Drivers of female and male body size in the Aegean wall lizard, *Podarcis erhardii*

by

Shelby R. Stadler

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Faculty Advisors:

Dr. Johannes Foufopoulos, Chair

Dr. Kinsey Brock, Co-Chair

Abstract

Biologists have noted since the days of Darwin and Wallace how island populations of vertebrates differ in body size from their mainland relatives. While much progress has been made in understanding global patterns in body size evolution across different species of wildlife (Benítez-López *et al*., 2021) scientists still don't have a good understanding of the ecological and environmental processes that generate these patterns. While many studies concerning vertebrate body size evolution have been performed, a hypothesis-driven approach that concerns life history differences in females and males is lacking, and it is not even known whether any putative factors influence female and male body size in the same way. We examined 36 populations of Aegean wall lizards (*Podarcis erhardii,* Lacertidae), a species widely distributed across the Balkan mainland and hundreds of Aegean islands. The species is unusual in that it not only occurs in a broad range of ecological conditions, but also that it varies substantially in body size (Males: 37%; Females: 33.9%) and that it occurs in numerous, clearly isolated and well-characterized island populations. It therefore constitutes an excellent model for determining the drivers of island body size across varying island environments. Here we evaluate multiple hypotheses ranging from predation pressure (predator species richness), resource availability (Normalized Difference Vegetation Index (NDVI), seabird density, island area), and competition for mates (lizard density) as possible factors affecting lizard body size.

We found that the factors affecting both female and male lizard body size depend on the presence of nesting seabird colonies on an island. Female body size on seabird islands was most strongly associated with seabird colony density, while male body size on seabird islands was only associated with conspecific lizard population density, suggesting a role for seabird subsidies and increased food resources for the evolution of female body size and intraspecific competition in the evolution of male body size. On non-seabird islands, female body size was positively correlated with island size, while male body size was not significantly associated with any of the factors we measured. This suggests that different factors were associated with female and male body size evolution in island populations of *P. erhardii*, and we propose that a general pattern like the island rule is subject not only to selective forces that are sex-specific, but also that there will important differences dictated by island ecology.

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Introduction

Species from mainland and island populations tend to have different body sizes (Foster, 1967; Van Valen, 1973; Benítez-López *et al*., 2021). Biologists have noted from early on the distinct ecological conditions experienced by island species (Darwin, 1859; Carlquist 1965). For a variety of animals, such as birds (Clegg and Owens, 2002), mammals (Foster, 1964), and reptiles (Pafilis *et al*., 2009), organismal biologists have noted the evolution of divergent body sizes in island taxa relative to their closest mainland relatives (Foster, 1967; Lomolino, 2005). Compared to the mainland, small-bodied vertebrates tend to show a shift towards gigantism on islands (Lomolino, 2005), whereas large-bodied vertebrates tend to display a tendency towards island dwarfism (Heaney, 1978), a phenomenon termed the ‘island rule’ (Van Valen, 1973). Nonetheless, the generality of the island rule has been also been challenged, with some studies finding often only weak, or clade-specific patterns (Meiri *et al*., 2008; Itescu *et al*., 2018). While a recent global-scale study (Benítez-López *et al*., 2021) appears to have now convincingly demonstrated the globally pervasive occurrence of this rule, it has not yet shed light on the specific processes that generate these patterns.

Possible factors driving island body size evolution

While numerous processes have been proposed as possible drivers of island body size much uncertainly still exists. The global occurrence of the island rule suggests that repeat patterns in resource availability, intrapopulation processes, or species interactions associated with island environments, lead to predictable evolutionary shifts in body size among island populations (Foster, 1964; Van Valen, 1973, Benítez-López *et al*., 2021). Below we review some of the most important ones.

Resource availability: vegetation/NDVI. Given that the shift towards larger body sizes requires increased and dependable access to resources in the broad sense, it is reasonable to assume that the presence of large-bodied island vertebrates will be associated with the presence of more readily available island resources. High primary productivity by plants forms the fundament of most terrestrial food webs, and *ceteris paribus*, is expected to support individual-rich populations of large-bodied taxa. On Mediterranean islands for example, increased plant growth supports, via rich populations of insects and other arthropods, dense *Podarcis* lizard populations (Pérez-Mellado and Traveset, 1999). At the landscape level, extent of vegetation cover is typically captured by calculating the NDVI (Normalized Difference Vegetation Index) (Huang *et al*., 2021). Assuming that vegetation cover and the resources it represents, also constitute a factor limiting lizard biology, one would expect that islands with higher NDVI scores would be positively correlated with increased lizard average body size.

Resource availability: seabirds. On many small islands, primary productivity is not dependent on autochthonous photosynthetic activity but rather on marine subsidies (Pafilis *et al*., 2011). Substantial research suggests that nesting seabirds can act as mobile ecological links connecting otherwise isolated island ecosystems, with marine food webs (Sánchez-Piñero and Polis, 2000). Seabird-derived resources can take a variety of forms including food scraps, guano, and bird carcasses, all of which can be utilized by island vertebrates (Pafilis *et al*., 2009b). As a result, it has been proposed that island lizard body size will be correlated to the density of nesting seabirds (Pafilis *et al*., 2009b).

Island size. Numerous studies have investigated the relationship between island size and body size (Heaney, 1976; Lomolino, 1985; Boback and Guyer, 2003). The majority of these have found that species body size is positively correlated to island size (Clegg and Owens, 2003; Lomolino, 2005; Benítez-López *et al*., 2021) although some have also found the opposite pattern (Boback, 2003; Meiri *et al*., 2005; Meiri, 2007; Meiri *et al.*, 2008). Functionally, island size may be related to resource availability and several possible mediating mechanisms may be responsible. For example, large islands tend to be more productive, especially in arid Mediterranean environments, because they have higher mountains generating more vegetation-supporting orographic precipitation (Zhao, 2018). This also likely translates into a more seasonally stable food supply which in turn would suggest that starvation risk during the arid summer period is less severe. In general, a significant positive relationship between body and island size is typically seen as an argument in favor of the importance of resource availability

Competition. Competition for food and mates in lacertid lizards is typically takes the form of intense physical altercations which can lead to toe and limb amputations, tail loss and even death (Deem and Hedman 2014, Madden and Brock, 2018). Because these contests have fitness consequences and are also often won by the largest individual, they can act as drivers of intense selection for the evolution of larger body sizes. Recent studies in the Aegean and other places have shown that such competitive interactions become more frequent and intense with rising population density (Pafilis *et al*., 2009b; Sagonas *et al*., 2014; Donihue *et al*., 2015). As such, population density can be used as a proxy for intraspecific competition and the associated selection pressure on the evolution of larger body sizes, especially in males, which are known to engage in significantly more agonistic encounters than females.

Predation. Predation has the potential of being a powerful factor shaping adult body sizes in many species of wildlife. High predation rates, typically the product of a diverse predator community, are likely to result in reduced life expectancy in average island prey species (Pafilis et al. 2009a). This, in turn, means that individuals that delay reproduction by postponing sexual maturity by one or more seasons, face the distinct possibility of completely missing the opportunity to procreate. Consequently, in high predation environments, there is a strong selective advantage to commence reproduction at the earliest possible age (Stibor, 1992; Reznick *et al.* 1990). Since body growth in lizards tends to slow down at sexual maturity, that would mean that average body size in a high-predation population would be smaller than in a low-predation environment. This phenomenon has been observed both in free-living wildlife populations as well as in human-managed fisheries populations (Olsen *et al*., 2004).

Present Study

The present study focuses on the processes driving body size in ectothermic island vertebrates. It accomplishes this by comparing a broad range of endemic island populations which have evolved under a spectrum of divergent environmental conditions (e.g. presence/absence of seabirds, variable vegetation structure, different predation regimes, etc.). The study focuses on the Aegean wall lizard (*Podarcis erhardii,* Lacertidae), a generalist reptile species that is found across hundreds of islands in the Aegean Sea (Greece), and on mainland southeast Europe (Hurston *et al*., 2009). This species can be found across a broad spectrum of habitats ranging from stone desert to Mediterranean scrubland to montane conifer forest. This diversity in prevailing ecological conditions, together with the existence in discrete, well-characterized island populations, has generated substantial variation in observed body size (Males: 37%; Females: 33.9%; this study). This range in prevailing conditions makes this an ideal natural system to study ecological and environmental influences on body size on islands.

Body size evolution of *Podarcis erhardii* on islands in the Aegean has been a focus of much early herpetological research including foundational work by Wettstein (1953) who - while noting the great variation body size across the various Cycladic populations - was not able to explain it. A recent comprehensive study, that combined data from numerous islands and several lizard taxa, revealed that while drivers of body size evolution likely differ across species, but failed to identify the processes responsible for any one species, including *P. erhardii* (Itescu *et al*., 2018). Research conducted in the last decade, has highlighted important behavioral, ecological, and life history differences between male and female Aegean wall lizards, indicating that they are likely subject to different selection forces, and as such should be analyzed separately (Donihue, 2016; Brock *et al*., 2020, BeVier *et al*., 2021). The present study therefore builds on the previous work by analyzing patterns in body size across islands separately for males and females, while at the same time taking island ecology explicitly into account.

More specifically, in this study we aim to:

1. quantify the extent of variation in body size and external morphology across numerous island populations of Aegean Wall lizards, and
2. test the extent to which different hypotheses centering on the importance of predation, competition, resource availability, and stability, are associated with the evolution of large body sizes in male versus female island lizards.

Methods

Study System

We conducted this study in the Cyclades, a cluster of islands in the central Aegean Sea, Greece (Figure 1). The climate of the region is typical of the Mediterranean, with warm, arid summers, and mild, wet winters (Giorgi and Lionello, 2008). The island vegetation has been shaped by several thousand years of human activity and disturbance (Grove and Rackham, 2003) and consists largely of various forms of Mediterranean scrub (Rackham and Moody, 1996). The present landscape is a mosaic of agricultural fields, sclerophyllous evergreen maquis, and *phrygana*, a diverse species community of aromatic, summer-deciduous shrubs (Fielding and Turland, 2008). Landscape greenness, typically captured by the Normalized Difference Vegetation Index (NDVI), varies significantly between islands in the region, and depends predominantly on amount of local precipitation and substrate. In general, larger Aegean islands, as well as mainland sites, receive more orographic precipitation and have more extensive vegetation cover, than smaller, low profile islets (Zhao, 2018).

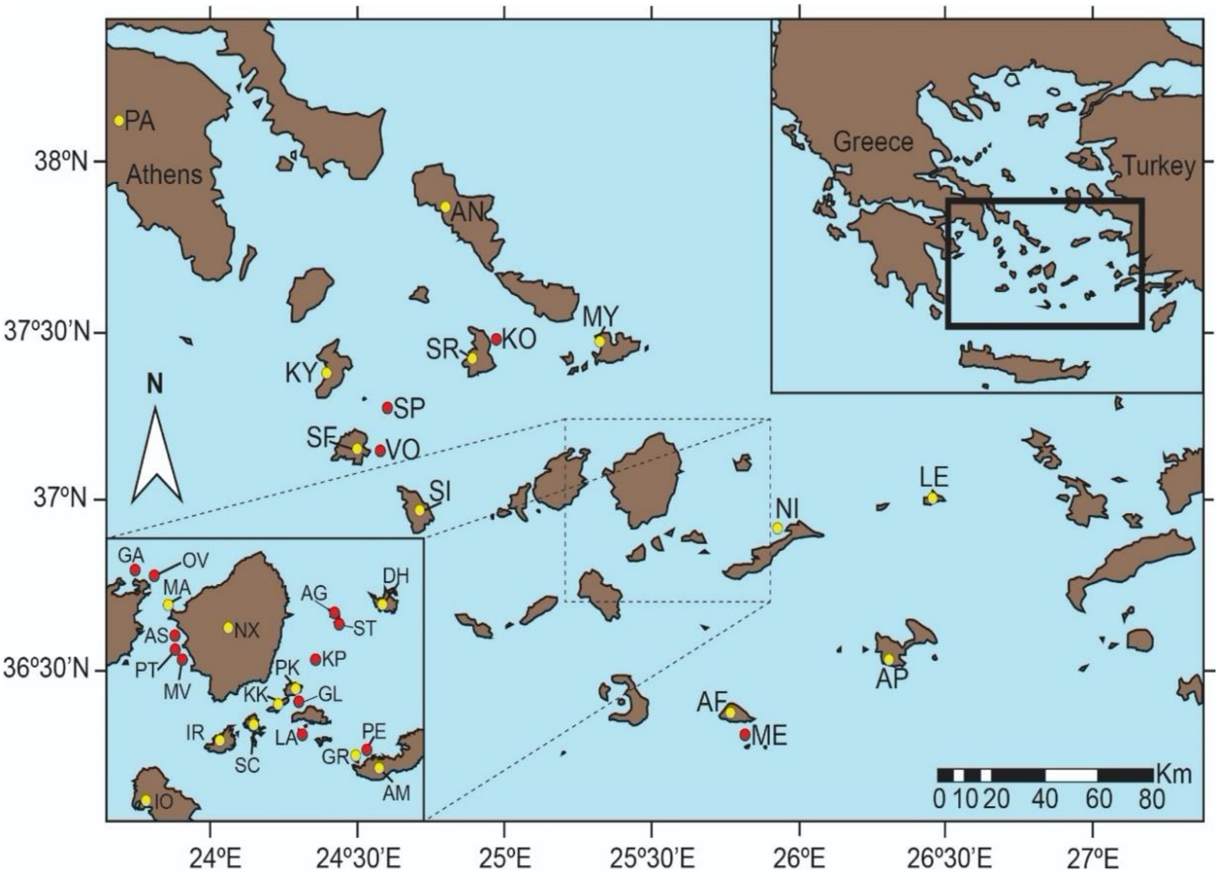

Figure 1. Map of study sites. One mainland site and 35 Cycladic island sites are indicated with a circle and acronym identifier. Sites are listed in alphabetical order. Agios Nikolaos (AG), Amorgos (AM), Anafi (AF), Andros (AN), Aspronissi (AS), Astypalea (AP), Dhonoussa (DH), Gaidouronissi (GA), Glaronissi (GL), Gramvoussa (GR), Ios (IO), Irakleia (IR), Kato Koufonissi (KK), Kommeno (KO), Kopria (KP), Kythnos (KY), Lazaros (LA), Levitha (LE), Mando (MA), Megalo Fteno (ME), Mikri Vigla (MV), Mykonos (MY), Naxos (NX), Nikouria (NI), Ovriokastro (OV), Pano Koufonissi (PK), Parnitha* (PA), Parthenos (PT), Petalidi (PE), Schoinoussa (SC), Serifopoula (SP), Serifos (SF), Sifnos (SI), Siros (SR), Strongyllo (ST), Vous (VO). Red circles indicate seabird islands, and yellow circles represent non-seabird islands. Asterick (*) indicates a mainland site.

The Aegean wall lizard (*Podarcis erhardii*, Figure 2) is a small- to medium-sized lacertid lizard that is native to the southern Balkans and inhabits many of the western Aegean Islands (Valakos *et al*., 2008). This species is mostly ground-dwelling and varies significantly in its body size across its distribution (Itescu *et al*., 2018). Adult body sizes range from 45-78mm, with a tail that can be twice as long as the body (Gruber, 1987; Donihue, 2015; Brock *et al*., 2020). *P. erhardii* is a generalist taxon with a broad distribution across different habitats and an opportunistic, omnivorous diet consisting primarily of various arthropods. However, on the islands this species is also known to opportunistically forage on plant material during the dry summer season (Brock *et al*., 2014).

Figure 2. A male Aegean wall lizard (*Podarcis erhardii*) from the isolated island of Astakida (SE Aegean Sea). Photo by Peter Oefinger.

Most of the islands that *P. erhardii* inhabits, sit on a shallow shelf and were connected during the last Ice Age forming one landmass known as Cycladia. Sea level rise since the end of the last glacial maximum led to the progressive flooding of the area, resulting in the formation of the present-day islands (Poulos *et al*., 2009). Because local reptile species like *Podarcis erhardii* are poor overwater dispersers, this history of island fragmentation also reflects the evolutionary history of the local island populations (Foufopoulos and Ives, 1999). Because of the significant period of isolation on these diverse island habitats, each island population appears to be closely adapted to the ecological conditions prevailing on each island (Hurston *et al*., 2009; Brock *et al*., 2015).

Island Characteristics

We visited 35 islands plus one mainland site, to obtain site-specific lizard population information, as well as local ecological and microenvironmental data (Table 1.). All study sites were all visited in May-June, for one to several days by at least one of the authors (K.M. Brock). Relative lizard population densities were quantified using a well-established approach of slowly walking one or two 100-meter long and 4-meter wide transects and recording any *P. erhardii* that were detected there (Brock *et al*., 2015; Donihue *et al*., 2015). This transect was always walked during peak lizard activity hours (0900-1100 and 1500-1700), on clear, sunny days with minimal wind (Brock *et al*., 2015).

In the Aegean Sea, the ecology of an island differs fundamentally dependent on the nesting presence of colonial seabirds (Pafilis *et al*., 2013; Gizicki *et al*., 2018). Smaller islands that harbor seabird nesting colonies have been shown to constitute intrinsically different environments for lizards than larger islands without seabirds (Pafilis *et al*., 2011; Pafilis *et al*., 2013; BeVier *et al*., 2021). Gull colonies provide crucial marine-derived subsides like guano, food scraps, and carcasses to otherwise dry, unproductive islet ecosystems, and these in turn represent important resources to resident lizards (Polis and Heard, 1996; Vervust *et al*., 2007). On each island, we therefore recorded the presence or absence of colonial seabirds (Yellow-legged gulls, *Larus michahellis*), as well as the density of these birds, measured as the number of nesting pairs per km^2. Presence of gull colonies is not just an important ecological driver of Aegean islands, but it also co-varies with many other putatively important factors. Thus, seabird islands tend to be small, predator free, and with high lizard densities, while non-seabird islands are greatly variable in size, with varying predator communities and vegetation cover and typically very low lizard densities. As a result, some of our hypotheses (e.g. competition and marine subsidies) could only be tested for seabird islands where these factors were important, while others (predation) could only be tested on non-seabird islands, therefore requiring separate analyses for the two types of islands.

Dense, shrubby vegetation is the preferred habitat for *P. erhardii*, as it represents both a food resource and provides shelter from predators (Brock *et al*., 2015). To quantify the amount of ecological resources available on each island and their possible effect on lizard body size, we calculated NDVI values (Normalized Difference Vegetation Index (NDVI)), a commonly used measure of landscape greenness (Huang *et al*., 2021). NDVI scores were obtained using images from the ESRI Landsat Explorer, which provides daily updated satellite images of Earth's surface (ESRI, 2018). The latitude and longitude of each study site was recorded, and input into the Landsat Explorer on ArcGIS Online to extract location-specific NDVI data. Each island's NDVI score was calculated by taking the date of field sampling at that site and finding the recorded data that was nearest date before and after the date of lizard capture and taking the average of the two values. This provided a specific, narrow NDVI calculation most relevant to the date the lizards were sampled.

To test for possible effects of predation pressure on body size, we calculated a metric of predation for each population. Previous work has shown that an index of predation pressure can be obtained by counting the number of different predator guilds found on each island (Brock *et al*., 2015). We assigned predator species into one of six predator guilds based on their ecological relationships to *P. erhardii,* and used the sum of the categories present on each island as a metric of predation pressure on that site. Following previously determined categories (Brock et al. 2015) we used the following 6 categories: 1. Rats (*Rattus rattus*), 2. Sand boas (*Eryx jaculus*), 3. Aerial predators (*Falco tinnunculus* and *Buteo buteo*), 4. Vipers (*Vipera ammodytes*), 5. Mammalian predators (feral cats [*Felis catus*], stone martens [*Martes foina*]), and 6. Colubrid (Other) snakes (*Dolichophis caspius, Elaphe quatuorlineata muenteri, Natrix natrix persa*. (Brock *et al*., 2015). Presence of predators on an island was determined using a combination published information (Handrinos and Akriotis, 1997; Valakos *et al*., 2008; Pafilis *et al*., 2009; Masseti, 2012; Brock *et al*., 2015) confirmed by field observations collected by two of the study authors (K.M.B. and J.F.). More specifically, each site was surveyed extensively by searching for signs of predator presence whether direct (live or dead individuals) or indirect (burrows, fecal matter, tracks) (Brock *et al*., 2015).

Lizard Measurements

We captured adult lizards from May to early July, in clear weather conditions (sunny with no wind). Adult animals were caught using telescopic, collapsible rods measuring ten feet in length, with a dental floss lasso attached to the end. Caught lizards were temporarily held in cotton cloth bags for further measurements. All animals were then taken temporarily into the lab; to reduce measurement error, morphometric measurements were performed by one of us (KMB) using precision digital calipers. As a measure of body size, we used Snout-Vent Length (SVL; expressed in mm) which is the most widely established relevant metric for lizards (Meiri, 2007). Lizards were then returned and released in the immediate vicinity of the capture site.

All research involving animals was conducted in accordance with the University of California-Merced Institutional Animal Care and Use Committee (IACUC protocol AUP17-0002) and permits provided by the Greek Ministry for Environment and Energy (ΑΔΑ: Ψ4Γ64653Π8-ΗΛ5, Ω8Δ84653Π8-ΒΞΧ, 6ΥΛΥ4653Π8-ΠΞΓ assigned to K.M. Brock).

Data Analysis

Data were analyzed in R (v1.3.959), using simple linear regressions in order to avoid overfitting the data (R Core Team 2020). Given known differences in life history and reproductive schedules which likely create different selection pressures and constraints, we analyzed female and male data separately (Donihue *et al.*, 2016; Brock *et al*., 2020). Female and male SVLs were averaged separately for each island, giving one female and one male average SVL value per each of the 36 sites. Given the aforementioned strong ecological differences between seabird and non-seabird islands, these were also analyzed separately.

The key variables thought to influence lizard body dimensions were lizard population density, seabird density, vegetation greenness (NDVI), intensity of predation, and log island area. To avoid collinearity issues these factors were correlated against each other using the *stats* package in R (R Core team, 2020). With the sole exception of the expected relationship between predator species nr and island size, all independent variables had correlation-coefficients less that 0.6 (Table 2). To determine which island factors are associated with average female and male SVL for seabird islands, we ran regressions of average female and male SVL against lizard density, seabird pairs per square kilometer, and Normalized Difference Vegetation Index (NDVI). Average female and male SVL values for non-seabird islands were regressed against lizard density, predator index, NDVI, and log island area.

Island	F Avg SVL (mm) (n)	M Avg SVL (mm) (n)	Lizard Density (Indiv/ 100m)	Seabird Density (Pairs/Km^2)	NDVI	Index of Predation (# predators/ island)	Log Island Area (Km^2)
Agios Nikolaos (AG)	61.26 ± 1.05 (11)	64.64 ± 0.58 (23)	10	37.48	0.25	2	-0.05
Amorgos (AM)	63.21 ± 2.39 (10)	68.73 ± 1.67 (12)	3	0	0.22	5	2.09
Anafi (AF)	53.45 ± 1.37 (10)	60.77 ± 2.0 (11)	4	0	0.23	3	1.69
Andros (AN)	60.34 ± 1.46 (11)	70.50 ± 0.99 (11)	7	0	0.54	6	2.58
Aspronissi (AS)	63.18 ± 1.14 (12)	65.57 ± 1.23 (10)	12	51.04	0.14	1	-1.42
Astypalea (AP)	64.54 ± 1.95 (7)	66.41 ± 1.21 (13)	2	0	0.15	3	2.00
Dhonoussa (DH)	54.51 ±1.02 (10)	56.44 ± 0.80 (10)	2	0	0.2	4	1.13
Gaidouronissi (GA)	69.01 ± 0.69 (15)	68.55 ± 0.65 (15)	8	45.88	0.25	1	-0.88
Glaronissi (GL)	62.07 ± 1.21 (6)	62.49 ± 0.66 (25)	1	13.87	0.24	1	-0.81
Gramvoussa (GR)	58.39 ± 1.01 (7)	64.39 ± 0.62 (23)	3.76	0	0.20	3	-0.12
Ios (IO)	59.31 ± 1.14 (8)	62.45 ± 1.04 (12)	5	0	0.11	6	2.01
Irakleia (IR)	56.64 ± 1.25 (11)	56.04 ± 1.0 (11)	3	0	0.18	6	1.26
Kato Koufonissi (KK)	57.73 ± 0.99 (10)	63.42 ± 0.53 (10)	2	0	0.25	3	0.66

Kommeno (KO)	65.76 ± 0.55 (12)	67.64 ± 1.29 (6)	13	11.95	0.12	3	-2.15
Kopria (KP)	62.35 ± 0.88 (12)	67.05 ± 0.78 (18)	5.5	27.22	0.20	0	-0.87
Kythnos (KY)	58.37 ± 1.72 (13)	62.16 ± 1.48 (17)	5	0	0.38	4	2.00
Lazaros (LA)	71.90 ± 1.53 (10)	74.12 ± 1.81 (10)	19	60.41	0.16	0	-1.86
Levitha (LE)	60.31 ± 1.68 (12)	69.63 ± 1.50 (19)	10	0	0.27	2	0.96
Mando (MA)	57.09 ± 1.65 (17)	59.30 ± 0.77 (32)	6	0	0.20	3	-1.60
Megalo Fteno (ME)	58.80 ± 1.72 (12)	60.20 ± 1.35 (23)	15	32.68	0.19	0	-1.23
Mikri Vigla (MV)	62.22 ± 1.16 (13)	61.70 ± 0.92 (12)	16	107.24	0.15	0	-2.70
Mykonos (MY)	62.79 ± 0.68 (22)	66.05 ± 0.38 (27)	2	0	0.17	5	1.61
Naxos (NX)	57.39 ± 1.73 (9)	60.24 ± 0.72 (27)	6	0	0.50	6	2.65
Nikouria (NI)	53.29 ± 0.88 (10)	57.82 ± 0.95 (11)	6	0	0.20	3	0.44
Ovriokastro (OV)	62.06 ± 1.27 (12)	62.79 ± 1.31 (13)	6	33.71	0.40	2	-0.66
Pano Koufonissi (PK)	55.43 ± 0.80 (13)	59.92 ± 1.10 (11)	3	0	0.22	5	0.76
Parnitha (PA)	63.99 ± 0.88 (12)	67.48 ± 1.16 (14)	7	0	0.32	6	3.00
Parthenos (PT)	63.73 ± 0.82 (27)	64.96 ± 0.73 (23)	14	52.22	0.13	2	-2.36
Petalidi (PE)	56.12 ± 0.96 (6)	54.61 ± 0.63 (8)	2	14.09	0.09	1	-1.30
Schoinoussa (SC)	54.73 ± 0.71 (13)	62.41 ± 0.53 (32)	1	0	0.14	5	0.95
Serifopoula (SP)	59.34 ± 1.13 (17)	65.66 ± 1.10 (13)	12	3.29	0.14	1	0.27
Serifos (SF)	60.67 ± 0.99 (25)	61.09 ± 1.02 (20)	3	0	0.32	4	1.84
Sifnos (SI)	62.26 ± 1.67 (11)	64.62 ± 1.33 (19)	2.3	0	0.37	5	1.86

Siros (SR)	66.58 ± 1.13 (16)	66.40 ± 1.24 (14)	9	0	0.30	5	2.01
Strongyllo (ST)	65.57 ± 2.45 (7)	71.41 ± 1.94 (9)	13	30.05	0.20	1	-0.44
Vous (VO)	66.62 ± 0.99 (10)	65.05 ± 1.11 (20)	12	24.68	0.34	0	-0.71

Table 1. Location and lizard characteristics for all 35 islands and the one nearby mainland site (Parnitha, PA). Islands are listed in alphabetical order and abbreviations correspond to labels on the map (Figure 1). Average female and male SVL, as well as 1 standard error are reported in millimeters, with the sample size *n* for each sex in parentheses. Lizard density was quantified as the number of individuals recorded per 100m transect. Seabird density is reported as the number of seabird pairs counted per square kilometer. Normalized Difference Vegetation Index (NDVI) is the measure of site vegetation greenness and was calculated using satellite imagery in Landsat Explorer Values can range from -1 to 1, with higher values indicating higher plant greenness. Index of predation is reported as the number of predator categories present on an island. Island areas are reported in km^2 as based on published information and have been log-transformed. (Foufopoulos and Ives, 1999; Poulos *et al*., 2009; Itescu *et al*., 2018).

Results

Islands in the data set range from the smallest islets (Kommeno at 0.007 km^2) to massive islands (Naxos at 429 km^2). Some islands are predator free, while others have up to 6 different types of predator. Out of the 36 islands, 14 had significant seabird colonies and were analyzed as “seabird islands”, and the remaining 21 islands were analyzed as “non-seabird” islands. Across our entire dataset, average female SVL varied from 53.29 mm to 71.90 mm, while male SVLs ranged from 54.61 mm to 74.12 mm. Seabird (SB) and non-seabird islands (NSB) differed significantly in important ecological characteristics: Area: -1.14 vs. 1.42; Average Index of Predation: 0 vs. 4.38; Average Lizard Density: 10.56 vs. 4.38; Average Seabirds per Km^2: 36.39 vs. 0, on seabird vs. non-seabird islands, respectively.

	Avg Female SVL	**Avg Male SVL**	**Log Island Area**	**Predator n**	**Lizard Density**	**Seabirds per Km^2**
Avg Male SVL	0.85					
Log Island Area	-0.22	0.04				

Predator n	-0.06	-0.01	0.00			
Lizard Density	0.45	0.50	-0.40	-0.17		
Seabirds per Km^2	0.29	0.12	-0.62	-0.32	0.52	
NDVI	0.19	0.10	0.54	0.05	-0.30	-0.23

Table 2. Spearman correlation matrix of the variables tested on seabird islands.

	Avg Female SVL	Avg Male SVL	Log Island Area	Predator n	Lizard Density
Avg Male SVL	0.74				
Log Island Area	0.48	0.41			
Predator n	0.23	0.05	0.60		
Lizard Density	0.24	0.34	0.10	-0.04	
NDVI	0.18	0.29	0.48	0.30	0.41

Table 3. Spearman correlation matrix of the variables tested on non-seabird islands.

Female body size

On seabird islands, average female SVL was positively correlated to nesting seabird density (pairs/km^2) (Linear Regression; $R^2 = 0.2458$, $P = 0.04105$, $N = 14$). In contrast, neither NDVI (Linear Regression; $R^2 = -0.0483$, $P = 0.538$, $N = 14$) nor lizard density (Linear Regression; $R^2 = 0.1242$, $P = 0.1176$, $N = 14$) were found to be significantly correlated with average female SVL.

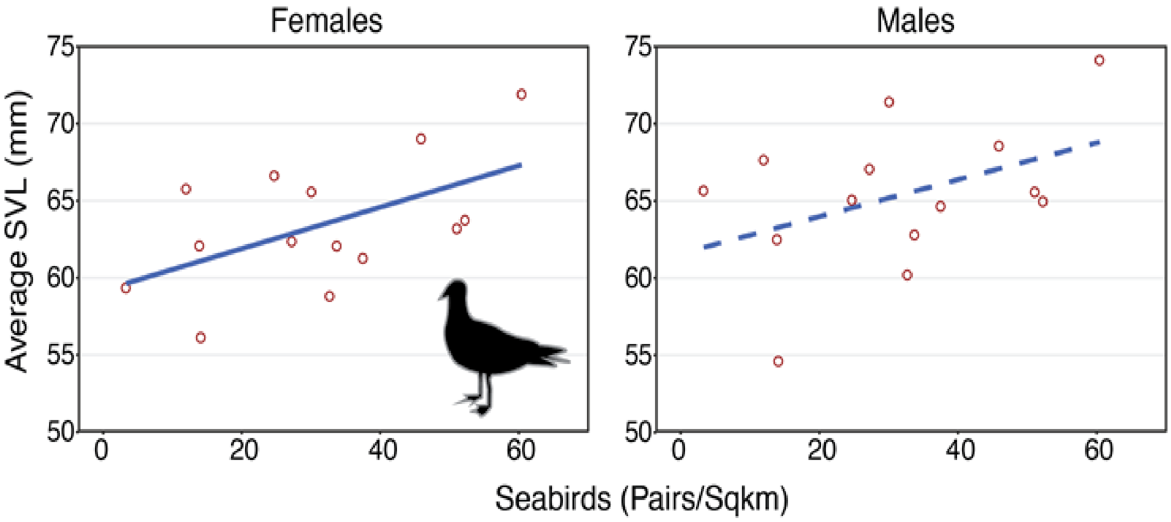

Figure 3. Scatterplots of seabird islands illustrating average female and male SVL by seabird density. Each circle represents one island. Average female SVL increases as seabird density increases R^2 = 0.2458, *P* = 0.04105, *N* = 14). The solid line represents the slope of a significant relationship, while the dotted line indicates the trendline in a non-significant pattern.

For non-seabird islands, average female SVL was not related to any of these variables, with a lack of significant linear relationships to lizard population density (Linear Regression; R^2 = 0.009058, P = 0.29, N = 21), index of predation (Linear Regression; R^2 = 0.002816, P = 0.317, N = 21), and NDVI (Linear Regression; R^2 = -0.01692, P = 0.424, N = 21). Instead, average female SVL was significantly correlated with log-transformed island area (Linear Regression; R^2 = 0.1872, P = 0.0287, N = 21; Figure 4).

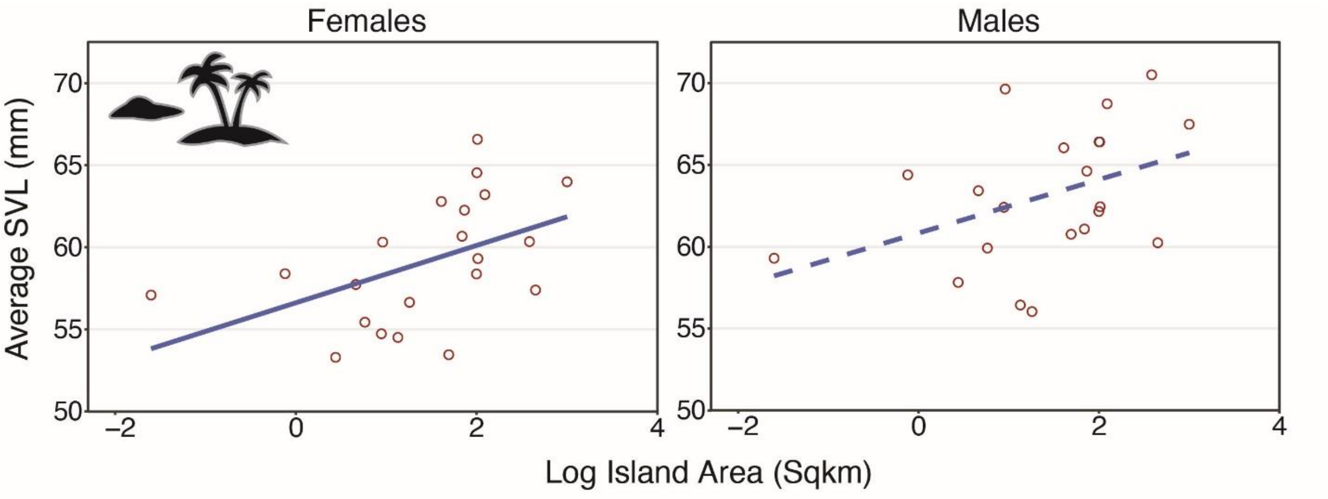

Figure 4. Scatterplots of average female and male SVL against log-transformed island area. Data shown are for non-seabird islands. Average female SVL (Left, solid line) rises with increasing island size (P = 0.0287, N = 21). For males (Right), a similar, but nonsignificant trend exists ($P > 0.05$; dashed line).

Male body size

We hypothesized that male body size was shaped by either resource availability—measured through seabird nesting density—or intensity of intraspecific competition (quantified through lizard population density).

Lizard density was positively correlated with average male SVL (Linear Regression; R^2 = 0.2967, P = 0.0256, N = 14) while all other variables failed to achieve statistical significance (Table 2).

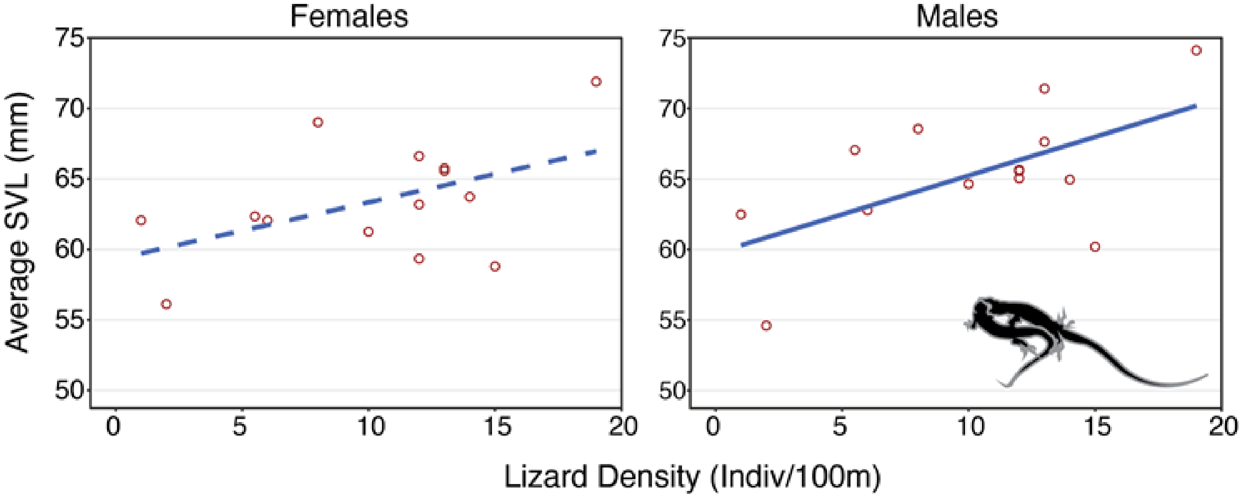

Figure 5. Scatterplots of average female (left) and male (right) SVL against lizard density. Data shown for seabird islands. Average male SVL rises significantly as lizard density increases ($P = 0.0256$, solid line). The corresponding pattern in females is similar but fails to achieve significance ($P > 0.05$).

For non-seabird islands, male average SVL was also regressed against lizard density, NDVI, and log island area. None of these variables were found to be significant ($P > 0.05$). Average male SVL for non-seabird islands showed a marginally non-significant positive trend to log-transformed island area (Linear Regression; $R^2 = 0.1219$, P =0.067, N = 14).

Seabird Islands	**Females**			**Males**		
	R^2	*p*	*AIC*	R^2	*p*	*AIC*
Lizard Density	0.124	0.118	80.687	**0.297**	**0.026***	**82.099**
Seabird Density	**0.246**	**0.041***	**79.503**	0.118	0.124	85.265
NDVI	-0.048	0.538	84.113	-0.082	0.923	88.137
Log Island Area	0.018	0.288	83.202	-0.078	0.813	88.078
Non-Seabird Islands						
Lizard Density	0.009	0.290	119.505	0.072	0.126	121.952
NDVI	-0.017	0.424	120.048	0.036	0.201	122.753
Index of Predation	0.003	0.317	119.637	-0.050	0.843	124.566
Log Island Area	**0.187**	**0.029***	**115.344**	**0.122**	**0.067**	**120.804**

Table 4. Data shown are seabird and non-seabird island regressions. Statistically significant values are marked with an asterisk. The model with the best fit (lowest AIC value) is bolded. Female SVL was found to be significantly correlated with seabird density (on seabird islands), and log island area (on non-seabird islands). Male SVL was found to be correlated with lizard density on seabird islands.

Discussion

Ecological and Environmental Variables

The purpose of this study was to examine the relative importance of different environmental factors that drive body size in island lizard populations. We hypothesized that female size would be associated with the amount of resources, along with intensity of predation, and that these eco-environmental differences between the sexes could explain why lizards do not show strong adherence to the island rule (Meiri 2007; Meiri *et al*., 2008; Itescu *et al*, 2018). We also predicted that male size is largely driven by male-male competition and resources. Overall, we found that female body size on seabird islands was associated with seabird density, while female body size on non-seabird islands was positively associated with increasing island size. In contrast, male body size on seabird islands was associated with lizard density, while male body size on non-seabird islands had no statistical relationship with any of the environmental factors predicted. Why these factors are significant for each sex will be explored below.

Females

Seabird effects. The strong association of female body size with the density of breeding seabirds suggests that it is at least partially, the reflection of the amount of resources available on a given island. Indeed, past research has demonstrated that seabird nesting density is a good metric of the amount of marine subsidies imported to an island, a process also reflected in the higher concentrations of nitrogen N, and phosphorus P, in the soil (Gizicki *et al*., 2018). Increased soil nutrients in turn provide resources for the growth of vegetation, which then supports more invertebrates, ultimately providing sustenance for lizards. More abundant food means lizards grow both faster and to a larger body size (Wright *et al*., 2013).

Resources on Non-Seabird Islands (Island Area). On non-seabird islands, marine subsidies are negligible and not likely to be relevant for lizards. Instead, we found that female body size correlates positively with island size. This corresponds to similar results from previous work (Meik *et al*., 2010; Itescu *et al*., 2018). The probable reason for this pattern is that larger islands represent not only more abundant, but also less variable natural resources, making an island's resource base more dependable for secondary consumers. Indeed, in the Mediterranean, larger islands have a higher elevational profile, intercepting more orographic precipitation and therefore receiving more rain (Zhao, 2018). The increased water availability translates into more substantial arthropod populations for the resident *Podarcis*, and into a shorter, less pronounced period of summer drought. It is during this summer period that pronounced aridity and lack of food results in intense selection pressure against large body size and the attendant large energetic needs (Stille and Stille, 2017). Interestingly, we did not detect an effect of vegetation cover (NDVI) on lizard body size. One possibility for this is that NDVI is not a good metric of resources available to lizards, or that the relationship between vegetation cover and lizard body size is not monotonic or linear.

Predation. Intensity of predation has been shown to be an important driver of species morphology and reproduction (Reznik *et al*., 1990; Cox *et al*., 2010; Lucas and French, 2012; Reedy *et al*., 2019). Life history theory predicts that populations experiencing higher predation rates would mature sexually at smaller body sizes. At least two different pathways may be responsible for this pattern: first, under intense predation conditions, it is adaptive to mature at an earlier age and at a presumably smaller body size (Stribor, 1992). Furthermore, intense predation pressure has been shown to select for significantly larger clutch size (Zhao, 2018). This – assuming conventional life-history tradeoffs between somatic grown and reproductive investment

– would translate into reduced growth and smaller adult body size. Given these theoretical predictions it was unexpected that we did not detect a relationship between number of predators and lizard body size. One possible explanation is that any reductions in predation rate result in strong increases in lizard population density (Foufopoulos *et al*., in prep.) and concomitant reductions in food availability. Hence any benefits stemming from reduced reproductive investment get negated by density-associated declines in food availability.

Competition. Extent of intraspecific competition is typically reflected in rising population density and can be an important factor shaping different aspects of life history (Pafilis *et al*., 2009). We did not expect competition to be an important factor in female body size, in part because females lacertids do not seem to experience the same level of competition for mates that has been observed in males. Confirming this prediction, we found no relationship between lizard density and female body size, neither on seabird nor on non-seabird islands.

Males

The initial predictions of this study were that male body size will be positively related to: 1. the amount of food resources available on an island (seabird density on seabird islands and island size on non-seabird islands), and 2. lizard population density, as the latter is known to be associated with increased intraspecific male-male competition. These predictions were supported only partially by the data. While there seemed to be positive associations between body size and seabird density as well as island size, in both cases these relationships failed to achieve significance (see Table

2). In contrast, we detected a significant positive relationship between lizard density and body size. The latter suggests that intraspecific competition is a potentially important driver for male body size. As already shown in other species of *Podarcis* (Pafilis *et al*., 2009), high population densities, as encountered on seabird islands, generate intense competition for food and mates. Male lizards engage in near constant agonistic interactions which often result in tail loss, digit amputation, and even death and subsequent cannibalism (Madden and Brock, 2018). In these circumstances, the largest male both survives and obtains the majority of matings. It is therefore not surprising that these conditions will represent intense selection pressure for large body evolution, especially if seabirds provide sufficient resources to buffer summer starvation (BeVier *et al*., 2021; Pafilis et al. 2009). Lizard density was not significantly associated with male size on non-seabird islands, presumably because lizard densities on these islands are almost an order of magnitude lower, relaxing the intensity and frequency of any intraspecific aggression.

Limitations of this study

This study has several potential limitations that are difficult to disentangle in this type of associative investigation. On one hand, there is no complete certainty that any observed differences in body size are the result of genuine evolutionary shifts. Because reptiles grow throughout their lifetime, albeit at a declining annual rate, body size may simply be the reflection of the average longevity individuals in a population are able to achieve. However, if that were the case, one would also expect to see body size declines in islands with higher number of predators, which are known to reduce lizard life expectancy and presumably average population body size. Such a relationship does however not occur, with larger, more predator-rich islands harboring larger-bodied lizard populations - hence suggesting that longevity is not an important underlying factor for observed body size patterns. Furthermore, it is not clear whether the body size differences we observe are the result of genuine genetic shifts or simply the results of plasticity (such as increased food availability) on the same genotype. The best only way to truly resolve these questions is to conduct common garden experiments between different island populations. Nevertheless, the strength and broad generality of the observed pattern across dozens of islands of very different environmental conditions indicates that these are ecologically significant patterns.

Conclusions

Body size in lizards at least, is a complex life history trait that like integrates effects from a variety of factors. Probably the most important conclusion of this study is that drivers affecting body size differ not just between males and females but are also critically dependent on island ecology. Both on regular islands and in the high population density, high agonistic intensity environment of seabird islands, stable availability of food resources allows females to achieve larger body sizes. In contrast for males, food resource availability seems to be of somewhat subordinate importance, while extent of selection pressure for large body size under conditions of intense intraspecific competition seems to take primacy.

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