Effects of island characteristics on parasitism in a Mediterranean lizard (*Podarcis erhardii*): a role of population size and island history?

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Abstract. Parasites are ubiquitous in wildlife populations and are regularly present in free-ranging vertebrates. Little research has been done on the impact of insularity on the patterns of parasitism. Islands, known for low genetic diversity and poor parasitic infracommunities, offer a tractable model to better understand the factors that shape parasitism. This study analyses helminth parasite loads from eight populations of the Erhard's Wall lizard (*Podarcis erhardii*, Lacertidae) occurring on islands of varying size, age and isolation in the Aegean Sea (Greece). By comparing burdens of infection among the different populations, we aimed to elucidate how island features shape levels of parasitism. Parasite communities on the islands were very species-poor, with only four genera of nematodes (*Spauligodon* sp., *Skrjabinodon* sp., *Parapharyngodon* sp. and *Skrjabinelazia* sp.) detected among the lizard populations. We found that aggregate worm infection level was positively correlated with island area, whereas total parasite prevalence was negatively correlated with island age, though marginally. This suggests that numbers of parasites are determined by the loss of genetic diversity as consequence of long-term population bottlenecks. Given that the island populations constitute an important model for the effects of habitat fragmentation on biodiversity, our findings raise concerns about the long-term prospects for many specialized parasite populations in the face of widespread anthropogenic habitat fragmentation.

Key words: islands, lizards, parasitism, helminths, Lacertidae, Mediterranean ecosystems.

Introduction

Parasitism is extremely widespread in natural ecosystems (Combes 2005). Vertebrates in particular harbour a great diversity of micro- and macroparasites that inhabit a broad range of ecological niches inside their hosts. Ecologists have only recently realized the importance of parasitic organisms in the workings of natural ecosystems (McCallum & Dobson 2002, Raymond et al. 2012). As a result, there is still relatively little understanding of the role that ecological factors play in determining levels of parasitism and in structuring parasite infracommunities. These gaps in knowledge are particularly pronounced in ectothermic vertebrates such as reptiles (Schneller & Pantchev 2008, Telford 2009).

Lizards are common hosts of different groups of parasites such as protozoans (Üçüncü et al. 2001, Roca & Galdón 2010, Arikan & Çiçek 2014), ticks (Scali et al. 2001, Meister et al. 2009, Ghira et al. 2013) and helminths (Galdón et al. 2006, Gürelli

et al. 2007, Carretero et al. 2011). Infected lizards may have poorer body condition, reduced social status, lower reproductive output, slower running speed, and poorer competitive ability than uninfected ones (Bauwens et al. 1983, Schall et al. 2000). All above may reduce viability at individual level and put at stake the survival of small, isolated populations (Pafilis et al. 2013).

Islands are typical examples of isolated habitats. Gene flow is dramatically restricted and insular populations may suffer from reduced genetic variability (Nei et al. 1975, Frankham et al. 2002). Furthermore, island populations often exhibit distinct changes in ecology, morphology, and behaviour because of the particular conditions prevailing on islands, collectively referred to as the "island syndrome" (van Valen 1973, Adler & Levins 1994). Limited research suggests that the structure and dynamics of parasite communities may change as well, deviating from the mainland patterns (Dobson et al. 1992, Roca et al. 2009, Garrido & Pérez-Mellado 2013). For instance, insular para-

site populations have been shown to lose their genetic diversity, while at the same time enlarge their host variety (Nieberding et al. 2006). Moreover, because islands harbour simpler and more manageable communities, they lend themselves more to the study of parasite-host relationships. Although a growing body of literature examines parasitism on insular populations (e.g. Roca & Hornero 1994, Roca 1996, Roca et al. 2005, Jorge et al. 2012), the impact of specific features of insularity, such as island age, island size, and distance from mainland, remains neglected. Here we focused on lizard parasitic helminths coming from eight Cycladic islands (Aegean Sea, Greece) in order to assess the effect of different aspects of insularity on lizard parasite patterns.

The Cyclades Islands separated from mainland Greece around the middle Pleistocene when rising sea levels led to a progressive break up and thus the proto-Cycladic block became increasingly fragmented (Mercier et al. 1989, Perissoratis & Conispoliatis 2003). Erhard's wall lizard, (*Podarcis erhardii*) is the most common lizard in the Cyclades. It is a poor over water disperser, (Foufopoulos & Ives 1999, Hurston et al. 2009) and thus its current populations, and their parasites, represent relict ice-age populations rather than recent overwater colonists. This means that island age is a close proxy for the history of the lizard and parasite populations living there (Li et al. 2014, Brock et al. 2015). Similarly, because the islands are ecologically homogenous and share the same climate, island size can be used as a proxy for host population size.

Trying to clarify the aspects of insularity that shape the patterns of parasitism, we assessed several aspects of parasites in regard to island features. The classical island biogeography theory predicts that insular communities comprise less taxa compared to mainland and that island size and age further affect this tendency (MacArthur & Wilson 1967). Indeed, recent studies using molecular approaches have shown that smaller and older isolated islands retain less genetic variability (Hinten et al. 2003, Hurston et al. 2009), which is reflected in depauperate parasite faunas (Roca & Hornero 1994, Roca et al. 2009). We thus anticipated that island size would positively affect parasite prevalence and infection levels, while island age and isolation would have the opposite effect. In other words, we expected that lizards from large and young islands that are closer to the mainland would host more parasites, whereas

their peers from small and old isolated islands would show lower levels of parasitism.

Materials and methods

Species background

Podarcis erhardii (Bedriaga, 1882) (Reptilia, Lacertidae) is a small lizard, with a snout vent length (SVL) of up to 70 mm and an average mass of 7.58 ± 1.4 g. The geographic range of the species encompasses the southern Balkan Peninsula and includes most of the islands in the W. Aegean Sea (Valakos et al. 2008). The species is best classified as an active-search hunter with a diet consisting of a variety of invertebrates, plant material and a preference for soft-bodied arthropods (Adamopoulou et al. 1999, Brock et al. 2014). The species is particularly common on the Cyclades Islands and is widespread across human-disturbed habitats such as agricultural terraces and drystone walls (Valakos et al. 2008). The parasite communities of the species are largely unknown and only geographically limited surveys have been conducted on some of these Aegean island populations (Roca 1995, Roca et al. 2009).

Study islands

All of the study islands belong to the Cyclades cluster, located in the central Aegean Sea (Greece) (Fig. 1). Typical for the region is a highly diverse coastal heath, consisting of spiny, summer-deciduous and strongly aromatic shrubs, collectively called *phrygana*. The region has a Mediterranean climate, with mild, rainy winters and long,
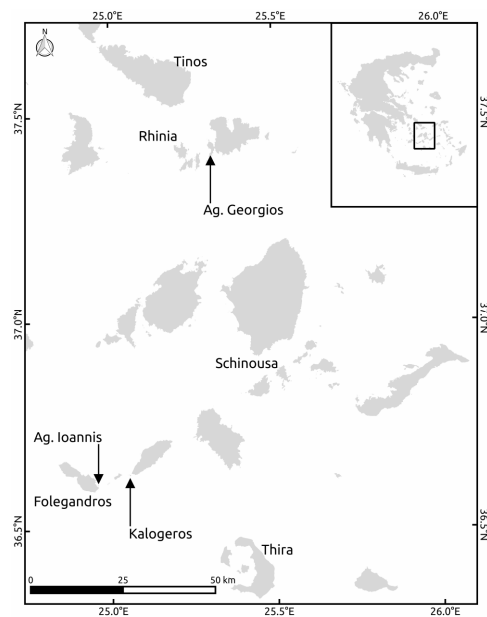

Figure 1. Map of the study area. Some islets (Agios Ioannis, Agios Georgios, Kalogeros) are too small to be visible at the scale of this map.

Table 1. Aegean islands from which the lizards were collected, their area (in km²), age (in years), distance from the nearest larger island (in km), prevalence (%), mean intensity (helminthes/host), mean richness (species/host taxa) and mean abundance (helminthes/host). Bold font: overall helminth fauna, Italics font: *Spauligodon sp*. N corresponds to the number of sampled lizards in each island (in parenthesis), n corresponds to number of parasite taxa (in parenthesis)

Island (N)	Island area	Island age	Distance	Prevalence	Intensity	Richness (n)	Abundance
Folegandros (49)	33	11,650	9.69	**34.78**/*16.32*	**4.87**/*3.62*	0.8(2)	**1.69**/*0.59*
Tinos (28)	195	5,800	1.912	**85.71**/*71.42*	**14.12**/*8.1*	1(3)	**12.52**/*5.79*
Schoinousa (21)	8.83	6,250	5.355	**90.38**/*4.76*	**17.06**/*1*	0.4(3)	**14.62**/*0.05*
Ag. Ioannis (21)	0.034	2,800	0.207	**76.19**/*14.28*	**3.60**/*1.5*	1.1(4)	**2.57**/*0.14*
Santorini (16)	71.2	-	18.1	**75**/*25*	**20.25**/*1.25*	0.3(4)	**15.19**/*0.31*
Kalogeros (14)	0.0598	7,150	0.382	**85.71**/*7.1*	**4.92**/*1*	1.1(3)	**4.21**/*0.07*
Rhinia (14)	13	9,500	4.56	**71.43**/*42.85*	**10.8**/*3.66*	1(3)	**7.71**/*1.57*
Ag. Georgios(11)	0.072	5,400	0.125	**81.82**/*28.57*	**5.67**/*2.66*	0.9 (3)	**4.64**/*14.54*

dry summers (Arianoutsou & Paraskevopoulos 1988). The average daily mean temperatures range between 9.3°C and 24.7°C. Rainfall is lower than that of other regions of Greece, averaging approx. 350-400 mm per year (Kotini-Zabaka 1983).

The study islands are broadly similar with respect to the prevailing ecological conditions, but vary greatly in their area, ranging from the smallest, Agios Ioannis – 0.34 km², to the largest, Tinos – 195 km² (Table 1.). In our analyses we parted the focal islands in two groups, large (inhabited by human, over 30 km²) and small (non inhabited and under the threshold of 30 km²). All islands with the exception of Santorini are landbridge islands, that is they were part of a larger continuous island landmass termed Cycladia during the Wisconsin-Würm ice age (Dermitzakis et al. 1990). As sea levels rose following the advance of the latest interglacial, and dependent on their elevation, various parts of this coastal landscape became inundated and formed today's archipelago. *Podarcis* lizards have been shown to be very poor overwater dispersers and most Aegean populations are considered today to be ice-age relics (Foufopoulos & Ives 1999, Foufopoulos et al. 2011). Thus, the islands, and by extension the lizard and parasite populations, have been isolated for long periods of time (2.800-11.650 years) and have been shaped by the prevailing conditions.

Specimen treatment

For the study we used specimens deposited in the Herpetological Collection of the Zoological Museum Alexander Koenig in Bonn, Germany. In the analysis, we included only islands for which more than 10 adult lizards were available (170 individuals from eight islands; ZMAK specimen numbers, Folegandros: 604, 654, 621-645, 670-693 – collected in June 1953, Tinos: 1170-1197 – collected in May 1959, Schoinousa: 345-353, 387-398 - collected in June 1952, Ag. Ioannis: 647-668 - collected in June 1953, Santorini: 9-17, 26-32 - collected in May 1952, Kalogeros: 606-619 - collected in June 1953, Rhinia: 846-859 - collected in June 1952, Ag. Georgios: 751-761 - collected in June 1953). To ensure that seasonality has no impact on parasite burden, we dissected only lizards that were collected within May and June. The body cavity of preserved lizards was opened, and the gastrointestinal tracts (hereinaf-

ter GI tract) were excised, preserved and labelled with location, date, and specimen ID number. Gastrointestinal tracts were processed according to the methods described by Roca and Hornero (1994). Parasite number and identity were quantified and recorded. Because of the scarce presence of male parasites, and the incomplete taxonomy state of these groups of helminths, identification was possible only to the level of the genus. As such, we adopted two different types of analysis. On the one hand, we reported aggregate worm intensity (average number of worms from all species, found in each infected lizard in a population), aggregate abundance (number of helminths, belonging to all taxa, in the average animal of a population i.e. including the uninfected hosts), and prevalence (the fraction of hosts parasitized divided by total number of hosts sampled). On the other hand, we repeated the aforementioned estimations using the specific metrics of the most prevalent helminth species in all islands (*Spauligodon* sp., Table 2).

Geographic data

Island area (in km²), and distance from the nearest larger landmass (in km) were obtained from the literature (Foufopoulos & Ives 1999) or calculated from GIS databases. Island area was log-transformed to normalize distributions. Age of an island was calculated by combining information from navigational charts identifying the depth of the underwater saddle connecting the island to its next largest landmass, and detailed sea level change charts (Pirazolli 1991, Perissoratis & Conispoliatis 2003), which provide sea levels since the Last Glacial Maximum (Foufopoulos & Ives 1999, Hurston *et* al. 2009, Foufopoulos et al. 2011). This allowed us to estimate duration of isolation for all islands with the exception of Santorini, an island that is located off the Cycladic shelf and for which there are no reliable estimates for age of separation (Table 1).

Statistical analyses

The Kolmogorov-Smirnov test was used to examine the normality of data. Wherever parametric assumptions were not met, data were log-transformed. To determine which factors might be shaping levels of parasitism, we conducted Pearson correlation analyses of parasitism patterns in regard to island characteristics, such as age and

Table 2. Infection parameters (prevalence, intensity of infection, abundance) of the helminths parasitizing *Podarcis erhardii* for the pooled sample of 137 hosts from all the islands.

Helminth species	% prevalence	Intensity of infection	Abundance
Spauligodon sp.	38 (52)	6.1 ± 9.6 (1 – 64)	2.3 ± 6.6 (0 – 64)
Skrjabinodon sp.	1.5 (2)	5 ± 4.2 (2 – 8)	0.07 ± 0.7 (0 – 8)
Parapharyngodon sp.	24.1 (33)	3.6 ± 2.7 (1 – 14)	0.9 ± 2.1 (0 – 14)
Skrjabinelazia sp.	11 (15)	2.2 ± 2.5 (1 – 10)	0.3 ± 1.1 (0 – 10)
Indeterm.	14.6 (20)	2.9 ± 2.5 (1 – 9)	0.4 ± 1.4 (0 – 9)

Table 3. Correlations between nematode burden, abundance, prevalence, and environmental characteristics. Bold font: overall helminth fauna, Italics font: *Spauligodon* sp.*Significance at the 0.1 level.

	Prevalence	Intensity	Abundance	Richness
LogIsland Area				
r	**-.264**/*.522*	**.710***/*.543*	**.632**/*.213*	.484
p	**.528**/*.184*	**.048**/*.163*	**.093**/*.611*	.223
n	8	8	8	8
Island Age (years)				
r	**-.716**/*.002*	**.004**/*.154*	**-.154**/*.243*	.138
p	**.070**/*.995*	**.993**/*.741*	**.742**/*.599*	.767
n	7	7	7	7
Distance (km)				
r	**-.397**/*.086*	**.630**/*.221*	**.473**/*.381*	.778*
p	**.330**/*.838*	**.094**/*.599*	**.237**/*.351*	.029
n	8	8	8	8

area. Relationship between the number of sampled host individuals and the number of parasite taxa found in each island was examined using Spearman rank correlation. All test were two-tailed (α=0.05). Statistical analysis was performed according to Zar (1984). All analyses were conducted in SPSS (Vs. 23, IBM Corporation).

Results

Dissection of the GI tracts revealed a largely insectivorous diet, with almost no vegetative material present. Interestingly, we also discovered that the species engages in cannibalism as well, as evidenced by the separate discoveries of a *Podarcis* foot and a tail among the various stomach contents – this observation has potentially important epidemiological ramifications since intraspecific predation can be an important mechanism of parasite transmission (Matuschka & Bannert 1987). We recovered a total of four different taxa of helminths (*Skrjabinodon* sp., *Spauligodon* sp., *Parapharyngodon* sp. and *Skrjabinelazia* sp.). Their global abundance, infection level, and prevalence are reported in Table 2. There is no relation between the number of sampled host lizards and the number of parasite taxa (Spearman R=0.498 p>0.05) so the sampling effort did not bias the results.

Effects of island characteristics on parasitism

Total helminth prevalence had marginal relationship with island age (r=-0.716, p=0.07). There were no significant relationships between island age and either worm intensity, worm abundance or richness (Table 3).

We detected a significant positive correlation between log-Island area and worm burden, (r=0.71, n=8, P=0.048, Pearson; Table 3). Hence, lizards from larger islands tended to carry heavier parasite populations (Fig. 2). In contrast, we did not detect any significant relationships between island area, global prevalence of infection, overall intensity and richness (p>0.05, Table 3). Similarly, there was no significant relationship between log-Island area and *Spauligodon* sp. (p>0.05, Table 3)

There was no significant correlation between distance from the nearest larger island and worm burden (r=0.63, n=8, P=0.095, Pearson; Table 3). This result was further supported while taking island area explicitly into account (r=0.475, n=8, P=0.326; partial correlation accounting for Log Area). There was also no significant correlation between distance and prevalence or abundance (see Table 3).
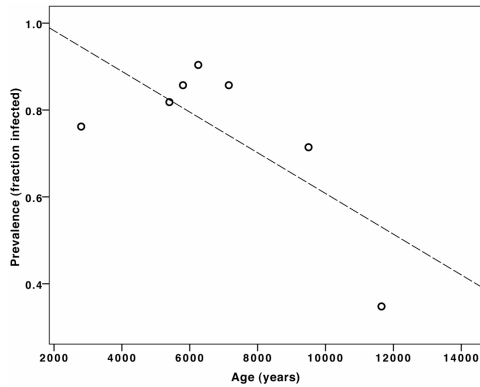
Figure 2. Parasite prevalence (fraction hosts infected) relative to island age. Longer population isolation results in lower levels of parasitism.
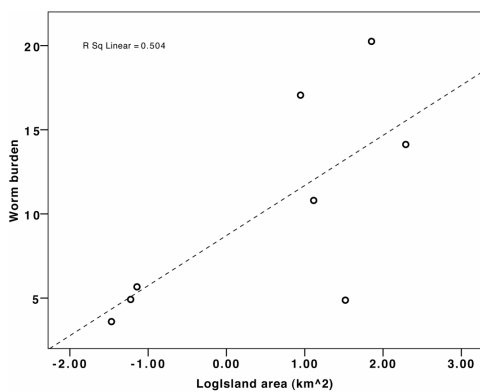

Figure 3. Worm intensity (worms per infected host) is related to island area. Lizards from larger islands tended to carry more nematodes.
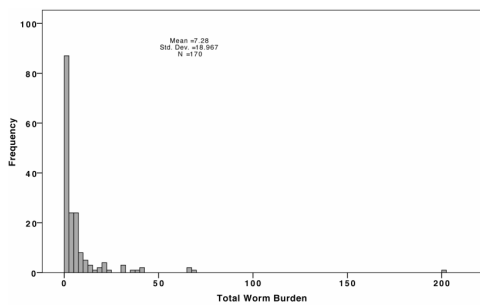

Figure 4. The total distribution of parasites for all hosts dissected (number of lizards carrying helminths is given as frequency in Y-axis).

Parasite burden distribution

The distribution of parasite burden is skewed right, such that the highest burdens occur in only a very few individuals (Fig. 4). Most lizards were found to carry few to no parasites, with the exception of a few super-spreaders (individuals with high parasite burden that are highly infectious) playing host to the majority of the parasites. The mean was 7.28 ± 18.967 worms per lizard, with a comparatively high standard deviation, higher than twice of the mean value.

Discussion

This study seeks to increase our understanding of the factors that determine levels of parasitism in ectothermic vertebrates surviving on small patches of habitat such as islands. This kind of knowledge becomes more and more important as increased anthropogenic activities are fragmenting natural habitats with unknown effects on both host, as well as parasite populations (Corti et al. 1999, McCallum & Dobson 2002, Zimmer 2011).

Our analyses suggest that certain island characteristics had a clear effect on the presence of parasites in the study populations. Both the highest worm burdens and the highest abundance were associated with lizard populations occurring on the largest islands. Large islands also supported the largest *P. erhardii* populations, in addition to other reptile communities, and are thus better able to maintain more substantial helminth populations. This may be either the result of larger host populations that will ensure transmission, or possibly because of more favourable prevailing environmental conditions such as increased soil moisture, which in turn boost transmission rates. At least one study has previously shown that parasite prevalence and burden in endothermic vertebrates increase with island size (Lindstrom et al. 2004). Thus the presence of several host populations may facilitate the spread of parasites and increase the presence of the "super spreader" individuals. In addition, it is possible that the small populations of worms surviving on small islands have lost genetic diversity due to the same genetic drift processes operating in their hosts (Hurston et al. 2009). Consequently, some of these species may have gone extinct producing smaller average helminth burdens. Even these parasite species that did persist, probably retain only low levels of genetic diversity. If this is the case, then this will likely undermine their ability to successfully establish themselves in hosts, further reducing parasite burdens.

Parasite prevalence was negatively correlated with island age. Thus lizard populations from younger islands had higher parasite prevalence than those that came from older islands. Since older island populations would have experienced longer periods of co-evolutionary bottlenecks (Frankham 1997; Frankham et al. 2002), parasite species that were unable to maintain a minimum viable population over thousands of years may have eventually gone extinct.

Parasite burdens were not equally represented as only few lizards carried the highest burdens, the so-called super-spreaders. This is very typical for wildlife populations (Roca & Hornero 1994). There was no clearly discernable pattern in the distribution of the nematode taxa investigated across the study islands. There was also little discernible effect of island size on species richness. In addition, there was little evidence for species nestedness, a pattern in which smaller islands harbour nested subsets of the communities of larger islands (Ulrich 2009; Morrison 2013). Most parasites were found on similar numbers of islands (four or five) with the possible exception of *Skrjabinodon* that was found only on two.

Our results are in accordance with a previous study on the insular parasites from another Aegean island cluster, the Sporades (Roca et al. 2009). Indeed, values for prevalence, mean intensity and mean abundance from helminths parasitizing the GI tract of *P. erhardii* fell within the same spectrum for Cyclades and Sporades. However, our findings deviate from the aforementioned study in the impact of island size on prevalence. Parasite infracommunities from both island clusters were poorer compared to mainland populations (Roca and Hornero 1991; Roca et al. 2009). At this point we have to stress out that the parasites we found in *P. erhardii* are generalists and common in many other species (Roca and Ferragut 1989; Martin and Roca 2004).

In summary, our study reveals that infection levels increase with island area, whereas island age has a negative effect on parasite prevalence. These findings indicate that parasitic infracommunities are affected by the loss of genetic diversity due to long-term isolation. In this regard, the study extends for the first time the existing paradigm of species community relaxation following habitat fragmentation into the parasite world.

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