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More and bigger lizards reside on islands with more resources

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Abstract

While global patterns in body size evolution in island vertebrates have been described extensively, the ecological processes that generate these patterns are not well understood. Here we used variation among lizard populations occupying an archipelago to test hypotheses about body size evolution. We examined 35 populations of Aegean wall lizards (*Podarcis erhardii*, Lacertidae), a species widely distributed across the Balkan mainland and hundreds of Aegean islands. We evaluated measures of resource availability (island area and seabird density), intraspecific competition (lizard abundance) and predation risk (presence of rats, carnivorous mammals, vipers, and birds of prey) as possible factors affecting lizard body size. Lizard body size increased with island size overall, as well as with seabird colony density, suggesting a role for increased food resources and especially seabird subsidies in the evolution of body size. Lizards were larger where lizard population density was higher, suggesting a possible role for intraspecific competition in the evolution of body size. In our sample, rats, carnivorous mammals, and vipers did not have obvious effects on lizard body size, and lizards were smaller on islands with resident birds of prey. Males were larger than females on average, yet sexual dimorphism did not vary consistently with measures of resource availability and competition. Overall, our results suggest that local resource levels predict population density and body size in these lizards, and that nesting seabirds in particular can substantially affect lizard body size.

Introduction

Islands make up just 1.86% of earth's surface area, yet harbor some of the most exceptional evolutionary lineages (Baldacchino, 2006; Foster, 1964). Isolation in island populations allows for the evolution of both unusual traits and dramatic size changes (Foster, 1964; Heaney, 1978; Lomolino, 2005; Van Valen, 2014), such as seen in giant Komodo dragons and pygmy three-toed sloths (Anderson & Handley, 2001; Jessop et al., 2006). For over a century, biologists have noted the distinct ecological conditions experienced by island species compared to the mainland (Darwin, 2004; Foster, 1964; Carlquist, 1965; Meiri et al., 2004; Van Valen, 2014). Evolution of divergent body sizes among different island species (Benítez-López et al., 2021; Foster, 1964; Lomolino, 2005) has been observed in a wide range of organisms including birds (Clegg & Owens, 2002), mammals (Foster, 1964), and reptiles (Pafilis, Meiri, et al., 2009). However, at least as much

variation in body size exists between different island populations of individual species (Itescu et al., 2018; Meiri et al., 2008). While investigating intraspecific patterns of body size variation may seem promising, it has only yielded a few generalizable insights, and studies have found only weak, or clade-specific patterns (Itescu et al., 2018; Meiri et al., 2008).

Multiple proposed patterns in resource availability, intrapopulation processes, or species interactions, may lead to evolutionary shifts in body size among different island populations (Benítez-López et al., 2021; Foster, 1964; Van Valen, 2014). Below we review some of the most important hypotheses to explain variation in body size on islands: island area, local resource availability, population density, sex, and predator presence.

Numerous studies have investigated the relationship between island size and body size (Boback & Guyer, 2003; Heaney, 1978; Lomolino, 1985; Thomas et al., 2009). The majority of these have found that species body size is positively

correlated with island size (Benítez-López *et al.*, 2021; Clegg & Owens, 2002; Lomolino, 2005), although some have also found the opposite pattern (Boback, 2003; Meiri, 2007; Meiri *et al.*, 2005; Meiri *et al.*, 2008). Large islands tend to be more productive, especially in arid Mediterranean environments, because they have higher mountains that generate more vegetation-supporting orographic precipitation (Zhao, 2018). This increase in precipitation likely translates into a more seasonally stable food supply, and lower starvation risk during the arid summer period. In general, a positive relationship between body and island size is seen as an argument in favor of the importance of resource availability.

High primary productivity by plants forms the fundament of most terrestrial food webs, and all things being equal, is expected to support individual-rich populations of large-bodied taxa. For example, on Mediterranean islands increased plant growth supports, via rich populations of insects and other arthropods, dense *Podarcis* lizard populations (Pérez-Mellado & Traveset, 1999). Primary productivity on many small islands depends not only on autochthonous photosynthetic activity but also 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 & 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, Meiri, *et al.*, 2009; Richardson *et al.*, 2019). As a result, island lizard body size should be positively correlated to the density of nesting seabirds (Pafilis, Meiri, *et al.*, 2009; Richardson *et al.*, 2019).

Island populations are thought to experience less interspecific competition because of lower species richness compared to the mainland (Meiri *et al.*, 2014), but potentially increased intraspecific competition due to increased population density, termed ‘density compensation’ (MacArthur *et al.*, 1972). Density compensation is common in island lizard species (Buckley & Jetz, 2007; Case, 1975; Donihue *et al.*, 2016), where local abundances of lizards tend to be an order of magnitude higher on islands than on the mainland, even when controlling for resource availability (Buckley & Jetz, 2007). Competition for food, space, and mates in lizards in the family Lacertidae often takes the form of intense physical altercations which can lead to toe and limb amputations, tail loss, and even death (Deem & Hedman, 2014; Madden & Brock, 2018; Pafilis, Meiri, *et al.*, 2009). Because these contests have fitness consequences and are often won by the largest individual, they can select for 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 (Donihue *et al.*, 2016; Lister, 1976; Pafilis, Meiri, *et al.*, 2009; Sagonas *et al.*, 2014). 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. Males tend to engage in more agonistic encounters than females (Cooper Jr *et al.*, 2015), though comparatively little attention has been paid to competition by females. Sexual dimorphism is predicted to be greater on smaller islands due to lower

overall species richness and reduced interspecific competition there (Meiri *et al.*, 2014).

Predation has the potential to shape adult body sizes in many species of wildlife. High predation rates will reduce life expectancy in prey species (Adler & Levins, 1994; Pafilis, Foufopoulos, *et al.*, 2009; Slobodkin, 1968). This, in turn, means that individuals that postpone 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 (Belk *et al.*, 2020; Reznick *et al.*, 1990; Stibor, 1992). 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).

This study examines body size in 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 (Valakos *et al.*, 2008). Foundational work by Wettstein (1953) noted great variation in body size across populations of *Podarcis erhardii*, but was not able to explain it. A recent comprehensive study with data from numerous Aegean islands and several lizard taxa, revealed that drivers of body size evolution likely differ across species, and 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 female and male Aegean wall lizards (BeVier *et al.*, 2021; Brock *et al.*, 2020; Donihue, 2016). The present study therefore builds on the previous work by analyzing patterns in body size across islands for females and males, 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 across numerous island populations of Aegean Wall lizards, and (2) test the extent to which resource availability, competition, and predation are associated with the evolution of body sizes in female and male lizards.

Materials and methods

Study system

We conducted this study in the Cyclades, a cluster of islands in the central Aegean Sea, Greece (Fig. 1). The climate of the region is typical of the Mediterranean, with warm, arid summers, and mild, wet winters (Giorgi & Lionello, 2008). The island vegetation has been shaped by thousands of years of human activity and disturbance (Grove & Rackham, 2003) and consists largely of various forms of Mediterranean scrub (Rackham & 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 *et al.*, 2005).

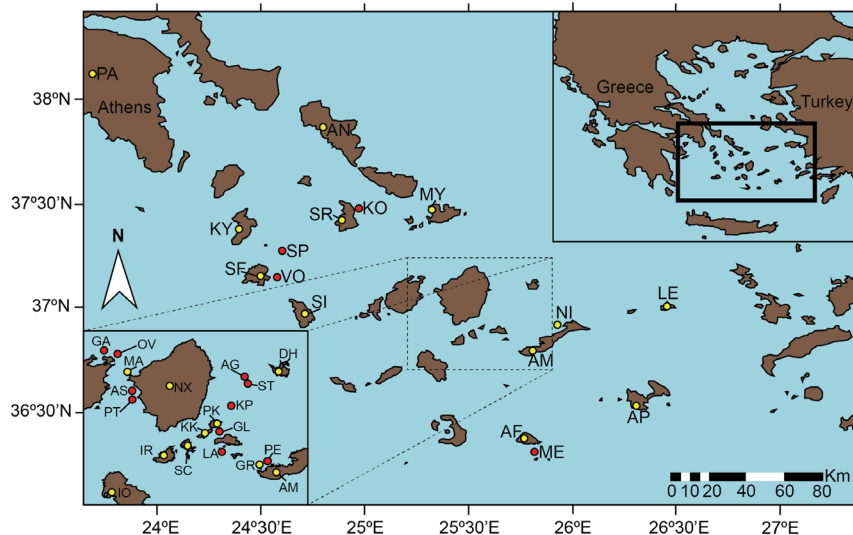


Figure 1 Map of study sites. One mainland site and 34 Cycladic island sites are indicated with a circle and acronym identifier. Sites are listed in alphabetical order. AG, Agios Nikolaos; AM, Amorgos; AF, Anafi; AN, Andros; AS, Aspronissi; AP, Astypalea; DH, Dhonnoussa; GA, Gaidouronissi; GL, Glaronissi; GR, Gramvoussa; IO, Ios; IR, Irakleia; KK, Kato Koufonissi; KO, Kommeno; KP, Kopria; KY, Kythnos; LA, Lazaros; LE, Levitha; MA, Mando; ME, Megalo Fteno; MY, Mykonos; NX, Naxos; NI, Nikouria; OV, Ovriokastro; PK, Pano Koufonissi; PA, Parnitha*; PT, Parthenos; PE, Petalidi; SC, Schoinoussa; SP, Serifopoula; SF, Serifos; SI, Sifnos; SR, Siros; ST, Strongylo; VO, Vouss. Red circles indicate seabird islands, and yellow circles represent non-seabird islands. Asterisk (*) indicates a mainland site.

The Aegean wall lizard (*Podarcis erhardii*, Fig. 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). Adult body snout-vent lengths range substantially from 45–78 mm, with a tail that can be twice as long as the body (Valakos *et al.*, 2008). *P. erhardii* is a generalist taxon with a broad distribution across different habitats and an opportunistic, omnivorous diet consisting primarily of various arthropods. On the islands this species is also known to occasionally forage on plant material during the dry summer season (Brock *et al.*, 2014). Across the archipelago Aegean Wall lizard populations have adapted to widely varying environmental conditions and can differ substantially in their ecology, morphology and antipredator behaviors (Brock *et al.*, 2015; Donihue *et al.*, 2016; Pafilis, Foufopoulos, *et al.*, 2009; Pafilis, Meiri, *et al.*, 2009; Zhao, 2018).

Cycladic islands investigated here are geologically homogeneous and are comprised mostly of sedimentary rocks. 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, or relatedness, of the local island populations (Foufopoulos & Ives, 1999). Because of the substantial period of isolation on these diverse island habitats, each island population appears to be closely adapted to the ecological conditions prevailing on each island (Brock *et al.*, 2015; Hurston *et al.*, 2009).



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

Island characteristics

We visited 34 islands and one mainland site to obtain site-specific lizard population information, as well as local ecological and microenvironmental data (Table 1). All study sites were visited in May–June 2018 and 2019, for one to several days by at least one of the authors. The sampled islands all formed from the last glacial maximum; they range in age from 5000 to 15 000 years old. Age data, along with island and mainland area (km²) data, were obtained from published and

governmental sources (Brock *et al.*, 2015; Foufopoulos & Ives, 1999; Poulos *et al.*, 2009). Relative lizard population abundances 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.*, 2016). This transect was always walked during peak lizard activity hours (0900–1100 and 1500–1700), on clear, sunny days with minimal wind (<2Bf; Brock *et al.*, 2015). Thus, we sampled much of the lizard habitat on smaller islands and one representative population of lizards on larger islands.

Several studies have indicated that the presence or absence of seabirds on islands can have profound impacts on lizard abundance; islands with seabirds have been found to have higher lizard abundances than islands without seabirds (Markwell & Daugherty, 2002; Pafilis, Meiri, *et al.*, 2009). In the Aegean Sea, some smaller islands harbor seabird nesting colonies and differ in important ways compared to larger islands without seabirds (BeVier *et al.*, 2021; Gizicki *et al.*, 2018; Pafilis *et al.*, 2011; Pafilis *et al.*, 2013). Seabird islands tend to not only have different predation regimes, but also different plant communities. Gull colonies provide crucial marine-derived subsidies like guano, food scraps, and carcasses to otherwise dry, unproductive islet ecosystems, and these in turn increase resources for resident lizards (Polis & Hurd, 1996; Richardson *et al.*, 2019; 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 km².

To test for possible effects of predator presence on lizard body size, we surveyed for the presence of rats, specialized mammalian predators, vipers, and birds of prey on each island. Previous work has shown that rats and larger mammalian predators such as cats can impact lizard populations (Li *et al.*, 2014; Pérez-Mellado *et al.*, 2008). Rats (*Rattus rattus*) are omnivores and likely a threat mainly to eggs and juveniles, whereas true Carnivores (feral cats [*Felis catus*], stone martens [*Martes foina*]) stalk and kill even the largest adults of *P. erhardii* (see Brock *et al.*, 2015). One of the main predators for adult *P. erhardii* is the long-nosed viper (*Vipera ammodytes*) (Simou *et al.*, 2008); *V. ammodytes* is a sit-and-wait predator that ambushes and envenomates its prey (Pafilis, Foufopoulos, *et al.*, 2009). Birds of prey, such as the common kestrel (*Falco tinnunculus*) and the common buzzard (*Buteo buteo*) are the most common aerial predators for *P. erhardii*; these species are active hunters who detect their prey visually from the air.

Presence of rats, cats, martens, vipers, and birds of prey on an island was determined using published information (Brock *et al.*, 2015; Handrinos & Akriotis, 1997; Masseti, 2012; Pafilis, Foufopoulos, *et al.*, 2009; Pafilis, Meiri, *et al.*, 2009; Valakos *et al.*, 2008) and 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, shed skins, and nests) (Brock *et al.*, 2015).

Lizard measurements

Adult lizards were captured during island visits using 3 m-long telescopic, collapsible fishing rods, with a dental floss lasso attached to the end. Captured lizards were temporarily held in cotton cloth bags. All animals were then taken briefly into captivity for measurements. To reduce measurement error, morphometric measurements were performed by one researcher (K.M.B.) 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). Animals were sexed based on the presence of post-anal swelling and femoral pores. Lizards were 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: Ω8Δ84653Π8-ΒΕΧ, 6ΥΛΥ4653Π8-ΠΕΓ assigned to K.M.B.).

Data analysis

Data were analyzed in R (v1.3.959), using linear mixed effects models and t-tests (R Core Team, 2020). Because of known differences in life history and reproductive schedules likely linked to body size (Algar & López-Darias, 2016; Brock *et al.*, 2020; Donihue *et al.*, 2016), female and male SVLs were averaged separately for each island. Given the strong predator regime differences between seabird and non-seabird islands, certain predator effects on SVL had to be analyzed in separate t-tests for seabird and non-seabird islands. For example, because large mammalian predators and vipers are completely absent from all seabird islets, their effect was evaluated on the non-seabird island dataset. Conversely, because rats were present on all non-seabird islands, their effect was tested by comparing seabird islands where they were absent to seabird islands where they occurred. Because birds of prey nest on both seabird and non-seabird islands, we analyzed the effects of the absence or presence of birds of prey on SVL for all islands together, while statistically controlling for seabird presence.

The key variables hypothesized to influence lizard body size were island area, seabird presence, and lizard abundance. Since lizards were sampled across two field seasons (2018 and 2019), we also included year in our analyses. We log-transformed female and male average SVL, island area, and lizard abundance to achieve normality and meet test assumptions. To test our hypotheses and determine which island factors are associated with average SVL, we ran linear mixed effects models of log average island SVL against log island area, seabird presence, log lizard abundance, year, and the interaction between seabird presence and island area. Males and females were analyzed separately. We also ran a linear mixed effect model with the same set of predictor variables and degree of sexual size dimorphism (SSD) as the dependent variable. We calculated SSD by dividing male average SVL by female average SVL.

Table 1 Location and lizard characteristics for all 34 islands and one nearby mainland site (Parnitha, PA)

Island	Latitude (°N) longitude (°E)	Sampling period month year	F Avg SVL (mm) (n)	M Avg SVL (mm) (n)	Lizard Abundance (Indiv/100 m)	Seabird density (Pairs/km ²)	Predator presence	Log Island area (km ²)
Agios Nikolaos (AG)	37.08841 25.69744	June 2019	61.26 (11)	64.64 (23)	10	37.48	R	-0.05
Amorgos (AM)	36.90331 25.99062	June 2018	63.21 (10)	68.73 (12)	3	0	R,B,M	2.09
Anafi (AF)	36.36367 25.74634	June 2018	53.45 (10)	60.7 (11)	4	0	R,B,M	1.69
Andros (AN)	37.82014 24.82999	June 2018	60.34 (11)	70.50 (11)	7	0	R,B,V,M	2.58
Aspronissi (AS)	37.04690 25.35061	May 2018	63.18 (12)	65.57 (10)	12	51.04	B	-1.42
Astypalea (AP)	36.55301 26.32940	June 2019	64.54 (7)	66.41 (13)	2	0	R,M	2.00
Dhonoussa (DH)	37.10371 25.79136	June 2018	54.51 (10)	56.44 (10)	2	0	R,B,M	1.13
Gaidouronissi (GA)	37.15583 25.26768	May 2019	69.01 (15)	68.55 (15)	8	45.88	R	-0.88
Giaronissi (GL)	36.91806 25.60635	May 2018	62.07 (6)	62.49 (25)	1	13.87	B	-0.81
Gramvousa (GR)	36.80349 25.74788	May 2019	58.39 (7)	64.39 (23)	3.76	0	R,B	-0.12
Ios (IO)	36.72659 25.27233	June 2019	59.31 (8)	62.45 (12)	5	0	R,B,V,M	2.01
Irakleia (IR)	36.85187 25.47120	June 2019	56.64 (11)	56.04 (11)	3	0	R,B,V,M	1.26
Kato Koufonissi (KK)	36.92055 25.59587	May 2019	57.73 (10)	63.42 (10)	2	0	R,B	0.66
Kommeno (KO)	37.46480 24.95076	June 2018	65.76 (12)	67.64 (6)	13	11.95	R,M	-2.15
Kopria (KP)	36.98658 25.63840	May 2019	62.35 (12)	67.05 (18)	5.5	27.22	none	-0.87
Kythnos (KY)	37.38379 24.39843	April 2018	58.37 (13)	62.16 (17)	5	0	R,M	2.00
Lazaros (LA)	36.87026 25.62302	June 2018	71.90 (10)	74.12 (10)	19	60.41	none	-1.86
Levitha (LE)	37.00452 26.46435	June 2018	60.31 (12)	69.63 (19)	10	0	R	0.96
Mando (MA)	37.08923 25.36130	May 2018	57.09 (17)	59.30 (32)	6	0	R,B	-1.60
Megaló Ftino (ME)	36.31094 25.80065	June 2018	58.80 (12)	60.20 (23)	15	32.68	none	-1.23
Mykonos (MY)	37.46930 25.32222	June 2018	62.79 (22)	66.05 (27)	2	0	R,V,M	1.61

Table 1 Continued.

Island	Latitude (°N) longitude (°E)	Sampling period month year	F Avg SVL (mm) (n)	M Avg SVL (mm) (n)	Lizard Abundance (Indiv/100 m)	Seabird density (Pairs/km ²)	Predator presence	Log Island area (km ²)
Naxos (NX)	37.08037 25.49156	May 2019	57.39 (9)	60.24 (27)	6	0	R,B,V,M	2.65
Nikouria (NI)	36.88224 25.91790	June 2019	53.29 (10)	57.82 (11)	6	0	R,B	0.44
Ovriokastro (OV)	37.15261 25.29635	May 2018	62.06 (12)	62.79 (13)	6	33.71	R	-0.66
Pano Koufonissi (PK)	36.93453 25.61505	June 2019	55.43 (13)	59.92 (11)	3	0	R,B,V,M	0.76
Parnitha (PA)	38.16045 23.72552	July 2018	63.99 (12)	67.48 (14)	7	0	R,B,V,M	3.00
Parthenos (PT)	37.02882 25.36067	May 2018	63.73 (27)	64.96 (23)	14	52.22	R,B	-2.36
Petalidi (PE)	36.81924 25.79369	May 2018	56.12 (6)	54.61 (8)	2	14.09	R	-1.30
Schoinoussa (SC)	36.87100 25.51940	June 2018	54.73 (13)	62.41 (32)	1	0	R,B,M	0.95
Serifopoula (SP)	37.25537 24.60690	May 2019	59.34 (17)	65.66 (13)	12	3.29	R	0.27
Serifos (SF)	37.14480 24.51450	May 2019	60.67 (25)	61.09 (20)	3	0	R,M	1.84
Sifnos (SI)	36.97770 24.74034	May 2019	62.26 (11)	64.62 (19)	2.3	0	R,V,M	1.86
Siros (SR)	37.42277 24.87979	June 2018	66.58 (16)	66.40 (14)	9	0	R,V,M	2.01
Strongylio (ST)	37.06940 25.70388	June 2018	65.57 (7)	71.41 (9)	13	30.05	R	-0.44
Vous (VO)	37.14247 24.56213	May 2019	66.62 (10)	65.05 (20)	12	24.68	none	-0.71

Islands are listed in alphabetical order and abbreviations correspond to labels on the map (Fig. 1). Latitude and longitude for sampling sites are given in decimal degrees. The sampling period is the month and year when we sampled lizards. Average female and male SVL are reported in millimeters, with the sample size *n* for each sex in parentheses. Lizard abundance was quantified as the number of individuals recorded per 100 m transect. Seabird presence is reported as the number of nesting seabird pairs counted on an island corrected for area (Pairs per square kilometer). Predator presence lists the predator categories present on seabird islands (none, rats [R]) and non-seabird islands (none, birds of prey [B], vipers [V], mammals [M]) (Brock *et al.*, 2015). Island area is reported in km² as based on published information and is log-transformed. (Foufopoulos & Ives, 1999; Itescu *et al.*, 2018; Poulos *et al.*, 2009).

To test our hypotheses that various predators on seabird and non-seabird islands influence female and male average SVL, we ran the following Welch's *t*-tests for females and males separately: one on the seabird island dataset that tested for mean differences in log average SVL between islands with and without rats, a second *t*-test on the non-seabird dataset that tested for mean differences in log average SVL between islands with and without large mammal predators, and a third *t*-test on the non-seabird dataset that tested for mean differences in log average SVL between islands with and without vipers. Finally, to test for mean differences in log average SVL between islands with and without birds of prey while correcting for the presence of seabirds, we ran two-way ANOVAs (one for females and one for males) with presence or absence of birds of prey and of seabirds as factors.

Results

Study island size ranged widely from the smallest islets (Kommeno at 0.007 km²) to massive islands (Naxos at 429 km²). Out of the 35 sampling locations, 14 islands had seabird colonies and were categorized as “seabird islands”, and the remaining 20 islands and one mainland location were categorized as “non-seabird” islands (Table 1). On average seabird islands were smaller than non-seabird islands (island area 0.072 km² vs. 26.303 km²) and had higher lizard abundances (10.18 indiv./100 m vs. 4.3 indiv./100 m). Seabird nesting density (i.e. nesting pairs/km²) was higher on smaller islands. Because seabirds prefer to nest at higher densities on the smallest islands, density of marine subsidies also increased with declining island area. Four seabird islands were completely predator free, while eight had rats present and three had birds of prey present. On non-seabird islands, five islands had rats but no other mammalian predators and fifteen had rats plus at least one other type of mammalian predator (Table 1); fourteen islands had bird of prey present, while eight were recorded as having vipers. Across our entire dataset, average female SVL varied from 53.29 mm to 71.90 mm, while average male SVL ranged from 54.61 mm to 74.12 mm (Table 1). Male lizards were larger than females on all but 5 islands (Table 1), with the sexual size dimorphism index ranging from 0.97 to 1.17 for different islands.

Predictors of average lizard SVL

Lizards tended to be larger on larger islands (Fig. 3), though this effect was statistically significant for females and not for males (Table 2). Sexual size dimorphism did not change consistently with island size (Table 2).

In our sample, seabirds nested on some of the smaller islands and lizards were large on most of the islands with seabirds (Fig. 3). While the relationship of lizard body size and island area differs depending on whether the islands harbor nesting seabirds, the interaction of seabird presence with island area was statistically significant for females and not for males (Table 2). Sexual size dimorphism tended to be least on very small islands with nesting seabirds (Fig. 3, Table 2). If we

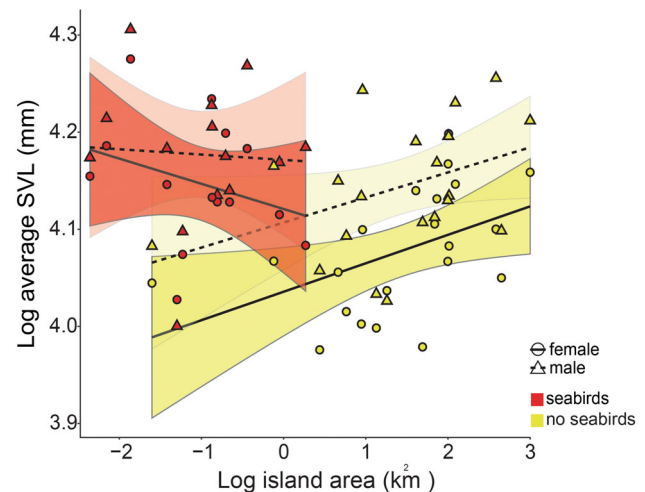


Figure 3 Scatterplot of log average island female and male SVL by log island area for seabird and non-seabird islands illustrating different mediating mechanisms of lizard body size. Each circle represents female average island SVL and triangles represent male average island SVL. An island is colored red if it is a seabird island or yellow if it is a non-seabird island.

correct seabird numbers for island size by dividing seabird nesting pairs by island area, both male and female body size increased with the density of nesting seabirds (Fig. 4).

Lizards tended to be larger on islands where lizard abundance was higher (Fig. 5), though this effect was statistically significant for males and not for females (Table 2). Sexual size dimorphism did not change dramatically with lizard abundance as the effects on male and female body size were roughly parallel (Fig. 5).

Predators and SVL on selected islands

Comparisons across islands with different combinations of nesting seabirds and resident predators showed no consistent effects of rats, carnivorous mammals, or vipers on female or male average SVL (Table 3). Lizards were smaller on islands with resident birds of prey, though this difference was statistically significant for females and not for males (Table 3).

Discussion

Our results reveal that body size in Aegean wall lizards depends on island size, the presence of nesting seabirds, conspecific density, and predatory birds in residence. Each of these factors is statistically significant for one sex and not the other, effects in the other sex are roughly parallel so that none of these factors has a statistically significant effect on sexual size dimorphism. We acknowledge two mutually exclusive null hypotheses -- that the effect is non-zero in one sex and zero in the other and that the effect is exactly the same for females and males -- and suggest that biologically plausible explanations for our data lie between these two extremes. Island size,

Table 2 Output from linear mixed effects model for log-transformed average female SVL, average male SVL, and sexual size dimorphism index (SSD)

Predictor variable	Female SVL		Male SVL		SSD	
	<i>r</i>	<i>P</i> -value	<i>r</i>	<i>P</i> -value	<i>r</i>	<i>P</i> -value
Year	0.147	0.4304	-0.043	0.8192	-0.263	0.1532
Log lizard abundance	0.296	0.1065	0.398	0.0265	0.220	0.2352
Seabird presence	0.290	0.1134	0.181	0.3303	-0.144	0.4402
Log island area	0.372	0.0396	0.299	0.1014	-0.083	0.6557
Log island area * Seabird presence	-0.358	0.0481	-0.122	0.5122	0.329	0.0703

Statistically significant predictors of island average SVL for females, males, and SSD are bolded.

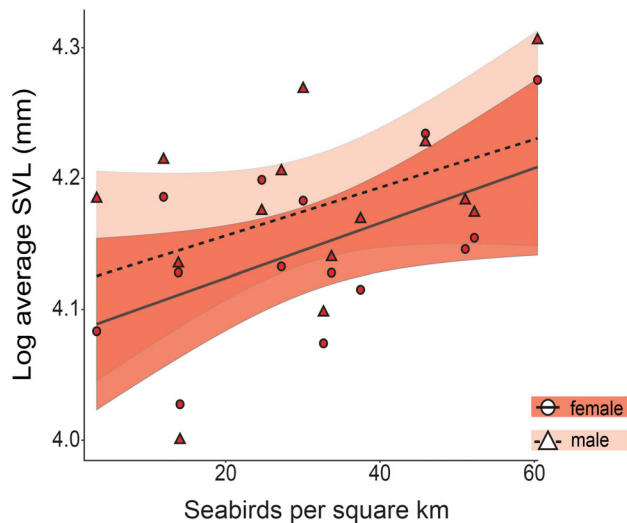


Figure 4 Scatterplot of female and male log average island SVL against number of seabirds per square km. Data shown are for seabird islands. Each circle represents female average island SVL and triangles represent male average island SVL. Both female and male average island SVL rises with increasing number of seabirds per square km (female $R^2 = 0.24$, $P = 0.04$, d.f. = 12, $N = 14$, male $R^2 = 0.11$, $P = 0.12$, d.f. = 12, $N = 14$).

the presence of nesting seabirds, conspecific density, and predatory birds in residence are likely important to both female and male lizards, yet the degree of importance to them may differ. In surveying this middle ground, we discuss first how each factor is likely to influence lizards of one or both sexes, and then turn to how the influence might be greater for one sex than the other.

In this study, average body size of Aegean wall lizard populations increased with island size if nesting seabirds were not present and increased with seabird nesting density when nesting seabirds were present (Figs 3 and 4). These results clarify and unify the conclusions of previous studies. Across various lizard taxa, both positive and negative relationships with island area have been reported, while for *P. erhardii* no consistent pattern has been demonstrated (Itescu *et al.*, 2018). Indeed, if we pool together islands with and without seabirds, our data do not show a convincing overall effect of island area. This study resolves this previously indeterminate pattern into a

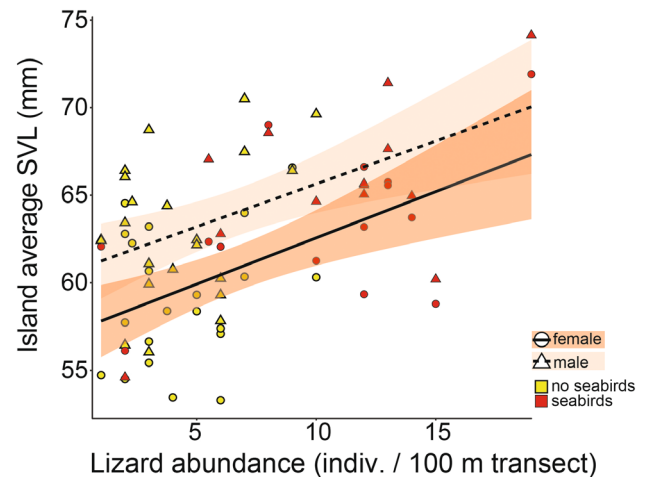


Figure 5 Scatterplot of average female (circle points, dark orange 95% CI) and male (triangle points, light orange 95% CI) SVL against lizard abundance for seabird (red) and non-seabird (yellow) islands. Average female SVL ($R^2 = 0.28$, $P < 0.001$, d.f. = 33, $N = 35$, solid line) and average male SVL ($R^2 = 0.24$, $P = 0.002$, d.f. = 33, $N = 35$, dotted line) rise significantly as lizard abundance increases.

positive relationship for islands without nesting seabirds and a negative relationship for islands with nesting seabirds (Fig. 3). Our results therefore support a unified explanation that centers on the importance of local food resources for body size. Local food resources, in turn, depend on different factors for different types of islands. On the larger islands – which are always without seabirds in our data – productivity increases with area (Zhao, 2018). In contrast, on seabird islands food resources are determined by the amount of marine inputs delivered by nesting seabirds.

On larger islands, locally produced resources are likely both more abundant and less variable, making an island's resource base more dependable for secondary consumers. In the Mediterranean, larger islands are taller on average, and so intercept more orographic precipitation and receive more total precipitation (Kalb, 2021). The increased water availability translates into a shorter, less pronounced period of summer drought, as well as into more substantial arthropod populations available to resident *Podarcis* (Zhao, 2018). Lack of food during the summer is hypothesized to be a strong negative selective force in Mediterranean reptiles (Stille & Stille, 2017).

Table 3 Effects of four types of predators on average female SVL and average male SVL

Predator type	Female SVL (mm)				Male SVL (mm)			
	Predator present	Predator absent	Test statistic	<i>P</i> -value	Predator present	Predator absent	Test statistic	<i>P</i> -value
Rat	62.86	64.15	$t_{10.50} = 0.55$	0.59	65.03	65.75	$t_{11.57} = 0.28$	0.78
Mammal (cat or marten)	59.92	57.04	$t_{10.15} = -1.42$	0.18	63.45	62.42	$t_{6.21} = -0.14$	0.89
Viper	60.53	58.02	$t_{17.71} = -1.55$	0.14	63.75	62.72	$t_{16.41} = -0.53$	0.60
Bird of prey	58.90	62.40	$F_{1,32} = 13.21$	0.00097	62.81	65.16	$F_{1,32} = 3.92$	0.057

The comparisons for rats are for islands with nesting seabirds. The comparisons for mammals and for vipers are for islands without nesting seabirds. The comparisons for birds of prey use all islands, while statistically controlling for the presence of nesting seabirds. Averages are given based directly on the measurements while statistical tests used log-transformed values. Statistically significant comparisons are bolded.

Marine subsidies provide critically important resources beyond those generated from local terrestrial production. The strong association of lizard body size with the density of breeding seabirds (Fig. 4) suggests that seabirds bring resources that, indirectly or directly, are important for lizards. Previous research has demonstrated that seabird nesting density is a good metric of the quantity of marine subsidies 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). In the Aegean Sea, because Yellow-legged gulls (*Larus michahellis*), the main seabird species, nest at higher densities on smaller islands (Carlberg, 2021), this translates into a negative lizard body size-island area relationship on those islands harboring seabird colonies. On these islands, marine subsidies are more concentrated (Gizicki *et al.*, 2018), resulting ultimately in the largest lizards found on the smallest seabird islands (Fig. 3).

In our study, lizards were larger where lizard abundances were higher (Fig. 5). One explanation for this pattern would be that lizard abundance and body size increase in parallel where more resources are available. While the pattern in our data is broadly consistent with this explanation, other information shows that lizards in high density populations are highly competitive. For example, on a separate set of small islands with seabirds, where lizard population densities were higher, lizards were able to bite more strongly and had more scars from having been bitten by other lizards (Donihue *et al.*, 2016).

In other species of *Podarcis* (Pafilis, Meiri, *et al.*, 2009), high population densities, as encountered on seabird islands, generate intense competition for food and mates. Lizards engage in near constant agonistic interactions which often result in tail loss, digit amputation, and even death and subsequent cannibalism (Madden & Brock, 2018). Competition, including potential cannibalism, may select for large body size, especially where seabirds or local production provide sufficient resources to buffer summer starvation (BeVier *et al.*, 2021; Pafilis, Foufopoulos, *et al.*, 2009; Pafilis, Meiri, *et al.*, 2009).

In our study, one kind of predator affected lizard body size, and three kinds of predators apparently did not (Table 2): On islands with nesting seabirds, lizards were about the same size

regardless of whether rats were also present. On islands without seabirds, lizards were very similar in size regardless of whether vipers or cats and stone martens, were present. These comparisons are limited by where these species occur naturally. Seabirds choose to nest on relatively small islands with few predators and in our study seabirds did not nest on any islands occupied by vipers, cats, or stone martens. Vipers, cats, and stone martens are most likely to persist on large, productive islands with many things to eat besides wall lizards. Future research could examine potential effects of these predators on such large islands. In particular, intense predation by domestic cats can reduce lizard population density by more than 50% near villages compared to away from villages (Li *et al.*, 2014). Such intense predation by cats is predicted to cause decreased lizard body size.

In our sample, lizards were smaller on islands they shared with a resident bird of prey. These birds can fly between islands and their distribution is far less limited by dispersal than is that of other predators. Islands with resident birds of prey need not support a population of these predators -- just provide a hunting ground for at least one individual.

Based on such prior research, we would have predicted that birds of prey would have a bigger effect on male than on female body size. Kestrel predation on green lizards is strongly biased toward males (Costantini *et al.*, 2007). Male *Podarcis erhardii* are more colorful than females in ways that should make them more conspicuous to the visual system of hunting birds (Marshall & Steven, 2014). Our results are not consistent with a greater effect on male than female body size. Instead, our results suggest that females may pay a greater growth cost for avoiding predation. Future research should examine sexual differences in habitat choice, thermoregulation, and foraging in response to risk of predation.

Across island differences, male lizards were consistently larger than females (Figs 3–5). Similar results have been reported in many other studies. The explanation must involve the relative costs and benefits of body size for reproduction by males and females. Our results hint that resources and predation may be more important for female body size and intraspecific competition for male body size in *Podarcis erhardii*, yet sexual dimorphism did not vary consistently with any factors in our study. The strongest pattern seen in our data is that dimorphism is lower on small islands with nesting seabirds, which

also tend to have more concentrated marine subsidies (Fig. 3). This pattern is counter to the prediction that sexual dimorphism will be greater on smaller islands (Meiri *et al.*, 2014).

While males are commonly larger than females in *Podarcis erhardii*, further research is needed to pinpoint why males might receive a relatively greater benefit or females might pay a relatively greater cost from being larger. Overall, our results show that body size differs between males and females on each island but differs far more between islands. The difference between the sexes likely can be understood by studying what males and females do differently during reproduction, but the differences between populations likely involve what both males and females need to do elsewhere in their lives.

In conclusion, our results show effects of island area, lizard abundance, presence of birds of prey, and seabird nesting density on the body size of *Podarcis* on islands, with the effects of island area, birds of prey, and nesting seabirds more pronounced for female lizards and the effects of lizard abundance more pronounced for male lizards. The effects of island area and seabird nesting density point to a central role of food resources in setting body size in these lizards, with food resources depending on two processes: primary productivity on islands without nesting seabirds and marine subsidies on islands with nesting seabirds. Predation may hold body size below the level allowed by food resources.

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Author contributions

Shelby Stalder wrote the manuscript and performed statistical analyses. Kinsey M. Brock collected the data, wrote the manuscript, and performed statistical analyses. Peter A. Bednekoff wrote the manuscript and performed statistical analyses. Johannes Foufopoulos collected the data and wrote the manuscript.

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