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## Resource partitioning in a Mediterranean lizard community

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### ABSTRACT

Some aspects of community ecology in a lizard assemblage composed of three sympatric and diurnal species (*Algyroides fitzingeri*, *Podarcis tiliguerta*, *Chalcides ocellatus*) were studied in a Mediterranean habitat of central Sardinia. The three lizards were characterized by significantly different mean body size. There was no spatial overlap between the smallest species (*A. fitzingeri*) and the largest one (*C. ocellatus*), while there was a certain amount of overlap between *P. tiliguerta* and each of the other two lizards. The three species preyed on a wide variety of invertebrates, but mainly on insects. Food niche breadth was higher in *P. tiliguerta*, and this could be related to the higher microhabitat heterogeneity of this lizard in the study area. Food niche overlap was high between *Chalcides ocellatus* and *Podarcis tiliguerta*, but low between *Algyroides fitzingeri* and *C. ocellatus*. Although further data are required before any firm conclusion can be drawn, the results of this investigation seem to indicate that (i) interspecific competition among the three lizards is rather limited, due both to food and spatial resource partitioning, and (ii) the lizard community is organized through the ecological needs of each species.

**KEY WORDS:** *Algyroides fitzingeri* - *Podarcis tiliguerta* - *Chalcides ocellatus* - Sauria - Reptilia - Body size - Food niche - Habitat partitioning - Sardinia.

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### INTRODUCTION

In the 1980's, after enjoying over two decades of brilliant success, the MacArthur and Hutchinson view of life, whereby interspecific competition is seen as the central factor in organizing living communities, partially declined. Thus, competition became only one factor among many, and spatial and temporal variability claimed more attention (e.g., Strong *et al.*, 1984; Diamond & Case, 1986; Barbault & Hochberg, 1992).

Birds were the vertebrate models most used in studies involving interspecific competition during the 1960's and 1970's, but when it was evident that forces other than competition were involved in the organization of living communities, the attention of ecologists was mainly addressed to other groups of vertebrates, such as amphibians and reptiles. Thus, herpetological communities were widely investigated, especially those occurring in tropical and desert ecosystems (e.g., Pianka, 1973, 1986; Barbault, 1977, 1991; Barbault & Maury, 1981; Barbault *et al.*, 1985). Very recently, however, several studies have been performed also on the community ecology of Mediterranean reptile assemblages, including both snakes (e.g., Luiselli & Rugiero, 1991) and lizards (e.g., Pollo & Pérez Mellado, 1988, 1989, 1990; Capula *et al.*, 1993; Capula & Luiselli, 1994).

In the present paper, some aspects of community ecology in a lizard assemblage from a large Mediterranean island (Sardinia) have been investigated.

### MATERIALS AND METHODS

Fieldwork was carried out in central Sardinia. The study area was a wide basaltic tableland located at about 550 m a.s.l. (Giara di Gesturi, 270 km SW of Nuoro). This area is characterized by grassy zones with dense bush (*Pistacia lentiscus*, *Arbutus unedo*, *Myrtus communis*, *Phyllirea angustifolia*), cork trees (*Quercus suber*) and dilapidated walls, with some historical and very ancient human dwellings (locally named «Nuraghi»).

In the study area, three diurnal lizard species occurred sympatrically: two Lacertidae [*Algyroides fitzingeri* (Wiegmann, 1834) and *Podarcis tiliguerta* (Gmelin, 1789)], and one Scincidae [*Chalcides ocellatus* (Forskål, 1775)]. These lizards were studied during three surveys carried out during April 1990, June 1992, and March 1993. In all, twenty days were spent in the field. Spatial partitioning of the three lizards was analyzed by designating a set of three predefined qualitative microhabitat categories along one transect: (A) grassy zone with dense bushy vegetation; (B) rocky zone with scarce bushy vegetation; (C) stonepiles and dilapidated walls of «Nuraghi». Each microhabitat was surveyed by random walks three hours a day, either in the morning or afternoon.

No specimen was killed during the course of the investigation. Lizards were captured by hand; thereafter, they were measured for snout-vent length (SVL) with a precision calliper (to  $\pm 0.1$  mm), sexed, marked by toe-clipping, and analyzed for any food item.

Snout-vent length and diet composition were recorded in 23 adult male and 20 adult female *Podarcis tiliguerta*, in 22 male and 18 female *Algyroides fitzingeri*, and in 17 male and 15 female *Chalcides ocellatus*.

To avoid killing any animals, their diet was studied by analyzing faecal pellets, which were collected by placing the lizards in small cages until defecation occurred. No faecal pellets were collected

from the ground. Only prey items which were clearly observed in the feces were identified to the lowest taxon possible, while food items which remained unidentified were excluded from the analysis.

Food niche breadth was calculated using the diversity index ( $B_S$ ) of Simpson (1949):

$$B_S = \frac{1}{\sum_{i=1}^n p_i^2}$$

and the standardized form ( $B_L$ ) of Levins (1968):

$$B_L = \frac{\sum_{i=1}^n (p_i^2)^{-1} - 1}{n - 1}$$

In these equations,  $p_i$  is the relative abundance of the  $i$ -th prey category in the sample, and  $n$  is the total number of prey items. Food niche overlap between species was estimated using Pianka's (1973) symmetric equation, in which values range from 0 (no overlap) to 1 (total overlap):

$$O_{JK} = \frac{\sum_{i=1}^n p_{ij} p_{ik}}{\sum_{i=1}^n p_{ij}^2 \sum_{i=1}^n p_{ik}^2}$$

where  $p_{ij}$  is the relative frequency of taxon  $i$  in the diet of species  $j$ , and  $p_{ik}$  is its relative frequency in the diet of species  $k$ . Unfortunately, as suggested by Ricklefs & Lau (1980) and Barbault *et al.* (1985), there is no simple statistical method for calculating the confidence limits of such estimates. Therefore, in order to assess the confidence limits of the  $B_S$  (Simpson, 1949) and  $B_L$  (Levins, 1968) indexes, we performed a Mantel test (see Manly, 1985).

Statistical analyses were performed using the Statistical Analysis System (SAS, PC version 6.0, 1985). All tests used in this study were two-tailed, with  $\alpha = 0.05$ .

## RESULTS

### Spatial distribution and population structure

The lizard community was composed by three diurnal lizards (*Algyroides fitzingeri*, *Podarcis tiliguerta*, *Chalcides ocellatus*) which could be considered potential competitors. Our observations allowed accurate

delineation of the spatial distribution of the three species along the habitat gradient of the study area (Fig. 1). *Chalcides ocellatus* was exclusively terrestrial and semi-fossorial, while *Algyroides fitzingeri* was mainly active on vertical surfaces (see also Capula & Luiselli, 1992). *Podarcis tiliguerta* was primarily terrestrial, but was also found on stonepiles and dilapidated walls.

Both *Algyroides fitzingeri* and *Chalcides ocellatus* were highly specialized with respect to their habitat choice, the former being limited to microhabitat C, the latter to microhabitat B. On the other hand, *Podarcis tiliguerta* appeared to be a generalist taxon. In fact, it was less specialized than the other two lizards in microhabitat choice, and occurred all over the three microhabitats, including both humid and dry spots.

Population structure was very different in the three species. According to our data (Capula & Luiselli, unpubl. observations), *Algyroides fitzingeri* was characterized by small and isolated demes (10-25 adults, closely grouped around a stonepile or Nurago). The population density of *Chalcides ocellatus* was higher (about 30 individuals per ha), with females more numerous than males, and the individuals were less grouped than in *Algyroides*. *Podarcis tiliguerta* was characterized by the highest density (more than 150 individuals per ha), without any spatial separation among different demes. No significant difference in population structure and microhabitat use was observed between the three study periods (April 1990, June 1992, March 1993). This could mean that population structure and habitat partitioning were not strongly influenced by year-to-year changes.

### Body size

In *Podarcis tiliguerta*, snout-vent length ranged from 56 to 67 mm in males, and from 54 to 59 mm in females. Males attained significantly larger SVL than females ( $\bar{X} = 62.91 \pm 2.79$  mm vs.  $\bar{X} = 56.15 \pm 1.46$  mm; two sample difference,  $t = 9.72$ ,  $df = 41$ ,  $P = 3.36^{-12}$ ). In *Algyroides fitzingeri*, males and females attained similar SVL (males:  $\bar{X} = 29.54 \pm 2.38$  mm; females:  $\bar{X} = 28.55 \pm 2.06$  mm;  $t = 1.386$ ,  $df = 38$ ,  $P = 0.173$ ), even though the biggest specimens in our sample were females. In *Chalcides*

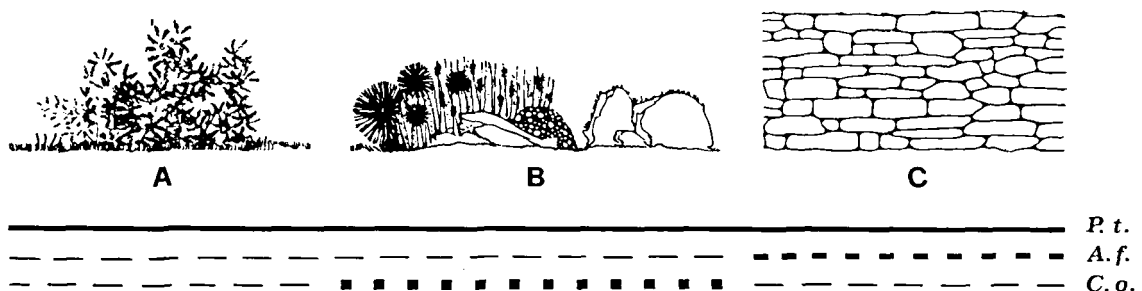


Fig. 1 - Relative frequency distribution of *Podarcis tiliguerta* (P.t. —), *Algyroides fitzingeri* (A.f. ---), and *Chalcides ocellatus* (C.o. ■■■■) with respect to the main microhabitats present in the study area. The broken line (---) means that the species does not occur in the indicated microhabitat. For detailed information on microhabitat categories (A, B, C) see Materials and Methods.

*ocellatus*, the male and female SVL did not differ in a statistically significant way (SVL: males:  $\bar{X} = 129.58 \pm 12.10$  mm; females:  $\bar{X} = 130.73 \pm 10.17$  mm; two sample difference,  $t = 0.287$ ,  $df = 30$ ,  $P = 0.775$ ).

There were significant differences in body size among the species. *Algyroides fitzingeri* was the smallest lizard in the area (average SVL = 30 mm), while *Chalcides ocellatus* was the largest one, its SVL ranging from 100 to 150 mm. *Podarcis tiliguerta* was intermediate in size between the other two species, its SVL ranging from 54 to 67 mm (body size differences between species:  $P < 0.001-0.0001$ ).

Diet

The diet data recorded in this study are summarized in Table I. In *Podarcis tiliguerta*, a mean of 2.84 prey/specimen was found, in *Algyroides fitzingeri* a mean of 2.35, and in *Chalcides ocellatus* a mean of 2.82. A positive correlation between number of ingested prey and lizard SVL was found in all species, Spearman's  $r$  ranging from 0.63 to 0.87 (in all cases  $P < 0.01$ ). Lizard diet consisted of a variety of invertebrates, mainly arthropods. Both flying (e.g., Diptera) and flightless (e.g., spiders and ants) prey were frequently found in the faecal pellets of *Podarcis tiliguerta* and *Algyroides fitzingeri*, while in *Chalcides ocellatus* flightless prey were almost exclusively found. This appears to be in agreement with the microhabitat partitioning of the three species. No preyed taxon amounted to over 17% of the diet either in

*Podarcis tiliguerta* or *Chalcides ocellatus*, while in *Algyroides fitzingeri* over 40% of spiders was recorded. This could mean that in the study area *Podarcis tiliguerta* and *Chalcides ocellatus* were more generalistic in prey use than *Algyroides fitzingeri*. This assertion seems to be confirmed by the higher niche breadth values observed in the two former species (differences statistically significant at a  $P < 0.001$  level, Mantel test) (see Table II).

The estimated values of food niche overlap among species are shown in Table III. It should be noticed that there was a high overlap in the taxonomic composition of the diets in coexisting *Podarcis tiliguerta* and *Chalcides ocellatus* (microhabitat B), but food niche overlap was lower in coexisting *Podarcis tiliguerta* and

TABLE II - Food niche breadth values for the three lizard species living in a Mediterranean habitat of central Sardinia.

Species	B <sub>s</sub>	B <sub>l</sub>
<i>Podarcis tiliguerta</i>	9.35	0.60
<i>Algyroides fitzingeri</i>	4.52	0.35
<i>Chalcides ocellatus</i>	8.62	0.76

B<sub>s</sub>, diversity measure of Simpson (1949); B<sub>l</sub>, standardized diversity measure of Levins (1968). For detailed information see text.

TABLE I - Diet composition of *Podarcis tiliguerta*, *Algyroides fitzingeri* and *Chalcides ocellatus* in a Mediterranean habitat of central Sardinia.

Preyed taxa	<i>P. tiliguerta</i>		<i>A. fitzingeri</i>		<i>C. ocellatus</i>	
	n	%	n	%	n	%
Coleoptera (adults)	10	8.2	4	4.2	7	7.3
Coleoptera (larvae)	7	5.7	3	3.2	8	8.3
Lepidoptera (adults)	1	0.8	5	5.3	0	0
Lepidoptera (larvae)	1	0.8	1	1.1	6	6.2
Diptera	20	16.4	8	8.5	2	2.1
Orthoptera	9	7.4	3	3.2	3	3.1
Formicoidea	14	11.5	11	11.7	0	0
Hymenoptera	6	4.9	2	2.1	0	0
Homoptera	5	4.1	0	0	0	0
Unidentified Insecta (larvae)	2	1.6	3	3.2	6	6.2
Araneidae	18	14.7	38	40.4	11	11.4
Miriapoda	2	1.6	0	0	0	0
Isopoda	3	2.4	0	0	16	16.7
Gastropoda	6	4.9	0	0	16	16.7
Oligochaeta	0	0	0	0	14	14.6
Unidentified Arthropoda	18	14.7	16	17.0	7	7.3
Total No of prey items	122		94		96	

TABLE III - Food niche overlap values among *Podarcis tiliguerta*, *Algyroides fitzingeri*, and *Chalcides ocellatus* living in a Mediterranean habitat of central Sardinia.

Species	$O_{jk}$
<i>Podarcis tiliguerta</i> - <i>Algyroides fitzingeri</i>	0.78
<i>Algyroides fitzingeri</i> - <i>Chalcides ocellatus</i>	0.43
<i>Chalcides ocellatus</i> - <i>Podarcis tiliguerta</i>	0.96

$O_{jk}$ , Pianka's (1973) symmetric overlap measure.

*Algyroides fitzingeri* (microhabitat C) (see Table III). This indicates that the diet of *Podarcis tiliguerta* was rather similar to those of the two sympatric lizards. Conversely, the diet of *Chalcides ocellatus* was extremely different from that of *Algyroides fitzingeri*, as indicated by the low value of food niche overlap (Table III). In *P. tiliguerta*, which is characterized by apparent sexual dimorphism, no evidence of intraspecific food competition was pointed out. However, it must be stressed that further data (e.g., stomach contents analysis) should be required to confirm our preliminary observations.

## DISCUSSION

From this study two main results emerge: (1) the three sympatric lizards were characterized by significantly different mean body size; (2) in the study area, there was a «partial» spatial segregation among the coexisting lizards.

With regard to the first result, there is both theoretical and empirical evidence showing that competition (e.g., food competition) tends to be reduced when there exist size differences between potential competitors (Ricklefs, 1973). Based on this assumption, one could expect to find that the food overlap value was (i) low between large- and small-sized lizards (*Chalcides ocellatus* and *Algyroides fitzingeri*, respectively), (ii) high between large- and medium-sized lizards (*Chalcides ocellatus* and *Podarcis tiliguerta*, respectively), (iii) intermediate between medium- and small-sized lizards (*Podarcis tiliguerta* and *Algyroides fitzingeri*, respectively) (see Table III).

With regard to the second result, it is well known that spatial segregation is extremely important to minimize competition between species, both from a theoretical (MacArthur & Pianka, 1966) and an empirical point of view (Schoener, 1974). In reptile communities, spatial segregation has been shown to be usually the main factor minimizing competition (e.g., Pianka, 1966; Jenssen, 1973; Saint Girons, 1975; Schoener, 1975, 1977), even though, in some cases at least, food resource partitioning seems to be as important as spatial segregation (e.g., Pianka, 1973, 1975; Fuentes, 1976; Huey & Pianka, 1977; Mushinsky & Hebrard, 1977; Luiselli & Rugiero, 1991).

With regard to spatial distribution, it appears that one lizard (*Podarcis tiliguerta*), i.e. the intermediate one in body size, can be considered a eurytopic species, while the other ones, viz. the largest (*Chalcides ocellatus*) and the smallest (*Algyroides fitzingeri*), are more specialized species. In fact, there was no spatial overlap between the smallest and the largest species, while there was a certain overlap between *Podarcis tiliguerta* and each of the other two lizards.

Our results on the food habits of *Podarcis tiliguerta*, which is characterized by a wide niche breadth (see Table II), give further evidence indicating that this is a eurytopic species. Thus, it may well be that the skill of this lizard to colonize the whole range of microhabitats existing in the study area partly depends on its very diversified diet. *Chalcides ocellatus* appeared to be another generalist predator, but it was observed to occupy some microhabitats only, probably due to morphological constraints (heavier body weight, short limbs etc.) which limit its climbing on vertical surfaces. *Algyroides fitzingeri* showed the lowest food niche breadth value and was the most specialized species in the lizard community.

From the results of this investigation, it can be inferred that (i) interspecific competition among the three lizards is rather limited, due both to food and spatial resource partitioning, and (ii) the studied lizard assemblage is organized through the ecological needs of each species rather than by species interactions. Although further data on several ecological aspects (e.g., thermal and reproductive ecology) are required before any firm conclusion can be drawn, it must be stressed that other significant differences emerge from a study of the life-history of the three species, and that these are in apparent agreement with the hypothesis of a very limited competition among the sympatric lizards. They concern (1) the reproductive pattern and phylogenesis: e.g., *Chalcides ocellatus* is an ovoviviparous scincid lizard, while *Algyroides fitzingeri* and *Podarcis tiliguerta* are two oviparous lacertid lizards; (2) population structure: e.g., each of the three species is characterized both by a peculiar deme size and a different migration rate between demes (Capula & Luiselli, unpubl. data); (3) sexual dimorphism: e.g., in *Podarcis tiliguerta* there is a clear sexual dimorphism, with males bigger and more powerfully coloured than females (Arnold & Burton, 1978), while in *Algyroides fitzingeri* and *Chalcides ocellatus* there is no apparent sexual dimorphism in colour or size.

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