo, 1987), extends its niche inversely, from a very stenophagous diet based on Formicidae (typical of the genus *Acanthodactylus*, see Saleh and Saber, 1988), towards more diverse feeding. As a result, this species seems to be more plastic than was considered previously (Pollo and Pérez-Mellado, 1988-1991). The decrease of interspecific competition may be an explanation of this niche extension but this needs to be tested. So, further studies on trophic availability, emphasizing food limitation, should be carried out.

Summary

The trophic dimension of the niche was analysed for two mediterranean Lacertidae, the Large *Psammodromus* (*Psammodromus algirus*) and the Fringe-toed Lizard (*Acanthodactylus erythrurus*), which live together in a sandy coastal area of NE Spain. 133 *Ps. algirus* and 87 *A. erythrurus* were captured during 1986 and 1987, in mothly campaigns, and their stomach contents were analyzed. Data are traited considering the whole population, the size and sex classes and the season of the year. Abudance (%N), occurrence (%P) and homogeneity are calculated for taxonomical and prey size categories. Moreover, individual, population and total accumulated diversities were obtained. Results show some surprising aspects. Diptera and Coleoptera are the main taxa consumed by *Ps. algirus* and *A. erythrurus*, respectively. Prey size depends on lizard size within each species but *A. erythrurus* eats larger (!) preys. Both species show high diversities and seasonal variation in the diet. However, the fringe-toed lizard is the more euryphagous individually. Sexual differences are irrelevant in all cases. The divergence of the trophic patterns of both lacertids, compared with other populations studied, may be explained in terms of prey availability (especially the dominance of Diptera), community composition and historical trends.

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