

## Helminth infracommunities of *Podarcis pityusensis* and *Podarcis lilfordi* (Sauria: Lacertidae) from the Balearic Islands (western Mediterranean basin)

V. ROCA AND M.J. HORNERO

Departament de Biología Animal (Parasitología Animal), Facultat de Ciències Biològiques, Universitat de València.  
Dr. Moliner, 50 46100-Burjassot (València), Spain

Received June 17, 1993

Accepted February 3, 1994

ROCA, V., and HORNERO, M.J. 1994. Helminth infracommunities of *Podarcis pityusensis* and *Podarcis lilfordi* (Sauria: Lacertidae) from the Balearic Islands (western Mediterranean basin). Can. J. Zool. 72: 658–664.

A survey of the helminth communities of *Podarcis pityusensis* (Boscá, 1883) and *Podarcis lilfordi* (Günther, 1874) (Sauria: Lacertidae) from the Pityusic and Gimnesic islands, respectively, in the Balearic Islands, Spain, was conducted. Both host species harbour similar though not identical helminth infracommunities. An analysis of the patterns of diversity for all helminths revealed that both lizards have depauperate isolationist infracommunities, possibly as a result of factors such as host ectothermy, the simplicity of their digestive canal, low vagility, and generalist feeding.

ROCA, V., et HORNERO, M.J. 1994. Helminth infracommunities of *Podarcis pityusensis* and *Podarcis lilfordi* (Sauria: Lacertidae) from the Balearic Islands (western Mediterranean basin). Can. J. Zool. 72: 658–664.

On trouvera ici les résultats d'un inventaire des communautés d'helminthes présentes chez les lézards *Podarcis pityusensis* (Boscá, 1883) et *Podarcis lilfordi* (Günther, 1874) (Sauria : Lacertidae), le premier dans les îles Pitiuses et l'autre dans les îles Géménées, Baléares, Espagne. Les deux espèces hébergent des infracommunautés semblables, mais non identiques. L'analyse de la diversité des helminthes a révélé que les deux lézards abritent des infracommunautés isolées et appauvries, sans doute à cause de caractéristiques qui leur sont inhérentes, notamment leur ectothermie, la simplicité de leur tractus digestif, leur faible motilité et leurs habitudes alimentaires généralistes.

### Introduction

Although several recent ecological studies are available on the helminth communities of marine mammals, birds, fish, and amphibians (e.g., Balbuena and Raga 1993; Edwards and Bush 1989; Goater and Bush 1988; Goater et al. 1987; Kennedy and Bakke 1989; Kennedy and Williams 1989; Muzzall 1991a, 1991b), very little effort has been devoted to studying the helminth communities of reptiles (Esch and Gibbons 1976; Esch et al. 1979). Aho (1990) provided a comprehensive review of the structure of the helminth communities of some reptiles and amphibians. More recently, Dobson and Pacala (1992) and Dobson et al. (1992) analysed the helminth communities of 10 lizard species from seven islands in the Caribbean. In contrast, there is a paucity of data on the structure of the helminth communities of European reptiles.

The indigenous fauna of most Mediterranean islands includes several saurian species. Among these, lizards of the genus *Podarcis* Wagler, 1830 are particularly abundant and geographically widespread. Two endemic lizards, *Podarcis pityusensis* (Boscá, 1883) and *Podarcis lilfordi* (Günther, 1874), can be found in the Balearic Islands. *Podarcis pityusensis* lives in the southern part of the archipelago, in Eivissa, and Formentera and the small islets around them. *Podarcis lilfordi* can only be found in the small islets surrounding the larger islands (Mallorca and Menorca) in the northern part of the archipelago. Both species display considerable inter-island variation in morphology; many subspecies have been described on the basis of their geographical isolation and limited interisland dispersal (Cirer 1980, 1981, 1989; Pérez-Mellado and Salvador 1988; Salvador 1979, 1984, 1986a, 1986b).

The biology and ecology of neither host species are yet completely known, but several preliminary papers provide data on daily and seasonal activity rhythms, population dynamics, thermoregulation, and feeding habits (e.g., Brown

et al. 1992; Pérez-Mellado 1989; Pérez-Mellado and Salvador 1981; Salvador 1986a, 1986b). In this paper we present the results of a study of the parasites of these two lizard species, including data on the structure of their infracommunities.

### Materials and methods

The Balearic Islands are located east of the Iberian peninsula (Fig. 1) and have a total area of 5014 km<sup>2</sup>. The habitats on the islands and small islets are fairly uniform, ranging in elevation from sea level to 200 m asl. The common landscape is a platform of lowlands with bush steppes and pine woods alternating with agricultural areas (Colom 1988). The smaller islands usually have xeric habitats.

Specimens belonging to several subspecies of *P. pityusensis* and *P. lilfordi* were collected from the islets surrounding Menorca, as well as from Eivissa and Formentera and surrounding islets (see Table 1). In all, 564 *P. pityusensis* and 386 *P. lilfordi* were analysed, of which 110 *P. pityusensis* were caught in the field in June 1987, October 1987, and June 1988; 242 were from the private collection of Dr. M. Cirer; and 212 were from the private collection of the senior author. Twenty *P. lilfordi* were caught in the field in June 1989, 253 were from the collection of Museo Nacional de Ciencias Naturales de Madrid, and 113 were from the private collection of the senior author. Lizards were killed with an overdose of chloroform. The digestive tract, heart, lungs, and liver were removed, opened, and placed in Ringer solution for examination. Helminths were removed, washed in distilled water, and fixed and mounted according to routine techniques (Roca 1985). Parasites were identified to the species level and the numbers and location of individuals of each species were recorded. The following helminths are deposited in the Parasitology Museum of the Animal Science Department of the University of València: *Paradistomum mutabile* (Accession No. 880615160-I), *Brachylaima* sp. (03040183), *Oochoristica gallica* (870610117-F), *Nematotaenia tarentolae* (871009074-I), *Diplopolydium acanthotetra* (871005009-I), *Mesocestoides* sp. (871009111-I), *Spauligodon cabrerai* (871008100-I), *Parapharyngodon bulbosus* (871008107-I), *Parapharyngodon micipsae* (871012156-I), *Parapharyngodon echinatus* (871008044-I), *Skrjabinezia hoffmanni* (82041130-ME), *Abbreviata* sp. (890620007-ME), *Acuaria* sp. (82041242-ME).

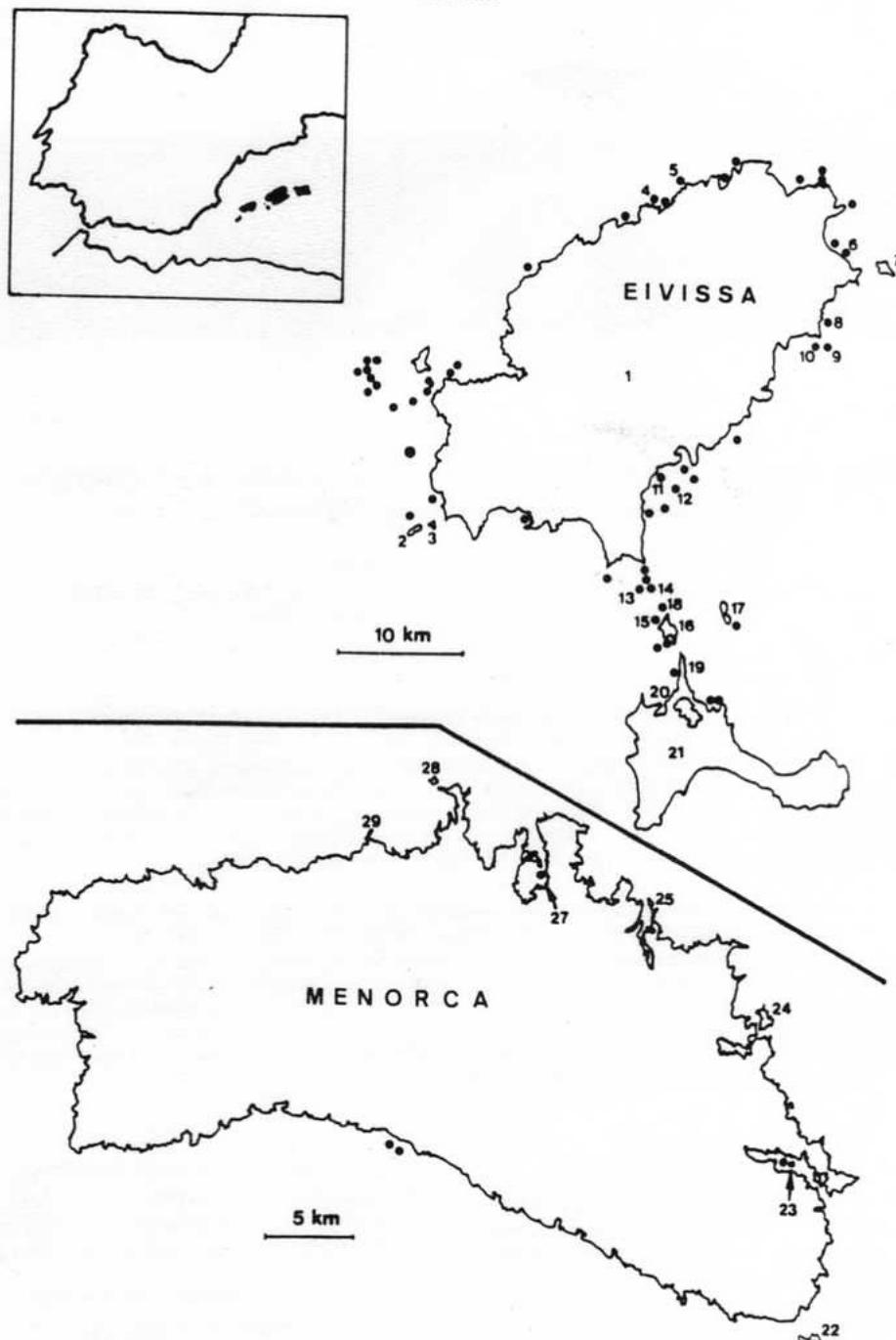


FIG. 1. The islands of the Balearic archipelago. The numbers correspond to those in Table 1.

*Spiruridae* (genus not identified) (82041148-ME), and *Centrorhynchus* sp. (82041140-ME). Types of *Strongyloides ophiurusensis* are deposited in the Institute of Parasitology, Czechoslovak Academy of Sciences, Czech Republic. Collection No. N-593. Voucher specimens of *Mesaphoruras mediniae* are deposited in The Natural History Museum, London, England, Reg. Nos. 1990.4863 and 1990.4864.

We follow Margolis et al. (1982) and Esch et al. (1990) in the use of descriptive ecological terms. Brillouin's index of diversity and evenness (Pielou 1977; Margurran 1988) was calculated, after

logarithmic transformation ( $\log_{10}$  to  $\log_{10}$ ), for each helminth infracommunity irrespective of the site of infection (Muzzall 1991a, 1991b), using DIVERS software (Krebs 1989). All statistical analysis was performed using standard methods (Sokal and Rohlf 1981).

### Results

Seventeen helminth species (2 Trematoda, 4 Cestoda, 10 Nematoda, and 1 Acanthocephala) were found. They were

TABLE 1. Islands and islets where lizards were collected

Island	Area (km <sup>2</sup> )	Elev. (m asl)	Age <sup>a</sup>	Subspecies <sup>b</sup>
1. Eivissa	541	475	—	<i>P. p. pityusensis</i>
2. Es Vedra	0.421	382	12	<i>P. p. vedrae</i>
3. Vedranell	0.200	124	12	<i>P. p. vedrae</i>
4. Murada	0.131	32	9	<i>P. p. muradae</i>
5. Calders	0.028	9	5	<i>P. p. pityusensis</i>
6. S'Hort	0.005	18	6	<i>P. p. hortae</i>
7. Tagomago	0.520	114	9	<i>P. p. tagomagensis</i>
8. Es Canar	—	27	7	<i>P. p. canensis</i>
9. Santa Eulalia	0.040	32	7.5	<i>P. p. redonae</i>
10. Rodona	—	25	7	<i>P. p. redonae</i>
11. Ses Rates	0.018	15	5	<i>P. p. ratae</i>
12. Es Malvins	0.097	16	8	<i>P. p. schreitmulleri</i>
13. Illetes Negres	0.037	4	6.5	<i>P. p. negrae</i>
14. Es Penjats	0.120	13	6.5	<i>P. p. ahorcadosi</i>
15. Sa Torreta	0.088	2	6.5	<i>P. p. torretensis</i>
16. S'Espalmador	2.090	24	6.5	<i>P. p. formenterae</i>
17. S'Espardell	0.850	29	8.5	<i>P. p. formenterae</i>
18. Illa den Pou	—	10	6.5	<i>P. p. formenterae</i>
19. Punta Trocadors	—	9	6.5	<i>P. p. formenterae</i>
20. La Savina	—	—	6.5	<i>P. p. formenterae</i>
21. Formentera	83	192	6.5	<i>P. p. formenterae</i>
22. Aire	0.342	15	8	<i>P. l. lilfordi</i>
23. Rey	0.042	10	7	<i>P. l. balearica</i>
24. Colom	0.402	43	6	<i>P. l. balearica</i>
25. Addaias	0.128	22	8	<i>P. l. addaya</i>
26. Sargantana	0.025	15	6	<i>P. l. sargantanae</i>
27. Rovells	0.005	2	6	<i>P. l. sargantanae</i>
28. Nitge	0.106	26	9	<i>P. l. fenni</i>
29. Bleda	0.046	61	7	<i>P. l. sargantanae</i>

<sup>a</sup>In thousands of years.<sup>b</sup>Subspecies of lizards living on each island.

identified by Roca and Hornero (1991) and Hornero and Roca (1994). The total number of parasite species and the infestation parameters for each host are given in Tables 2 and 3. The host species do not harbour identical parasite communities, although compositional similarities do exist.

#### Digenea and Acanthocephala

The digenleans *Paradistomum mutabile* and *Brachylaima* sp. (metacercariae) occur in both hosts. The prevalence of infestation of *P. mutabile* in *P. pityusensis* (22.9%) and *P. lilfordi* (10.9%) reveals that this is a common parasite.

The acanthocephalan *Centrorhynchus* sp. (larvae) shows a low prevalence and intensity of infestation in both hosts.

#### Cestoda

Cestodes were found only in *P. pityusensis*. Two species, *O. gallica* and *N. tarentolae*, were found as adults, while *D. acanthotetra* and *Mesocestoides* sp. were found in the larval stage in the body cavity of the host.

#### Nematoda

Nematodes are the main component of the helminth infracommunities of *P. pityusensis* and *P. lilfordi*. *Skrjabinodon medinae*, *S. cabrerae*, *P. bulbosus*, and *P. micipsae* are present as adults in the two host species. *Acuaria* sp. and *Spirurida* (genus not identified) were found as larvae in the body cavity of both hosts. *Strongyloides ophiussensis* was recovered only from *P. pityusensis*, not from *P. lilfordi*; *S. hoffmanni* and *Aboviania* sp. were found only in *P. lilfordi*.

#### Helminth community diversity

Although 15 helminth species were recorded from *P. pityusensis* and 11 from *P. lilfordi*, the average number per lizard never exceeded 1.35 and 0.93, respectively, and the maximum number of helminths found in any individual lizard was 5 and 4, respectively (Table 4). The total number of helminth species in the populations of *P. pityusensis* and *P. lilfordi* greatly exceeded both the average and the maximum number of species per individual lizard.

Table 4 shows diversity parameters for the helminth infracommunities of both hosts. Helminth richness, abundance, and Brillouin's index are all higher in *P. pityusensis* than in *P. lilfordi*. Nevertheless, the low values of Brillouin's index for both hosts emphasize the low diversity of their helminth infracommunities.

Except for *P. mutabile*, the monoxenous species, mainly the pharyngodonid nematodes, show the highest prevalences and intensities of infection, so they make a greater contribution to the structure of the infracommunities.

#### Discussion

*Paradistomum mutabile* seems to be an exclusively insular species because it is present in islands of the Mediterranean basin and absent from the mainland. The presence of *Brachylaima* sp. (metacercariae) in some of the lizards is probably due to ingestion of snails that are intermediate hosts of the parasite; the life cycle of *Brachylaima* sp. requir-

TABLE 2. Infestation parameters of the helminths parasitizing *Podarcis pityusensis*

Helminth species	Site of infection	Prevalence <sup>a</sup>	Intensity of infection		
			Range	$\bar{x}$	Mean abundance
<b>Digenea</b>					
<i>Paradistomum mutabile</i>	Gall bladder	129 (22.9)	1-56	8.1	1.8
<i>Brachylaima</i> sp.	Intestine	1 (0.2)	—	—	—
<b>Cestoda</b>					
<i>Oochoristica gallica</i>	Intestine	25 (4.4)	1-264	30.4	1.3
<i>Nematotaenia tarentolae</i>	Intestine	19 (3.4)	1-10	2.6	0.1
<i>Diplopylidium acanthotetra</i>	Body cavity	16 (2.8)	1-35	10.1	0.3
<i>Mesocestoides</i> sp.	Body cavity	9 (1.6)	1-56	12.4	0.2
<b>Nematoda</b>					
<i>Skrjabinodon medinae</i>	Cloaca	67 (11.9)	1-20	4.8	0.6
<i>Spauligodon cabrerae</i>	Cloaca	193 (34.2)	1-222	20.9	7.2
<i>Parapharyngodon bulbosus</i>	Cloaca	104 (18.4)	1-134	17.6	3.2
<i>Parapharyngodon echinatus</i>	Cloaca	9 (1.6)	1-14	4.6	0.1
<i>Parapharyngodon micipsae</i>	Cloaca	123 (21.8)	1-15	4.6	1.0
<i>Strongyloides ophiensis</i>	Intestine	7 (1.2)	1-37	9.7	0.1
<i>Acuaria</i> sp.	Body cavity	5 (0.9)	1-8	3.8	0.03
<i>Spirurida</i> gen. sp.	Body cavity	6 (1.1)	1-6	2.8	0.03
<b>Aganchocephala</b>					
<i>Centrorhynchus</i> sp.	Body cavity	4 (0.7)	1-4	2.5	0.01

<sup>a</sup>Number of hosts parasitized divided by the number of hosts sampled (564). Values in parentheses are percentages.

TABLE 3. Infestation parameters of the helminths parasitizing *Podarcis lilfordi*

Helminth species	Site of infection	Prevalence <sup>a</sup>	Intensity of infection		
			Range	$\bar{x}$	Mean abundance
<b>Digenea</b>					
<i>Paradistomum mutabile</i>	Gall bladder	42 (10.9)	1-26	6.5	0.7
<i>Brachylaima</i> sp.	Intestine	3 (0.8)	1-2	1.3	0.01
<b>Nematoda</b>					
<i>Skrjabinodon medinae</i>	Cloaca	96 (24.9)	1-17	4.1	1.0
<i>Spauligodon cabrerae</i>	Cloaca	161 (41.7)	1-109	12.2	5.1
<i>Parapharyngodon bulbosus</i>	Cloaca	14 (3.6)	1-14	6.5	0.2
<i>Parapharyngodon micipsae</i>	Cloaca	25 (6.5)	1-11	3.8	0.2
<i>Skrjabinelazia hoffmanni</i>	Intestine	4 (1.0)	1-5	2.0	0.02
<i>Abbreviata</i> sp.	Intestine	1 (0.3)	1	—	—
<i>Acuaria</i> sp.	Body cavity	4 (1.0)	1-20	6.8	0.1
<i>Spirurida</i> gen. sp.	Body cavity	4 (1.0)	1-6	2.8	0.02
<b>Acanthocephala</b>					
<i>Centrorhynchus</i> sp.	Body cavity	4 (1.0)	1-5	2.3	0.02

<sup>a</sup>Number of host parasitized divided by the number of hosts sampled (386). Values in parentheses are percentages.

two terrestrial gastropods as intermediate hosts and a rodent as the definitive host (Mas-Coma and Esteban 1983; Mas-Coma and Feliu 1984). The presence of this trematode in lizards is accidental (Roca et al. 1989).

Stades have not been found in *P. lilfordi*. Larval forms (*D. acanthotetra* and *Mesocestoides* sp.) are probably absent because their life cycle cannot be completed owing to a lack of definitive hosts (cats or genets) in the islets near Menorca (Hornero and Roca 1994).

The common nematodes in the infracommunities of *P. pityusensis* and *P. lilfordi* are members of the Pharyngodonidae, of which *S. cabrerae* is an endemic species in the Balearic Islands. *Strongyloides ophiensis*, also an endemic species, is the only Pityusic lizard specialist. No specialist helminths have been described for the Balearic lizard *P. lilfordi*. The rest of the adults that parasitize both hosts are from generalist species (sensu Edwards and Bush 1989). *Spauligodon cabrerae* could also be considered a specialist in

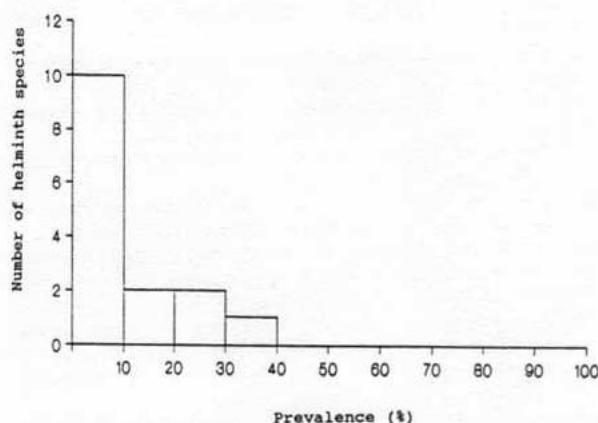


FIG. 2. Frequency distribution of the species of the helminth community in *P. pityusensis*.

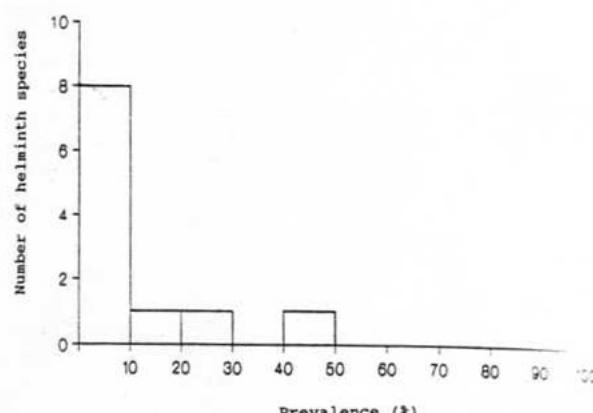


FIG. 3. Frequency distribution of the species of the helminth community in *P. lilfordi*.

TABLE 4. Overall diversity parameters of the helminth infracommunities from both hosts

Host	n	No. of helminth species/host <sup>a</sup>	No. of helminths/host <sup>a</sup>	Brillouin's index <sup>a</sup>	Proportion of sample with 0 or 1 helminth species
<i>P. pityusensis</i>	564	1.35±1.02 (0-5)	16.44±31.22 (0-420)	0.242±0.292 (0-1.211)	0.60
<i>P. lilfordi</i>	386	0.93±0.74 (0-4)	7.45±12.84 (0-110)	0.108±0.200 (0-0.815)	0.81

<sup>a</sup>Values are given as the mean ± SD, with the range in parentheses.

TABLE 5. Host characteristics proposed by Kennedy et al. (1986) to be used for predicting the diversity of the *Podarcis pityusensis* and *P. lilfordi* communities

	Depauperate community (isolationist)		Diverse community (interactive)
Alimentary canal	Simple	↔	Complex
Thermoregulation	Ectothermy	↔	Endothermy
Vagility	Low	↔	High
Diet	Simple	→?	Complex
Selective feeding (generalists or specialists)	No	↔	Yes
Life cycles of helminths	Indirect	↔	Direct
General trend	Depauperate (isolationist)	↔	Diverse (interactive)

lizards of the Balearic Islands because it is present in both *P. pityusensis* and *P. lilfordi* but not in other European lizards. We also suggest that the trematode *P. mutabile* is a *Podarcis* specialist because it is always found parasitizing lizards of this genus.

The low values of helminth richness and abundance indicate that many members of the helminth infracommunities occurred only irregularly and occasionally (Figs. 2 and 3). This agrees with the typical pattern of helminth infection of many reptiles, in which few species occur frequently, few species occur with moderate prevalence, and many species

are rare (García-Adell and Roca 1988; Roca 1985; Roca et al. 1986, 1989).

The helminth infracommunity of *P. lilfordi* is less diverse than that of *P. pityusensis*. This is probably due to differential infection by species with an indirect life cycle; for example, *O. gallica* and *N. tarentolae* are absent in *P. lilfordi*, and the intensity and abundance of *P. mutabile* are higher in *P. pityusensis* than in *P. lilfordi*. In the case of heteroxenous helminths parasitizing lizards, the number of helminth species and the number of individual helminths per host are closely related to helminth diversity. As *P. pityusensis* lives on b

islands (Eivissa, Formentera) and *P. lilfordi* only on small islets, prey availability is greater for the former species. The feeding analysis by V. Pérez-Mellado (personal communication) and Corti and Pérez-Mellado (1991) showed that *P. pityusensis* from Eivissa and Formentera fed on more arthropod taxa than *P. lilfordi*, increasing the possibility of infection by heteroxenous species.

The low diversity of the helminth infracommunities of *P. pityusensis* and *P. lilfordi* suggests that they are depauperate communities. Several characteristics of the host may be responsible for the existence of these isolationist depauperate communities (Table 5): ectothermy, the simplicity of the alimentary canal, low vagility, a simple diet, generalist feeding, and the small number of helminth species with a direct life cycle (Aho 1990; Kennedy et al. 1986; Muzzall 1991a). Since lizards are ectotherms, environmental conditions limit potential recruitment and community development of helminths by affecting both the feeding rates and foraging behaviour of their hosts (Aho 1990). Lizards possess a relatively simple enteric system which does not seem to be too suited to supporting rich and abundant helminth faunas. It is assumed that simple habitats provide fewer niches for colonization. The lizards show low vagility and do not move over large distances, usually living in very small isolated islets. Their restricted movements facilitate the exploitation of hosts by parasites with a direct life cycle (such as the cloacal oxyurids). Altogether, the infracommunities of *P. pityusensis* include 10 species with an indirect life cycle and 15 monoxenous species; *P. lilfordi*, on the other hand, has heteroxenous and 4 monoxenous species. But in both, monoxenous species are most prevalent and abundant. On the generalist-specialist continuum, V. Pérez-Mellado (personal communication) suggests that *P. pityusensis* and *P. lilfordi* should be considered generalist feeders. Nevertheless, it can be shown that in some places, circumstances, and (or) time periods, these lizards feed on only one or a few prey types. This pseudospecialization is due to a reduction in prey availability and does not entail physiological or morphological changes, relaxing when the trophic limitations no longer exist. The relative complexity of the lizards' diet does not seem to play an important role in the establishment of diverse communities, since in many cases this complexity is drastically reduced as a result of low trophic availability because of the small size of the islets and (or) the poor fauna on them.

Thus, we can conclude that the helminth infracommunities of *P. pityusensis* and *P. lilfordi* are basically isolationist because of their low diversity, the presence of few infrapopulations, and the peculiar characteristics of the hosts, such as ectothermy, the simplicity of the digestive tract, and low vagility. The depauperate character of these helminth infracommunities agrees with those observed in other lizard species (García-Adell and Roca 1988; Roca 1985; Roca et al. 1986, 1989, 1990), these patterns being widespread amongst saurian reptiles.

#### Acknowledgements

The authors thank Prof. V. Pérez-Mellado, Department of Animal Biology, University of Salamanca, Spain, Dr. Antonia María Cirer, University of Barcelona, Spain, and Museo Nacional de Ciencias Naturales de Madrid, Spain, for herpetological material, and Prof. E. Font Bisier, Department

of Faunal Ecology, University of València, Spain, for suggestions concerning an earlier version of the manuscript. Comments and suggestions from two anonymous reviewers are much appreciated. We also thank the Conselleria d'Agricultura i Pesca de les Illes Balears for permits (6399, 7027, 3990, 30/5/80) for collecting living hosts. This work was financed through project PB 87-0707-C02-01 of the Spanish Comisión Interministerial de Ciencia y Tecnología.

- Aho, J.M. 1990. Helminth communities of amphibians and reptiles: comparative approaches to understanding patterns and processes. In Parasite communities: patterns and processes. Edited by G. Esch, A. Bush, and J. Aho. Chapman and Hall, London. pp. 157–195.
- Balbuena, J.A., and Raga, J.A. 1993. Intestinal helminth communities of the long-finned pilot whale (*Globicephala melas*) off the Faroe Islands. *Parasitology*, **106**: 327–333.
- Brown, R.P., Pérez-Mellado, V., Diego-Rasilla, J., García, J.A., Naranjo, A., and Speakman, J.R. 1992. Individual and population energetics of a lizard on a Mediterranean islet. *Oecologia*, **91**: 500–504.
- Cirer, A.M. 1980. Descripción de dues subespecies noves de *Podarcis pityusensis*. *Bull. Inst. Cat. Hist. Nat.*, **45**(3): 121–126.
- Cirer, A.M. 1981. La lagartija ibicenca y su círculo de razas. *Consell Insular d'Eivissa i Formentera*, Eivissa. pp. 1–106.
- Cirer, A.M. 1989. Algunos datos colorimétricos de *Podarcis pityusensis*. *Rev. Esp. Herp.*, **3**: 197–208.
- Colom, G. 1988. El medio y la vida en las Baleares. Conselleria de Cultura, Educació i Esports, Govern Balear, Ciutat de Mallorca.
- Corti, C., and Pérez-Mellado, V. 1991. Feeding ecology of insular populations of *Podarcis* lizards in the North Tyrrhenian Sea (Corsica and Tuscan Islands) and Balearic Islands: a preliminary study. In Abstracts of the 6th Ordinary General Meeting of the Societas Europaea Herpetologica, Budapest, Hungary, 19–23 August 1991. Edited by Z. Korsós and I. Kiss. The Hungarian Natural History Museum, Budapest. p. 25.
- Dobson, A.P., and Pacala, S.W. 1992. The parasites of *Anolis* lizards in the northern Lesser Antilles. II. The structure of the parasite community. *Oecologia*, **92**: 118–125.
- Dobson, A.P., Pacala, S.W., Roughgarden, J.D., Carper, E.R., and Harris, E.A. 1992. The parasites of *Anolis* lizards in the northern Lesser Antilles. I. Patterns of distribution and abundance. *Oecologia*, **91**: 110–117.
- Edwards, D.D., and Bush, A.O. 1989. Helminth communities in avocets: importance of compound community. *J. Parasitol.*, **95**: 439–445.
- Esch, G.W., and Gibbons, J.W. 1976. Seasonal incidence of parasitism in the painted turtle *Chrysemys picta marginata* Agassiz. *J. Parasitol.*, **63**: 818–821.
- Esch, G.W., Gibbons, J.W., and Bourque, J.E. 1979. The distribution and abundance of enteric helminths in *Chrysemis s. scripta* from various habitats on the Savannah River plain in South Carolina. *J. Parasitol.*, **65**: 624–632.
- Esch, G.W., Shostak, A.W., Marcogliese, D.J., and Goater, T.M. 1990. Patterns and processes in helminth parasite communities: an overview. In Parasite communities: patterns and processes. Edited by G. Esch, A. Bush, and J. Aho. Chapman and Hall, London. pp. 1–19.
- García-Adell, G., and Roca, V. 1988. Helmintofauna de Lacertidos de los Pirineos Centrales Ibéricos. *Rev. Iber. Parasitol.*, **48**: 257–267.
- Goater, C.P., and Bush, A.O. 1988. Intestinal helminth communities in long-billed curlews: the importance of congeneric host-specialist. *Holarct. Ecol.*, **11**: 140–145.
- Goater, T.M., Esch, G.W., and Bush, A.O. 1987. Helminth parasites of sympatric salamanders: ecological concepts at infracommunity, component and compound community levels. *Am. Midl. Nat.*, **118**: 289–300.

- Hornero, M.J., and Roca, V. 1994. Helmintofauna de *Podarcis lilfordi* (Günther, 1874) (Sauria: Lacertidae) de los islotes de Menorca (Islas Baleares, Mediterráneo Occidental). *Misc. Zool.* In press.
- Kennedy, C.R., and Bakke, T.A. 1989. Diversity patterns in helminth communities in common gulls, *Larus canus*. *Parasitology*, **98**: 439–445.
- Kennedy, C.R., and Williams, H.H. 1989. Helminth parasite community diversity in a marine fish, *Raja batis* L. *J. Fish Biol.* **34**: 971–972.
- Kennedy, C.R., Bush, A.O., and Aho, J.M. 1986. Patterns in helminth communities: why are birds and fish different? *Parasitology*, **93**: 205–215.
- Krebs, C.J. 1989. Ecological methodology. Harper and Row, New York.
- Magurran, A.E. 1988. Ecological diversity and its measurement. Croom Helm Ltd., London.
- Margolis, L., Esch, G.W., Holmes, J.C., Kuris, A.M., and Schad, G.A. 1982. The use of ecological terms in parasitology (report of an ad hoc committee of the American Society of Parasitologists). *J. Parasitol.* **68**: 131–133.
- Mas-Coma, S., and Esteban, J.G. 1983. Nuevos datos sobre las helmintofaunas parásitas de micromamíferos en las islas Pitiusas. II. Platelmintos. III. Estado actual de conocimientos. *Bol. Soc. Hist. Nat. Balears*, **27**: 181–194.
- Mas-Coma, S., and Feliu, C. 1984. Helminth fauna from small mammals (insectívoros and rodents) of the Pityusic Islands. In Biogeography and ecology of the Pityusic Islands. Edited by H. Kuhbier, J.A. Alcover, and C. Guerau d'Arellano Tur. Dr. W. Junk Publishers bv, The Hague. pp. 469–525.
- Muzzall, P.M. 1991a. Helminth infracommunities of the newt, *Notophthalmus viridescens*, from Turkey Marsh, Michigan. *J. Parasitol.* **77**: 87–91.
- Muzzall, P.M. 1991b. Helminth infracommunities of the frogs *Rana catesbeiana* and *Rana clamitans* from Turkey Marsh, Michigan. *J. Parasitol.* **77**: 366–371.
- Pérez-Mellado, V. 1989. Estudio ecológico de la lagartija balear *Podarcis lilfordi* (Günther, 1874) en Menorca. *Rev. Menorca*, **80**: 455–511.
- Pérez-Mellado, V., and Salvador, A. 1981. Actividad y termorregulación estival de *Podarcis pityusensis* (Boscá, 1883) (Sauria: Lacertidae) en Ibiza y Formentera. *Amphib.-Reptilia*, **2**: 181–186.
- Pérez-Mellado, V., and Salvador, A. 1988. The balearic lizard *Podarcis lilfordi* (Günther, 1874) (Sauria: Lacertidae) of Menorca. *Arq. Mus. Bocage*, **1**(10): 127–195.
- Pielou, E.C. 1977. Mathematical ecology. John Wiley and Sons, New York.
- Roca, V. 1985. Contribución al conocimiento de la helmintofauna de los Lacértidos y Gekkónidos del piso termomediterráneo del Levante ibérico. Tesis doctoral, Facultad Biológicas, Universitat de València, València, Spain.
- Roca, V., and Hornero, M.J. 1991. Helmintofauna de *Podarcis pityusensis* (Boscá, 1883) (Sauria: Lacertidae). *Rev. Esp. Herpetol.* **5**: 77–87.
- Roca, V., Lluch, J., and Navarro, P. 1986. Contribución al conocimiento de la helmintofauna de los herpetos ibéricos. V. Parásitos de *Psammodromus algirus* (L., 1758) Boulenger. *Psammodromus hispanicus* Fitzinger, 1826 y *Acanthodactylus erythrurus* (Schinz, 1833) Mertens, 1925 (Reptilia: Lacertidae). *Bol. R. Soc. Esp. Hist. Nat. Secc. Biol.* **81**(1–4): 69–78.
- Roca, V., Lopez-Balaguer, E., and Hornero, M.J. 1989. Helmintofauna de *Podarcis hispanica* (Steindachner, 1870) y *Podarcis hispanica* (Seoane, 1884) (Reptilia: Lacertidae) en el Cuadrante Noroccidental de la Península Ibérica. *Rev. Ibér. Parasitol.* **49**: 127–135.
- Roca, V., Ferragut, M.V., and Hornero, M.J. 1990. Estimaciones ecológicas acerca de la helmintofauna de *Lacerta schreiberi* Bedriaga, 1878 (Sauria: Lacertidae) en el Sistema Central (España). *Rev. Esp. Herpetol.* **4**: 93–100.
- Salvador, A. 1979. Taxonomía de las lagartijas baleares del archipiélago de Cabrera. *Bonn. Zool. Beitr.* **30**(1/2): 176–191.
- Salvador, A. 1984. A taxonomic study of the Eivissa wall lizard *Podarcis pityusensis* (Boscá, 1883). In Biogeography and ecology of the Pityusic Islands. Edited by H. Kuhbier, J.A. Alcover, and C. Guerau d'Arellano Tur. Dr. W. Junk Publishers bv, The Hague. pp. 393–427.
- Salvador, A. 1986a. *Podarcis lilfordi* (Günther, 1874) Balearen Eidechse. In Handbuch der Reptilien und Amphibien Europas Echsen III (*Podarcis*). Edited by W. Böhme. Aula-Verlag, Wiesbaden. pp. 83–110.
- Salvador, A. 1986b. *Podarcis pityusensis* (Boscá, 1883) Pityusic Eidechse. In Handbuch der Reptilien und Amphibien Europas Echsen III (*Podarcis*). Edited by W. Böhme. Aula-Verlag, Wiesbaden. pp. 231–253.
- Sokal, R.R., and Rohlf, F.J. 1981. Biometry. 2nd ed. W.H. Freeman and Co., San Francisco.