The diet of an introduced population of *Podarcis pityusensis.*

Is herbivory fixed?

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Abstract. The Ibiza Wall Lizard (*Podarcis pityusensis*), a Balearic endemism, has been observed in its original habitat to feed not only on Arthropoda but also on plants. The diet of an introduced population living in the city of Barcelona (continental Spain) was analyzed in order to test the feeding habits of this species excluding the insular effect. As in the islands, the clumped prey (Homoptera and Formicidae) represented the bulk of the diet (>50%). The trophic use of these taxa changed drastically throughout the year but not among classes (especially both sexes) which differed only in the secondary preys. The prey size depended on the lizard size and the trophic diversity was high except in winter. The plant portion was limited (5.3%) but it was completely absent in the syntopic *Podarcis hispanica*. Seeds, flowers and other plant matter were mainly eaten by adults in summer. This trophic strategy is considered to be a derived feature which has probably evolved several times under insular conditions. However, conversely to other non-balearic *Podarcis*, its persistence in *Podarcis pityusensis* after a translocation to a continental locality indicates some kind of historical constraints. Nevertheless, this species still remains highly adaptable showing that the endogenous influence is only partial.

Key words. Diet, herbivory, *Podarcis pityusensis*, lizards, islands, translocations.

Introduction

Some members of the genus *Podarcis* (Reptilia, Lacertidae) living in Mediterranean islands have been observed to feed not only on Arthropoda like most Lacertidae but also on plant matter like fibers, fruits, flowers, nectar or pollen (Eisentraut, 1949; Salvador, 1986a,b; Sorci, 1990; Pérez-Mellado and Corti, 1993). Herbivory seems to be energetically inefficient for small lizards (<50 g) under standard conditions (Pough, 1973). So, this dietary shift was been explained as a consequence of the insular conditions which often involve food scarcity, lack of interspecific competition and low predation pressure (Stephens and Krebs, 1986; Williamson, 1981). However, among all the insular populations of *Podarcis sp* studied, only the Balearic species *Podarcis lilfordi* and *Podarcis pityusensis* consume a considerable amount of vegetal matter (Pérez-Mellado and Corti, 1993). Could then herbivory have become a partially fixed feature in these cases?

This study investigates these aspects in the Ibiza Wall Lizard (Podarcis pityusensis), a medium-sized lacertid which is endemic to the Pityusic Archipelago (Eivissa, Formentera and islets around them). In contrast to other insular lizards, this species has proved its ability to colonize areas outside its original range, like the city of Palma, Ses Illetes and, probably, Cap Formentor in Mallorca (Mayol, 1985; Barbadillo, 1987; Buttle, 1986) and, recently, the city of Barcelona in the Iberian Peninsula (Carretero *et al.*, 1991). This last population allows us to test the feeding habits of this species excluding the insular effect in order to determine the importance of such historical constraints. Moreover, since previous studies showed mainly the data in spring and summer, not only the global diet but also its interspecific and seasonal variation are analyzed. Additionally, some information about other sympatric lacertids is given.

Unfortunately, most of the area was strongly altered after the study (1992) due to roadworks which limited possibilities of field work and finally produced a drastic reduction in the population size (Carretero *et al.*, in press).

Material and methods

The study zone was an urban area of Barcelona (Plaça de les Glòries, UTM 31TDF3384). An introduced colony of *Podarcis pityusensis* occupied some abandoned lots in high densities for the past 15 years. Animals were observed over debris, blocs of concrete and slopes covered by weedy vegetation (see Carretero *et al.*, 1991, for a complete description of the environment). Climate can be defined as littoral Mediterranean, with warm temperatures, irregular precipitation and a dry season in summer (mean annual temperature: 16.6∞C; total annual rainfall: 598.4 mm; means of 30 years, Panareda & Nuet, 1973).

The only lacertid found sympatrically was *Podarcis hispanica*. This species was always observed in low numbers and in the margins of the introduced population. Some adults of this species were seen being attacked by Podarcis pityusensis (Carretero *et al.*, 1991).

The population was divided into three classes: adult males, adult females and immatures. The last one grouped all non-adult individuals observed throughout the year since sexual maturity was probably attained in the second year of life (Carretero *et al.*, in press). Minimum snout-vent lengths (SVL) of adults were 49 mm for males and 50 mm for females. Males were larger than females (Carretero *et al*, in press). Annual activity was discontinuous. No adults and only some isolated immatures were seen between November and February (observation of the authors).

145 *Podarcis pityusensis* (and 19 *Podarcis hispanica*) were collected from March 91 to February 92 in monthly campaigns. Most of these lizards were captured during the period of activity but some were also actively sought under stones in winter. At the laboratory, their SVL were measured using a digital calliper (0.01 mm precision). Animals were injected with 70% ethanol and stored in that liquid. These specimens were used not only in this study but also in the analysis of their biometrical and reproductive traits.

The stomach was the only segment of the digestive tract that was used since it was considered the most accurate and the most uniform representation of the real diet (Carretero and Llorente, this volume). Stomach contents were analyzed under a binocular dissecting microscope. The minimum numbers criterion was used in the prey counting of every stomach content (Vericad and Escarré, 1976). The Order level was used as operational taxonomic unit (OTU, Sneath and Sokal, 1973) with some exceptions (see Figures and Tables). Prey lengths were measured using a micrometer eyepiece or a calliper (0.01 mm precision) and grouped into classes of 1 mm interval (see Figures and Tables).

Jover's method (Jover, 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 I'' (Ruiz and Jover, 1981) and the resource use index (IU, Jover, 1989). The last one emphasizes the homogeneity as the feature which must be measured by a trophic descriptor (see advantages in Jover, 1989; see also Carretero and Llorente, 1991, 1993, for two examples of application of this index to the diet of lacertids). Repletion index was calculated as the percentage of empty stomachs from a sample.

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 method (Jover, 1989) and total accumulated diversity (Hn) were calculated. Populational diversities were compared by Student's t tests (considering the Bonferroni correction) instead of using the analysis of variance, because of their non-additivity (Carretero and Llorente, 1991).

Diet overlap was calculated applying the Schoener's index (Schoener, 1968) to the percentages of resource use for OTUs and size classes. This index has proved to be more accurate than others for estimating intermediate real overlaps (Linton *et al.*, 1981).

Results

After dissection, 38 stomachs of *Podarcis pityusensis* were found to be empty. So, 107 contents were available for the analysis (60 males, 55 females and 30 immatures, considering the classes and 36 spring, 33 summer, 28 autumn and 36 winter, considering the seasons). 4 from the 19 *Podarcis hispanica* stomachs were also empty.

676 prey items were determined for *Podarcis pityusensis*. The number of preys per stomach (total mean 4.66) showed significant seasonal variation (Kruskal-Wallis test, H = 21.51, p = 0.00015). Dunn's *a posteriori* test ($p < 0.05$) detected significant differences between winter and spring/summer numbers and between autumn and spring (fig. 1). No intraspecific differences of any kind were found. The seasonal variation of the repletion index followed an inverse pattern to the number of preys (fig. 1).

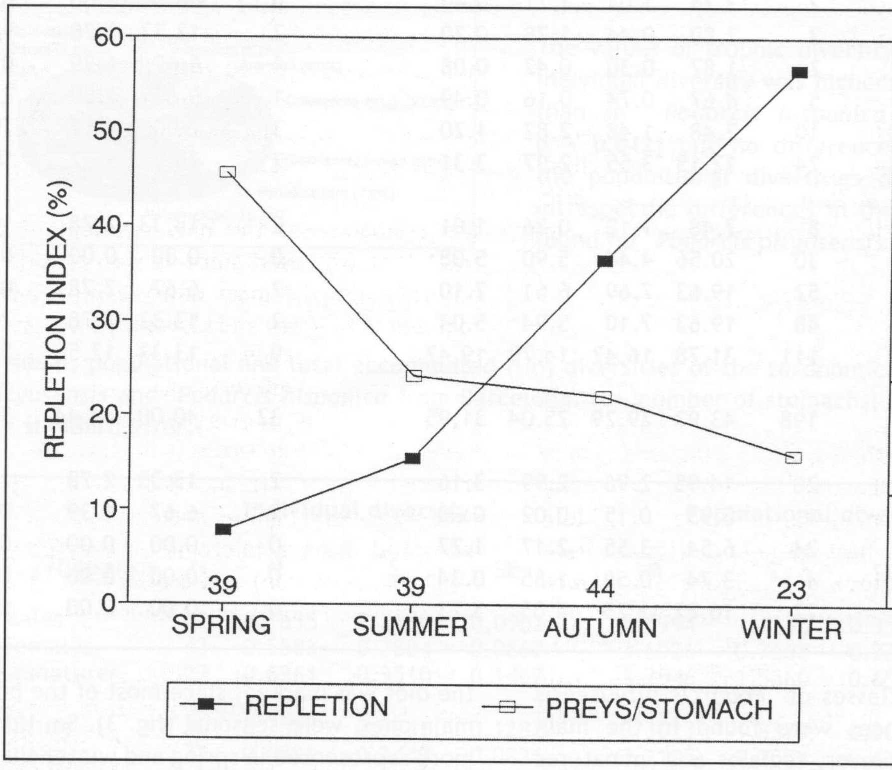

Fig.1 *Seasonal variation of the repletion index and the number of prey per stomach in Podarcis pityusensis (Barcelona). Numbers represent the sample size (empty stomachs included).*

Table 1 shows the comparative values of the trophic descriptors for the different prey taxa. The diet of *Podarcis pityusensis* was mainly of animal origin but plant items (seeds, flowers and other plant matter) were also consumed (IU=5.30%). Arthropoda represented most of the animal preys, except some small snails and slugs (2.62%). It is interesting to remark that a case of cannibalism was detected. Homoptera (mainly

Aphididae, 31.95%) and Formicidae (19.47%) were the main OTUs consumed, the rest being secondary preys. Both OTUs were also the main preys found in the small sample of *Podarcis hispanica*. No remains of vegetal origin were found in this species.

Table 1. Comparative descriptors of the taxonomical categories consumed by *Podarcis pityusensis* and *Podarcis hispanica* in Barcelona. T = total number of preys; %P = percentage of occurrence; %N = percentage of abundance; IP = Probabilistic index (I'' of Ruiz and Jover, 1981); IU = resource use index (Jover, 1989).

	Podarcis pityusensis					*Podarcis hispanica*				
OTU	T	%P	%N	IP	IU	T	%P	%N	IP	IU
Stylommatophora	17	13.08	2.52	3.50	2.62	2	13.33	2.78	2.56	2.38
Isopoda	41	13.08	6.07	6.05	5.65	4	13.33	5.56	4.77	4.75
Opiliones	1	0.93	0.15	0.00	0.00	0	0.00	0.00	0.00	0.00
Araneae	37	26.17	5.47	9.91	7.17	2	6.67	2.78	0.61	0.00
Acari	4	3.74	0.59	0.42	0.34	0	0.00	0.00	0.00	0.00
Lithobiomorpha	5	3.74	0.74	0.44	0.39	0	0.00	0.00	0.00	0.00
Geophilomorpha	1	0.93	0.15	0.10	0.00	0	0.00	0.00	0.00	0.00
Glomerida	1	0.93	0.15	0.01	0.00	0	0.00	0.00	0.00	0.00
Collembola	7	3.74	1.04	1.71	0.40	0	0.00	0.00	0.00	0.00
Dictyoptera	3	2.80	0.44	1.78	0.20	2	13.33	2.78	1.19	2.38
Dermaptera	2	1.87	0.30	0.42	0.08	1	6.67	1.39	0.02	0.00
Lepidoptera imagi	5	4.67	0.74	0.16	0.49	1	6.67	1.39	2.46	0.00
Lepidoptera larvae	10	7.48	1.48	2.82	1.20	3	20.00	4.17	10.13	5.65
Diptera imagi	24	12.15	3.55	2.97	3.31	7	26.67	9.72	10.94	11.37
Diptera larvae	8	7.48	1.18	0.36	1.01	2	13.33	2.78	10.45	2.38
Coleoptera imagi	30	20.56	4.44	5.90	5.08	0	0.00	0.00	0.00	0.00
Coleoptera larvae	52	19.63	7.69	6.61	7.10	2	6.67	2.78	0.39	0.00
Hymenoptera (no F)	48	19.63	7.10	5.94	5.04	2	13.33	2.78	2.61	2.38
Formicidae	111	31.78	16.42	14.79	19.47	9	13.33	12.50	5.42	10.50
Homoptera	198	43.93	29.29	25.04	31.95	32	40.00	44.44	38.18	55.84
Heteroptera	20	14.95	2.96	2.99	3.16	2	13.33	2.78	10.23	2.38
Squamata	1	0.93	0.15	0.02	0.00	1	6.67	1.39	0.02	0.00
Seeds	24	6.54	3.55	2.17	1.27	0	0.00	0.00	0.00	0.00
Flowers	4	3.74	0.59	1.85	0.34	0	0.00	0.00	0.00	0.00
Other plant matter	22	16.82	3.25	4.05	3.73	0	0.00	0.00	0.00	0.00

When considering the classes of *Podarcis pityusensis* separately, no differences were found in the main taxa eaten (fig. 2). However, females and immatures showed higher consumption of the secondary preys than males. Vegetal matter was almost absent in immatures (0.67%).

The seasonal variation in the taxonomical composition of the diet was marked, since most of the preys, even the main ones, were seasonal (fig. 3). So, Homoptera were more represented in spring and winter than in the other seasons whereas Formicidae reached the highest use in summer but they were absent in winter. In contrast, Araneae remained relatively constant throughout the year. The vegetal portion of the diet was slightly higher in summer than in the rest of the year.

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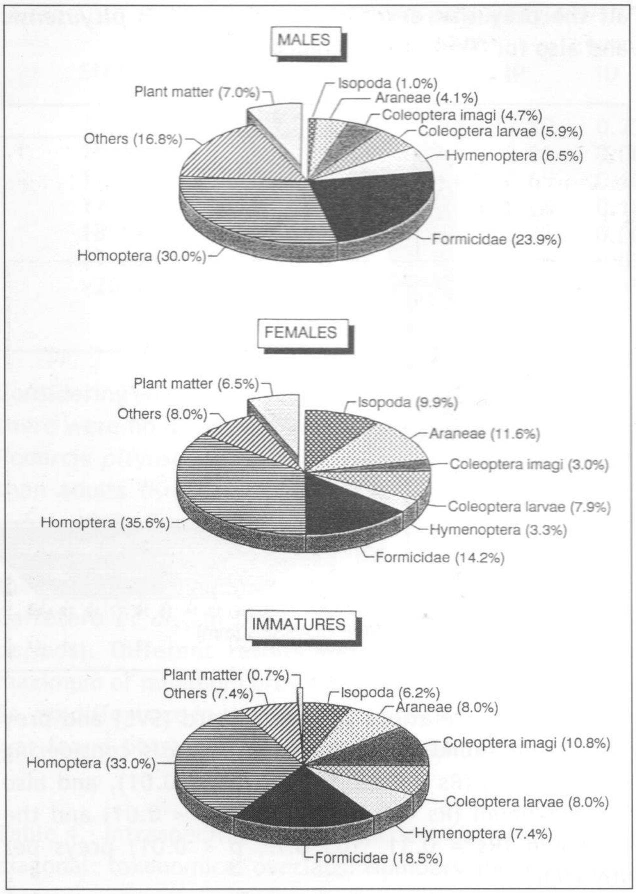


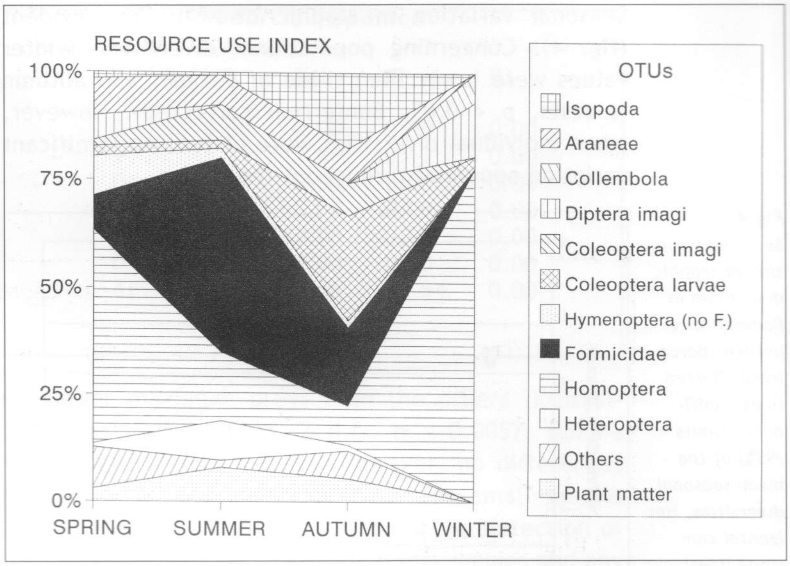


Fig.3
Seasonal variation of the taxonomical diet in Podarcis pityusensis (Barcelona).

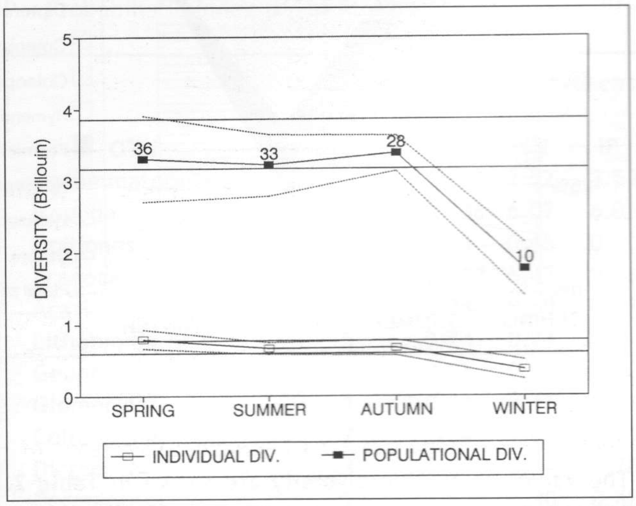
The values of trophic diversity are shown in Table 2. Individual diversity was higher in *Podarcis pityusensis* than in *Podarcis hispanica* (t = 2.52, 120 d.f., p = 0.012) but no differences were found between the populational diversities of the two species. No intraspecific differences in the trophic diversity were found for *Podarcis pityusensis* in any case.

Table 2.- Individual, populational and total accumulated (Hn) diversities of the taxonomical categories in the diet of *Podarcis pityusensis* and *Podarcis hispanica* from Barcelona. N = number of stomachs; M = mean; S = standard deviation; SE = standard error.

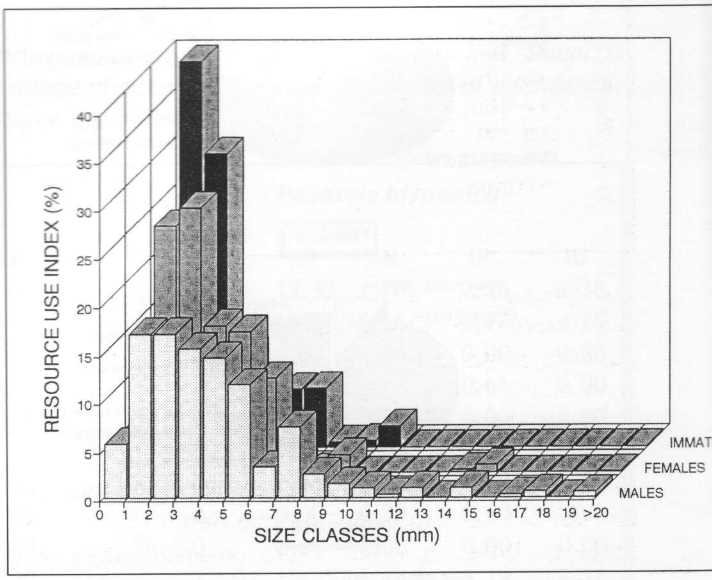
		Individual diversity			Populational diversity			
P. pityusensis	N	M	S	SE	M	S	SE	Hn
Males	42	0.7635	0.3180	0.0962	3.4994	1.1136	0.3368	3.25
Females	43	0.5888	0.2884	0.0862	3.6026	0.7668	0.2292	3.28
Immatures	22	0.6861	0.3510	0.1467	3.2546	1.5560	0.6502	2.89
Spring	36	0.7898	0.3941	0.1287	3.3023	1.8379	0.6004	3.03
Summer	33	0.6591	0.2449	0.0836	3.2105	1.2574	0.4290	2.91
Autumn	28	0.6677	0.2992	0.1108	3.3765	0.6768	0.2507	3.08
Winter	10	0.3602	0.2211	0.1371	1.7585	0.1162	0.3619	1.51
Total	107	0.6774	0.3129	0.0593	3.5450	1.4896	0.2823	3.40
P. hispanica	15	0.4694	0.1591	0.0805	3.0116	1.6041	0.8118	2.53

Seasonal variation in trophic diversity was evident (fig. 4). Concerning populational diversities, winter values were lower than those of summer and autumn (t tests, $p < 0.05$, Bonferroni corrected). However, when individual diversities were tested, no significant variation appeared throughout the year.

Fig.4
Seasonal variation of trophic diversities in Podarcis pityusensis (Barcelona). Dotted lines: confidence limits (95%) of the mean seasonal diversities. Horizontal continue lines: confidence limits (95%) of the mean annual diversities. Numbers represent the sample size (only full stomachs).



The spectrum of prey sizes consumed by *Podarcis pityusensis* ranged from 0.5 mm to more than 30 mm. The modal prey size consumed was displaced to low values and the distribution of resource use followed a logarithmic curve (fig. 5). Table 3 shows the values of all the prey size descriptors for *Podarcis pityusensis* and also for *Podarcis hispanica.*



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Significant correlations between lizard (SVL) and prey sizes were found in *Podarcis pityusensis* considering all the preys (Rs = 0.28, 675 d.f., $p < 0.01$), and also the maximum (Rs = 0.29, 105 d.f., $p < 0.01$) and the minimum (Rs = 0.31, 105 d.f., $p < 0.01$) preys per stomach.

Table 3.- Comparative descriptors of the prey sizes consumed by *Podarcis pityusensis* and *Podarcis hispanica* in Barcelona. T = total number of preys; %P = percentage of occurrence; %N = percentage of abundance; IP = Probabilistic index (I'' of Ruiz and Jover, 1981); IU = resource use index (Jover, 1989).

	Podarcis pityusensis					*Podarcis hispanica*				
Size class	T	%P	%N	IP	IU	T	%P	%N	IP	IU
0-1mm	32	15.89	4.73	6.62	3.99	10	20.00	13.89	2.90	6.27
1-2mm	188	43.93	27.81	20.19	26.32	18	40.00	25.00	21.69	27.91
2-3mm	118	56.07	17.46	24.20	22.81	8	46.67	11.11	8.19	22.42
3-4mm	79	39.25	11.69	12.95	14.07	8	20.00	11.11	11.01	12.90
4-5mm	65	31.78	9.62	7.25	11.18	8	33.33	11.11	14.99	14.05
5-6mm	72	33.64	10.65	7.06	8.80	0	0.00	0.00	0.00	0.00
6-7mm	29	16.82	4.29	2.71	3.93	2	13.33	2.78	3.85	2.09
7-8mm	26	14.95	3.85	1.60	3.01	2	13.33	2.78	1.56	2.09
8-9mm	15	13.08	2.22	2.67	2.08	3	13.33	4.17	0.80	2.66
9-10mm	10	9.35	1.48	1.84	1.23	5	26.67	6.94	2.60	9.61
10-11mm	6	5.61	0.89	0.60	0.58	1	6.67	1.39	12.31	0.00
11-12mm	3	2.80	0.44	0.05	0.18	1	6.67	1.39	1.37	0.00
12-13mm	5	4.67	0.74	0.37	0.43	1	6.67	1.39	3.08	0.00
13-14mm	2	1.87	0.30	1.78	0.07	0	0.00	0.00	0.00	0.00

	Podarcis pityusensis					*Podarcis hispanica*				
Size class	T	%P	%N	IP	IU	T	%P	%N	IP	IU
14-15mm	7	6.54	1.04	3.80	0.73	0	0.00	0.00	0.00	0.00
15-16mm	1	0.93	0.15	0.01	0.00	1	6.67	1.39	0.12	0.00
16-17mm	3	2.80	0.44	0.65	0.18	0	0.00	0.00	0.00	0.00
17-18mm	3	2.80	0.44	0.64	0.18	0	0.00	0.00	0.00	0.00
18-19mm	1	0.93	0.15	0.20	0.00	0	0.00	0.00	0.00	0.00
19-20mm	2	1.87	0.30	1.76	0.07	0	0.00	0.00	0.00	0.00
>20mm	9	7.46	1.33	3.05	0.15	4	26.68	5.56	15.54	0.00

Considering all the preys consumed throughout the year, there were no differences between males and females *Podarcis pityusensis*, but immatures ate smaller sizes than adults (Kruskal-Wallis test, H = 31.98, 2 d.f., p = 5 · 10-7, Dunn's *a posteriori* test, $p < 0.05$). No changes in the results for adults were found between the reproductive and the postreproductive seasons (see Carretero *et al.*, in press, for the definition of these periods). Different results were observed when only maximum or minimum prey per stomach were analyzed. So, no difference in the maximum prey size per stomach was found between females and immatures but males ate larger maximum preys than the others (Kruskal-Wallis tests, H = 10.38, 2 d.f., p = 0.0057; Dunn's *a posteriori test*, $p < 0.05$). However, no differences were found in the minimum sizes. The small sample size of *Podarcis hispanica* prevented the detection of any significant difference between this species and any other group.

Finally, the trophic overlaps between the classes of *Podarcis pityusensis* are shown in table 4. For the both *Podarcis* species, the total overlaps were 60.05% (OTUs) and 84.31% (size classes).

Table 4.- Intraspecific overlap matrices between the classes of *Podarcis pityusensis* (Barcelona). Numbers below the diagonal: taxonomical overlaps. Numbers above the diagonal: size overlaps.

Schoener Index	**Males**	**Females**	**Immatures**
Males	---	80.69	60.00
Females	71.63	---	75.49
Immatures	78.09	78.99	---

Discussion and conclusions

From these results, there appears to be a similarity in the feeding habits of *Podarcis pityusensis* and other insular populations (see references below). However, some dietary shifts have been detected as well. The number of preys per stomach is similar to those found in other *Podarcis*, usually smaller than this species (Pérez-Mellado, 1983; Valakos, 1986) but this result appears rather low when compared to the similar-sized members of other genera (e.g. *Psammodromus algirus* or *Acanthodactylus erythrurus*, Carretero and Llorente, 1993). Moreover, the number of empty stomachs throughout the year is relatively high. This could mean a limitation in food availability, especially but not exclusively, in winter.

As to the taxonomical composition of the diet, the presence of vegetal food deserves comment. Although, the percentage found here is lower than in the insular populations of *Podarcis pityusensis* (see Eisentraut, 1949; Salvador, 1986b; Pérez-Mellado and Corti, 1993), it is higher than in other *Podarcis* species living on the continent, some of which do not eat plants at all (Mellado *et al.*, 1975; Mou, 1987; Pérez Mellado, 1983). It is noteworthy that vegetal matter was completely absent in the stomachs of the syntopic *Podarcis hispanica*. This was also the case of another urban *Podarcis hispanica* population from Barcelona studied by Llorente (1988). Reversely, except *Podarcis lilfordi* from the islets around Mallorca and Menorca (see Salvador, 1986a), the insular populations of other *Podarcis spp* of the Mediterranean (see Valakos, 1986, 1987; Sorci, 1990; Castilla and Bauwens, 1991; Pérez-Mellado and Corti, 1993) lack vegetal matter in their diets (*Podarcis erhardii*, *Podarcis tiliguerta*) or this is present in low proportions (*Podarcis filfolensis*, *Podarcis hispanica*, *Podarcis muralis*, *Podarcis sicula*, *Podarcis wagleriana*). So, the presence of vegetal food in the diet of *Podarcis pityusensis* cannot be explained only in terms of resource availability, but may also be a result of historical influences.

The animal diet differs from those of most Mediterranean Lacertidae since the main items consumed are clumped preys (Aphididae and ants), which together represent more than a half of the total diet. Moreover, these taxa are also the most important for the insular populations of *Podarcis pityusensis* (Eisentraut, 1949; Salvador, 1986b; Pérez-Mellado and Corti, 1993), indicating a tendency to food specialization.

Cannibalism has been reported for this and other Lacertidae, not only insular (Mellado *et al*., 1975; Salvador, 1986a and b; Pérez-Mellado and Corti, 1993). The coincident result of adult males predating on immatures, usually hatchlings (see also Carretero, 1993) could be related with phenomena of intraspecific competition, which is expected to be high in islands and/or dense populations as in Barcelona (Carretero *et al*., 1991).

The intraspecific differences in the taxa eaten are also relevant. Results found here fit the prediction of Pough (1973) about the reduction of vegetal consumption for small lizards, but applied here to a smaller scale (the different size classes within the same species). The limitation in the intestine length and, consequently, in the time of food retention by immatures is obviously implied (Dearing, 1993, unpubl. data). Intersexual segregation, which is higher than that due to body size, could be a secondary result of the sexual dimorphism (see below).

Seasonal variation of the diet can be used to elucidate what is the strategy of food consumption. The optimal foraging theory (Stephens and Krebs, 1986) states that foraging involves the optimization of different variables such as prey-switching, energy input, nutrients balance and time (Murdoch, 1969; Schoener, 1969; Rapport, 1971; Paullian, 1975; Stamps *et al*., 1981). It has been proposed (Nagamuna and Roughgarden, 1990; Pérez-Mellado and Corti, 1993) that, under insular conditions, the low predation risk would free lizards from part of the temporal constraints when they search and handle their preys. Then, foraging would be more dependent on the other factors, mainly the energy demands. Since the arthropod availability in islands is usually scarce, especially in summer, lizards could use other kinds of food (plants, but also Stylommatophora) which requires more time investment for obtaining the same amount of energy. Ants, which are abundant in the diet of insular Lacertidae (see references and Outboter, 1981; Quayle, 1983; Di Palma, 1984), represent in general an emergency resource when other preys are scarce (Fuentes, 1976). Moreover, despite they are heavily chitinized and hence energetically defective (Díaz and Carrascal, 1993), their searching costs per prey are lower than expected because they are found in aggregations (Pollo & Pérez-Mellado, 1991; Pérez-Mellado, 1992; Pérez-Mellado and Corti, 1993). The same applies to Homoptera, although they show a thinner exoskeleton and higher profitability than ants (Díaz and Carrascal, 1993).

In the present case, if only environmental constraints were involved, the return to the continent should have induced a reversion of *Podarcis pityusensis* to a "typical" diet, as a consequence of a time minimizing tactic which has often been reported to change throughout the year and between sexes (Durtsche, 1992; Díaz and Carrascal, 1993; Preest, 1994). Results found here do not agree with this hypothesis because Homoptera, ants and, to a lesser extent, plants continue to be highly consumed. The seasonal patterns of the consumption of ants and plants are similar to those of the insular populations (see also Carretero and Llorente, 1993, for the continental *Acanthodactylus erythrurus*). Homoptera (Aphididae) are consumed in a different, opportunist way replacing Formicidae as dominant prey in spring and winter. So, the foraging strategy seem to be partially fixed in this species. As a criticism of this statement, it should be noted that *Podarcis hispanica*, which have probably no endogenous specializations, consumes many Aphididae. Nevertheless, it should be taken into account that most *Podarcis hispanica* were captured in autumn. If a specific analysis is performed in this season, the importance of Homoptera for *Podarcis hispanica* it increases whereas in *Podarcis pityusensis* decreases (see fig. 3), the last species consuming other alternative preys. A possible explanation would be that other preys (Isopoda, Coleoptera larvae) are more consumed by *Podarcis pityusensis* than Homoptera (and Formicidae) in autumn, when food availability could be higher and non-constraining. This could imply a relaxing of interspecific competition between species, *Podarcis hispanica* then eating the most abundant resource. As in other studies (Pérez-Mellado, 1983; Carretero and Llorente, 1991a; Carretero, 1993), Araneae remain constant for *Podarcis pityusensis* throughout the year because of their continuous activity (Jones, 1985).

From the results of the diversity analysis, like most of the species of Lacertidae, diet is characterized by a wide trophic niche, manifested in high trophic diversities. However, the values of individual (but not the populational) diversities are lower than in other species (Carretero and Llorente, 1991, 1993; Carretero, 1993). Moreover, the populational diversity is nearly five times the individual diversity in every group analyzed. This means that there is a considerable heterogeneity among individuals which tend to stenophagy in different ways. Thus, it is common to find a great number of ants or Aphididae in a stomach but it is rather rare to find both together. The comparative results indicate that this strategy remains constant among classes. Seasonally, winter represents a period of scarcity not only in the number but also in the types of prey and diversity because of the arthropod diapause.

The modal size class consumed by *Podarcis pityusensis* is lower than those of other similar-sized Lacertidae of nearby continental localities (see for instance, Carretero, 1993; Carretero and Llorente, 1993) and similar to smaller species of this family (Pérez-Mellado, 1983; Carretero and Llorente, 1991). If foraging activity was under strong time constraints without a nutrient restriction, size should be the most important factor involved in the selection of preys assuming that larger preys provide more energy than small ones (Stamps *et al.*, 1981; Pérez-Mellado *et al.*, 1991). In fact, the individual selection of largest preys has been reported for the continental lacertid *Psammodromus algirus* in the postreproductive season when intraspecific relationships decrease and predation pressure has a determinant role (Díaz and Carrascal, 1990, 1993). However, as it has been mentioned above, ants and Aphididae are not selected individually. So, the modal prey size consumed is biassed to the lowest values, as in the islands. This pattern is the same for sexes and seasons (see results), contrasting with those of other continental lizards (Durtsche, 1992; Díaz and Carrascal, 1993; Preest, 1994) with the exception of those with highly myrmecophagous diets (see for instance, Pérez-Mellado, 1992).

Nevertheless, the body size of the predator continues to be important (Pianka, 1986) and the size of the prey consumed is dependent of it. Pérez-Mellado and Corti (1993) did not detect any significant relation between the lizard and prey sizes in Mediterranean islands and they interpreted this as a result of the foraging tactics. Then, is there a prey size shift in the Barcelona population? As it has been remarked (Carretero and Llorente, 1991), the detection of significant correlations depends not only on the prey sizes but on the sample size and the SVL ranges of the lizards as well. So, the data of the immatures (not analyzed by these authors) have probably increased the power of our analysis and there may be no real difference with the insular populations. As a consequence, prey-predator size correlations have been found and adults eat larger preys than immatures. Furthermore, the large body of adult males allows them to eat some extremely large preys that cannot be subdued by females or, of course, by immatures. This may be explain the considerable sexual segregation observed in the taxonomical composition of the diet (see table 4 and also Carretero, 1993). Since, this kind of prey is rare in comparison with the rest, they do not influence on the results of the total prey analysis.

In conclusion, the trophic specialization found in *Podarcis pityusensis* consists mainly in the consumption of aggregated small preys and vegetal matter. This strategy and especially the herbivory is common in most small lizards, living in islands and/or under in arid conditions (see previous works and Sadek, 1981; Rocha, 1989; Dearing and Schall, 1993; Van Sluys, 1993; Paulissen and Walker, 1994; and the revision by Green, 1982). However, its persistence in this species after a translocation to a continental locality indicates that some historical constraints exist

Whereas the genus *Podarcis* is about 20-18 m.y. old (Böhme & Corti, 1993), it is estimated that its arrival to the Balearic Islands occurred during the Messinian regression (7-5 m.y.) when they were connected to the continent by dry, saline plains (Alcover *et al.*, 1981). Herbivory (and the consumption of clumped prey) is then a derived feature which has probably arisen several times in this primarily entomophagous and euriphagous lineage. However, only the balearic species seem to have become deeply specialized in this way. In fact, the other balearic lacertid, *Podarcis lilfordi*, very close genetically to *Podarcis pityusensis* (Bischoff, 1973; Ramón *et al.*, 1986) is the only one which shares these trophic features (Salvador, 1986a; Pérez-Mellado and Corti, 1993). In addition, the reproductive traits of this population of *Podarcis pityusensis* also show the same conservative character (Carretero *et al.*, in press). This trophic specialization could be associated with the fact that the Balearic species are probably the most ancient insular *Podarcis*. Nevertheless, the decrease in vegetal consumption and the seasonal variations observed here indicate that this species remains highly adaptable. So, the trophic ecology can still shift widely when the environment change and the endogenous influence is only partial (see a similar case in *Acanthodactylus erythrurus*, Carretero *et al.*, 1993).

What does specialization consist of? Excluding the elongation of the intestine (unplubl. data, see also Dearing, 1993) probably allowing animals to retain the food in the digestive tract for a longer time, no other anatomical features have been observed. The differences in the feeding behaviour (foraging tactics, feeding stimulus of slow-moving or immobile preys as Stylommatophora and plants, etc...) would require further research.

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