

Parasitic infracommunities of the Aegean wall lizard *Podarcis erhardii* (Lacertidae, Sauria): isolation and impoverishment in small island populations

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Abstract. The Aegean wall lizard *Podarcis erhardii*, is widely distributed across the islands of the Aegean Sea (Greece). While there exists a relatively substantial body of knowledge on the ecology and life history of the species, the parasite communities of the taxon remain almost completely unknown. Quantifying the composition of these communities in *P. erhardii* is not only important for autoecological reasons, but also because inter-island comparisons of this lizard's parasite communities can shed light on the factors that structure parasite diversity in general. Here we investigate the gastrointestinal parasite communities of *P. erhardii* populations occurring on 16 landbridge islands of the Sporades group in the NW Aegean Sea by examining the gastrointestinal tracts of 113 lizards. In all, 8 species of helminths were found: 1 Trematode (*Paradistomum mutabile*), 1 Cestode (*Oochoristica* sp.) and 6 Nematodes (*Parapharyngodon micipsae*, *Parapharyngodon bulbosus*, *Parapharyngodon echinatus*, *Spauligodon* sp., *Abbreviata* sp., and *Skrjabinelazia* sp.). The prevalence, mean intensity, and mean abundance of infection were respectively 63.71%; 6.01 (± 11.71 ; range 1-90); and 3.57 (± 9.5 ; range 0-90). Brillequin's index of diversity for the Sporades was 0.048 (± 0.13 ; range 0-0.142). These values were lower than for most other mainland and insular lacertid populations, and suggest that the investigated island populations harbor very depauperate helminth communities. The severe impoverishment of the parasite communities and the differential persistence of generalist parasite species with simple life cycles is most likely the result of a combination of insular environmental conditions (spatial and temporal isolation, arid climate, small host population sizes) and host life history characteristics (diet, simple gastrointestinal tract architecture). The paucity of parasites in these relictual island populations suggests that small reptile populations fragmented by anthropogenic activities may not be able to sustain their native parasite communities over the long term.

Keywords: Aegean Sea, Greece, helminth communities, lacertids, lizards.

Introduction

Lacertid lizards of the genus *Podarcis* (Wagler, 1830) probably evolved in the Mediterranean Basin (Harris and Arnold, 1999; Arnold, et al., 2007) and are today widespread across both mainland and island ecosystems of the region (Alcover, 1988). Recent research has lead

to greatly improved understanding of the evolution and systematics, as well as the ecology and physiology of the members of the genus (Gálán, 1997, 2000; Pafilis et al., 2005, 2007; Carretero, Marcos and de Prado, 2006; Valakos et al., 2007; Vervust, Grbac and van Damme, 2007). In contrast, little work has been done on the parasite communities infecting the genus *Podarcis*, and especially those species occurring on islands (Roca, 1995; Galdón et al., 2006; Roca, Lo Cascio and Martin, 2006; Burke et al., 2007). Nonetheless, parasitological investigations of such island populations are particularly interesting because: (i) they often display unusual life history characteristics thus helping to shed light on the processes driving parasitism in vertebrate populations, (ii) both hosts and parasites have often been isolated for very long periods of time hence setting the stage for a better understanding of their interaction details.

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To address some of these questions we investigated the parasite communities of the Aegean wall lizard *Podarcis erhardii* (Bedriaga, 1882) found on the Sporades islands of the NW Aegean Sea (Greece). Although we have currently a reasonably good understanding of the ecology and life history of this lizard (Chondropoulos, 1986; Gruber, 1986; Valakos, 1990; Pafilis, 2003), the parasite communities of the taxon remain almost completely unknown. To date, only a single study (Roca, 1995) has been published on a limited sample of *P. erhardii* parasites from the Cyclades cluster in the C. Aegean Sea; the present paper provides the opportunity to compare parasite communities across two different Aegean archipelagos. In addition, because of the relative simplicity of the island communities and the large number of islands on which the species occurs, this study offers the opportunity to understand better the general patterns of distribution of parasites on islands in general.

Recent research (Foufopoulos and Ives, 1999; Hurston et al., 2009) has confirmed that, similar to other Mediterranean lacertids (Capula, 1996; Capula and Ceccarelli, 2003), *P. erhardii* is a very poor overwater disperser. Thus Aegean island populations, rather than being considered recent overwater colonists, constitute Pleistocene relicts that became isolated when rising sea separated large landmasses into the present day landbridge islands (Foufopoulos and Ives, 1999; Poulakakis et al., 2005). As a result, it is likely that parasite communities on these islands also reflect this long history of isolation and survival in often-small populations of hosts. Elucidating the composition of the parasite communities on the study populations of *P. erhardii* has not only implications for understanding the ecology of the species, but can also help shed light on the general factors that determine parasitism in islands.

The question of which factors underlie parasitism on islands has to our knowledge been asked only rarely and little is known about the underlying drivers (e.g., Lindstrom et al., 2004).

The only studies to date to investigate the issue in a formal fashion and attempt to answer it in a rigorous way suggests that little order exists in the structure of island parasite communities (Dobson and Pacala, 1992; Dobson et al., 1992; Roca and Hornero, 1994). An simple issue for example that has not been addressed is to which extent the species – area relationship holds up for parasitic helminthes and one of the chief aims of this paper is to answer this question.

Materials and methods

Aegean wall lizard, Podarcis erhardii ruthveni (Werner, 1930)

P. erhardii is widely distributed across the islands of the western Aegean Sea. The species prefers open, richly structured habitats, but is an ecological generalist and can be found in essentially all island ecosystems ranging from the shoreline to the highest peaks (Wettstein, 1953). *P. erhardii* has been shown to be a generalist arthropod predator with an opportunistic diet ranging from Coleopterans and ants to Hemipterans and spiders, but which also appears to preferentially seek out soft-bodied invertebrates such as larvae and snails (Adamopoulou, Valakos and Pafilis, 1999). In contrast to other insular lacertids (Pérez-Mellado, Corti and Valakos, 1991; Van Damme, 1999) the diet of *P. erhardii* does not appear to contain significant amounts of plant material (Adamopoulou et al., 1999). In this study we used exclusively on adult animals.

Study islands

The Sporades Islands are located in the northwestern section of the Aegean Sea. This study focuses on the Sporades cluster *sensu stricto*; the outlying Skyros cluster, while administratively considered to be part of the Sporades archipelago, has a different geologic and biogeographic history (Perissaratis and Conispoliatis, 2003; Triantis et al., 2005), is inhabited by the congeneric lizard *P. gaigeae* and will not be considered in this study. This proper Sporades group consists of approx. 33 islands and islets, of which only the largest three (Alonnisos, Skiathos and Skopelos), are inhabited by humans (see fig. 1). While the climate in the region is generally dry (Andreakos, 1978) it is not as arid as other parts of the Aegean Sea region, and all of the larger islands are covered by a mosaic of – frequently dense – thermo-mediterranean vegetation such as *Pinus halepensis* pine forest, *Pistacea lentiscus* maquis, and *Sarcopoterium*-dominated phrygana (Economidou, 1975). Smaller islets, especially to the east of the cluster tend to be covered by low but dense phrygana communities (Economidou, 1975).

At the end of the Wisconsin-Würm glaciation, ~20 000 years ago, sea levels were an estimated 121 m lower than at

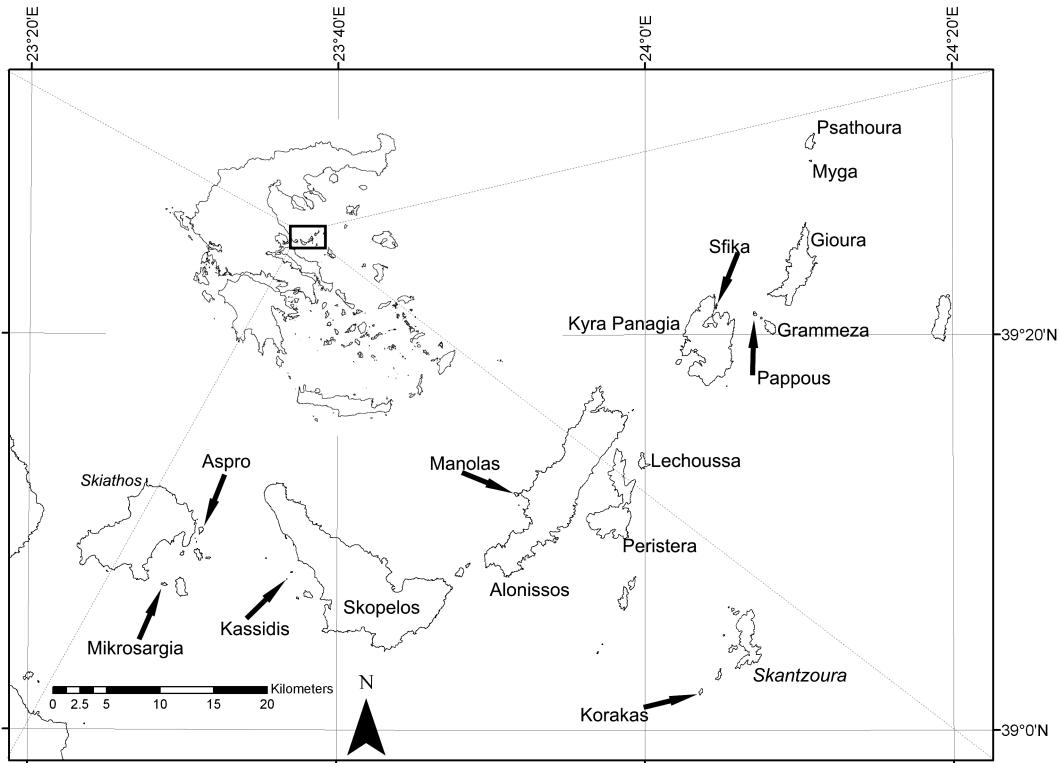


Figure 1. Map of the Sporades island group (NW Aegean Sea, Greece). Islands that were not sampled are in italics.

present, and all of the study islands were either connected to the Greek mainland or fused into larger island blocks (van Andel and Schackleton, 1982; Fairbanks, 1989). As the climate warmed up, rising sea levels lead to the progressive fragmentation of these extended landmasses into the present-day islands (Erol, 1981; Perissoratis and Conispoliatis, 2003). Whereas all of the study islands are located on the same general underwater bank, only the western Sporades (W. of Lechoussa and Alonnisos, or W. of 24°E longitude; fig. 1) were connected to the mainland during the last ice age (and have therefore a maximum island age < 18 250 ybp, Fairbanks, 1989). In contrast, all of the eastern islands are separated by deeper waters (>121 m) from the mainland or the near-shore islands and as such have been isolated for >200 000 years from the continental landmass (Foufopoulos and Ives, 1999; Perissoratis and Conispoliatis, 2003).

Methods

All specimens examined here were collected by K.F. Buchholz during two collecting trips conducted in August (Aspro, Grammeza, Pappous, Kassidisi) and September (Kyra Panagia) of 1957, as well as in April 1958 (Skopelos, Alonnisos, Manolas, Korakas, Gioura, Sfika, Peristera, Lechoussa, Mikrosargia, Psathoura, Myga). The specimens were deposited in collections of the Zoological Museum Alexander Koenig in Bonn, Germany. Preserved lizards

were sexed, snout-vent length (SVL) was measured, and preserved gastrointestinal tracts (including liver) were excised, and later on dissected using standard parasitological techniques (Hornero, 1991). Parasites were identified by one of us (VR), if possible to the species level, and the number and location of parasites in each lizard were recorded.

We follow here the use of descriptive ecoparasitological terms according to Bush et al. (1997). Brillouin's index was used for calculating diversity, in accordance to Magurran (2004). The following prevalence (*P*) cut-off values for determining status in the *P. erhardii* infracommunities were adapted from Galdon et al. (2006): core species *P* > 30%; secondary species 8% < *P* < 30% and satellite species *P* < 8%. Summary statistics (prevalence, intensity of infection, abundance) were calculated for each species of parasite, as well as for each island. Because sample sizes for some islands were small, we report – and include in subsequent analyses – summary statistics only for those island samples that are larger than an arbitrarily selected cut-off value of *n* = 6. All statistical analyses were conducted using SPSS-16.0 (SPSS Inc., 2007).

One of the chief aims of this paper is to compare parasitism data to abiotic island characteristics such as island size and geographic, as well as temporal isolation. All of these factors have been proposed as possible drivers of parasitism (Dobson et al., 1992). Island areas were obtained from the literature or, whenever unavailable, were calculated from aerial photographs. To obtain an index of geographic

isolation we quantified remoteness from the next largest land mass (generally a larger island) by measuring the corresponding distance on a navigational chart (USDMA, 1984, 1986). Lastly, to estimate the age (duration of isolation) of an island we identified the maximum depth of the underwater saddle connecting an island to its next largest neighbor using detailed available navigational charts (USDMA, 1984, 1986). Since detailed global (Fairbanks, 1989; Pirazzoli, 1991, 1996), as well as local (Erol, 1981; Papageorgiou et al., 1990) curves of Holocene sea level rise are now available, it is possible to estimate at which point in the past, under an eustatic sea level rise assumption, rising waters ‘pinched off’ an island from a larger landmass. To determine the importance of population history on parasite prevalence we employ two different, though related metrics of island history: (i) time of isolation from the next largest island and (ii) a categorical variable (Holocene Island vs. Pleistocene Island) denoting whether an island was connected to the mainland during the last glaciopluvial maximum when sea levels dropped to their lowest level (-121 m) in the recent past (table 1).

Table 1. Geographic characteristics and major parasitological parameters for the study islands. Estimated island age reflects time of isolation from the next largest island. All islands marked with (*) are off the main shelf and have been isolated for more than 200 000 years from the mainland. Islands with sufficient sample sizes to have parasitological parameters estimated and which are included in the quantitative analyses are starred (*). For the last four parasitological parameters (mean intensity, mean richness, mean abundance, Brillouin’s Diversity Index) mean island values \pm standard errors are indicated.

Island	Area (km 2)	Distance (km)	Island age (years)	Number of sampled lizards	Preva- lence (%)	Mean intensity (helminths/ host)	Mean richness (species/ host)	Mean abundance (helminths/ host)	Brillouin’s diversity
Alonnisos	69.2	4.2	13 450	3	—	—	—	—	—
Aspro*	0.1536	0.354	5700	10	50	2.40 ± 1.85 (1-4)	0.60 ± 0.66 (0-2)	1.20 ± 1.78 (0-4)	0.045 ± 0.13 (0-0.450)
Gioura*	10.9555	3.908	18 250 [†]	16	31.25	8.0 ± 8.76 (1-23)	0.31 ± 0.46 (0-1)	2.50 ± 6.14 (0-23)	—
Grammeza*	0.8230	2.778	13 450 [†]	8	75	4.0 ± 4.5 (1-14)	1.0 ± 0.87 (0-3)	3.0 ± 4.27 (0-14)	0.046 ± 0.12 (0-0.371)
Kassidis*	0.0035	2.022	10 050	13	53.85	20.85 ± 28.73 (3-90)	0.77 ± 0.89 (0-3)	11.23 ± 23.51 (0-90)	0.06 ± 0.15 (0-0.536)
Korakas*	0.0861	1.496	9950 [†]	7	100	2.30 ± 1.28 (1-10)	1.14 ± 0.34 (1-2)	2.30 ± 1.28 (1-10)	0.054 ± 0.13 (0-0.380)
Kyra Panagia	25.16	7.2	18 250 [†]	5	—	—	—	—	—
Lechoussa	0.47	1.25	12 800	3	—	—	—	—	—
Manolas*	0.0056	0.19	5850	6	0	0	0	0	0
Mikrosagria	0.071	1.28	7650	2	—	—	—	—	—
Myga	0.01603	1.07	5900 [†]	4	—	—	—	—	—
Pappous*	0.0616	1.838	13 450 [†]	7	42.85	2.0 ± 0.82 (1-3)	0.57 ± 0.73 (0-2)	0.86 ± 1.12 (0-3)	0.050 ± 0.12 (0-0.346)
Peristera*	13.338	0.604	9550	14	78.57	7.18 ± 8.02 (1-31)	1.14 ± 0.74 (0-2)	5.64 ± 7.69 (0-31)	0.142 ± 0.19 (0-0.534)
Psathoura	0.72	6.4	12 800 [†]	4	—	—	—	—	—
Sfika*	0.0318	0.067	1500 [†]	6	50	5.67 ± 4.64 (1-12)	0.50 ± 0.50 (0-1)	2.83 ± 4.33 (0-12)	—
Skopelos	96.1	7.0	13 450	5	—	—	—	—	—

Results

We dissected the gastrointestinal tract of 113 lizards collected on 17 islands, and were able to confirm the sex for 97 of them (65 males and 32 females). The examined *P. erhardii* populations were parasitized by 8 species of helminths (1 Digenean, 1 Cestode and 6 species of Nematodes, see table 2). All the helminths were found in the digestive tract except *Paradistomum mutable* that was dissected out of the gall bladder. The average number of parasite species per lizard was 0.75, and the maximum number of parasite taxa found in any individual lizard never exceeded 3. Hence, the island populations of *P. erhardii* harbor very impoverished parasite communities consisting largely of monoxenous Pharyngodonid nematodes. The helminths

Table 2. Infection parameters of the helminths parasitizing *P. erhardii* for the pooled sample of 113 hosts from all islands.

Helminth species	% prevalence ¹ (number of infected hosts)	Intensity of infection ²		Abundance ³	
		Range	Mean	Range	Mean
Digenea					
<i>Paradistomum mutabile</i>	8 (9)	1-85	15.8 ± 25.5	0-85	1.4 ± 8.5
Cestoda					
<i>Oochoristica</i> sp.	2.7 (3)	1-1	1	0-1	0.02 ± 0.13
Nematoda					
<i>Parapharyngodon micipsae</i>	15 (17)	1-4	2.2 ± 1.1	0-4	0.34 ± 0.91
<i>Parapharyngodon echinatus</i>	0.8 (1)	—	—	—	—
<i>Parapharyngodon bulbosus</i>	9.1 (10)	1-12	5.8 ± 3	0-12	0.51 ± 1.87
<i>Spauligodon</i> sp.	18.6 (21)	1-31	4.4 ± 6.4	0-31	0.77 ± 3.23
<i>Abbreviata</i> sp.	0.8 (1)	—	—	—	—
<i>Skrjabinelazia</i> sp.	11 (13)	1-7	2.4 ± 1.7	0-11	0.28 ± 0.94

¹ Number of hosts parasitized divided by total number of hosts sampled (113).

² Helminths/host defined as total number of worms divided by number of infected hosts.

³ Helminths/host defined as total number of worms divided by the total number of hosts sampled (113).

encountered had a global prevalence (all taxa) of 63.71% (72/113). While the mean intensity of infection (all taxa) was of 6.01 ± 11.71 worms/infected host (range 1-90), the abundance (all taxa) was 3.57 ± 9.5 worms/host (range 0-90). Brillouin's Diversity Index was 0.048 ± 0.13 (range 0-0.142).

Parasites and host characteristics

There were no significant effects of host sex on individual parasite species burden (for all species $p > 0.05$); total burden (total number of worms all species) ($U = 944$, $n = 97$, $p = 0.712$, Mann-Whitney test) or whether a host was infected with a parasite (any species) ($U = 950$, $n = 97$, $p = 0.421$, Mann-Whitney test). Furthermore, we did not detect any significant relationship between host body size (measured as snout-vent-length [SVL]) and intensity of infection for the helminth taxa encountered in this study. The only exception was *P. bulbosus* where we found a significant positive relationship to host body size ($r = 0.215$, $p = 0.03$); in fact, only hosts with an SVL > 60 mm were infected.

Species characteristics

Of the species encountered, *Spauligodon* sp. was the most common with 18.6% of all hosts

infected. However, the species with the highest absolute numbers, intensity of infection and abundance was the digenetic *P. mutabile* where a single host was found carrying 85 helminths of this species. Detailed infection parameters for individual species of parasites are given in table 2.

Parasites and island characteristics

To understand how island characteristics might shape patterns of parasitism, we correlated parasite diversity, aggregate prevalence, intensity of infection and abundance (table 1) for the nine islands for which minimum sample size criteria were met, against island characteristics [(log-transformed) Island size, (log-transformed) Distance from next largest landmass, and Island Age] (see table 3). We detected no statistically significant relationships with the single exception of finding a marginally positive relationship between Brillouin's Diversity Index and island size (fig. 2). Furthermore, we failed to detect any significant effects of island age status (Holocene vs. Pleistocene Island) on aggregate prevalence ($t = 0.027$, 7 df, $p = 0.979$), intensity of infection ($t = 0.750$, 7 df, $p = 0.478$), abundance ($t = 0.975$, 7 df, $p = 0.362$), and parasite diversity index ($t = 0.335$, 5 df, $p = 0.751$). Lastly, time of the year (Spring

Table 3. Correlation coefficients, and associated sample sizes (n) between key parasitological variables and abiotic island characteristics. Significant correlations ($p < 0.05$) are shown in bold and are starred (*). NS – not significant.

	Total prevalence	Abundance	Intensity of infection	Brillouin's Diversity Index
Log island area (km 2)	0.123 (9) NS	-0.111 (9) NS	-0.132 (9) NS	0.756* (7)
Log distance (km)	0.008 (9) NS	0.271 (9) NS	0.308 (9) NS	0.192 (7) NS
Island age (years)	-0.129 (9) NS	0.074 (9) NS	0.157 (9) NS	0.235 (7) NS

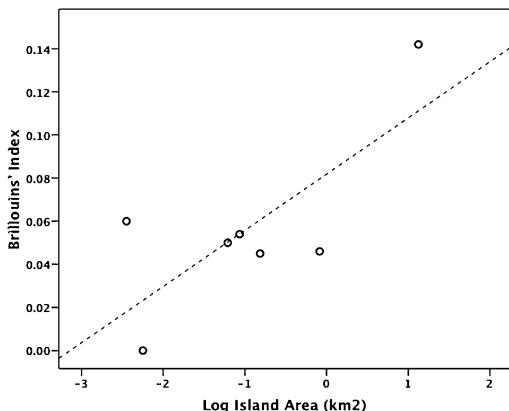


Figure 2. Parasite diversity (quantified using Brillouin's Diversity Index) was positively correlated with the size of the island from which the sampled host population originated ($r = 0.756$, $p < 0.048$, $n = 7$).

vs. Fall collection) was not significantly related to aggregate prevalence ($t = 0.668$, 7 df, $p = 0.525$), intensity of infection ($t = -0.619$, 7 df, $p = 0.556$), abundance ($t = -0.599$, 7 df, $p = 0.568$), and Brillouin's parasite diversity index ($t = 0.363$, 2.027 df, $p = 0.751$).

Discussion

This study reports for the first time on the parasite communities of *Podarcis erhardii ruthveni* occurring on the Sporades archipelago. Despite the study's focus on gastrointestinal parasites, the results are notable in revealing a severely impoverished infracommunity consisting largely of Pharyngodonid nematodes.

The detection of the digenetic *Paradistomum mutabile* – one of only two non-nematode genera – in our samples corroborates an earlier notion that this species is a likely island specialist (Roca and Hornero, 1994). The species

has a wide distribution in different Mediterranean island regions such as Balearic Islands, Spain; Rioux, France; Sicily, Italy; Kimolos and Naxos islands (Cyclades), Greece (Hornero, 1991; Roca, 1995), but appears to be largely lacking from lizard populations on the Iberian mainland (Hornero, 1991). This is probably related to the general absence of Pulmonate mollusks, which constitute the first intermediate host in the life cycle of the parasite, from mainland ecosystems. This species is also probably the only member of the infracommunities of *P. erhardii* that can be considered a specialist (*sensu* Edwards and Bush, 1989) since it parasitizes exclusively lizards of the genus *Podarcis* (Roca and Hornero, 1994). The remainder of the parasite assemblage consists of generalist taxa that are known both from the genus *Podarcis*, as well as from other lizards (Roca, Lluch and Navarro, 1986; Roca and Ferragut, 1989; Martin and Roca, 2004).

Our documentation of the tapeworm *Oochoristica* sp. is the first record for this genus from the Greek islands. The low prevalence of this cestode mirrors previously collected data from the Mediterranean lacertids *Podarcis pityusensis*, *P. lilfordi*, *P. muralis*, and *P. siculus* (Roca, 1995). The generally poor trophic availability in insular ecosystems (Pérez-Mellado and Corti, 1993) likely translates into a corresponding rarity of intermediate hosts that this tapeworm needs to complete its life cycle. The simplicity of island food webs therefore impacts this species more than the other monoxenous members of the parasite infracommunity.

Four of the six species of nematodes in the infracommunities of *P. erhardii ruthveni* are members of the family Pharyngodonidae.

In this family, two evolutionary lineages have been recognized, parasitizing carnivorous and herbivorous reptiles respectively (Petter, 1966; Roca, 1999). The genera found in *P. erhardii ruthveni* (*Parapharyngodon*, *Spauligodon*), belong to the ‘carnivorous host’ lineage, confirming the broadly carnivorous diet of *P. erhardii* (Adamopoulou et al., 1999). The presence of these genera on the Sporades mirrors similar prevalence patterns of congeners in other insular lizard populations from the western (Roca and Hornero, 1994), central (Roca, 1995; Roca et al., 2006) and eastern (Roca, 1995) Mediterranean Basin.

In general, the parasite assemblages found in our Sporades samples are very similar to those collected in the past from some Cyclades Islands (Naxos, Milos) to the south (Roca, 1995) with many of the same helminth species found in both surveys. The only notable absence is *Oochoristica* sp., which has not yet been documented from the Cyclades. However, considering the scarce occurrence of this cestode in the Sporades, and the low number of hosts sampled in the south Cyclades (Roca, 1995), it may be well possible that this species has a broader distribution across the Aegean region but has not yet been detected from the Cyclades (Roca, 1995).

Correlations with host body size and sex

We detected no relationship between lizard SVL and parasite load, except for *P. bulbosus* where a positive relationship between host body size and parasite load was found. In essence, only the largest lizards (SVL > 60 mm) were infected with this helminth; furthermore, the larger the host’s size, the larger the average number of worms found. A possible explanation for this pattern is that only the largest lizards are involved in behaviors – such as territorial aggression – that lead to infection.

Relationship to island characteristics

Parasite diversity varied moderately between the islands. We detected a weak, but statistically

significant, positive relationship between Brillouin’s Diversity Index (BDI) and island size (fig. 2). However, neither parasite species number, nor prevalence, nor intensity of infection were related to island size or any other island characteristics. Consequently, the relationship between BDI and island size, while in line with general predictions of the equilibrium theory of island biogeography (MacArthur and Wilson, 1967), needs to be interpreted with caution until more substantial datasets can be evaluated.

Nestedness and order of the parasite community

For landbridge islands that originate from an ancestral landmass through a process of progressive fragmentation, Atmar and Patterson (1993), as well as Foufopoulos and Ives (1999) have shown that species assemblages are structured by quasi-deterministic extinction processes which produce taxon communities that decline in a predictable manner on progressively smaller islands. As a result, smaller island species assemblages can be almost perfectly nested subsets of all larger species-rich communities. Contra these expectations, we observe a notable absence of nestedness in the helminth infracommunities from the Sporades (table 4). This general lack of order suggests that parasite presence in this archipelago is not the result of simple deterministic processes, but more likely the outcome of idiosyncratic interactions between abiotic island characteristics, local ecological conditions, seasonality and individual host traits (Dobson and Pacala, 1992; Dobson et al., 1992). On the other hand, the observed lack of nestedness can also be interpreted as the result of environmental stochasticity (Dobson et al., 1992), or be the result of variable or inadequate sampling effort.

Impoverishment of parasite communities

Even in comparison to other depauperate Mediterranean lizard populations, the species assemblages hosted by *P. erhardii ruthveni* on the

Table 4. Distribution of parasites across the islands of the study region. Only those islands for which a sufficient sample size was available (see text) are included. Islands are ordered by decreasing number of parasite species diversity. Parasites are ordered by decreasing number of islands encountered. In two cases (*) worms of the genus *Parapharyngodon* could not be identified to species. Under an expectation of nestedness, parasite occurrences would crowd into the upper left corner of the table.

Island	<i>Parad</i>	<i>Spaul</i>	<i>Ooch</i>	<i>Skrz</i>	<i>Pbul</i>	<i>Pmic</i>	<i>Pech</i>	<i>Abbre</i>	Total
Gioura	1	1			1*			1	4
Aspro	1	1		1	1*				4
Pappous	1		1		1				3
Korakas			1	1		1			3
Grammeza	1	1	1						3
Kassidis	1				1		1		3
Peristera		1		1					2
Sfika					1	1			2
Manolas									0
Total	5	4	3	3	3	2	1	1	

Table 5. Prevalence and diversity (Brillouin's Diversity Index) of helminth communities of *Podarcis* lizards from other islands in the Mediterranean Basin. Data based on the present study as well as Roca (1995).

Species	Islands	Prevalence (%)	Diversity
<i>Podarcis erhardii</i>			
<i>ruthveni</i>	Sporades	61	0.048
<i>Podarcis erhardii</i>	Cyclades	73	0.108
<i>Podarcis lilfordi</i>	Balearic	72	0.100
<i>Podarcis milensis</i>	Milos	71	0.197
<i>Podarcis muralis</i>	Rioux	66	0.147
<i>Podarcis pityusensis</i>	Balearic	79	0.242
<i>Podarcis siculus</i>	Rioux	62	0.141
<i>Podarcis tiliguertus</i>	Corsica	47	0.034

Sporades appear to be particularly impoverished. Only *P. tiliguertus* on Corsica has had lower parasite prevalences or less diverse infracommunities (table 5). The low parasite prevalences and depressed diversity indices on the Sporades indicate that the helminth infracommunities of *P. erhardii ruthveni* are best characterized as isolationist (*sensu* Kennedy et al., 1986; Aho, 1990). The depauperate nature of these infracommunities of the Aegean wall lizard populations is highlighted by the notable absence of core taxa (i.e., species with a prevalence > 30%), and the presence of only 4 secondary taxa (*Spauligodon* sp., *Skrjabinelazia* sp., *Parapharyngodon bulbosus* and *P. micipsae*; 30% > prevalence > 8%). The remainder of the assemblage consists of

rare satellite species with prevalences less than 8%: *Oochoristica* sp., *Paradistomum mutabile*, *Parapharyngodon echinatus* and *Abbreviata* sp. These data are in broad agreement with the general parasitological patterns observed in other Mediterranean island populations where usually only a single core species can be detected (generally in the genus *Spauligodon*).

What are the drivers that are responsible for this pronounced impoverishment of the Aegean wall lizard infracommunities? Most likely, the answer can be found in a combination of factors relating to host life history traits and prevailing environmental characteristics.

Effects of lizard life history on helminth infracommunities

Past research has revealed that ectothermy, as seen in these lizards, is associated with low levels of parasitism, probably because ectothermic animals have more modest energetic requirements than endotherms, and as such reduced opportunities to become infected through ingestion of contaminated food items (Roca, 1999). In addition, the small size and structural simplicity of the gastrointestinal tract of *P. erhardii*, like in all *Podarcis* members, means that fewer ecological niches are available for parasitic helminths to occupy, thus further limiting parasite diversity possible (Roca & Hornero, 1994; Roca, 1999). As a result, a generalist, car-

nivorous diet – whether through the resulting gastrointestinal tract simplicity, or some other mechanism – is associated with lower infection rates and impoverished parasite communities (Kennedy et al., 1986; Roca and Hornero, 1991, 1994; Roca, 1999; Martin and Roca, 2004). The diet of *P. erhardii* contains mostly small terrestrial arthropods (Adamopoulou et al., 1999) and the species, in contrast to other island-dwelling lizards, has been shown to not include significant amounts of plant matter in its diet. In contrast, *P. pityusensis*, which has the greatest incidence of herbivory among the Mediterranean island lizard populations, also has the highest parasitism rates, as well as the most diverse parasite communities (Pérez-Mellado et al., 1991; Roca, 1995).

Effects of island characteristics on helminth infracommunities

A constellation of abiotic environment characteristics probably also contributes to the paucity we found in the helminth communities of the study islands. The climate of the region, especially on the smaller islands, which lack orographic precipitation, is relatively dry (Andreakos, 1978). Lizard populations occurring in xeric habitats have been shown to exhibit comparatively low levels of parasitism, possibly because of reduced survival of parasite eggs outside the host (Dobson et al., 1992 and references therein). In addition, since lizard populations occurring on these islets are frequently very small, they can only sustain relatively modest parasite communities. Indeed, although little work has been done on this subject, at least one study has shown that in island vertebrates, parasite prevalence and average burden decline with decreasing island- and presumably host-population size (Lindstrom and Foufopoulos, 2004). The isolated nature of the study islands and the relict character of the reptile populations occurring there (Foufopoulos and Ives, 1999), together with the impoverished reptile communities, suggest that infection of island lizards by new parasite species via overwater dispersal of

either infected hosts or parasite propagules is likely to be rare.

In general, the depauperate nature of the parasite community, as well as the observed low prevalence and infection intensities in the Sporades, follow a general island pattern (see table 5) and suggest that the island populations of *P. erhardii* are not subject to a heavy burden of disease. If this is indeed the case, low levels of parasitism may be partially responsible for the high densities of lacertids lizard populations observed on many of the small islands in the region.

To summarize, the parasite communities of the *P. e. ruthveni* island populations are unusually impoverished. Infection rates are modest, parasite burdens are low, and most of the helminths we found were generalist taxa with simple life cycles. Because this is a relict system with little between-island dispersal, it can serve as a model for the effects of ongoing anthropogenic fragmentation on reptile populations with poor dispersing abilities. This study suggests that such isolated populations will likely lose many of the parasites that can be found in larger, continuous populations. This in turn can have important long-term conservation implications when it comes to the preservation of parasitic organisms, which constitute an important component of the global biodiversity. At the same time, loss of parasitic communities can have important effects on the surviving lizard populations themselves. The removal of this important selection agent can lead to a possible attenuation of host immune responses, a process that can ultimately render the species susceptible to new, invasive pathogens.

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