

Dietary adaptations and herbivory in lacertid lizards of the genus *Podarcis* from western Mediterranean islands (*Reptilia: Sauria*)

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A b s t r a c t. We examined the diets of several species of *Podarcis* from different western Mediterranean islands. We tested the prediction of more generalized diets in lizards from poor environments. We also examined the extent and mode of herbivory in relation to arthropod diversity in the diet. Lizards from the Tuscan Archipelago, *P. sicula* from Menorca, and *P. tiliguerta* from Corsica all show a rather generalized diet. In contrast, *P. lilfordi* and *P. pityusensis* from the Balearic Islands and, to a lesser extent, *P. hispanica* from Benidorm Island, appear much more stenophagous, including a high proportion of clumped prey in their diets. Plant matter is a common food item in most of the population studied, specially in Balearic lizards. A marked seasonal shift in the degree of herbivory was observed in these species where high-energy plant parts are frequently consumed during summer. In one of the Balearic Islands (Nitge), the bulk of the summer diet was formed by pollen and nectar of one particular plant species. Herbivory, consumption of clumped prey and other dietary peculiarities of insular populations of Mediterranean lizards indicate a very flexible feeding behaviour compared to mainland congeners. This could result from a lack of predation pressure allowing high population densities to be reached in islets with poor trophic resources. Differences found in dietary characteristics among island populations can be interpreted as a consequence of different current ecological conditions, as well as historical and biogeographical differences among the islands.

Key words. Diet, herbivory, lizards, *Podarcis*, island-ecology.

Introduction

Ecological responses to insularity can involve, among other effects, changes in diets and foraging behaviours (Gorman 1979). The Mediterranean climate is characterized by strong short-term as well as seasonal fluctuations (Fuentes 1984), leading to corresponding variations in food resources. Current foraging theories predict that a decrease in food abundance should lead to a lesser food specialization (Schoener 1971; Stephens & Krebs 1986). Small lacertid lizards, considered as food generalists (Arnold 1987), should therefore be well adapted to this environment by means of their opportunistic, generally insectivorous, feeding behaviour. In order to examine this hypothesis we studied insular lizards of the genus *Podarcis* of the Western Mediterranean basin. Here, we consider two species *Podarcis sicula* and *Podarcis muralis* from Tuscan Archipelago, *Podarcis tiliguerta* endemic to Corsica, *Podarcis hispanica* from the small island of Benidorm (eastern Spain) the two endemic species of the Balearic Islands, *Podarcis pityusensis* and *Podarcis lilfordi*, as well as the introduced species *Podarcis sicula*.

In this paper we examine dietary characteristics of these insular populations to test the expectation of a more generalized diet in islands with very poor trophic resources (Schoener 1971; Krebs & Stephens 1986). There are some indications in the literature

about the existence of herbivory in Mediterranean insular lizards (Eisentraut 1949; Salvador 1976, 1986a and b; Sadek 1981; Pérez-Mellado 1989). But the true extent of this feeding behaviour and its ecological relevance are not documented. The second aim of this work, therefore, was to test the relationship between body size and the degree of herbivory (Pough 1973), and the relationship between herbivory and prey availability (Schluter 1984).

Material and Methods

Species and study sites

The Tuscan Archipelago is situated in the Tyrrhenian Sea, between the Tuscan coast and Corsica. The *P. muralis* inhabiting the Tuscan Archipelago are differentiated from the continental ones at most at a subspecific level, so that one may hypothesize that they colonized it not earlier than during one of the sea regressions (Azzaroli 1983) that occurred in the Pliocene (Acquatraversa regression, ended about 2 m. y. ago) and Pleistocene, namely in the course of the most important one, the so-called Cassia regression, 0.8–1.0 m. y. ago. On the other hand, *P. sicula* almost surely reached the Tuscan Archipelago later; the populations more diverging from the continental *P. s. campestris*, i.e. those from Giglio and Capraia, presumably populated those islands, judging also from the electrophoretic data (Corti et al. 1989), during the upper Pleistocene, about 200,000–250,000 years ago, while *P. s. campestris* (Elba and probably Formica di Burano and Sparviero Islets) and the *P. s. campestris*-like lizard from Montecristo reached their island more recently, sometimes (Elba) even by human agency.

Corsica is a large island situated to the west of the central Italian coast and south of France. The ancestor of *Podarcis tiliguerta* may have populated the Cyrno-Sardinian complex between the Messinian salinity crisis and the Pleistocene Cassia regression, but more probably during the Pliocene (Lanza 1985).

Benidorm Island, situated 3.5 km off the eastern coast of Alicante (Spain), is a part of the continental platform and was colonized by *Podarcis hispanica* during the Holocene. Subspecific differentiation does not appear to have occurred in the population of this island (Pérez-Mellado unpub. data).

The Balearic Islands form an archipelago geologically divided into Gymnesic (Mallorca, Menorca and islets around them) and Pityusic Islands (Eivissa, Formentera and islets). The Balearics were occupied by terrestrial vertebrates during the Messinian period (Alcover & Mayol 1982). Hence, geological data indicate a last connection with the Iberian peninsula from approximately 5 million years ago (Alcover et al. 1981; Riba 1981).

Minor Gymnesic Islands (e.g., islets around Mallorca and Menorca) are occupied by *Podarcis lilfordi*, extinct in the main islands of Mallorca and Menorca (Alcover et al. 1981), while the Pityusic Archipelago shelters the endemic lizard *Podarcis pityusensis*. The main island of Menorca is inhabited by two introduced species, *Lacerta perspicillata* from Morocco, and *Podarcis sicula* from the Italian peninsula. Both introductions seem to be very recent and undertaken by man.

Balearic and Benidorm Islands have a Mediterranean mesothermic climate (*csa* in the Köppen-Geiger classification, see Strahler 1986) characterized by mild winters and hot dry summers. The average daily temperature is 22°C in the hottest month in the middle of the dry season (see Cirer 1981 and Guijarro 1984). Corsica and the Tuscan Archipelago are included in the *csb* climate type (Strahler 1986), also having a mesothermic climate, but with greater annual rainfall and, hence, a less pronounced dry season. The duration of the dry season in Corsica and the Tuscan Archipelago varies between 3 and 4 months, while in Balearic and Benidorm Islands it lasts, at least, 5 months (Henry 1977; Miller 1983).

The vegetation of the areas under study is typically Mediterranean, from an extremely poor plant cover with only two or three plant species in some islets as Nitge (Pérez-Mellado 1989) to a true thermomediterranean maquis or garrigue sparsely covered by patches of oak and pine forests, and cultivated areas, as in bigger islands such as Eivissa, Menorca or Formentera (see more details in Colom 1978 and Rivas-Martínez & Costa 1987).

Sampling

We studied 12 insular populations of *Podarcis lilfordi* from the islets around Menorca and 16 populations of *Podarcis pityusensis* from Ibiza, Formentera, and some islets around them. From the Tuscan Archipelago, we included 6 populations of *Podarcis muralis* and 6 of *Podarcis sicula*. From Corsica, we studied a sample of 21 specimens from 13 different localities widely distributed throughout the island and covering the main range of habitats and altitudes. Finally, we studied 29 specimens from Benidorm Island, where there is a very dense population of *Podarcis hispanica* (Gil and Guerrero pers. comm.).

To avoid the capture of specimens in these threatened populations of insular lizards, stomach samples were obtained only from Museum specimens which had been sacrificed just after collecting. Samples of *Podarcis sicula* and *Podarcis muralis* were from specimens deposited in the Zoological section "La Specola" of the Natural History Museum of the University of Florence (Italy). Samples of *Podarcis lilfordi* from Menorca islets were from specimens deposited at the Museo Nacional de Ciencias Naturales, C.S.I.C., Madrid (Spain), while specimens of *Podarcis hispanica* from Benidorm Island and *Podarcis pityusensis* were from the Herpetological collections of the Department of Animal Biology, University of Salamanca and the Department of Animal Biology, University of Valencia (Spain). In addition, several faecal pellets were collected in Menorca islands (table 1) corresponding to sampling periods in spring and summer (excepting the winter sample from Rei Island, Menorca, table 1). We obtained samples for different periods to make an analysis of dietary seasonal effects. From the island of Nitge, we obtained samples in two successive summers (samples II and III from 1987 and 1988 respectively, see table 2).

Stomach and faecal pellet contents were identified at order and family levels. The length and width of each prey item were measured with a micrometer eyepiece under a binocular dissecting microscope. The volume was estimated as an approximation to an appropriate geometrical shape (see, for example, López et al. 1991). The snout-vent-length (SVL) of the lizards was taken to the nearest mm (table 2).

The conclusions on the relative importance of each prey type that are based only on volume or only on numerical abundance may misrepresent the true contribution of the prey to the diet of the lizard (Robinson & Cunningham 1978). Hence, the diet was summarized as the proportion of the total number of prey items in the stomach or faecal pellet, the proportion of lizards eating a prey type, and the proportion of the total volume of prey in the stomach.

Trophic niche breadth (B) was calculated according to the formula given by Levins (1968), as well as its standardized value (Bs, see Hespenheide 1975) the most common equations used in dietary studies of lizards (Pianka 1986).

Results

General diets

In the Tuscan Archipelago the diet of *P. sicula* and *P. muralis* showed significant differences in proportions of prey items consumed (pooled data of all populations in both species, G-test of independence, $G=39.63$, $p<0.01$), while we did not find a significant difference between diets of *P. sicula* from Menorca and Tuscan Archipelago (tables 3 and 8, $G=18.51$, $p>0.05$).

Podarcis sicula showed a terrestrial diet, with a relatively important presence of Gastropoda (table 3). The use of Isopoda (13.79 % by number) is also important in comparison with the remaining populations. By volume the most important prey items were Isopoda, Insect larvae, Amphipoda, and Diptera (figure 1).

In *Podarcis muralis* the bulk of the diet is formed by Coleoptera, Formicidae and, in some cases (e.g. Elba Island), Diptera (table 4). Hymenoptera, Heteroptera and Diptera were the most important groups by volume (figure 2). Hence, the diet of *P. muralis* in Tuscan Archipelago shows a higher proportion of flying insects than *P. sicula* and lower values of trophic diversity.

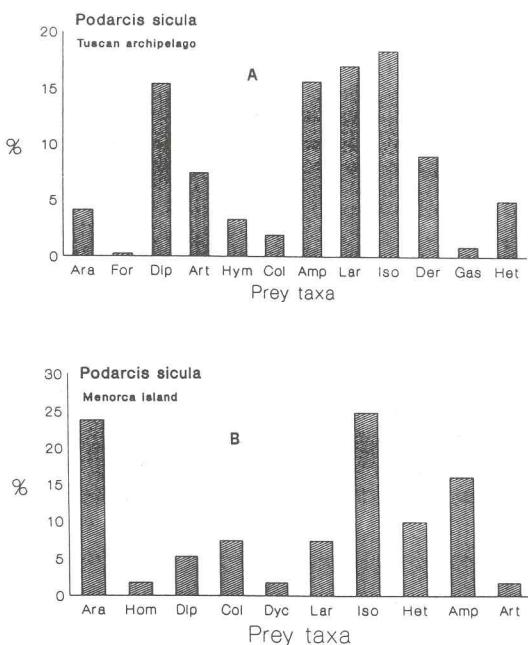


Fig. 1: Proportion by volume of the most important prey taxa (above 1 % of the total volume) in *Podarcis sicula* from Tuscan Archipelago (A) (pooled data of all populations under study) and Menorca (B). Ara = Araneae, For = Formicidae, Dip = Diptera, Art = Arthropoda undertermined, Hym = Hymenoptera (other than Formicidae), Col = Coleoptera, Amp = Amphipoda, Lar = Insect larvae, Iso = Isopoda, Der = Dermaptera, Gas = Gastropoda, Het = Heteroptera, Hom = Homoptera, Dyc = Dyctioptera.

The small sample sizes precluded any deeper inference and an analysis of dietary differences between islands of the Tuscan Archipelago. The threatened situation of these populations discouraged the capture of additional specimens.

In the Balearic Islands, dietary differences were observed between the two endemic species studied. *Podarcis pityusensis* has a diet dominated by ants and beetles (table 5). Coleoptera is also the most important prey type by volume (figure 3). Some differences were also found between islets and the main islands of Eivissa and Formentera. The diet of *Podarcis lilfordi* seems to be more uniform than of *P. pityusensis*, and mainly based on clumped prey such as Formicidae, Homoptera, and Coleoptera, the vast majority of them from the family Curculionidae. But in some very small islets (e.g. Porros) we observed an acute euryphagy (tables 6 and 7).

Podarcis tiliguerta appears highly variable in its diet (table 8), as corresponding to the widespread distribution of sampling sites throughout the Corsica Island (see above).

Finally, the terrestrial diet of *Podarcis hispanica* from Benidorm Island included a high proportion of ants and other Hymenoptera (table 8).

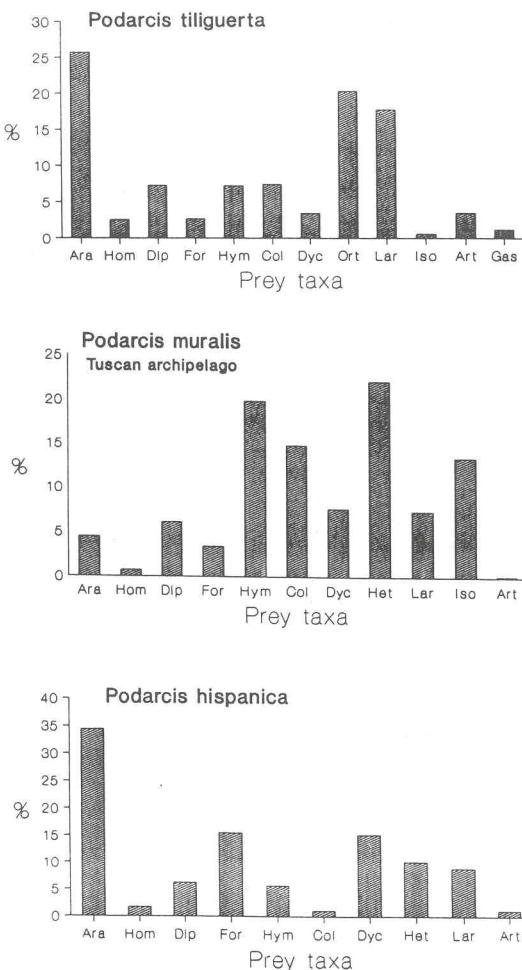


Fig. 2: Proportion by volume of the most important prey taxa in *Podarcis muralis* (pooled data of all islands under study), *Podarcis tiliguerta* and *Podarcis hispanica*. Ort = Orthoptera, remaining abbreviations as in Fig. 1.

Prey size

We detected a significant difference between prey sizes of species under study (table 2, Kruskal-Wallis analysis, $H=63.73$, $p<0.001$). The Dunn test indicates the following pairwise comparisons: *P. pityusensis* and *P. sicula* from the Tuscan Archipelago took larger prey than *P. muralis*, *P. hispanica* and *P. lilfordi*. On the other hand, the more diverse diet of *P. sicula* in the Tuscan Archipelago was reflected by a significant difference in prey sizes between samples from different islands studied ($H=31.98$, $p<0.001$), while *P. muralis* showed similar prey sizes among all populations under study ($H=2.77$, $p=0.091$).

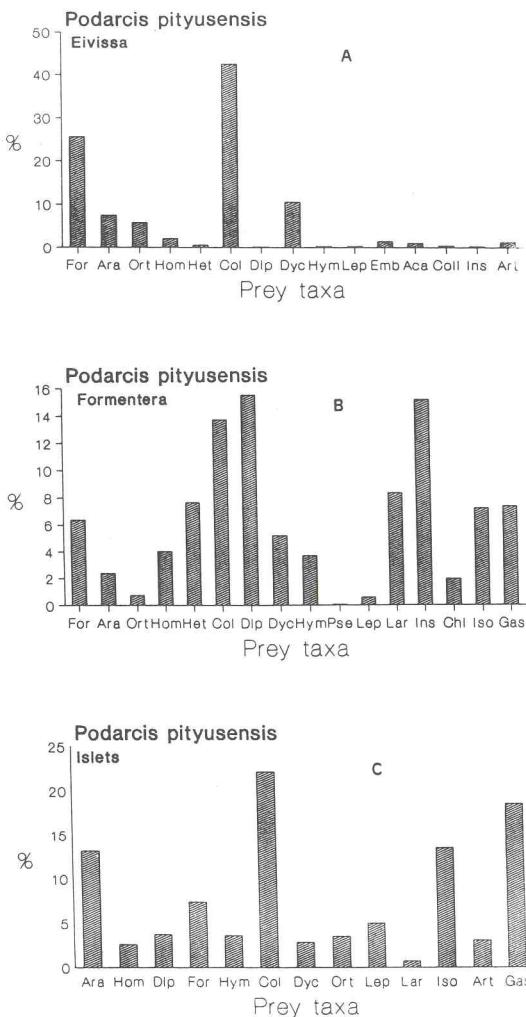


Fig. 3: Proportion by volume of the most important prey taxa in *Podarcis pityusensis* for Eivissa Island (A), Formentera (B) and pooled data for the remaining islets studied (C). Lep = Lepidoptera, Emb = Embioptera, Aca = Acarida, Coll = Collembola, Ins = underdetermined Insects, Chl = Chilopoda, remaining abbreviations as in Fig. 1.

We were not able to detect any significant correlations between body size of lizards (average of adult SVL, see table 2) and prey size taking into account all populations studied (Spearman Rank Correlation, $Rs=0.06$, $p=0.64$), in spite of differences between body sizes of each lizard population (table 9, see also Pérez-Mellado & Salvador 1988 for *P. lilfordi* populations and Cirer 1987 for *P. pityusensis*).

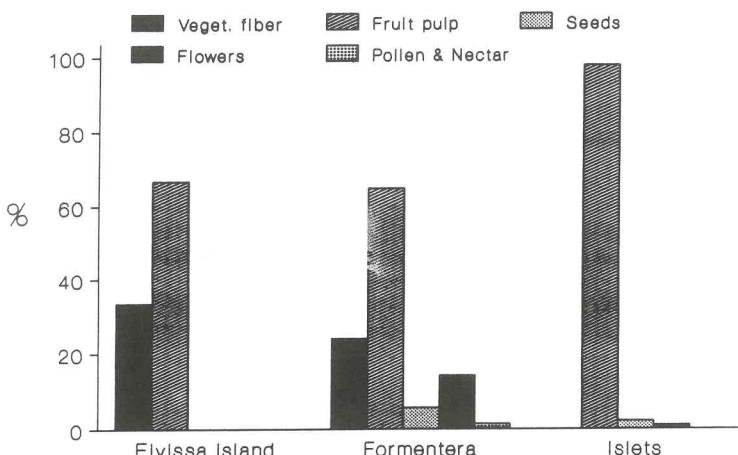


Fig. 4: Proportion in which different plant parts (see text) were found in stomach contents of *Podarcis pityusensis*.

A significant correlation between average prey size and trophic diversity was found (with B index, $R_s=0.68$, $p<0.001$, and with Bs index, $R_s=0.66$, $p<0.001$). Hence, a less diverse diet, obviously based on clumped prey (see also below), implies a lower average prey size. This appears to be one of the reasons for the lack of a correlation between prey size and body size of the lizards. Also, the high variability in prey size taken will mask any existing smaller difference.

Herbivory

Plant consumption seems to be very variable in the Tuscan Archipelago (table 3 and 4) and not widespread among individuals of the populations, judging from the relatively low proportion of stomachs with plant matter. The importance of plants in the diet seems to be less pronounced in *P. muralis* than in *P. sicula*.

Plant matter was found only in a minor proportion of the stomachs of *P. hispanica* from Benidorm Island (table 8). This kind of food type is even less important in *P. sicula* from Menorca and completely absent from the sample of *P. tiliguerta* (table 8).

Finally, plant matter was frequently found in the diet of *P. pityusensis* and *P. lilfordi* (tables 5, 6, and 7). The Balearic species (pooled data) showed a significantly higher percentage of individuals consuming plant matter than both *Podarcis* species (pooled) from the Tuscan Archipelago (Mann-Whitney U test, $Z=2.074$, $p=0.038$), but we did not find a significant difference between both archipelagos concerning the average volume of plant matter ($Z=1.36$, $P=0.17$).

Spearman rank correlation analyses were computed between principal dietary factors and other characteristics of the populations under study supposedly related with plant consumption (table 9). We found a negative correlation between dietary

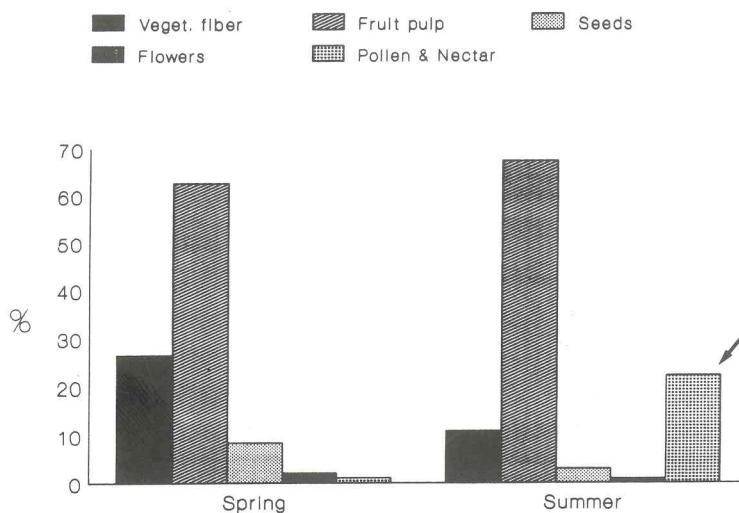


Fig. 5: Proportion of different plant parts eaten by *Podarcis lilfordi* during spring and summer (pooled data of all populations under study). The arrow indicates the relatively high proportion of pollen and nectar in summer sample (see text for more details).

diversity and plant consumption, and also between dietary diversity and the number of prey per stomach. This last result indicates that the consumption of clumped prey significantly reduced dietary diversity, mainly by the inclusion of Formicidae. Hence, we also found a positive correlation between plant consumption and the proportion of Formicidae in the diet.

In summary, *Podarcis* which include a higher proportion of plants in their diets (e.g., those of Balearic Islands, especially *P. lilfordi*) are characterized by a high proportion of clumped prey, principally ants.

It is also interesting to point out the lack of correlation between body size of lizards and all trophic factors analyzed.

Because we lack a direct estimation of trophic availability in islands, we used surface area and maximum elevation above sea level of the island, the best predictors of species abundance in Mediterranean islands (Parlanti et al. 1988). We were unable to find any relation between dietary factors and those variables (table 9). Hence, we can conclude that plant use and dietary diversity are rather independent of the islands size.

In the Balearic Islands, where plant use is widespread, we were able to distinguish in stomach contents the different parts of plants eaten by lizards. Hence, we classified plant remains in five categories: 1. vegetable fibre from leaves or soft stems, 2. flowers, 3. fruit pulps, 4. seeds, and 5. nectar and pollen. As we see in figures 4 and 5, the bulk of plant matter is formed by fruit pulp both in *P. pityusensis* and *P. lilfordi*.

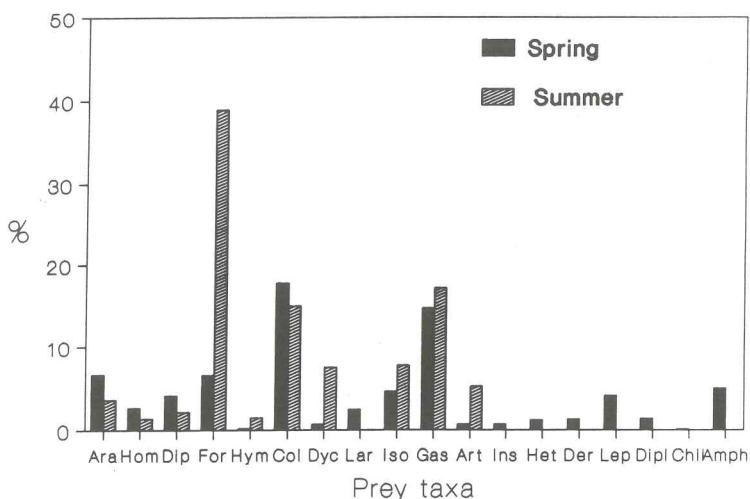


Fig. 6: Seasonal changes in the proportion of the most important prey taxa eaten by *Podarcis lilfordi* in spring and summer. Abbreviations as in Figures 1, 2, and 3.

Seasonal effects

We studied seasonal dietary shifts in *Podarcis lilfordi* populations. Results from spring and summer samples are summarized in tables 6 and 7 respectively.

In general, dietary diversity was lower during summer. The relative abundance in the diet of Coleoptera, Isopoda, and Formicidae exhibited significant variations (G-tests, in all cases $p < 0.001$), whereas the relative abundance of Araneae, Diptera (for both $G = 10.33$, $p > 0.05$), Chilopoda ($G = 10.91$, $p > 0.05$), Homoptera, Heteroptera, and larvae ($G = 0.85$, $p > 0.05$) remained fairly constant. Hence, the seasonal dietary shifts can be summarized in a higher importance of Coleoptera during spring and a predominance of Isopoda and Formicidae during summer. In fact, the trend to myrmecophagy is so strong that ants are the main prey even by volume (fig 6), what is particularly noteworthy given the small size of ant species involved.

Also plant consumption is significantly higher during summer, concerning the proportion of individuals consuming plant matter (fig 7, Kruskal-Wallis analysis, $H = 5.73$, $p = 0.015$), as well as the average volume of plants in stomachs or faecal pellets (fig 8, $H = 13.21$, $p = 0.0003$).

The rather high proportion of pollen and nectar from summer samples of *P. lilfordi* deserves special attention. This amount of nectar and pollen came from the Nitge lizards faecal pellets (fig 5). The spring diet of Nitge lizards is similar to that of the lizards of other islands (table 6) but with the arrival of summer trophic resources seems to decline drastically in this islet (Pérez-Mellado pers. obs.) and the diet shifts to a highly herbivorous composition. Faecal analyses indicate that the main item (70 %) were anthers, nectar and pollen of the sea fennel *Critchmum maritimum*

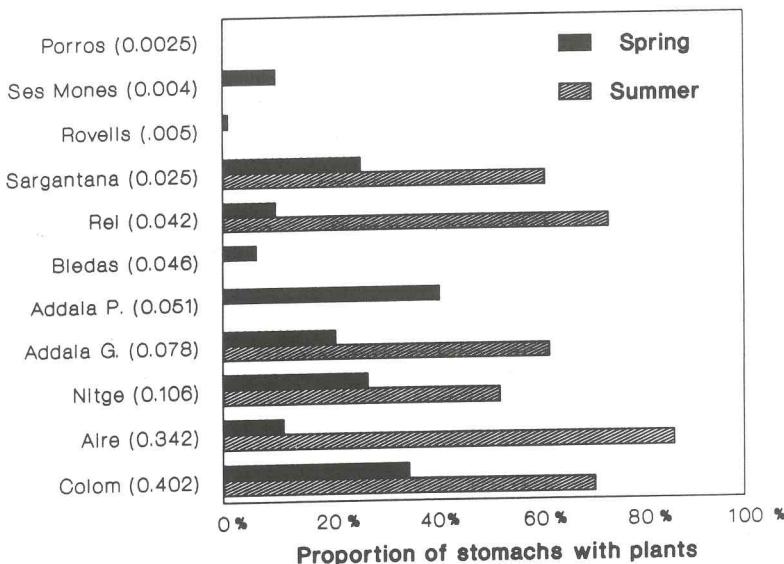


Fig. 7: Proportion of stomach or faecal pellets with plant matter of *Podarcis lilfordi* during spring and summer (in parentheses the size of the island in km²).

(Umbelliferae), the most common plant species on the island (see also Pérez-Mellado 1989). During hot days of late July and August it is possible to observe numerous active lizards on Nitge, even at midday, engaged in a "nectaring" behaviour clumped on the top of *C. maritimum* inflorescences.

Discussion

One might predict similar diets in both Mediterranean groups of islands, Balearics and Tuscan Archipelago. However, *P. sicula* and *P. muralis* (from the latter group) showed a more diverse diet in which plant material plays a secondary role. The diet of these species is composed of the most common terrestrial arthropods found in Mediterranean ecosystems (see similar results in Valakos 1986, 1987; Pollo & Pérez-Mellado 1988). It is also of interest to point out the similarity of the diets shown by populations of *Podarcis sicula* from the Tuscan Archipelago and Menorca, in spite of the distance between them. This result indicates that dietary characteristics of the populations under study cannot be explained solely by different trophic availabilities in the two archipelagos.

In the Balearic Islands, we observe that stenophagy occurs in both species, *P. lilfordi* and *P. pityusensis*, and that it is directed toward clumped prey such as Homoptera, some families of Coleoptera as Curculionidae, and, specially, ants. How can this high consumption of ants and other very small prey be explained? Ants are strongly chitinized and of comparatively small size in the dietary samples studied. Taking into account current time-minimizing predation risk models (see, for exam-

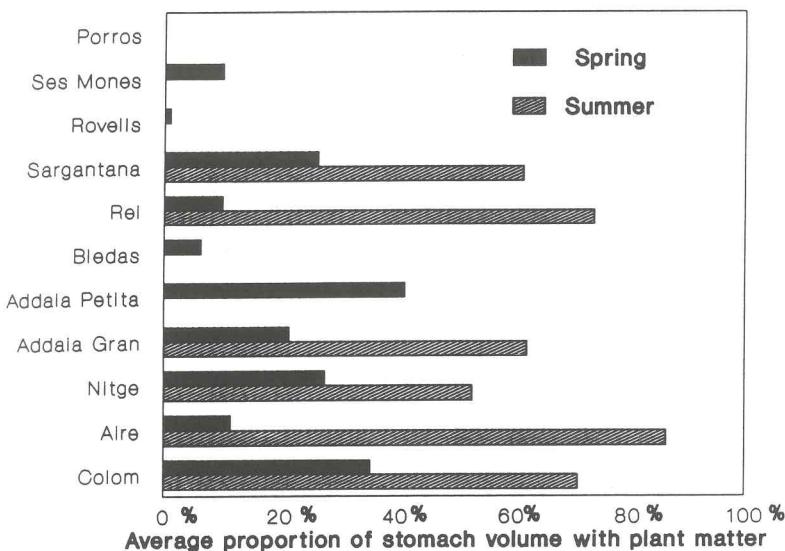


Fig. 8: Average proportion of stomach or faecal pellets volume of plant matter in *Podarcis lilfordi* during spring and summer.

ple, Schoener 1969 and Stephens & Krebs 1986), prey of this size is not profitable for the predator (Fuentes 1974). However, the searching costs are lower because of their clumped distribution in nests, columns or aggregations (see also Darewskij 1967 for a similar approach). In addition, as Naganuma & Roughgarden (1990) pointed out, the time-minimizing predation risk model (Schoener 1969) is more appropriate to continental conditions (McLaughlin & Roughgarden 1989, fide Naganuma & Roughgarden 1990) than to insular conditions with little or no predation pressure as in the Balearic Islands (Pérez-Mellado 1989, and pers. obs.). Here, it may be more appropriate to employ a net energy gain per time of activity approach (Naganuma & Roughgarden 1990). In this context, even if the energy-maximizing criterion favoured the consumption of the largest ingestible prey item, because such large items are much less frequently encountered, very small items can be included in an optimal diet (*sensu* Schoener 1971). In fact, the myrmecophagy is common among insular populations of *Podarcis* lizards (Quayle 1983; Ouboter 1981; Salvador 1976, 1986a, b) and it is postulated as the optimal strategy in arid environments (Pianka 1986; Pérez-Mellado 1992; Pollo & Pérez-Mellado 1988, 1991), or during periods of dry conditions (see similar conclusions in James 1991 for termites). Ballinger & Ballinger (1979) found a reduction in trophic diversity in *Sceloporus jarrovi* during years of low trophic availability and a corresponding rise in the consumption of small Hymenoptera (e.g. Formicidae). Thus, ants can be considered a quite general dietary alternative in situations of poor trophic availability.

Pianka & Parker (1975) explained the bizarre morphology of some myrmecophagous species of lizards as *Phrynosoma* spp. and *Moloch horridus* as an adaptation of body form to this kind of trophic ecology. But the extent of myrmecophagy in Mediterranean lizards, lacking any special adaptation, challenges this interpretation (see other examples in Greene 1982). As Greene (1982) pointed out, a highly modified morphology is not a prerequisite for being an ant specialist.

Plant matter is important in the diet of several populations of insular *Podarcis*. Assuming that dietary diversity is, at least partially, related to arthropod availability, we can expect an inverse relation between trophic diversity and plant consumption as we showed above (see Results). But we were unable to detect a relationship between plant consumption and island area.

If arthropod availability is an important factor in determining the extent of plant consumption we might also expect a higher plant consumption during dry summer. The comparison between spring and summer diets of *P. lilfordi* confirmed such an expectation, also predicted by Eisentraut (1949). Hence, the appearance of herbivory seems to be linked in this case to a temporary poverty of arthropod prey (see similar results for *Liolaemus* species inhabiting Chilean Andes in Fuentes & Di Castri 1975 and for *Tropidurus* lizards in Schlüter 1984, but see also several examples of nectarivory apparently not related to arthropod availability in Whitaker 1968, 1987; Vinson 1975; Thorpe & Crawford 1979, and Cheke 1984).

Pough (1973) indicated that because small lizards have higher energy requirements in proportion to their body weight, it is not possible for them to acquire a herbivorous diet. But Greene (1982) demonstrated that herbivory is much more common among small lizards than previous data suggested. Among lacertid lizards, plant consumption is fairly common in insular populations (Castilla et al. 1989 for *Lacerta bedriagae*; Eisentraut 1949; Koch 1928; Salvador 1976, 1986a, b; Pérez-Mellado 1989 for Balearic lizards; Elvers 1977; Sadek 1981, Lunn 1991 for *Podarcis dugesii*; Sorci 1990 for *Podarcis filfolensis*; Di Palma 1984 for *Psammodromus algirus*; Henle & Klaver 1986 for *Podarcis sicula*).

In general, these previous works did not mention the proportion of different parts of the plant consumed by lizards (Mautz & Nagy 1987). Our data indicates that the highest proportion of plant matter corresponds to fruit pulps, seeds, nectar, and pollen. Thus, high energy-content materials were consumed, in some cases with a caloric value close to that of animal origin (Golley 1961), and can be assimilated at a very high efficiency (see, for example, Martínez del Río 1990 for nectar). Such special herbivory can explain the lack of morphological specializations of Balearic lizards (Greene 1982). True herbivory, primarily based on vegetal fibre, is unlikely in lacertid lizards because they lack suitable masticatory capacities as a consequence of their kinetic skull and streptostylic mandibular suspension (Ostrom 1963; Szarski 1962). Pough (1973) pointed out that a true herbivorous behaviour could develop only in tropical ecosystems, where these plant materials are available throughout the year. In the Balearics we observed a higher plant consumption in summer coinciding with the apparition of fruits in several Mediterranean plant species as *Pistacia lentiscus* frequently found in stomach contents and faecal pellets. The occurrence of seasonal changes in abundance of this food type does not preclude its effective use by lizards.

The most interesting foraging behaviour among populations under study was observed in Nitge Island where *Podarcis lilfordi* feeds during summer almost exclusively on nectar and pollen of *Crithmum maritimum* (more than 70 % by volume in one of the summer samples) and a few arthropods, mainly ants. Koch (1928) and Salvador (1976) reported a similar behaviour in *P. lilfordi* from Na Foradada Islet (Cabrera Archipelago, south of Mallorca), where individuals were seen climbing on Umbelliferae, catching insects, and licking nectar.

Nitge, and possibly other Balearic islets, have special conditions that might explain the appearance of this feeding strategy. The islet is patchily covered by three small plant species (Pérez-Mellado 1989) two of them, *Allium ampeloprasum* and *Crithmum maritimum* used as food resources by lizards. In summer the drought of the islet is extreme and very few arthropods can be seen. During the first half of summer 1991 lizards were observed feeding on flowers of *Allium ampeloprasum* (R. Brown pers. comm.). This demonstrates adaptability to a new food resource as the height and structure of these plants means that they are not generally available to the lizards (unless flattened by wind or domestic goats). *C. maritimum* comes into flower during the second half of summer, when it is possible to observe dozens of lizards climbing these plants and licking nectar and pollen from the small flowers while pending from the inflorescences to which they climb by the forelimbs.

In summary, herbivory of Mediterranean *Podarcis* can be considered as part of a very opportunistic foraging behaviour. In fact, our data indicate the usual consumption of other unexpected foods such as crustaceans of the order Amphipoda that were taken from the shore of the islets. A similar behaviour was described by Lukina (1963 in Darevskii 1967) in *Lacerta sascicola szcerbaki* (see also Henle & Klaver 1986 for *Podarcis sicula*). These insular populations are also frequently observed taking unusual food such as carcasses or any organic matter left by visiting tourists (Corti & Pérez-Mellado pers. obs.; see also Elvers 1977; Kramer 1946; Lunn 1991; Sadek 1981; Salvador 1976, 1979). On the other hand, malacophagy seems to be uncommon (see tables 3–8) in Mediterranean lizards under study, in spite of the usually high snail abundance in insular ecosystems (Corti & Pérez-Mellado pers. obs.) and their potential profitability. This fact can be explained by the high costs of handling and crushing their shells (Greene 1982).

Finally, we made only three observations of cannibalism by adult male *Podarcis lilfordi* on hatchlings. This behaviour seems to be relatively common in other populations of insular lacertids (Kramer 1946; Salvador 1976, 1986a and b), but we do not know its importance from a trophic point of view.

Summarizing our results, we found a highly adaptable feeding behaviour in *Podarcis pityusensis* and *Podarcis lilfordi* with very variable food materials in their diets. Like the Balearic Islands' *Podarcis*, the diet of *Podarcis hispanica* from Benidorm Island also appears to be fairly well adapted to a dry environment, including a large proportion of ants. Why did we not find similar results in *P. tiliguerta*, *P. sicula* and *P. muralis*? Concerning the Tuscan Archipelago, the drought during late spring and summer is less severe (see above), thus, we can expect a higher arthropod availability that allows a more diverse diet based on larger and more profitable prey such as Coleoptera, Dycloptera, or Diptera. In the case of *P. tiliguerta*, it inhabits an island with highly variable ecological conditions, similar to those in the continent. Hence,

its diet does not show any insular characteristics. However the diet of the introduced *Podarcis sicula* in Menorca is similar to that of the two *Podarcis* inhabiting the Tuscan Archipelago, indicating the importance of historical factors.

The isolation of *P. lilfordi* and *P. pityusensis* on the Balearic Islands took place during the Messinian period, which was characterized by very dry climatic conditions. The Balearic territory was at this time in the centre of a saline steppe that acted as a filter for the colonization of the area (Alcover & Mayol 1982). It is therefore feasible that there was strong natural selection for lizards with higher trophic adaptability and/or a capability to adopt a narrow myrmecophagous diet. In fact, it seems that the original distribution of *Podarcis lilfordi* in the island of Mallorca was limited to Vindobonian limestone areas, indicating that it was an arid adapted species (Colom 1978).

In conclusion, trophic characteristics of insular populations of *Podarcis* species can be explained by a combination of factors including present day ecological conditions as well as historical factors. Trophic behaviour of Mediterranean *Podarcis* is well adapted to present ecological conditions considering the extremely dense populations attained in several islets, specially in the case of Balearic Islands (Pérez-Mellado 1989 and unpub. data; see a similar conclusion for *Aporosaura anchietae* in Robinson & Cunningham 1978, for *Podarcis filfolensis* in Sorci 1990, and for some populations of *Podarcis sicula* in Henle & Klaver 1986). We lack appropriate information about predation pressure in the Tuscan Archipelago, Corsica, and Benidorm Islands, but in the case of the Balearics it is probable that the absence of predators in islets permits foraging behaviour on plants, characterized by higher time investment, and related dense populations of lizards. Barbault (1991) stressed the strong relation between predation and the density of lizard populations, and the relationship between high lizard densities and low predator abundance in islands has been widely recognized (e.g. Case 1983; Case & Bolger 1991).

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Zusammenfassung

Wir haben die Nahrung von mehreren Mittelmeerarten der Gattung *Podarcis* untersucht und die Voraussage einer breiteren Nahrungsbasis von Eidechsen unter kargen Umweltbedingungen getestet. Wir haben noch dazu den Grad und die Art von Herbivorie in Relation zur Vielfalt von Arthropoden in der Nahrung untersucht. Die Eidechsen vom Toskanischen Archipel, *P. sicula* von Menorca und *P. tiliguerta* von Korsika, haben eine ziemlich breite Nahrungsbasis. Im Gegensatz dazu waren *P. lilfordi* und *P. pityusensis* von den Balearischen Inseln und, in geringerer Weise, *P. hispanica* von der Insel Benidorm stenophag, inklusive einem verhältnismäßig hohen Anteil von Früchten in der Nahrung. Pflanzenmaterial ist eine gewöhnliche Speise in den meisten untersuchten Populationen, besonders auf den Balearischen Inseln. Eine

besonders hohe saisonale Änderung im Herbivoriegrad wurde bei den Populationen von *P. lilfordi* und *P. pityusensis* beobachtet, wo energiehaltige Pflanzenteile im Sommer häufig verzehrt werden. Auf einer der Balearischen Inseln (Nitge) besteht die gesamte Sommer-nahrung aus Pollen und Nektar einer bestimmten Pflanzenart. Herbivorie und andere Nah-rungsbesonderheiten der Mittelmeereidechsen zeigen ein flexibles Nahrungsverhalten im Ver-gleich zu den Festlandeidechsen gleicher Gattung. Dies könnte auf einen Mangel an Prädato-ren auf kleinen Inseln mit kargen Umweltbedingungen zurückzuführen sein, der eine hohe Populationsdichte erlaubt. Verschiedene Nahrungscharakteristiken zwischen Inselpopulatio-nen können als Konsequenz mehrerer ökologischer Bedingungen angesehen sowie auf histori-sche und biogeographische Unterschiede zurückgeführt werden.

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Table 1: Samples from insular Mediterranean lizards and general characteristics of the islands studied. In sample column, Sp = spring, Su = summer. P column = type of material analyzed, S = stomach contents, F = faecal pellets (see text for more details).

Island	Species	Area (km ²)	Maximum elevation (m)	Sample	P
Tuscan Archipelago					
Elba	<i>Podarcis sicula</i>	223.5	1019	Sp	S
Montecristo	<i>Podarcis sicula</i>	10.4	645	Sp	S
Formica di Burano	<i>Podarcis sicula</i>	0.006	11	Su	S
Sparviero	<i>Podarcis sicula</i>	0.013	38	Su	S
Giglio	<i>Podarcis sicula</i>	21.2	498	Sp	S
Capraia	<i>Podarcis sicula</i>	19.6	449	Sp	S
Topi	<i>Podarcis muralis</i>	0.013	33	Su	S
Ortano	<i>Podarcis muralis</i>	0.012	22	Sp	S
Paolina	<i>Podarcis muralis</i>	0.002	13	Sp	S
Elba	<i>Podarcis muralis</i>	223.5	1019	Su	S
Gorgona	<i>Podarcis muralis</i>	2	255	Su	S
Pianosa	<i>Podarcis muralis</i>	10.3	29	Sp	S
Corsica	<i>Podarcis tiliguerta</i>	8722	2710	Su	S
Iberian peninsula (eastern coast)					
Benidorm	<i>Podarcis hispanica</i>	0.07	50	Su	S
Balearic Islands					
Menorca	<i>Podarcis sicula</i>	701	357	Su	S
Eivissa	<i>Podarcis pityusensis</i>	541	475	Su	S
Formentera	<i>Podarcis pityusensis</i>	82	192	Su	S
Espalmador	<i>Podarcis pityusensis</i>	2.09	27	Su	S
Penjats	<i>Podarcis pityusensis</i>	0.12	16	Su	S
Espardell	<i>Podarcis pityusensis</i>	0.85	29	Su	S
Torretes	<i>Podarcis pityusensis</i>	0.088	8	Su	S
Tagomago	<i>Podarcis pityusensis</i>	0.52	114	Su	S
Ses Rates	<i>Podarcis pityusensis</i>	0.018	13	Su	S
Santa Eulària	<i>Podarcis pityusensis</i>	0.049	31	Su	S
s'Hort	<i>Podarcis pityusensis</i>	0.005	20	Su	S
En Calderas	<i>Podarcis pityusensis</i>	0.028	6	Su	S
Negra	<i>Podarcis pityusensis</i>	0.037	7	Su	S
Vedrà	<i>Podarcis pityusensis</i>	0.621	380	Su	S
Murada	<i>Podarcis pityusensis</i>	0.013	37	Su	S
Malví Plà	<i>Podarcis pityusensis</i>	0.008	9	Su	S
Malví Gros	<i>Podarcis pityusensis</i>	0.012	18	Su	S
Nitge I	<i>Podarcis lilfordi</i>	0.106	26	Sp	S
Nitge II	<i>Podarcis lilfordi</i>			Su	F
Nitge III	<i>Podarcis lilfordi</i>			Su	F
Bledas	<i>Podarcis lilfordi</i>	0.046	61	Sp	S
Addaia Gran I	<i>Podarcis lilfordi</i>	0.078	22	Sp	S
Addaia Gran II	<i>Podarcis lilfordi</i>			Su	S
Addaia Petita	<i>Podarcis lilfordi</i>	0.051	20	Sp	S
Ses Mones	<i>Podarcis lilfordi</i>	0.004	2	Sp	S
Aire I	<i>Podarcis lilfordi</i>	0.342	15	Sp	S
Aire II	<i>Podarcis lilfordi</i>			Su	F
Codrell	<i>Podarcis lilfordi</i>			Su	F
Sargantana I	<i>Podarcis lilfordi</i>	0.025	15	Sp	S
Sargantana II	<i>Podarcis lilfordi</i>			Su	F
Rovells	<i>Podarcis lilfordi</i>	0.005	7	Sp	S
Porros	<i>Podarcis lilfordi</i>	0.002	1	Sp	S
Rei I	<i>Podarcis lilfordi</i>	0.042	10	Sp	S
Rei II	<i>Podarcis lilfordi</i>			Su	F
Colom I	<i>Podarcis lilfordi</i>	0.402	43	Sp	S
Colom II	<i>Podarcis lilfordi</i>			Su	F

Table 2: Length of prey in different populations under study. N = number of prey measured, SVL = average snout-vent-length in adult individuals, x = average prey length, Min. = minimum prey length, Max. = maximum prey length. Numbers II and III correspond to summer samples in six populations of *Podarcis lilfordi*.

Island	Species	SVL	N	x	Min.	Max.
Tuscan Archipelago						
Formica di Burano	<i>Podarcis sicula</i>	69.5	43	8.22	2.2	35
Sparviero	<i>Podarcis sicula</i>	69	17	7.8	2.5	11
Giglio	<i>Podarcis sicula</i>	60.7	19	6.5	1	21
Topi	<i>Podarcis muralis</i>	62.3	13	6.4	2	12
Ortano	<i>Podarcis muralis</i>	55.5	4	6.6	1.5	17
Paolina	<i>Podarcis muralis</i>	59.5	7	6.58	2.6	15
Elba	<i>Podarcis muralis</i>	62.1	9	4.5	2	12
Pianosa	<i>Podarcis muralis</i>	71.7	8	16.06	2	50
Corsica	<i>Podarcis tiliguerta</i>	57.8	58	6.06	1.5	21
Iberian peninsula						
Benidorm	<i>Podarcis hispanica</i>	57.5	52	3.94	2	16
Balearic Islands						
Menorca	<i>Podarcis sicula</i>	80	17	5.85	2	14.5
Eivissa	<i>Podarcis pityusensis</i>	65	286	2.22	0.8	20
Formentera	<i>Podarcis pityusensis</i>	74	320	4.3	1	30
Espalmador	<i>Podarcis pityusensis</i>	75.5	50	4.46	1.5	15
Penjats	<i>Podarcis pityusensis</i>	77.5	22	5.43	2	15
Espardell	<i>Podarcis pityusensis</i>	78.5	42	3.25	1.5	10
Torretes	<i>Podarcis pityusensis</i>	67.8	6	2.81	1.7	7
Tagomago	<i>Podarcis pityusensis</i>	78	119	2.25	1.8	10
Ses Rates	<i>Podarcis pityusensis</i>	79.5	19	2.27	2	6
Santa Eulària	<i>Podarcis pityusensis</i>	77.8	93	2.8	1.8	15
s'Hort	<i>Podarcis pityusensis</i>	73.5	7	6.33	2	15
En Calders	<i>Podarcis pityusensis</i>	69	16	2.47	2	3.5
Negra	<i>Podarcis pityusensis</i>	77.5	37	4.01	1.7	16
Vedrà	<i>Podarcis pityusensis</i>	77.8	29	3.06	2	10
Murada	<i>Podarcis pityusensis</i>	75	43	3.68	1.1	15
Malví Plà	<i>Podarcis pityusensis</i>	80	64	2.04	2	4
Malví Gros	<i>Podarcis pityusensis</i>	80	13	2.69	2	10
Nitge I	<i>Podarcis lilfordi</i>	61.9	406	2.21	0.6	37
Nitge II	<i>Podarcis lilfordi</i>		33	3.29	1.5	7
Nitge III	<i>Podarcis lilfordi</i>		263	2.58	1.8	15
Bledas	<i>Podarcis lilfordi</i>	64.5	13	6.43	2.7	21
Addaia Gran I	<i>Podarcis lilfordi</i>	62.4	114	3.24	0.8	12
Addaia Gran II	<i>Podarcis lilfordi</i>		11	3.68	1.5	7
Addaia Petita	<i>Podarcis lilfordi</i>	62.5	190	1.94	0.7	23
Ses Mones	<i>Podarcis lilfordi</i>	64.1	11	3.62	1.1	9
Aire I	<i>Podarcis lilfordi</i>	69.9	292	1.42	0.8	31
Aire II	<i>Podarcis lilfordi</i>		8	6.25	3	12
Codrell	<i>Podarcis lilfordi</i>	61.5	147	2.68	1.5	8
Sargentana I	<i>Podarcis lilfordi</i>	57.3	489	1.71	0.6	15
Sargentana II	<i>Podarcis lilfordi</i>		122	2.66	1.5	15
Rovells	<i>Podarcis lilfordi</i>	64	20	3.33	0.8	12
Porros	<i>Podarcis lilfordi</i>	66.8	28	4.25	1.5	11
Rei I	<i>Podarcis lilfordi</i>	68.6	25	4.4	1	21
Rei II	<i>Podarcis lilfordi</i>		20	3.23	1.2	6
Colom I	<i>Podarcis lilfordi</i>	65.7	34	4.25	0.4	18
Colom II	<i>Podarcis lilfordi</i>		13	5.06	1.8	11

Table 3: Diet of *Podarcis sicula* from Tuscan Archipelago. $\%_0N$ = proportion of the prey by number, $\%_0P$ = proportion of individual lizards having eaten the prey, B = trophic niche width, Bs = standardized niche width (see text). In the column $\%_0N$ vegetable matter is expressed as the average of the proportion of volume occupied by plant matter in individual stomachs, while in column $\%_0P$ we show the proportion of individual lizards having plant matter in their stomachs or faecal pellets.

Taxa	Overall $\%_0N$	$\%_0P$	Elba $\%_0N$	$\%_0P$	Montecristo $\%_0N$	$\%_0P$	Formica di Burano $\%_0N$	$\%_0P$	Sparviero $\%_0N$	$\%_0P$	Giglio $\%_0N$	$\%_0P$	Capraia $\%_0N$	$\%_0P$
Aranee	16.23	52.38	46.15	100	20	37.5	3.45	18.18	7.14	40	27.27	20	42.86	75
Isopoda	12.98	33.33			20	37	24.14	81.82	7.14	20	3.03	80		
Diplopoda	0.65	2.38					1.72	9.09						
Chilopoda	1.29	4.76					3.45	18.18						
Dictioniera	3.24	11.9	7.69	25					7.14	40		6.06	20	
Homoptera	1.94	4.76	15.38	25	6.67	12.5	6.9	27.27	3.57	20				
Heteroptera	5.19	16.66			12.5	39.66	36.36	7.14	40		6.06	20	14.29	25
Diptera	18.83	23.8			6.67	8.62	8.62	36.36			9.09	30	14.29	25
Coleoptera	8.44	21.42	7.69	25					3.57	20	18.18	30	14.29	25
Hymenoptera	1.94	7.14									3.03	10	14.29	25
Formicidae	7.79	19.04	7.69	25	13.33	25	3.45	9.09	21.43	60				
Insecta larvae	10.38	23.0			26.66	50	1.72	9.09	32.14	60	6.06	20		
Arthropoda undet.	7.78	19.04	7.69	25	6.67	12.5	3.45	18.18	10.71	40	15.15	20	14.29	25
Gastropoda	3.24	11.9	7.69				3.45	18.18			3.03	10		
Vegetable matter			17.5	40	50	11.11	5	9.09	50	20	30	10	50	25
No. of stom./faeces	42	4							11	5	10		4	
No. of prey	154	13							58	28	33		7	
No. of prey/stom.	3.66	3.25							5.27	5.6	3.3		1.75	
B	8.9	3.75							5.48	4.26	7.02		3.76	
Bs.	0.56	0.45							0.74	0.32	0.55		0.69	

Table 4: Diet of *Podarcis muralis* from Tuscan Archipelago.

Taxa	Overall % _N P	% _N Topi	% _N P	Ortano % _N	% _N P	Paolina % _N	% _N P	Elba % _N	% _N P	Gorgona % _N	% _N P	Pianosa % _N	% _N P
Araneae	9.73	34.3	17.65	42.86	11.11	50	22.22	80	4.55	12.5			
Isopoda	7.07	18.7	11.76	14.29	3.7	16.67	11.11	40	9.09	25	30	50	
Diplopoda	2.65	9.03			3.7	16.67							
Diptera	5.3	15.6	11.76	14.29	7.41	33.33			9.09	25			
Dictionptera	3.53	15.6			3.7	16.67	5.56	20	4.55	12.5	3.27	50	10
Homoptera	4.42	15.6			3.7	16.67	11.11	40			20	25	50
Homoptera	4.42	15.6			3.7	16.67							
Diptera	9.73	21.9	5.88	14.29	7.41	33.33			31.32	37.5			
Coleoptera	15.92	46.9	29.41	71.43	14.81	50	5.56	20	22.72	50			
Hymenoptera	7.07	18.7	11.76	28.57	7.41	16.67	11.11	20	4.55	12.5	30	50	
Formicidae	23.66	25	11.76	28.57	11.11	16.67	40	9.09	25	93.45	50	10	25
Insecta larvae	6.5	12.5			14.81	33.33	5.56	20			3.27	50	
Arthropoda undet.	4.42	15.6			11.11	50	5.56	20	4.55	12.5			
Vegetable matter			10	14.28		70	20	25	14.28		5	22.5	40
No. of stom./faeces	31	7			6		5			8		2	4
No. of prey	113	17			27		18			22		21	10
No. of prey/stom.	3.64	2.42			4.5		3.6			2.75		10.5	2.5
B	7.02	5.66			10.56		7.71			5.37		1.21	4.16
Bs.	0.55	0.77			0.77		0.74			0.54		0.10	0.79

Table 5: Diet of *Podarcis pityusensis* from Pityusic Islands.

Table 5 (continued): Diet of *Podarcis pityusensis* from Pityusic Islands.

Table 6: Diet of *Podarcis lilfordi* during spring.

Table 6: (continued).

Table 7: Diet of *Podarcis liofordi* during summer.

Taxa	Nitge II % _N	Nitge II % _P	Nitge III/IV % _N	Nitge III/IV % _P	Addaia Gran % _N	Aire % _N	Codrell % _N	Sargentana % _N	Rei % _N	Colom % _N	Colom % _P
Pseudoscorpionida	0.14	0.88	0.96	23.68	1.29	6.66	4.38	2.23	15.38	4.59	11.9
Araneae	0.69	4.39	0.53	13.15	2.59	13.33	6.14	2.67	23.07	1.32	4.4
Isopoda	4.16	26.32	0.1	2.63	1.29	6.66	1.75	3.22	0.18	1.12	0.57
Diplopoda									0.09	0.56	1.5
Chilopoda											5.06
Orthoptera	0.28	1.75	0.42	10.52	1.29	6.66	2.63	4.83	7.69	4.15	22.59
Dyctioptera	0.14	0.88	1.5	31.57	3.89	13.33	9.64	17.34	0.44	0.37	2.25
Dermaptera			0.1	2.63			0.89	0.89	7.69	0.28	1.69
Homoptera									0.47	2.82	0.57
Heteroptera	0.42	2.63	0.42	10.52	5.19	20	5.26	9.67	2.67	2.29	5.97
Diptera	0.14	0.88						0.44	3.84	1.14	0.42
Lepidoptera	3.05	13.16	1.82	36.84	15.58	73.33	17.54	27.41	5.35	10.34	1.26
Coleoptera									46.15	2.07	10.34
Hymenoptera										25.37	3.79
Formicidae	86.82	77.19	91.4	92.1	67.53	93.33	0.87	1.61	1.13	0.57	1.49
Insecta larvae	0.28	1.75	0.21	5.26	1.29	6.66	36.84	83.48	92.3	88.09	71.26
Insecta undet.	0.28	1.75	0.53	13.15			1.75	3.22	3.22	0.57	1.49
Arthropoda undet.	0.97	5.26	0.53	42.1			4.38	8.06	0.44	0.94	0.56
Gastropoda	2.64	10.53	1.71				3.5	6.45	0.44	3.84	5.64
Vegetable matter	72.61	73.38	33.51	81.57	62.5	66.66	86.52	74.19	55	34.61	61.84
No. of stom./faeces	114				15		62		26	177	67
No. of prey	721				38		114		224	1058	79
No. of prey/stom.	6.32				931		5.13		8.61	5.97	233
Bs.	1.32				24.5		2.05		1.42	1.28	2.9
					1.19		0.13		0.04	0.02	1.47
					0.06		0.32			0.07	0.04

Table 8: Diets of *Podarcis tiliguerta* from Corsica, *Podarcis hispanica* from Benidorm and *Podarcis sicula* from Menorca.

Taxa	<i>Podarcis tiliguerta</i> Corsica		<i>Podarcis hispanica</i> Benidorm		<i>Podarcis sicula</i> Menorca	
	%N	%P	%N	%P	%N	%P
Pseudoscorpionida			3.57	13.79	23.8	58.33
Araneae	9.2	38.1	3.57	10.34	11.9	25
Isopoda	1.15	4.76			2.38	8.33
Diplopoda					2.38	8.33
Chilopoda					2.38	8.33
Orthoptera	4.6	19.05	2.67	10.34	2.38	8.33
Dyctioptera	2.3	9.52	4.46	17.24	2.38	8.33
Homoptera	13.79	28.57	1.78	6.89	2.38	8.33
Heteroptera	1.15	4.76	6.25	13.79	4.76	16.67
Diptera	22.99	57.14	1.78	6.89	7.14	25
Lepidoptera	2.3	9.52	1.78	6.89		
Coleoptera	5.75	19.05	1.78	3.44	21.42	58.33
Hymenoptera	4.6	14.29	25.89	31.03		
Formicidae	20.69	47.62	44.64	65.51		
Insecta larvae	8.05	14.29	1.78	6.89	9.52	16.67
Insecta undet.			1.78	6.89	4.76	8.33
Arthropoda undet.	1.15	4.76			4.76	16.67
Gastropoda	1.15	4.76	42.75	29		
Vegetable matter				13.79	2.38	8.33
No. of stom./faeces	21				12	
No. of prey	87				42	
No. of prey/stom.	4.14				3.5	
Bs.	7.2				7.17	
	0.44				0.47	

Table 9: Spearman Rank Correlation analysis of dietary and general characteristics of populations under study. B = trophic niche width, Bs = standardized niche width, FOR = proportion of Formicidae in the diet, NP = number of prey per stomach, %S = proportion of individuals with plant remains, AV = average volume of plant matter, SUR = surface (km^2) of the island, SVL = average snout-vent-length of adult individuals, ALT = maximum altitude of the island (* = $p < 0.05$, ** = $p < 0.01$).

	B	Bs	FOR	NP	%S	AV	SUR	SVL
B								
Bs	0.83**							
FOR	-0.71**	-0.72**						
NP	-0.38*	-0.52**	0.30*					
%S	-0.37*	-0.16	0.32*	-0.07				
AV	-0.36*	-0.27	0.45*	-0.24	0.59**			
SUR	0.08	0.05	-0.16	-0.10	0.02	-0.08		
SVL	-0.07	-0.02	0.03	-0.17	0.19	0.22	-0.05	
ALT	0.18	0.10	0.01	-0.11	-0.001	-0.04	0.70	-0.11