Biogeographic patterns of blood parasitism in the Aegean Wall Lizard across the cycladic islands

Permalink
https://escholarship.org/uc/item/3kn7r7zm

Journal
Frontiers of Biogeography, 13(2)

Authors
Fornberg, Johanna L.
Semegen, Sarah L.

Publication Date
2021

DOI
10.21425/F5FBG49428

Supplemental Material
https://escholarship.org/uc/item/3kn7r7zm#supplemental

Copyright Information
Copyright 2021 by the author(s). This work is made available under the terms of a Creative Commons Attribution License, available at https://creativecommons.org/licenses/by/4.0/

Peer reviewed
Biogeographic patterns of blood parasitism in the Aegean wall lizard (*Podarcis erhardii*) across the Cycladic Islands

Johanna L. Fornberg¹,²* and Sarah L. Semegen¹

¹School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI, 48104, USA; ²Department of Ecology, Evolution, and Marine Biology, University of California - Santa Barbara, Santa Barbara, CA, 93117, USA. *Correspondence: Johanna Fornberg (fornberg@ucsb.edu), Address: University of California Santa Barbara, Santa Barbara, CA, 93106, USA.

Abstract

The biogeography of host-parasite dynamics is an area that has received little attention in studies of island ecology. While a few studies have shed insight on patterns of parasitism in insular host populations, more empirical evidence is needed to ascertain how isolation impacts parasites. Biogeography generally theorizes that the physical size of islands and the duration of each island's isolation can be driving geographic factors controlling species interactions and populations dynamics. To test this, we assessed the effect of island structure and population isolation on the endemic insular lizard *Podarcis erhardii* and its native hemogregarine parasite (Apicomplexa: Adeleorina) in the Cyclades (Aegean Sea). We analyzed the relationships of prevalence and parasitemia of hemogregarine infection with several factors concerning the island (size, time of isolation, spatial isolation, population density) and host (body size) levels using regression and structural equation models, respectively. Regressions indicate that islands with greater host density and islands which have been isolated for shorter timespans tend to have higher hemogregarine prevalences; structural equation models suggest a similar pattern for parasitemia. We hypothesize this may be driven by insular density compensation. Hosts on islands that are more temporally and spatially isolated also tend to have higher prevalence and parasitemia of hemogregarines. Our results indicate that island area, island isolation, and host population density are likely to be significant drivers of changes in host-parasite interactions in fragmented populations.

Keywords: Aegean Sea, biogeography, fragmentation, hemogregarines, host-parasite interactions, insularity, land-bridge islands, lizards.

Introduction

Research in island biogeography has uncovered a variety of ecological patterns and processes that affect fragmented and isolated biotic communities. Many studies focus on the effect of fragmentation and insularity on community structure, physiology, morphology, and predator-prey interactions (MacArthur and Wilson 1967, Adler and Levins 1994, Blondel 2000, Blumstein and Daniel 2005, Hurston et al. 2009, Novosolov et al. 2013), but less is known about the impact of insularity on host-parasite dynamics (i.e., infectious species which decrease host fitness with a pathology that is intensity-dependent, Lafferty and Kuris 2002) (McCallum and Dobson 2002). In a recent survey, biologists determined that...
One of island biology’s top research priorities was understanding how island isolation and size affected population dynamics (Patiño et al. 2017).

Evidence has shown that isolation can have wide-ranging impacts on host-parasite distributions and interactions (Perkins 2001, Morand and Krasnoz 2010). Hosts may effectively lose parasites when isolated if host populations become small or dispersed (Clay 2003, Torchin et al. 2003), or parasites may evolve to have a wider niche, thereby infecting new additional hosts (Nieberding et al. 2006). Hosts may also be more susceptible to parasitism if hosts are inbred, which could be determined by spatial and temporal isolation trends (Reed and Frankham 2003, Charpentier et al. 2008). Parasitologists and ecologists have developed theory detailing the possibilities of host-parasite evolution following isolation, but there is still much opportunity for empirical and observational study of island biogeography in natural systems (Poulin 2004, Illera et al. 2015).

Generally, insular systems often exhibit higher aggregate population densities on small islands as compared to larger islands and mainland areas, a process known as density compensation (MacArthur et al. 1972, Wright 1980, Rodda and Dean-Bradley 2002). Studies that have investigated the relationships between parasitism and island biogeography suggest that isolation tends to lead smaller islands with denser host populations to harbor higher parasite prevalence and infection intensity, and lower richness of parasite diversity (Gouy de Bellocq et al. 2002, Roca et al. 2009). While density compensation is documented in faunal populations (Wright 1980, Rodda and Dean-Bradley 2002), it is not clear how this process manifests in a host-parasite system when isolation also varies spatially and temporally.

Related biogeography research suggests that more intense isolation lead to a distinct loss of genetic diversity in the parasite and subsequently impoverished parasite populations in hosts (Reed and Frankham 2003, Nieberding et al. 2006, Pérez-Rodríguez et al. 2013, Koop et al. 2014). Two related study found insular parasite populations to be increasingly depauperate the longer the period of isolation from the mainland (Roca et al. 2009, Pérez-Rodríguez et al. 2013). There is also evidence that isolation leads to higher parasitism in inbred populations (Charpentier et al. 2008, Luikart et al. 2008, Chapman et al. 2009). Another study found that island hosts, compared to mainland hosts, had significantly more parasitism as a result of reduced genetic variability and increased host population density (Loiseau et al. 2017). Similarly, spatial isolation of island communities can dramatically alter species composition by affecting immigration and dispersal opportunities (MacArthur and Wilson 1967, Simberloff and Wilson 1969, Simberloff 1976, Whittaker et al. 2007, Rosindell and Harmon 2013), which may affect population size in remaining species. Islands that are more spatially isolated from mainland or other possible “source” land masses are expected to experience lower diversity and more apparent evolutionary divergence than islands that are less isolated but of the same size (Simberloff and Wilson 1969, Simberloff 1976).

The predictions of island biogeography theory have been developed for several decades in the context of free-living species, and little of this work has been extended to consider symbiotic species like parasites, pathogens, and mutualists. Insular communities are, in some cases, depauperate of symbiotic species. Parasites, for example, may be entirely lost in the process of isolation from the host species (Torchin et al. 2003, Tomé et al. 2018). Loss or reduction of symbiotic species may be a result of restrictions in host species abundance, environmental or dispersal limitations, or a consequence of evolutionary changes in hosts, parasites, or both. For parasites infecting isolated host species, we may expect that parasites evolve to be less host specific over time as this may be expected to increase transmission and abundance, however, a depauperate host population or low immigration may reduce or prevent parasite survival. Integrating parasitism into island biogeography theory requires a careful assessment of how free-living species dynamics affect symbiotic species that operate at a finer spatial scale than their hosts. Parasites (and other symbionts) are so intimately associated with hosts that host individuals or populations are functionally equivalent to habitat and patches for parasite species (Kuris et al. 1980, Combes 2001).

The Cycladic islands are an archipelago of landbridge islands in the Aegean Sea, located off the eastern coast of Greece (Fig. 1). Most of the islands, and the vertebrate populations inhabiting them, became progressively isolated during the gradual rise in sea levels following the last glacial maximum 18000 years ago (Pirazzoli and Pluet 1991, Kapsimalis et al. 2009, Poulos et al. 2009). Duration of island isolation depends on the depth of the underwater saddle between two islands and varies greatly between 25 years and 5.33 million years (Foufopoulos and Ives 1999). Multiple lines of evidence indicate that the Aegean wall lizard (Podarcis erhardii, Reptilia: Lacertidae) is a very poor over-water disperser; as a result, the evolutionary history of Cycladic populations reflects the fragmentation history of the islands they inhabit (Foufopoulos and Ives 1999, Hurston et al. 2009). The resulting diversity of habitat and population characteristics of the Cycladic islands present an excellent study system to investigate the long-term effects of habitat fragmentation on the evolutionary ecology of host-parasite interactions.

We determined how island geography and host ecology affect the prevalence and intensity (sensu Margolis et al. 1982, and hereafter, parasitemia) of parasite infections in the Aegean wall lizard host. Podarcis erhardii is a native host for a vector-transmitted hemogregarine parasite (Apicomplexa: Adeleorina). Recent work has shown that hemogregarine parasites on islands are surprisingly host-specific, and that insular parasites tend to reflect the evolutionary history of their hosts (Tome et al. 2018). Consistent with traditional island biogeography theory, island
effects on host-parasite interactions should be most apparent in relation to changes in island size and island isolation (i.e., temporal and spatial isolation) (MacArthur and Wilson 1967, Dobson et al. 1992, Galdón et al. 2006). We hypothesized that island geography and biology have significantly influenced the prevalence and parasitemia of hemogregarine parasitism of *P. erhardii* over time. Specifically, we predicted that both prevalence and parasitemia would be negatively associated with island size (km²), island age (years since isolation occurred), and spatial isolation (distance) (km) (cf. MacArthur and Wilson 1967, Hess 1996, Roca et al. 2009), but positively associated with insular host density.

**Materials and Methods**

**Study System**

The Cycladic island archipelago comprises several hundred islands and islets. Larger islands are covered by a patchwork of open habitats, ranging from sclerophyllous maquis and coastal heaths to

---

**Figure 1.** Map of islands sampled for Apicomplexan parasites and their host, *Podarcis erhardii*. Islands in the Cyclades were chosen based on variety of age (in years) and area (in km²) of each island. Islands sampled are shown in grey. Island acronyms: Amorgos (AM), Anafi (AF), Andros (AN), Antikeros (AT), Fidoussa (FD), Glaronissi (GL), Ios (IO), Iraklia (IR), Keros (KE), Kisiri (KS), Lazaros (LZ), Makria (MK), Mando (MN), Megalo Fteno (MG), Mikro Fteno (MF), Naxos (NX), Pacheia (PC), Tinos (TN).
agricultural areas, riverine thickets, and exposed rock glades. The islands experience typical Mediterranean climate with wet, mild winters and hot, dry summers. In total, we sampled 18 Cycladic islands in this study. Islands sampled were chosen to represent a sufficiently broad range of periods of isolation (25 to 200,000 years) and sizes (0.008 to 379.95 km²) to reflect the varying conditions in the island system (Table S1). All sampling and data collection was conducted at low elevation (< 500 m above sea level) sites dominated by phrygana or marquis shrubland.

*Podarcis erhardii* is native to the southern Balkans, ranging as far north as Bulgaria and west into Albania; it is found throughout mainland Greece and the Aegean islands, including the Cyclades archipelago (Valakos et al. 1999). The complex geologic history of the Cycladic islands has driven notable divergence in *Podarcis* morphology (Brock et al. 2015, Donihue 2016), behavior (Pérez-Mellado and Casas 1997, Deem and Hedman 2014, Donihue et al. 2015), and genetic diversity (Poulakakis et al. 2003, Hurston et al. 2009). In natural habitats, *P. erhardii* is commonly infected with mites (*Ophionyssus* sp., *Acari: Trombiculidae*), as well as with ticks (*Haemaphysalis* sp., *Acari: Ixodidae*) on islands with domestic livestock (Pafilis et al. 2013). *Podarcis* lizards are also commonly infected with hemogregarine parasites in native populations (Harris et al. 2011, Garrido and Pérez-Mellado 2013).

Hemogregarine parasites (Apicomplexa: Adeleorina) infect red blood cells (RBCs) of their hosts and are found in a wide range of vertebrate species, including all orders of Reptilia (Telford, 2008) and several *Podarcis* species (Roca and Galdón 2009). Hemogregarinines are vectored by a diverse group of invertebrates, including mites (*Acari*), fleas (*Siphonaptera*), and sandflies (*Phlebotominae*) (Smith 1996). The effects of hemogregarine infection on reptile hosts, including *Podarcis* lizards, are not widely understood.

**Data Collection**

We determined island age using bathymetric data and historic estimates of rising sea levels in the region (from the Pleistocene until present) (see Brock et al. 2015). Island area is represented as the size of islands in square kilometers. Host population density was determined as the number of *P. erhardii* individuals seen across a 100-meter transect (individuals/100-m) on each island at the site of sampling. Along the same transect at each study site, we estimated vegetation cover as the percent ground covered by plants in 1-squared meter quadrat. Spatial isolation of each island from the mainland was measured as the distance in kilometers separating the focal island to the nearest larger land mass (i.e. a potential source land mass for overwater dispersion). All field sampling was conducted in 2016.

Resident *P. erhardii* populations at a single representative site on each island (Fig. 1) were sampled in habitat patches at low elevation dominated by phrygana or marquis shrubland. Sites were non-adjacent to roads, towns, agriculture, or other forms of development, and were comparable across islands.
framework to explicitly test hypotheses on both direct and indirect causal relationships among data (Ullman 2001, Arhonditsis et al. 2006, Schreiber et al. 2006). Unlike other methods used in hypothesis testing, SEM is a robust technique for assessing relationships among data with complex interrelationships and interactions (Arhonditsis et al. 2006) making it ideal for ecological data collected at two scales that are expected to be correlated. SEM models were generated using the ‘lavaan’ package (Rosseel 2012). The first hypothesized SEM (Model A) is based on two latent variables that we predicted to be related to parasitism of Podarcis hosts: ‘island’ is defined by direct paths to island area (km$^2$), time of isolation of each island population (age in years), the spatial isolation, i.e. distance of each island to the nearest larger land mass (km), vegetation cover (percent cover averaged on a 100-m transect) and host density (indiv/100-m) (Fig. 2). ‘Host’ was defined by direct paths to body mass (g), snout-vent length (cm), age class (adult or juvenile), and sex. ‘Island’ and ‘host’ latent variables were predicted to have direct connections to parasitemia (at the host-individual scale). We used modification indices to explore additional links in the data that may not have been included in the original conceptualization of Model A. Of the relationships suggested by modification indices, four additional indirect paths were included in the second SEM (Model B) of parasitemia data, which represent interaction terms. An indirect path was created between host age class and snout-vent length, between host sex and host body mass, and between vegetation cover and both island area and host density. We also included indirect paths between island area and host density in both Model A and B, because a large amount of island research has found significant correlation between island size and population density (MacArthur et al. 1972, Wright 1980, Rooda and Dean-Bradley 2002, Keesing et al. 2006).

Among the measurements of island characteristics, some variables violated normality assumptions (even when transformed) used for maximum likelihood estimation procedures in traditional SEMs, so we used diagonally-weighted least squares estimation for these models (Mindrilă 2010). Model fit was assessed using chi-square tests, root-mean square error of approximation, and comparative fit index.

| Results of multiple regressions on prevalence of hemogregarine infection in insular P. erhardii populations |
|---------------------------------------------------------------|
| **Dependent variable:** |
| Prevalence (% infection) |
| (1) | (2) |
| Island Age | -0.075* | -0.075** |
| (0.036) | (0.027) |
| Island Area | -0.050 | 0.073 |
| (0.054) | (0.059) |
| Host Density | 0.201** | 0.222*** |
| (0.073) | (0.059) |
| Island Distance | 0.072 | 0.099 |
| Vegetation Cover | -0.074 | (0.130) |
| Average Snout-Vent Length | 5.307** | 4.234** |
| (2.349) | (1.817) |
| Average Body Mass | -1.868** | -1.737** |
| (0.695) | (0.616) |
| Intercept | -17.284* | -13.356* |
| (8.573) | (6.549) |
| Observations | 18 | 18 |
| $R^2$ | 0.717 | 0.690 |
| Adjusted $R^2$ | 0.519 | 0.594 |
| Residual Std. Error | 0.202 (df = 10) | 0.185 (df = 13) |
| F Statistic | 3.624** (df = 7; 10) | 7.219*** (df = 4; 13) |

Note: *p<0.1 **p<0.05 ***p<0.01
Fig. 2 illustrates the causal relationships that were hypothesized for this host-parasite system.

**Results**

Hemogregarine infections were ubiquitous across all 18 study islands, but prevalence varied widely. Infection prevalence ranged between 7% in the island population on Antikeros to 100% on the island Mando; on average, 68% of all lizards were infected (of 511 total individuals sampled: see Table S1). Overall parasitemia ranged from 0.0001 to 0.1211% infected RBCs (per 10000 RBCs). The average parasitemia for all infected *P. erhardii* hosts was 0.0044% infected RBCs; average parasitemia for *P. erhardii* populations ranged from 0.0002 to 0.027% infected RBCs.

**Prevalence Among Islands**

Our first model indicated that vegetation cover, distance to mainland, and island area were not significant predictors for parasite prevalence (adjusted $R^2 = 0.52$, $p = 0.032$; Table 1). Removing these terms from our regression did not dramatically improve our model fit (adjusted $R^2 = 0.59$, $p = 0.0028$; Table 1). This model indicates that prevalence is negatively correlated with island age and average host body mass, and positively correlated with host density and snout-vent length. These models also suggest that prevalence is non-significantly negatively correlated with island area and vegetation cover, and non-significantly positively correlated with distance to mainland. This suggests that islands with more dense host populations and
more recent (younger) islands tend to have higher hemogregarine prevalences.

**Structural Equation Models of Parasitemia**

Model A did not meet criteria for model fitting parameters (chi-square = 187.383, df = 32, RMSEA = 0.100, CFI = 0.909). We rejected this model because the root-mean square error of approximation suggests a poor fit (Browne and Cudeck 1993). The second SEM of parasitism among individual hosts (Model B) provided a better fit to the data (chi-square = 89.321, df = 28, RMSEA = 0.067, CFI = 0.964) than did Model A. Following Browne and Cudeck (1993), the root-mean square error of approximation falls in the bounds of a ‘close’ fit (<0.08). The comparative fit index 0.968 also suggests a close fit (CFI should be close to 1) for this model (Bentler, 1990), and the chi-square of Model B (89.321) is nearly half that of Model A (187.383).

**Discussion**

Fragmentation and isolation of landscapes have complex effects on the ecology of host-parasite interactions; they are often mediated through a variety of ecological processes that may operate at different spatial scales. The natural history of land-bridge islands reflects the natural history of insular populations and can ultimately inform their evolutionary responses to isolation (Foufopoulos and Ives 1999, Hurston et al. 2009) and thus provide a suitable model system to examine the factors driving ecological processes at multiple scales. Our results support that island geography can shape not only the ecology of insular host populations, but also the interactions between hosts and their parasites.

Our analyses show that habitat fragmentation and insularity can significantly alter prevalence and parasitemia of hemogregarine infection in Podarcis hosts over evolutionary time, and this effect of insularity on parasitism likely occurs through two primary ecological mechanisms. The first mechanism concerns change in host population density initiated, in part, by changing island size (i.e., density compensation); the second is the effect of isolation time, which likely leads to changes in genetic variability (Whittaker and Fernández-Palacios 2007, Hidasi-Neto et al. 2018).

Specifically, the regression and SEM indicate that increasing island area reduces prevalence of hemogregarine infection, as well as parasitemia in the host *P. erhardii* in Aegean island populations, although this yielded a statistically non-significant p-value. We interpret the output as potential evidence that smaller islands harbor more infected individuals, and infected individuals harbor more parasites. Two of the smallest islands sampled, Kisiri and Mando, also had particularly high prevalence (96% and 100%, respectively) and average parasitemia (0.027% and 0.0053% infected RBCs, respectively) of all islands sampled. While this finding was not statistically significant (α = 0.05) we argue it provides enough correlational evidence to suggest that island area is an important factor to consider in future explorations of island host-parasite communities.

We also found significant positive relationships between host density and prevalence and parasitemia. Lizard populations are significantly denser on smaller Cycladic islands, consistent with the operation of density compensation, by which islands which are smaller in area support higher density of insular species compared to mainland populations (MacArthur et al. 1972, Wright 1980, Rooda and Dean-Bradley 2002, Keesing et al. 2006). The resulting associations between hemogregarine infection and island area and host density, taken together, support that density compensation for *P. erhardii* populations effectively extended to its native blood parasite. To this end, host density is greater on smaller islands and infection is subsequently more prevalent and intense. This indicates that biogeography in the region has shaped the distribution and intensity of hemogregarine parasitism. For example, on the small island Megalo Fteno (area: 0.06 km², host density: 20 indiv./100-m) prevalence (96%) and average parasitemia (0.00325% infected RBCs) were markedly higher than on the larger, less dense island Antikeros (area: 1.05 km², host density: 1 indiv./100-m), where prevalence was only 7%, and average parasitemia was 0.0002% infected RBCs.

It is also worth noting that our SEM analyses on parasitemia indicated that our models (Model B) better fit empirical data when including interaction terms among variables (see Results). The complex interrelationships of these island- and host-level variables illustrate the value of robust tools like SEM for testing ecological data (Ullman 2001, Arhonditsis et al. 2006) because it allows flexibility to consider interacting ecological variables. Some of the interaction terms that were added to fit Model B represent biological realism, e.g. the well-studied relationship between an organism’s age and sex with individual body size (Hill et al. 2016). More notable, however, is the interaction terms between vegetation cover and both island area and host density, as well as an interaction term between island area and host density which was included in both model A and B (Fig. 2). We interpret the interaction of these terms as evidence for potentially important trophic relationships among species in this system, and the role of resource availability on parasitism of *P. erhardii*. Hemogregarines are trophically-transmitted parasites, with invertebrates often serving as vectors (Telford 2008). Therefore, we might expect that differences in vegetation and variation in *P. erhardii* population size between islands may be drivers of heterogeneity in invertebrate (i.e., potential vectors) distribution (Wu et al. 2019). Hematophagous ectoparasites were not explicitly explored in this study, but we did observe common (and occasionally heavy) occurrence of mites (Ophionyssus sp.) on *P. erhardii*. *Ophionyssus* sp. may be another possible vector of hemogregarines (Allison and Desser 1981, Hlavová-Kočíková et al. 2014). This would be a valuable area of future research to understand the transmission
biology and biogeography of the entire life cycle of this hemogregarine parasite.

The time since isolation of each island was negatively related to hemogregarine prevalence and parasitemia, while spatial isolation (distance to mainland) was positively (though non-significantly) related to prevalence and parasitemia. Island populations that have been isolated for increasingly long periods of time have lower prevalence of hemogregarines and lower levels of parasitemia. One possibility is that reduced genetic diversity of isolated populations of hemogregarine parasites leads to impoverished parasite populations in insular hosts that are isolated for long periods (Pérez-Rodríguez et al. 2013, but see also Illera et al. 2015). However, other research on isolation of hosts and their parasites has demonstrated that host may be more susceptible to parasitism due to inbreeding over time (Acevedo-Whitehouse and Cunningham 2006, Chapman et al. 2009, Luikart et al. 2008). Genetic diversity is reduced over time following isolation of a population, and the implications of reduced genetic variability in hosts as well as in parasites has cascading impacts on host-parasite interactions (Nieberding et al. 2006, Plaisance et al. 2008, Ishtiaq et al. 2009). In cases where hosts are inbred, genetic inbreeding may lead to immunosuppression and thereby increase parasitism (Reed and Frankham 2003, Charpentier et al. 2008). This study suggests that isolation leads to lower parasitism prevalence and lower parasitemia in host populations isolated for longer periods. A possible mechanism for this pattern is a loss of parasite genetic diversity over evolutionary time, thereby reducing the ability of parasites to maintain transmission cycles. Spatial isolation, however, was positively (though not significantly) related to prevalence and parasitism. Islands that are spatially isolated likely have less colonization events (MacArthur and Wilson 1967, Valente et al. 2020). This suggests that the causative factor for increased or decreased parasitism in this system is connected to the prevalence of opportunities for inputs (of hosts) from other land masses, rather than temporal isolation per se (Ishtiaq et al. 2009).

The significance of island area, host density, and island spatial and temporal isolation on the distribution and intensity of hemogregarine infections in P. erhardii populations demonstrate several important ecological changes that occur following isolation of insular populations. The onset of density compensation following restriction of habitat size leads to notable changes in the ecology of insular species (Blumstein and Daniel 2005, Keesing et al. 2006) and their parasites, as shown here. The influence these changes have on host-parasite interactions has not previously received much attention in disease ecology literature or in studies on the biogeography of parasites.

This study provides a model of how host-parasite interactions can change over evolutionary time when populations become isolated following fragmentation. We found that changes in amount of available habitat and density of populations can effectively change the prevalence and intensity of native infections. Our analyses also suggest that reduction in genetic diversity, a function in part of how long a population has been isolated, could be involved in reducing prevalence and parasitemia, although this remains to be formally tested. This in turn suggests that spatial fragmentation can drive changes in host-parasite dynamics over time. In particular, the size of island habitats and the density of populations on those islands may significantly alter the interactions between hosts and hemogregarine parasites through the mechanism of density compensation following isolation (MacArthur et al. 1972, Wright 1980, Keesing et al. 2006). The temporal and spatial isolation of islands also affects these interactions over evolutionary time, potentially by impacting the genetic variability of hosts and parasites, however, further exploration is this area is necessary for understanding genetic responses to geographic isolation in host-parasite island systems (Illera et al. 2015). The influence of these island characteristics on host-parasite interactions implies that parasitism can be significantly altered by the characteristics of the islands or island-like fragments. Such implications are important for when predicting how fragmentation may alter host-parasite ecology in natural systems, and by what mechanism.

Acknowledgements
The authors thank Dr. Bobbi Low and Dr. Donald Zak for their support and insight throughout the conception and assembly of this research. The authors also appreciate Dr. Johannes Foufopoulos for support during field work. Thanks especially to Cassandra Coulter, Blake Graber, Eric Krawczyk, Kasey McDonald, Lauren Vesprani for invaluable assistance in lab and field collection. All work was approved by the University of Michigan Institutional Animal Care & Use Committee (Protocol PRO00006987) and in accordance with the Greek Government (Permit ΑΔΑ: ΩΘΤ84653Π8-Β3Μ). This work was funded School of Natural Resources and Environment and the Rackham Graduate School at the University of Michigan.

Author Contributions
JF and SM contributed to field work planning, data collection, manuscript drafting and editing, and approval of the final manuscript and associated figures and materials. JF also conducted project design, laboratory work, and data analysis.

Data Accessibility
The datasets generated and/or analyzed during the current study are available in the figshare repository at 10.6084/m9.figshare.5673421 and 10.6084/m9.figshare.5673415. The authors will provide any additional data or analyses upon reasonable request.
Supplementary Material

The following materials are available as part of the online article from https://escholarship.org/uc/fb

Table S1. Measures of island geographic characteristics and aggregate results of host biology, parasite prevalence, and parasitemia per island population of Podarcis erhardii.

Figure S1. Image of infected mature erythrocytes from a blood smear of Podarcis erhardii.

References

Acevedo-Whitehouse, K. & Cunningham, A. (2006) Is MHC enough for understanding wildlife immunogenetics? Trends in Ecology and Evolution, 21, 433–438.

Adler, G.H. & Levins, R. (1994) The island syndrome in rodent populations. The Quarterly Review of Biology, 69, 473–490.

Allison, B. & Desser, S.S. (1981) Developmental stages of Hepatozoon lygosomarum (Doré 1919) comb. n. (Protozoa: Haemogregarinidae), a parasite of a New Zealand skink, Leiolopisma nigriplantare. The Journal of Parasitology, 67, 852-858.

Arhonditsis, G.B., Stow, C.A., Steinberg, L.J., Kenney, M.A., Lathrop, R.C., McBride, S.J. & Reckhow, K.H. (2006) Exploring ecological patterns with structural equation modeling and Bayesian analysis. Ecological Modelling 192, 385–409.

Bentler, P.M. (1990) Comparative fit indexes in structural models. Psychological Bulletin, 107, 238–246.

Blondel, J. (2000) Evolution and ecology of birds on islands: trends and prospects. Life and Environment, 50, 205 – 220.

Blumstein, D.T. & Daniel, J.C. (2005) The loss of anti-predator behaviour following isolation on islands. Proceedings of the Royal Society B, 272, 1663–1668.

Brock, K.M., Bednekkoff, P.A., Pafilis, P. & Foufopoulos, J. (2015) Evolution of antipredator behavior in an island lizard species, Podarcis erhardii (Reptilia: Lacertidae): the sum of all fears? Evolution, 69, 216–231.

Browne, M.W., Cudeck, R. (1993) Alternative ways of assessing model fit. In: Testing Structural Equation Models (ed. by K.A. Bollen, and J.S. Long), pp.136-162. Sage, Newbury Park, USA.

Burnham, K.P. & Anderson, D.R. (2002) Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach (Second). Springer-Verlag, New York.

Chapman, J.R. Nakagawa S., Colman, D.W., Slate, J. & Sheldon, B.C. (2009) A quantitative review of heterozygosity–fitness correlations in animal populations. Molecular Ecology, 18, 2746–2765.

Charpentier, M.J.E., Williams, C.V. & Drea, C.M. (2008) Inbreeding depression in ring-tailed lemurs (Lemur catta): genetic diversity predicts parasitism, immunocompetence, and survivorship. Conservation Genetics, 9, 1605–1615.

Clay, K. (2003) Parasites lost. Nature, 421, 585–586.

Combes, C. (2001) Parasitism: the ecology and evolution of intimate interactions. The University of Chicago Press, Chicago, USA.

Deem, V. & Hedman, H. (2014) Potential cannibalism and intraspecific tail autotomy in the Aegean wall lizard, Podarcis erhardii. Hyla, 2014, 33–34.

Donihue, C.M. (2016) Aegean wall lizards switch foraging modes, diet, and morphology in a human-built environment. Ecology and Evolution, 6, 7433–7442.

Donihue, C.M., Brock, K.M., Foufopoulos, J. & Herrel, A. (2015) Feed or fight: testing the impact of food availability and intraspecific aggression on the functional ecology of an island lizard. Functional Ecology, 30, 566-575.

Foufopoulos, J. & Ives, A.R. (1999) Reptile extinctions on land bridge islands: life history attributes and vulnerability to extinction. The American Naturalist, 153, 1–25.

Galdón, M.A., Roca, V., Barbosa, D. & Carretero, M.A. (2006) Intestinal helminth communities of Podarcis bocagei and Podarcis carbonelli (Sauria: Lacertidae) in NW Portugal. Helminthologia, 43, 37–41.

Garrido, M. & Pérez-Mellado, V. (2013) Prevalence and intensity of blood parasites in insular lizards. Zoologischer Anzeiger, 252, 588–592.

Gouy de Bellocq, J., Morand, S. & Feliu, C. (2002) Patterns of parasite species richness of Western Palearctic micro-mammals: island effects. Ecography, 25, 173–183.

Haklová-Kočíková, B., Hůžkanová, A., Majláth, I., Račka, K., Harris, D.J., Földvári, G., Tryjanowskii, P., Kokošová, N., Malčeková, B. & Majláthová, V. (2014) Morphological and molecular characterization of Karyolysus – a neglected
but common parasite infecting some European lizards. Parasites and Vectors, 7, doi: 10.1186/s13071-014-0555-x.

Harris, D.J., Maia, J.P.M.C. & Perera, A. (2011) Molecular survey of Apicomplexa in Podarcis wall lizards detects Hepatozoon, Sarcocystis and Eimeria species. The Journal of Parasitology, 98, 1–7.

Hess, G. (1996) Disease in metapopulation models: implications for conservation. Ecology, 775, 1617–1632.

Hidasi-Neto, J, Bailey, R.I., Vasseur, C., Woas, S., Ulrich, W, Jambo, O., Santos, A.M.C., Cianciaruso, M.V. & Prinzing, A. (2018) A forest canopy as a living archipelago: why phylogenetic isolation may increase and age decrease diversity. Journal of Biogeography, 46, 158–169.

Hill, R.W., Wyse, G.A. & Anderson, M. (2016) Animal physiology. 4th edn. Sinauer Associates Inc. Publishers, Sunderland, USA.

Hlavac, M. (2018) stargazer: well-formatted regression and summary statistics tables. R package version 5.2.1. Digital resource available at https://cran.r-project.org/web/packages/stargazer/stargazer.pdf.

Hurston, H., Voith, L., Bonanno, J., Foufopoulos, J., Pafilis, P., Valakos, E. & Anthony, N. (2009) Effects of fragmentation on genetic diversity in island populations of the Aegean wall lizard Podarcis erhardii (Lacertidae, Reptilia). Molecular Phylogenetics and Evolution, 522, 395–405.

Illera, J.C., Fernández-Álvarez, Á., Hernández-Flores, C.N. & Foronda, P. (2015) Unforeseen biogeographical patterns in a multiple parasite system in Macaronesia. Journal of Biogeography 42, 1858–1870.

Ishtiaq, F., Clegg, S.M., Phillimore, A.B., Black, R.A., Owens, I.P.F. & Sheldon, B.C. (2009). Biogeographical patterns of blood parasite lineage diversity in avian hosts from Southern Melanesian islands. Journal of Biogeography, 37, 120–132.

Kapsimalis, V., Pavlopoulos, K., Panagiotopoulos, I., Drakopoulou, P., Vandarakis, D., Sakelariou, D. & Anagnostou, C. (2009) Geoarchaeological challenges in the Cyclades continental shelf (Aegean Sea). Zeitschrift Für Geomorphologie, Supplementary Issues, 53, 169–190.

Keesing, F., Holt, R.D. & Ostfeld, R.S. (2006) Effects of species diversity on disease risk. Ecology Letters, 9, 485–498.

Koop, J.A.H., DeMatteo, K.E., Parker, P.G. & Whiteman, N.K. (2014) Birds are islands for parasites. Biology Letters, 10, 6–10.

Kuris, A.M., Blaustein, A.R. & Aio, J.J. (1980) Hosts as islands. American Naturalist, 116, 570–586.

Lafferty, K.D. & Kuris, A.M. (2002) Trophic strategies, animal diversity and body size. Trends in Ecology and Evolution, 17, 507–513.

Lefcheck, J. (2021). Structural equation modeling in R for ecology and evolution. Digital resource available at https://jslefche.github.io/sem_book/index.html.

Loiseau, C., Melo, M., Lobato, E., Beadell, J.S., Fleischer, R.C., Reis, S., Doutrelant, C. & Covas, R. (2017) Insularity effects on the assemblage of the blood parasite community of the birds from the Gulf of Guinea. Journal of Biogeography, 44, 2607–2617.

Luikart, G., Pilgrim, K., Visty, J., Ezenwa, V.O. & Schwartz, M.K. (2008) Candidate gene microsatellite variation is associated with parasitism in wild bighorn sheep. Biology Letters, 4, 228–231.

MacArthur, R.H. & Wilson, E.O. (1967) The theory of island biogeography. Princeton University Press.

MacArthur, R.H., Diamond, J.M., & Kerr, J.R. (1972) Density compensation in island faunas. Ecology, 53, 330–342.

Margolis, L.L., Esch, G.W., Holmes, J.C., Kuris, A.M., & Schad, G.A. (1982) The use of ecological terms in parasitology. The Journal of Parasitology, 68, 131–133.

McCallum, H. & Dobson, A. (2002) Disease, habitat fragmentation and conservation. Proceedings of the Royal Society B, 269, 2041–2049.

Mîndrilă, D. (2010) Maximum likelihood (ML) and diagonally weighted least squares (DWLS) estimation procedures: a comparison of estimation bias with ordinal and multivariate non-normal data. International Journal of Digital Society, 1, 60–66.

Morand, S. & Krasnov, B.R. (2010) The Biogeography of Host-Parasite Interactions, 1st edn. Oxford University Press, Oxford, UK.

Nieberding, C., Morand, S., Libois, R. & Michaux, J.R. (2006) Parasites and the island syndrome: the colonization of the western Mediterranean
islands by *Heligmosomoides polygyrus* (Dujardin, 1845). Journal of Biogeography, 33, 1212–1222.

Novosolov, M., Raia, P. & Meiri, S. (2013) The island syndrome in lizards. Global Ecology and Biogeography, 22, 184–191.

Patiño, J., Whittaker, R.J., Borges, P.A.V., et al. (2017) A roadmap for island biology: 50 fundamental questions after 50 years of The Theory of Island Biogeography. Journal of Biogeography, 44, 963–983.

Pena, E.A. & Slate, E.H. (2006) Global validation of linear model assumptions. Journal of the American Statistical Association, 101, 341-354.

Pérez-Mellado, V. & Casas, J.L. (1997) Pollination by a lizard on a Mediterranean island. Copeia, 1997, 593-595.

Pérez-Rodríguez, A., Ramírez, Á., Richardson, D.S. & Pérez-Tris, J. (2013) Evolution of parasite island syndromes without long-term host population isolation: parasite dynamics in Macaronesian blackcaps *Sylvia atricapilla*. Global Ecology and Biogeography, 22, 1272–1281.

Pirazzoli, P.A. & Pluet, J. (1991) World atlas of Holocene sea-level changes. Elsevier.

Plaisance, L., Rousset, V., Morand, S. & Littlewood, D.T.J. (2008) Colonization of Pacific islands by parasites of low dispersal ability: phylogeography of two monogenean species parasitizing butterflyfishes in the South Pacific Ocean. Journal of Biogeography, 35, 76–87.

Poulakakis, N., Lymberakis, P., Antoniou, A., Chalkia, D., Zourou, E., Mylonas, M. & Valakos, E. (2003) Molecular phylogeny and biogeography of the wall-lizard *Podarcis erhardii* (Squamata: Lacertidae). Molecular Phylogenetics and Evolution, 28, 38-46.

Poulin, R. (2004) Macreocological patterns of species richness in parasite assemblages. Basic and Applied Ecology 5, 423–434.

Poulos, E., Ghionis, G. & Maroukian, H. (2009) Sea-level rise trends in the Attico – Cycladic region (Aegean Sea) during the last 5000 years. Geomorphology, 107, 10–17.

R Core Team. (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Digital resource available at https://www.R-project.org/.

Reed, D.H. & Frankham, R. (2003) Correlation between fitness and genetic diversity. Conservation Biology, 17, 230–237.

Roca, V. & Galdón, M.A. (2009) Haemogregarine blood parasites in the lizards *Podarcis bocagei* (seoane) and *P. carbonelli* (Pérez-Mellado) (Sauria: Lacertidae) from NW Portugal. Systematic Parasitology, 75, 75–79.

Roca, V., Foufopoulos, J., Valakos, E. & Pafilis, P. (2009) Parasitic infracomunities of the Aegean wall lizard *Podarcis erhardii* (Lacertidae, Sauria): isolation and impoverishment in small island populations. Amphibia-Reptilia, 30, 493–503.

Rodda, G. H. & Dean-Bradley, K. (2002) Excess density compensation of island herpetofaunal assemblages. Journal of Biogeography, 29, 623–632.

Rosindell, J. & Harmon, L. J. (2013) A unified model of species immigration, extinction and abundance on islands. Journal of Biogeography, 40, 1107–1118.

Rosseel, Y. (2012) lavaan: an R Package for Structural Equation Modeling. Journal of Statistical Software, 48, 1–36.

Schall, J.J. (1990) The ecology of lizard malaria. Parasitology Today, 6, 264–269.

Schreiber, J.B., Nora, A., Stage, F.K., Barlow, E.A. & King, J. (2006) Reporting structural equation modeling and confirmatory factor analysis results: a review. The Journal of Educational Research, 99, 323–338.

Simberloff, D.S. (1976) Experimental zoogeography of islands: effects of island size. Ecology, 57, 629–648.

Simberloff, D.S. & Wilson, E.O. (1969) Experimental zoogeography of islands: the colonization of empty islands. Ecology, 50, 278–296.

Smith, T.G. (1996) The genus Hepatozoon (Apicomplexa: Adeleina). The Journal of Parasitology, 82, 565–585.

Telford, S. (2008) Hemoparasites of the reptilia: color atlas and text. CRC press. 376 pp.

Tomé, B., Pereira, A., Jorge, F., Carretero, M.A., Harris, D. J., & Perera, A. (2018) Along for the ride or missing it altogether: exploring the host specificity and diversity of haemogregarines in the Canary Islands. Parasites & Vectors, 11, doi: 10.1186/s13071-018-2760-5.

Torchin, M.E., Lafferty, K.D., Dobson, A.P., Mckenzie, V.J. & Kuris, A.M. (2003) Introduced species...
and their missing parasites. Nature, 421, 628–630.

Whittaker, R.J. & Fernández-Palacios, J.M. (2007) Island biogeography: ecology, evolution and conservation. 2nd Ed. Oxford University Press, Oxford.

Wright, S.J. (1980) Density compensation in island avifaunas. Oecologia, 45, 385–389.

Wu, Q., Richard, M., Rutschmann, A., Miles, D.B. & Clobert, J. (2019) Environmental variation mediates the prevalence and co-occurrence of parasites in the common lizard, Zootoca vivipara. BMC Ecology, 19, doi: 10.1186/s12898-019-0259-3.