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TROPHIC PARTITIONING AND COMMUNITY ORGANIZATION IN A GUILD OF LIZARDS IN LA SIERRA DE QUADARRAMA (SPAIN)

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Food partitioning relationships among six sympatric lizard species were studied in the La Sierra de Quadarrama, Spain. The results of this study show that in spite of these lizards are eclectic predators feeding on a wide range of invertebrate prey, there exists three species with marked food preferences. Food -niche overlap values varies depending on the way of estimation, by one hand considering only the number of prey and, by the other, taking in consideration also the prey volume. Total food -niche overlap values were high in a few cases among the members of this guild. The importance of food -niche partitioning among these co -occurring species as an evolutionary force that had lead species coexistence is a topic that deserves further experimental work.

Key words: trophic, lizards, food niche, prey.

The importance of ecological segregation to minimize actual or potential competition between co -occurring lizard species, and thus contributing to their coexistence has been outlined frequently (Barbault, 1981; Barbault and Celecia, 1981; Pianka, 1974; Schoener, 1974). Study of food partitioning among the members of a guild is an important aspect to be considered. First, because differential utilization of trophic resources could contribute to reduce competition (Barbault et. al., 1978, Barbault et al., 1985) and, second, because competition for food may be the dominant factor in the ecological organization of assemblages of sympatric species (Schoener, 1974, Toft, 1985).

It has been even sugested that species diversity in a given guild depends upon the breadth of the niches and on the importance of overlap which such species can tolerate (Barbault and Celecia, 1981). From this viewpoint it could be considered as a direct approach to the analysis of the organization of guilds the study of the utilization of resources in terms of breadth of the niche and the overlap of the niches.

Thus, the purpose of the present work is to examine the trophic aspects of one mountain lizard guild through a comparative analysis of species diets.

Material and Methods

Field work was carried out at la Sierra de Quadarrama on the southern slope of Sistema Central, north of Madrid (Spain), along an altitudinal gradient (Gandullo et al., 1976) from mediterranean at the lower parts, to a characteristic high -montain in the upper parts. The latter, climate includes 5 months with reduced temperatures (under 0 °C) and has 1.033 mm of annual precipitation, concentrated in two peaks: April and November. Geologically, the area lies on igneous and metamorphic rocks, mainly granite and gneiss (Gandullo, 1976).

Four physiognomic -floristic units occur at the zone (Ruiz del Castillo, 1976): 1) El Piso Basal, a mediterranean forest with a rock rose (*Cistus ladaniferus*), and oak (*Quercus ilex*), an ash (*Fraxinus angustifolia*) and a juniper (*Juniperus oxicedrus*) as the main species. 2) El Piso Montano, a forest with an oak (*Quercus pyrenaica*) as the dominant species, accompanied by a juniper (*Juniperus communis*) and a shrub (*Sarothamnus vulgaris*).

3) El Piso Subalpino, a pine forest dominated by a pine (*Pinus silvestris*), accompanied by a broom (*Cytisus purgens*), by a juniper (*Juniperus communis*) and by *Sambucus nigra* and *Pteeridium aquilinum*, and 4) El Piso Alpino with a broom (*Cytisus purgans*) as the solitary species.

The lizard community of the zone is dominated by six lacerted species: *Lacerta monticola*, *L. lepida*, *Podarcis hispanica*, *P. muralis*, *Psammodromus algirus* and *P. hispanicus*. Among these species two groups were recognized on the basis of their microhabitat usage: the ground -dwellers *Psammodromus algirus* and *P. hispanicus*, and the rock -dwellers, *Lacerta monticola*, *L. lepida*, *Podarcis muralis* and *P. hispanica*.

Lizards were captured in the field by hand or with rubber bands, from June to August 1984 and preserved in 10 % formalin. The following data were recorded for each individual captured: species, sex, snout -vent lengt and mass. Stomach contents were removed and examined with a binocular microscope. A total of 176 stomachs that yielded 769 individual food items were analyzed. Length an wedth of each prey item were measured with an optical mircometer and their volumes were caldulated assuming that the bodies were cylindrically shaped.

Food niche breadt (Bs) values were calculated using the Spimson's diversity index (Levins, 1968) in a standardized form / varying between 0 and 1:

$$Bs = \frac{(p_i^{\,2})^{-1} - 1}{N - 1}$$

Where p_i is the relative occurence of i^{th} taxonomic prey category in the sample, or the relative volume of the i^{th} prey category. Prey items were classified both by taxon (order) and by volume categories.

Food niche overlap among species were measured using Pianka's index (1973);(O_{jk}):

$$O_{jk} = \frac{P_{ij} \cdot P_{ij}}{p_{ij}^{\,2} \cdot p_{ij}^{\,2}}$$

Where P_{ij} is the relative volume of taxon, or the relative occurenee, of taxon in the diet of species j and P_{ik} is the relative volume, or the relative occurenee in the diet of species k.

The values of food niche breadth and overlap were statistically tested considering the null hypotheses that observed values were beyond random expectationl, using the Kolmogorov-Smirnov two tailed test (Kreyszig, 1987). As emphasized by Ricklefs and Lau (1980), there are no simple statistical methods for calculating the confidence limits of such estimates, but this lack did not impede the discussion of our results.

Results

Prey taxa consumption

Taking in consideration that observed food niche dimensions are beyond random expectation ($D>0.049$; $p<0.005$) the studied lizards could be differentiated into the following groups according to the diversity of prey taxa in the diet of each species (tab. 1), as well as by the prey volume:

Specialists: Species with low trophic diversity ($Bs<0.100$) such as *Lacerta monticola* ($Bs = 0.046$) and *Psammodromus hispanicus* ($Bs = 0.099$) which are specialized in *Coleoptera* consumption, and *L. lepida* for which vertebrates occupy a high relative volume ($Bs = 0.063$).

Generalists: Species displaing a relatively high trophic diversity ($Bs<0.300$), such as *Podarcis muralis* ($Bs = 0.250$), *Psammodromus algirus* ($Bs = 0.300$), and *Podarcis hispanica* ($Bs = 0.354$).

Table 1

Prey taxa number standardized niche breadth. The data concerning the compostition by prey taxa (frequency by volume) and prey taxa volume standardized niche breadth are shown among parentheses.

Species	Lacerta		*Podarcis*		*Psammodromus*	
	monticola	*lepida*	*hispanica*	*muralis*	*algirus*	*hispanicus*
Number of stomachs	30	P	45	39	40	15
Number of items	226	64	187	100	130	54
Coleoptera (ad)	0.65	0.50	0.13	0.06	0.16	0.33
	(0.73)	(0.07)	(0.14)	(0.02)	(0.06)	(0.71)
Coleoptera (l)	0.03	0.06	0.06	0.11	0.06	0.05
	(0.03)	(0.04)	(0.05)	(0.04)	(0.03)	(0.03)
Lepidoptera (ad)	0.02				0.02	
	(0.01)				(0.04)	
Lepidoptera (l)	0.01	0.06	0.09	0.06	0.15	
	(0.02)	(0.06)	(0.20)	(0.02)	(0.29)	
Hymenoptera (Formicidae)	0.01		0.01		0.01	0.06
Hymenoptera (ad)	0.04	0.06	0.07	0.13	0.06	0.06
	(0.02)	(0.05)	(0.09)	(0.29)	(0.03)	(0.01)
Hymenoptera (l)	0.01	0.06	0.04	0.01	0.01	
	(0.05)	(0.09)	(0.06)	(0.20)	(0.03)	
Diptera (ad)	0.08		0.04	0.17	0.14	0.05
	(0.02)		(0.03)	(0.11)	(0.07)	(0.06)
Diptera (l)			0.02	0.02	0.02	
			(0.06)	(0.01)	(0.04)	
Orthoptera (ad)	0.01	0.06	0.01	0.04	0.06	
	(0.07)	(0.03)	(0.02)	(0.13)	(0.19)	
Orthoptera (l)			0.01		0.14	
			(0.03)		(0.12)	
Hemiptera	0.01		0.09	0.09	0.06	0.11
	(0.01)		(0.05)	(0.02)	(0.09)	(0.07)
Homoptera	0.01	0.03	0.21		0.01	0.06
	(0.02)	(0.01)	(0.05)		(0.05)	(0.07)
Isoptera	0.02					
	(0.01)					
Odonata			0.01			
			(0.01)			
Diplura				0.02		

Table 1 (Continuation)

				(0.02)		
Protura		0.06				
		(0.01)				
Contipeda			0.01			
			(0.05)			
Thysanura			0.04			
			(0.02)			
Dermaptera			0.01		0.01	
			(0.02)		(0.01)	
Mecoptera			0.01			
			(0.04)			
Pseudocopiadeae				0.02	0.01	
				(0.02)	(0.03)	
Aranaeae	0.10	0.05	0.14	0.22	0.08	0.28
	(0.08)	(0.01)	(0.15)	(0.17)	(0.05)	(0.09)
Vertebrate		0.06				
		(0.27)				
Standardized diversity	0.055	0.112	0.318	0.302	0.355	0.157
	(0.044)	(0.014)	(0.357)	(0.133)	(0.244)	(0.039)

The two trophic groups are more easily observed by graphical representation of the frequency distributions (by volume) of major prey taxa consumed (fig. 1). As it could be observed in this figure the patterns of prey use are very different among all paired species except between *Lacerta monticola* and *Psammodromus algirus* (λ^2 16.75; $p < 0.005$).

Prey size.

Overall patterns of prey utilization by volume categories are shown in fig. 2. As it is possible to observe the diet spectra varies significantly among all paired species λ^2 14.86; $p < 0.005$), which shows differential peaks of frequency consumption.

As prey size is usually related to predator size, such relationship were searched in this lizard guild. To avoid biases introduced by taxonomic-size related differences among prey, these relationships were analyzed only for four well-defined insects groups, all of them commonly consumed by all lizards species: *Coleoptera adults* (ad), *Coleoptera larvae* (l), *Hymenoptera* and Araneae (fig. 3). In the four groups I found statistically significant correlations between mean snout-vent length and mean prey volume.

Food niche overlap.

Overlap values based on the percentage contribution of prey by taxon, and by volume contribution of prey size categories are both shown in tab. 2 observed values that were beyond random expectation ($D > 0.049$); $p > 0.005$). Overall food niche overlap were estimated by calculating the

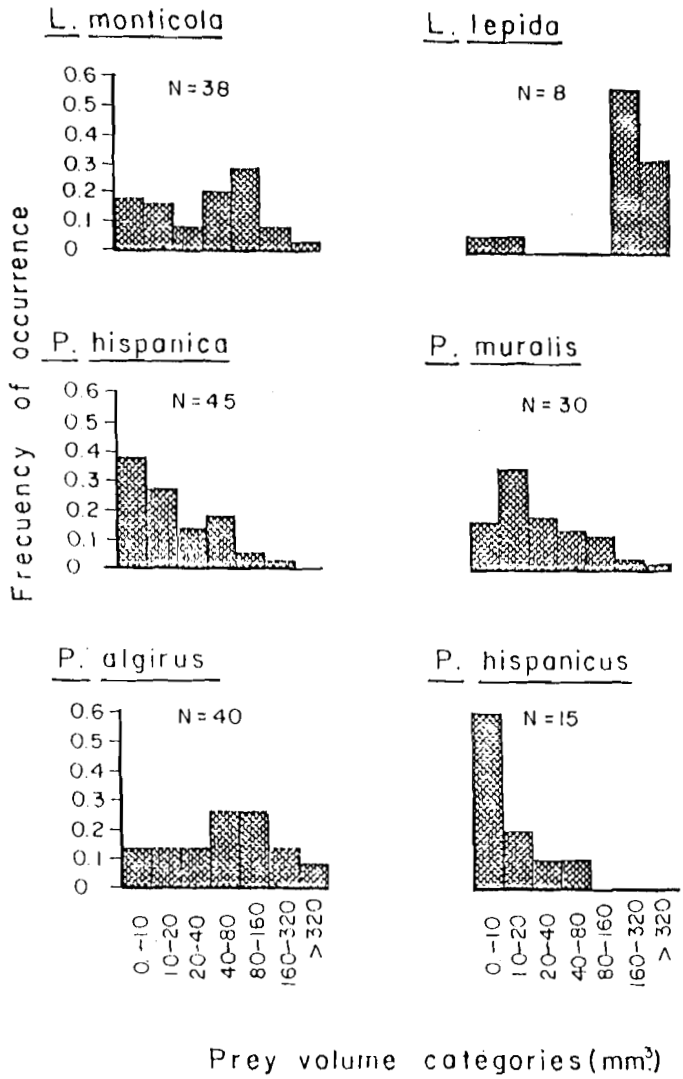

Fig. 1. Frequency distribution by volume of prey consumed by each species.

products of these two niche components (tab. 3). This total niche overlap could be biased because it uses niche dimensions which are probably not perfect orhogonals, but this lack doesn't impede the analyses.

Along the prey taxa niche dimension, overlap values were generally from medium to high (around 0.637), whereas prey size overlap values observed were low, with the only expectation between *L. monticola* and *P. hispanicus*.

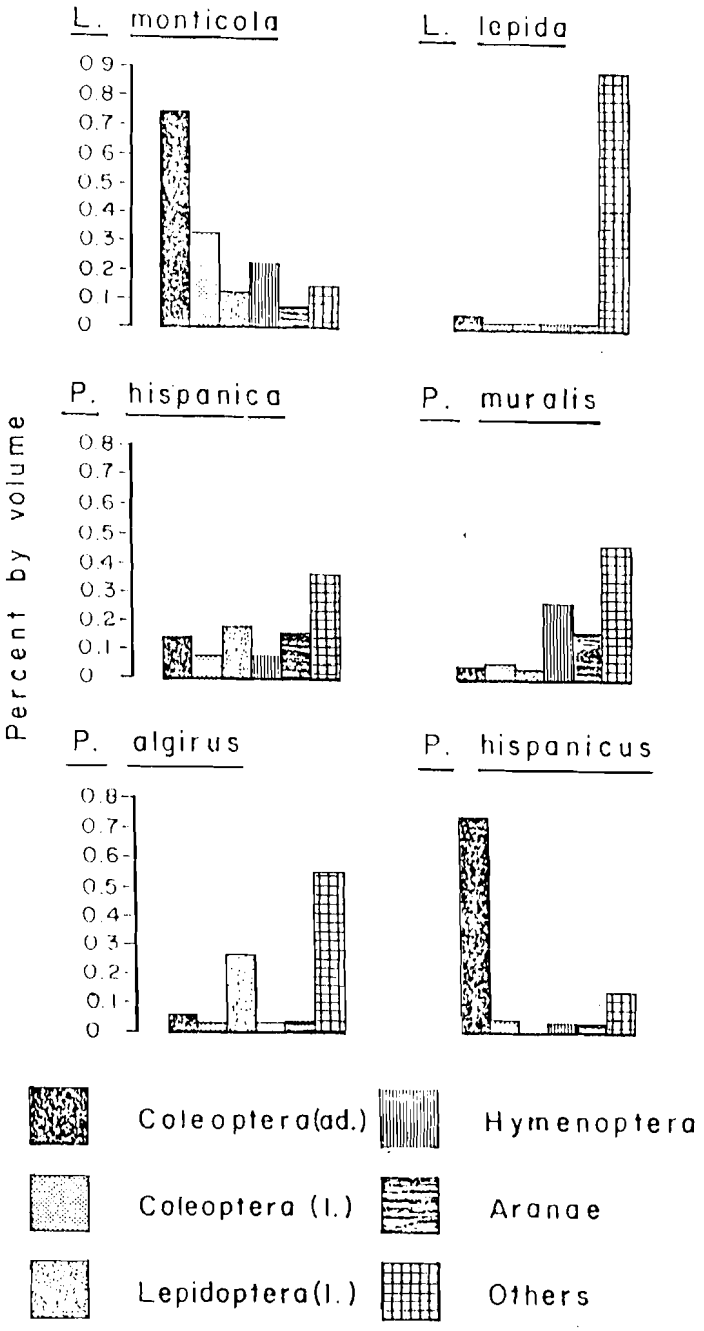

Fig. 2. Prey size (volume of items in mm^3) consumption spectra for the six studied species.

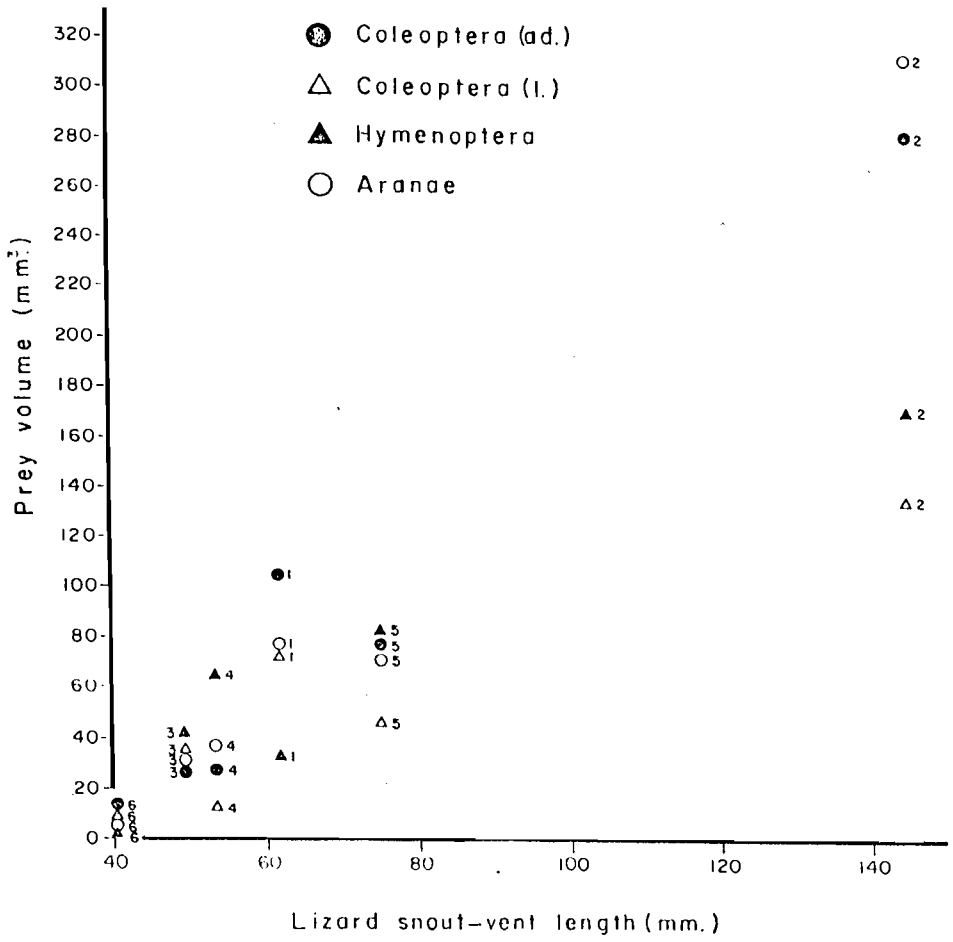

Fig. 3. Relationship between average prey volume and average lizard body length among the six species (1 = *L. monticola:* 2 = *L. lepida;* 3 = *P. hispanica,* 4 = *P. muralis,* 5 = *P. algirus* and 6 = *P. hispanicus).*

Discussion

The results of this study are consistent with those previously reported for these lizards (M e l l a n d o et al., 1975; M o u, 1987; M o u and B a r b a u l t, 1986). These species are eclectic predators feeding on a wide range of invertebrates. The most abindant prey were beetles, spiders, and larvae of *Coleoptera* and *Lepidoptera,* but a broad variety of prey were eaten including for example *Diptera, Hymenoptera* and *Hemiptera.*

In relation to size of the prey consumed, M e l l a d o et al., (1975) found the same differences for three species common to both studies. *Lacerta lepida* shows the higher mean prey size, followed *Psammodromus algirus,* and in the last place *P. hispanicus.*

Table 2

Trophic niche overlap values for the studied species. Data based on prey taxe diversity (lower part of the Table) and prey volume (upper pert)

Ojk volume / Ojk number	*L. monticola*	*L. lepida*	*P. hispanica*	*P. muralis*	*P. algirus*	*P. hispanicus*
L. monticola	-	0.082	0.512	0.157	0.247	0.989
L. lepida	0.959	-	0.052	0.027	0.033	0.079
P. hispanica	0.501	0.540	-	0.574	0.687	0.516
P. muralis	0.360	0.341	0.651	-	0.369	0.143
P. algirus	0.596	0.602	0.655	0.708	-	0.194
P. hispanica	0.870	0.764	0.738	0.687	0.634	-
Ojk number	0.647	0.641	0.617	0.549	0.637	0.729
Ojk volume	0.397	0.055	0.468	0.254	0.306	0.384

Table 3

Total trophic niche overlap among the lizard species of the La Sierra de La Guadarrama

	L. monticula	*L. lepida*	*P. hispanica*	*P. muralis*	*P. algirus*	*P. hispanicus*
L. montiocola	-					
L. lepida	0.521	-				
P. hispanica	0.507	0.296	-			
P. muralis	0.259	0.184	0.613	-		
P. algirus	0.422	0.319	0.671	0.519	-	
P. hispanicus	0.904	0.422	0.627	0.415	0.414	-
Ojk	0.523	0.348	0.543	0.462	0.473	0.556

Concerning the trophic ecology of *Lacerta muralis,* this species shows a narrow trophic niche breadth than other populations studied in France (M o u, 1987; M o u and B a r b a u l t, 1986). However, we must take into consideration the particular conditions of both studied populations in relation to their environment and potencial competitors. At La Sierra de Guadarrama *L. muralis* are spatially overlapped with *L. monticola* and *Psammodromus algirus,* whereas in France *L. muralis* is the only lizard species in the studied zone. Some of the data of the french populations were taken in the season of spring, than it is also necessary to take into account the season in which these studies were performed, because lizard diet strongly depends on availability of prey items in the environment (O r t e g a and H e r n a n d e z, 1983, K h o d a d o o s t et al., 1987).

It is also remarkable that in the mountain lizard community of La Sierra de la Guadarrama has no ants or termites specialists, which are very common in the case in desert lizard guilds (B a r b a u l t et al., 1978; B a r b a u l t and M a u r y, 1981).

Ecological organization of the guild. In this is evident that prey items were identified only to very basic categories. However, even at the order level, it is possible to emphasize the following salint features of this lizard guild in relation to their food niche. The overlap values observed are

high in a few cases, which indicates that, even at the leve of analysis perfomed, the food resource partitioning is probably an important determinant in the ecological organization of this assemblage of species, and a key factor to take into consideration in order to explain species coexistence.

This hypothesis could be supported by the fact that two of the most abundant and widely distributed species among the different habitats of the study area (O r t e g a per. abs), are also the more generalized in relation to the kind and size of prey'items consumed: *Podarcis hispanica* and *Psammodromus algirus*.

Certainly, much experimental work remains to be done to test this and other hypotheses regarding the ecological organization of this lizard guild.

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TROFICKÉ ROZDELENIE A ORGANIZÁCIA ZOSKUPENÍ JAŠTERÍC V OBLASTI LA SIERRA DE GUADARRAMA (ŠPANIELSKO)

Alfredo Ortega-Rubio

V práci sa analyzovalo spoločenstvo jašteríc a využívanie potravných zdrojov. Potravná nika a jej prekrývanie varíruje v závislosti od dostupnosti a početnosti potravy, ako aj od jej zloženia. Vypočítala sa šírka trofickej niky pre jednotlivé druhy jašteríc vyskytujúcich sa v pohorí Gaudarrama. Potravné zložky (ich frekvencia) sa v jednolitvých radoch určili rozborom žalúdkov.

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