

Inconsistent patterns of body size evolution in co-occurring island reptiles

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Abstract

Aim: Animal body sizes are often remarkably variable across islands, but despite much research we still have a poor understanding of both the patterns and the drivers of body size evolution. Theory predicts that interspecific competition and predation pressures are relaxed on small, remote islands, and that these conditions promote body size evolution. We studied body size variation across multiple insular populations of 16 reptile species co-occurring in the same archipelago and tested which island characteristics primarily drive body size evolution, the nature of the common patterns, and whether co-occurring species respond in a similar manner to insular conditions.

Location: Aegean Sea islands.

Time period: 1984–2016.

Major taxa studied: Reptiles.

Methods: We combined fieldwork, museum measurements and a comprehensive literature survey to collect data on nearly 10,000 individuals, representing eight lizard and eight snake species across 273 islands. We also quantified a large array of predictors to assess directly the effects of island area, isolation (both spatial and temporal), predation and interspecific competition on body size evolution. We used linear models and meta-analyses to determine which predictors are informative for all reptiles, for lizards and snakes separately, and for each species.

Results: Body size varies with different predictors across the species we studied, and patterns differ within families and between lizards and snakes. Each predictor influenced body size in at least one species, but no general trend was recovered. As a group, lizards are hardly affected by any of the predictors we tested, whereas snake size generally increases with area and with competitor and predator richness, and decreases with isolation.

Main conclusions: No factor emerges as a predominant driver of Aegean reptile sizes. This contradicts theories of general body size evolutionary trajectories on islands. We conclude that overarching generalizations oversimplify patterns and processes of reptile body size evolution on islands. Instead, species' autecology and island particularities interact to drive the course of size evolution.

KEYWORDS

body size, competition, island area, isolation, lizards, predation, snakes

1 | INTRODUCTION

The identification of general pathways in the evolution of body size variation among insular populations has received decades of attention, and multiple patterns and drivers have been proposed and contradicted. Trait evolution on islands is often perceived as strong, predictable and consistent across taxa (Köhler, Moyà-Solà, & Wrangham, 2008; Lomolino, 2005; Van Valen, 1973). The most debated pattern is the 'island rule', suggesting that insular animals tend to evolve a medium body size (Faurby & Svenning, 2016; Lomolino, 2005; Van Valen, 1973; cf. Itescu, Karraker, Raia, Pritchard, & Meiri, 2014; Leisler & Winkler, 2015; Meiri, 2007). Insular faunas are generally depauperate, becoming species poor as islands become smaller and more isolated (e.g., Darlington, 1957; MacArthur & Wilson, 1963). Therefore, insular animals are thought to experience relaxed interspecific competition and predation pressures, which, in turn, promote higher population densities and, consequently, stronger intraspecific competition (Melton, 1982). Together with resource limitation, these ecological processes are commonly thought to drive body size evolution on islands (Case, 1978; Lomolino, 2005; Melton, 1982). Heaney (1978) suggested that the effect of each of these factors changes with the size of the focal island and animal. He hypothesized that interspecific competition is more important to small animals than to large ones and that food limitation is more important to large animals than to small ones. He also hypothesized that the effect of predation is equally important at all sizes, but produces different trends at different body sizes. Additionally, he hypothesized that food limitation is the most important selection agent on small islands, predation on medium-sized islands, and interspecific competition on large islands and the mainland. Alternative explanations for body size variation on islands, suggesting indirect selection of these ecological factors on body size, via direct selection on life-history traits, have also been proposed (Adler & Levins, 1994; Palkovacs, 2003; Raia et al., 2003).

Area and isolation are the two main island characteristics thought to affect animal body size. Lomolino (2005) suggested that small species increase in size on smaller and more isolated islands, whereas large species become smaller on such islands. Other studies, however, found minor support for such relationships in mammals (Meiri, Dayan, & Simberloff, 2005, 2006), snakes (Boback, 2003) and lizards (Meiri, 2007). Heaney (1978) predicted that the body size of small mammals decreases whereas that of large mammals increases with increasing area (see also Marquet & Taper, 1998; Melton, 1982). He further predicted that medium-sized animals are largest on intermediate-sized islands, becoming smaller on both smaller and larger islands (Heaney, 1978). However, Meiri et al. (2005) found no support for Heaney's prediction, or for a linear response of size to island area.

Isolation can be defined both in space and in time. Spatial isolation, usually calculated as the distance of the island from the nearest mainland (e.g., Anderson & Handley, 2002; Meik, Lawing, Pires-daSilva, & Welch, 2010), reduces immigration (i.e., gene flow) rates and makes in situ adaptations more likely (Heaney, 2000). The effect of spatial isolation on body size is possibly indirect, reflecting factors such as predation and competition pressures (Arnold, 1979; Heaney, 1978).

Anderson and Handley (2002) suggested that, where over-water dispersal is unlikely (as in the case of Aegean Sea reptiles; Foufopoulos & Ives, 1999), body sizes on close and far islands would not differ. Temporal isolation is thought to be associated with body size in systems where sufficient time since isolation has not yet passed to allow a unidirectional change towards an optimum to be completed (Anderson & Handley, 2002). However, accelerated trait evolution on recently isolated islands has also been suggested (Aubret, 2015). As increased isolation is expected to drive the same phenotypic changes as decreasing island area (Adler & Levins, 1994), Heaney's (1978) prediction for island area is possibly true for isolation as well (i.e., that intermediate-sized species are smallest at intermediate isolation, and larger at low and high degrees of isolation). Furthermore, as Heaney suggested, island area reflects predation and interspecific competition, and therefore, the pattern suggested for island area should apply to predation and interspecific competition, with the latter possibly showing a stronger effect in small species.

Reptiles are well known for their extreme-sized insular forms: giant tortoises and Komodo dragons on the one hand, and the world's smallest lizards (*Sphaerodactylus* geckos and *Brookesia* chameleons; Glaw, Köhler, Townsend, Vences, & Salamin, 2012; Hedges & Thomas, 2001) and snakes (Caribbean *Tetracheilostoma* threadsnakes; Hedges, 2008) on the other. Whether reptile body sizes tend to grow or diminish on islands compared with the mainland seems to be a clade-specific characteristic (c.f. e.g., Boback & Guyer, 2003; Case, 1978; Meiri, 2007, 2008). How island area and isolation affect reptile body size evolution is unclear. Previous studies provided inconsistent results (cf. Boback, 2003; Donihue, Brock, Foufopoulos, Herrel, & Grindstaff, 2016; Hasegawa & Moriguchi, 1989; Meiri, 2007; Meik et al., 2010; Soulé, 1966). Release from predation is thought to drive size increase in small species and size decrease in large species by relaxing direct selection on size-related anti-predatory adaptations (Heaney, 1978; Vervust, Grbac, & Van Damme, 2007). Relaxed interspecific competition allows niche shifts and promotes size changes (Case, 1978; Hasegawa, 2003; Schoener, 1970; Soulé, 1966; but see Dunham, Tinkle, & Gibbons, 1978). Ecological release (both from predators and from interspecific competitors) is also thought to promote higher population densities, and consequently, stronger intraspecific competition and aggressiveness (Donihue et al., 2016; Pafilis, Meiri, Foufopoulos, & Valakos, 2009), which in turn favours large sizes, although smaller size is expected where early maturity is advantageous (Melton, 1982; Palkovacs, 2003; Raia et al., 2003).

To date, insular reptile body size evolution studies have either contrasted mainland and island species or populations (e.g., Boback & Guyer, 2003; Case, 1978; Itescu et al., 2014; Meiri, 2007) or have examined the effects of some predictors across populations of a single species (e.g., Meik et al., 2010; Soulé, 1966) or genus (Dunham et al., 1978). It remains unclear which island characteristics primarily drive body size evolution, the nature of common patterns, and whether co-occurring species respond in a similar manner to insular conditions. Which factor is most influential is sometimes debated even for a single species (cf. Calsbeek & Cox, 2010, 2011; Losos & Pringle, 2011). Therefore, we approached these questions by directly quantifying the

effect of multiple potential selection agents across multiple island populations of multiple reptile species within a single archipelago. Comparing species co-occurring within the same archipelago allows one to eliminate island-specific factors that vary across different regions, such as latitude, climate, vegetation and primary productivity, but remain relatively uniform among such co-occurring species (Meiri, Meijaard, Wich, Groves, & Helgen, 2008). This study design potentially enables us to distinguish between patterns driven by the island conditions we studied and those that are species specific.

We assembled a database of unprecedented coverage, encompassing body size data for nearly 10,000 individuals of 16 reptile species (eight lizard and eight snake species), from 273 islands in the Aegean Sea. These islands vary widely in area, isolation and faunal composition. Body size in reptile populations on these islands also varies greatly (and, in some species, even reaches the maximal documented size; Itescu, Schwarz, Moses, Pafilis, & Meiri, 2016), making this system ideal to study size evolution on islands. We aimed to test several hypotheses, as follows: (a) small species increase in size whereas large species become smaller as islands decrease in area, increase in isolation (in time and space) and harbour fewer predators and competitors for the focal species (Heaney, 1978; Lomolino, 2005); (b) medium-sized species are largest on intermediate-sized islands and intermediate degrees of isolation, predation and competition (Heaney, 1978); (3) interspecific competition affects small species more strongly than large species, whereas the effect of predation is not size dependent (Heaney, 1978); and (d) body size patterns on islands are consistent across taxa (Köhler et al., 2008; Lomolino, 2005).

2 | METHODS

2.1 | Study system

The Aegean Sea has several thousand islands varying across six orders of magnitude in area. Their geological histories are diverse (Lymberakis & Poulakakis, 2010), and the landscapes are a patchwork of dwarf Mediterranean scrub (locally called 'phrygana'), sclerophyllous evergreen maquis and agricultural areas (Fielding, Turland, & Mathew, 2005). Consequently, faunal composition and resource availability vary greatly across islands. Fifty reptile species inhabit Aegean Sea islands, with the gecko *Mediodactylus kotschy* and the lacertid *Podarcis erhardii* being most common, inhabiting even very small islets (Valakos et al., 2008).

2.2 | Data collection

We measured specimens in the field during spring and summer periodically over 33 years (1984–2016). We also measured specimens in eight museum collections (Zoologische Staatssammlung München, Zoologische Forschungsmuseum Alexander Koenig in Bonn, Natural History Museum of Crete, Goulandris Natural History Museum, British Natural History Museum, French National Museum of Natural History, Museum of Comparative Zoology at Harvard University and Yale Peabody Museum of Natural History). Finally, we comprehensively

surveyed literature and recorded body size information for as many Aegean island reptiles as possible (data were extracted from 97 sources; see Supporting Information Appendix S1 for a list). We recorded sex and body size for 9,951 adult individuals of eight lizard and eight snake species originating from 273 islands (Table 1; Supporting Information Appendix S2). We used the most commonly reported size indices: snout–vent length (SVL) for lizards, and total length for snakes. Mean body mass for each species was calculated from data we recorded in the field and from the literature. To ensure that our use of multiple data sources did not bias the results, we compared the mean body size of specimens measured in museum collections and specimens measured in the field for several islands. We compared only islands from which we recorded body size data of at least five males and five females for each data source. For the two species with sufficient data we found no differences between sources (*P. erhardii*, field mean SVL = 61.05 mm, museum = 60.43 mm, $n = 38$ islands, $t = 1.22$, $p = .23$; *M. kotschy*, field = 43.35 mm, museum = 43.68 mm, $n = 25$, $t = -1.05$, $p = .30$). We therefore pooled museum, literature and field data in all further analyses.

Following most island biogeography studies (studies of body size included; e.g., Boback, 2003; Lomolino, 2005; Meiri et al., 2005), we tested the distance from the nearest mainland as an index of spatial isolation. However, for land-bridge island systems this index might not adequately quantify effective isolation (Itescu, 2017), especially in the Aegean Sea archipelago (Foufopoulos & Ives, 1999). Therefore, we also studied the distance from the closest larger island and a temporal isolation index, the time since isolation. Distances were calculated using Google Earth tools. Periods of isolation for islands isolated during the past 20,000 years [since the end of the Last Glacial Maximum (LGM)] were calculated by crossing data for the maximal depth between a focal island and the last landmass to which it was connected with region-specific charts of sea-level change since the LGM (see Foufopoulos & Ives, 1999; Foufopoulos, Kilpatrick, & Ives, 2011). Maximal depths were drawn from fine-resolution bathymetric maps of the Hellenic Navy Hydrographic Service (www.hnhs.gr/geoindex/). Estimations were calculated to a 1-year resolution, and we did not round values, although we acknowledge our method cannot accurately estimate isolation time at such a fine resolution. Temporal isolation data for islands isolated earlier than the LGM were assembled from the literature (Supporting Information Appendix S3). We assembled island-specific faunal lists based on the literature and our own field observations to count the potential predator and competitor species of each focal population. Predators were defined as all mammals and reptiles likely to prey upon focal species (Supporting Information Appendix S4). Birds were excluded because their mobility across islands and their seasonal migration allows them to hunt well away from their breeding sites, making it impossible to create reliable island-specific lists. To ensure that the exclusion of birds did not significantly affect our predator richness values we tested the correlation between predatory bird richness values and the combined counts of predatory mammal and predatory reptiles across 41 islands for which we did have reasonably reliable predatory bird lists (Itescu, Schwarz, Meiri, Pafilis, & Clegg, 2017). The correlation coefficient (r) was 0.90 ($p < .01$). We therefore

TABLE 1 Summary of data and the effects of each predictor on each species

Group	Family	Species	Islands (n)	Individuals (n)	Population mean size range (mm)	Species mean body mass (g)	Area (squared km)	Distance from the mainland (km)	Distance from closest larger island (km)	Time since isolation (years)	Predators	Competitors	
Lizards	Gekkonidae	<i>Hemidactylus turcicus</i>	27	270	42.04–59.89	3.3	+	n.s.	n.s.	n.s.	n.s.	n.s.	
		<i>Mediodactylus kotschy</i>	86	2,071	33.52–49.88	2.8	–	n.s.	n.s.	n.s.	n.s.	n.s.	∩
	Lacertidae	<i>Podarcis erhardii</i>	118	5,323	52.87–75.23	6.0	–	–	+	+	–	n.s.	n.s.
		<i>Podarcis gaigeae</i>	14	641	57.37–77.67	8.4	n.s.	–	–	+	–	n.s.	n.s.
		<i>Podarcis milensis</i>	8	116	53.65–67.09	4.1	–	n.s.	+	+	+	n.s.	n.s.
		<i>Lacerta trilineata</i>	16	231	107.33–141.85	69.9	–	+	n.s.	n.s.	n.s.	n.s.	n.s.
Scincidae	<i>Ophisops elegans</i>	14	143	40.10–48.53	2.0	+	n.s.	n.s.	n.s.	n.s.	–	n.s.	
	<i>Ablepharus kitaibelii</i>	24	180	35.66–44.84	1.4	n.s.	+	n.s.	n.s.	n.s.	n.s.	n.s.	
Snakes	Boidae	<i>Eryx jaculus</i>	8	48	269.79–516.33	52.5	n.s.	–	n.s.	n.s.	–	n.s.	
		<i>Dolichophis caspius</i>	11	72	1,085.40–1,886.00	625.2	n.s.	n.s.	n.s.	n.s.	n.s.	–	+
	Colubridae	<i>Eirenis modestus</i>	8	33	386.00–543.00	19.8	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
		<i>Elaphe quatuorlineata</i>	11	70	1,036.20–1,525.61	846.9	n.s.	–	n.s.	n.s.	n.s.	n.s.	n.s.
		<i>Natrix natrix</i>	11	55	566.25–910.00	91.6	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
		<i>Telescopus fallax</i>	12	56	477.43–903.33	44.9	∩	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
		<i>Vipera ammodytes</i>	15	152	281.33–592.25	28.1	n.s.	–	n.s.	n.s.	n.s.	n.s.	n.s.
		<i>Vipera xanthina</i>	8	51	490.78–1,493.33	276.0	n.s.	n.s.	n.s.	n.s.	U	n.s.	n.s.

Note. Full statistics of all models (with sample sizes) are given in Table 2. Population mean size range refers to snout–vent length in lizards and total length in snakes. +, positive correlation; –, negative correlation; ∩, positive quadratic relationship; ∩, negative quadratic relationship; n.s., non-significant correlation.

feel confident to exclude bird counts from our database. We could not quantify potential predatory arthropods (e.g., spiders, scorpions, centipedes), because reports of predation on reptiles by arthropods and island-specific faunal lists for them are too rare. Competitors were defined as other lizards (for lizards) or other snakes (for snakes), assuming that juveniles of large species potentially compete with adults of smaller species.

2.3 | Analyses

We examined 16 reptile species for which we had measurements of at least three individuals per population sampled across at least eight islands. This approach allowed us to maximize the number of species and populations as well as the range of islands; hence, to maximize variation in the predictor variables. To avoid size biases attributable to sexual size dimorphism, we calculated the population mean body size by averaging male and female means. Only for *Ablepharus kitaibelii* we used a mean of all individuals regardless of sex, because reliably determining their sex in the field in a non-invasive manner is extremely difficult.

We first explored, for each species, whether the relationship of body size with each of the six island characteristics (island area, distance from the mainland, distance from the closest larger island, time since isolation, predator richness and competitor richness) is linear or curvilinear. To test Heaney's (1978) prediction that the relationship between size evolution of species and each of the predictor variables is affected by the species body size, we regressed the correlation coefficient of the relationship between body size (i.e., body length) and each of the six predictor variables against the \log_{10} -transformed body mass of each species. We expected to find a positive relationship where Heaney's prediction holds, because it asserts that small species would show negative body size–predictor slopes, medium-sized species would have slopes equal to zero, and large species would show positive slopes (see Meiri et al., 2005). To test Heaney's prediction that interspecific competition is more important for small species than for large species, whereas predation is equally important across all size classes, we regressed the absolute value of the correlation coefficients against \log_{10} -transformed body mass. Here, we expected to find a significant negative trend for interspecific competition and no trend for predation if the prediction holds. We used body mass as the predictor variable in these analyses, because it is comparable across taxa, eliminating biases driven by body shape, and therefore is more suitable for interspecific comparisons than body length (Feldman & Meiri, 2013; Feldman, Sabath, Pyron, Mayrose, & Meiri, 2016).

We then took a meta-analytic approach to explore whether any island characteristic significantly affects body size across all reptiles we studied in general or across each suborder (snakes and lizards) separately. We conducted DerSimonian–Laird random-effect meta-analysis of correlation coefficients (r) of the linear regressions of body size against each predictor variable in all species as effect sizes, for each group separately. We used the correlation coefficients from regressions of \log_{10} -transformed body size (against tested predictors) for all

TABLE 2 Best models by species

Group	Family	Species	n	Predictor	Slope	SE	Intercept	SE	p-value	Adjusted R ²	
Lizards	Gekkonidae	<i>Hemidactylus turcicus</i>	27	Log area	1.91	0.59	46.37	1.01	< .01	0.26	
		<i>Mediodactylus kotschy</i>	86	Log area	-0.86	0.44	39.64	0.88	.05	0.10	
			Competitor richness	2.81	0.81				< .01		
	Lacertidae	<i>Podarcis erhardii</i> *	118	Competitor richness (²)	-0.38	0.12	1.80	<0.01			0.07
				Log area	(-)<0.01	<0.01				.02	
				Distance from the mainland	(-)<0.01	<0.01				.01	
		<i>Podarcis gaigeae</i> *	14	Log distance from closest larger landmass	0.01	0.01	2.53	0.19		.04	
				Distance from the mainland	(-)<0.01	<0.01				< .01	0.51
				Log distance from closest larger landmass	0.07	0.02				.01	
				Log time since isolation	-0.08	0.02				< .01	
<i>Podarcis milensis</i>	8	Log area	-2.23	0.74	48.63	3.80		.03	0.75		
		Log time since isolation	2.06	0.68				.03			
<i>Lacerta trilineata</i>	16	Log area	-7.28	3.01	136.02	7.45		.03	0.43		
		Distance from the mainland	0.14	0.05				.01			
<i>Ophisops elegans</i>	14	Log area	3.06	1.00	41.61	1.28		.01	0.36		
		Predator richness	-0.67	0.28				.04			
<i>Ablepharus kitaibelii</i>	24	Distance from the mainland	0.03	0.01	39.13	0.73		< .01	0.30		
Snakes	Boidae	<i>Eryx jaculus</i>	8	Distance from the mainland	-5.77	0.55	1,302.57	89.63	< .01	0.94	
			Predator richness	-26.20	3.56				< .01		
	Colubridae	<i>Dolichophis caspius</i>	11	Predator richness	-326.08	88.43	2,751.25	391.42	.01	0.58	
			Competitor richness	447.95	116.38				< .01		
			None	-	-				-		
	<i>Eirenis modestus</i>	8	Distance from the mainland	-2.79	0.48	1,482.29	37.59		< .01	0.77	
		11	None	-	-				-		
		11	Log area	0.55	0.21	2.04	0.26		.03	0.43	
		11	(Log area) ²	-0.09	0.04				.04		
		12	Distance from the mainland	(-)<0.01	<0.01	2.74	0.04		< .01	0.63	
Viperidae	<i>Vipera ammodytes</i> *	15	Log time since isolation	-6.94	1.86	19.42	4.39		.01	0.65	
	<i>Vipera xanthina</i> *	8	(Log time since isolation) ²	0.71	0.19				.01		

Note. n is island sample size. *Body size was log₁₀-transformed in this species.

species, to standardize the r values we analysed. The meta-analyses were performed using the 'metacor' R package (Laliberté, 2011).

Finally, we examined, for each species, which of the six island characteristics comprise the model that best predicts its body size on islands and compared the selected best models across species. To this end, we performed a multiple regression test for each species, followed by a backward-stepwise model-selection procedure based on p -values ($\alpha < .05$), using both linear and quadratic terms. We avoided using the Akaike information criteria (AIC) for model selection [AIC or corrected AIC (AICc) scores] because the models with the lowest scores often had predictors that were poorly associated with size (i.e., they had p -values $> .05$ when significance levels were estimated), making them non-informative (models with the lowest scores merely being the best of a collection of poor models; Arnold, 2010; Mac Nally, Duncan, Thomson, & Yen, 2017). Thus, the much maligned p -value approach proved more conservative. Nevertheless, we present the AICc-based best models for each species in Supporting Information Appendix S5 to highlight that our general conclusions are robust for using different model-selection approaches. We avoided overparameterization by limiting models to include a maximum of three data points (i.e., islands) per tested predictor. We discarded predictors that were highly collinear with others (variance inflation factor ≥ 5) in the same model. To meet the assumptions of parametric tests, we \log_{10} -transformed island area, time since isolation, and where needed, body size (residual distributions of six of the 16 species were not normal before transformation; Shapiro-Wilk normality test) in all analyses. In all cases where we analysed correlation coefficients (r) as the dependent variable, we used the r values from regressions of \log_{10} -transformed body size (against tested predictors) for all species to standardize the analysed values.

3 | RESULTS

The best models for body size were highly inconsistent across species. Each of the predictors we tested was correlated with the body size of at least one species, but most predictor-body size relationships were non-significant, and no predictor was important for all species (Table 1). We found 14 different models (in terms of variables included and trend signs) across the 16 studied species. Only the snakes *Elaphe quatuorlineata* and *Vipera ammodytes* shared a similar model. For two snake species (*Eirenis modestus* and *Natrix natrix*), no predictors were significant. Explanatory power and effect sizes of each predictor varied greatly across the 16 species examined, within snakes and lizards separately, and even within families (Table 2). In only one out of 16 reptile species (the snake *Telescopus fallax*) was a quadratic model of body size for island area significant, and only five species showed a significant linear relationship (three positive and two negative) between size and area, when area was tested in univariate models (Figure 1; see full univariate model statistics in Supporting Information Appendix S6). After model selection, *T. fallax* still showed the same quadratic pattern, and significant linear relationships emerged only in lizards (positive in two species and negative in four). In fact, for lizards the island area was the most frequently significant predictor. For snakes, the distance from the

mainland was the most frequently significant predictor, negatively correlated with body size in three species and positively so in one.

When we regressed the correlation coefficient (r) from the regression of body size against each predictor variable in each study species against its log body mass, we found a significant negative relationship for the three isolation indices (distance from the mainland, distance from the closest larger island and time since isolation). The results for island area, predator richness and competitor richness in this analysis were non-significant (Table 3; Figure 2). Regressing the absolute values of the correlation coefficients from body length-predator richness and body length-competitor richness regressions against body mass ($n = 16$) showed that the importance of both predation (slope = $.06 \pm .07$, $p = .40$, $R^2 = .05$) and interspecific competition (slope = $.08 \pm .06$, $p = .23$, $R^2 = .10$) for body size variation is not size dependent (Figure 3).

The meta-analyses (Table 4) revealed that none of the predictors we tested had a significant effect on body size in reptiles overall. Only the distance from the closest larger island seemed to have a general (positive) effect on lizards (and a weak one at that). Snake body size, however, significantly increased with island area, as well as with competitor and predator richness, and declined with the distance from the mainland and with the time since isolation. The only predictor variable that did not significantly affect snake body size was the distance from the closest larger island (i.e., the opposite of the lizard pattern).

4 | DISCUSSION

Aegean island reptiles show great idiosyncrasy in the way their sizes respond to the factors we studied. We found great pattern diversity among the species we studied, with effects of the predictor variables varying in sign, shape (linear, curvilinear) and significance. None of the predictor variables consistently affected even the majority of species, and a comparison of the best models across species showed that nearly all species were affected by a different combination of factors. Very few consistent patterns emerged, except that most predictors were uninformative for most species (a consistency of sorts). In line with this finding, the meta-analysis of effect sizes showed that none of the three isolation indices significantly drives insular body size of the studied reptiles in a particular direction (i.e., patterns are inconsistent across species). Island area, predator richness and competitor richness probably have no general effect on insular reptile body size. Our results also revealed striking differences in the response of body size on islands to environmental conditions in lizards and those in snakes. That said, small reptile species tend to become larger on more isolated islands, whereas large species tend to become smaller as geographical and temporal isolation increases.

A common perception in island biogeography is that as islands get smaller and more isolated, the effects of the insular environment on the traits of their inhabitants intensify (Filin & Ziv, 2004; Lomolino, 2005; Melton, 1982). However, when the effects of area and isolation on reptile body size are tested directly, results are often inconsistent. For snakes, Hasegawa and Moriguchi (1989) found a negative

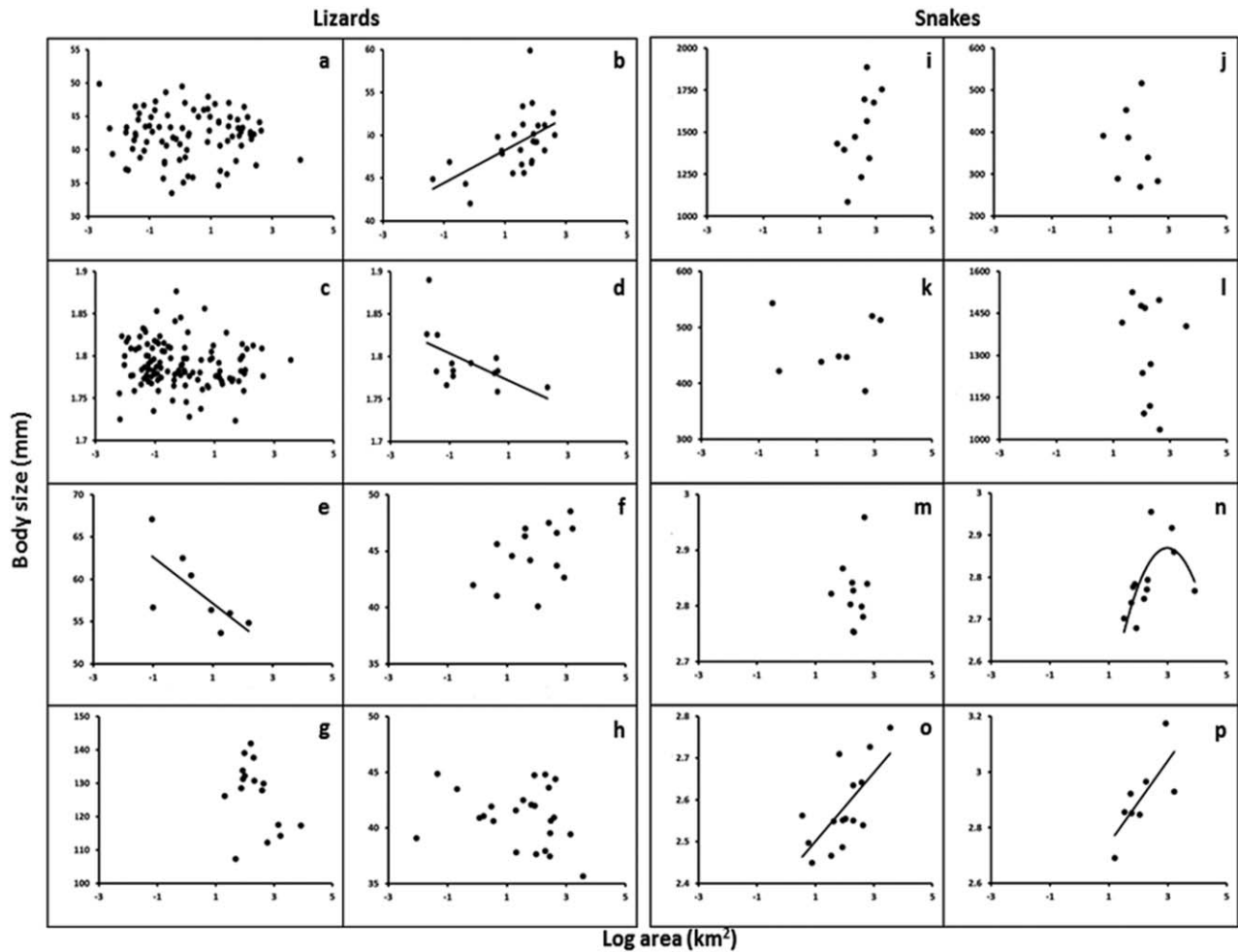


FIGURE 1 Body size as a function of island area. (a) *Mediodactylus kotschyi*. (b) *Hemidactylus turcicus*. (c) *Podarcis erhardii*. (d) *Podarcis gaigeae*. (e) *Podarcis milensis*. (f) *Ophisops elegans*. (g) *Lacerta trilineata*. (h) *Ablepharus kitaibelii*. (i) *Dolichophis caspius*. (j) *Eryx jaculus*. (k) *Eirenis modestus*. (l) *Elaphe quatuorlineata*. (m) *Natrix natrix*. (n) *Telescopus fallax*. (o) *Vipera ammodytes*. (p) *Vipera xanthina*. Body size index is as follows: snout-vent length (SVL) for species a, b, e, f, g and h; log SVL for species c and d; total length for species i, j, k and l; and log total length for species m, n, o and p. Trend lines indicate a significant relationship ($p < .05$)

correlation between body size and island area, Boback's (2003) meta-analysis revealed no correlation between them, and Meik et al. (2010, 2012) found a strong positive correlation in speckled rattlesnakes (*Crotalus mitchellii*). Our meta-analysis results for snakes in general support the findings of Meik et al. (2010, 2012), but for most species we

studied (seven out of the eight species) island area is not a particularly important predictor of body size according to model selection (for *T. fallax* it is, but the relationship with body size is hump shaped). Boback (2003) and Meik et al. (2010) found no association between size and either temporal or geographical isolation, whereas we found a negative

TABLE 3 Results of the regression of the correlation coefficient (r) between body size and each predictor variable in each of the 16 study species against its log body mass (in grams)

Predictors	Slope	SE	Intercept	SE	p -value	R^2
Log area	.14	.13	-.11	.21	.32	.07
Distance from the mainland	-.30	.12	.22	.20	.03	.29
Log distance from closest larger island	-.20	.08	.33	.13	.03	.30
Log time since isolation	-.30	.09	.36	.15	.01	.42
Predator richness	.20	.11	-.18	.19	.11	.17
Competitor richness	.13	.11	-.04	.18	.27	.08

Note. Significant results are highlighted in bold.

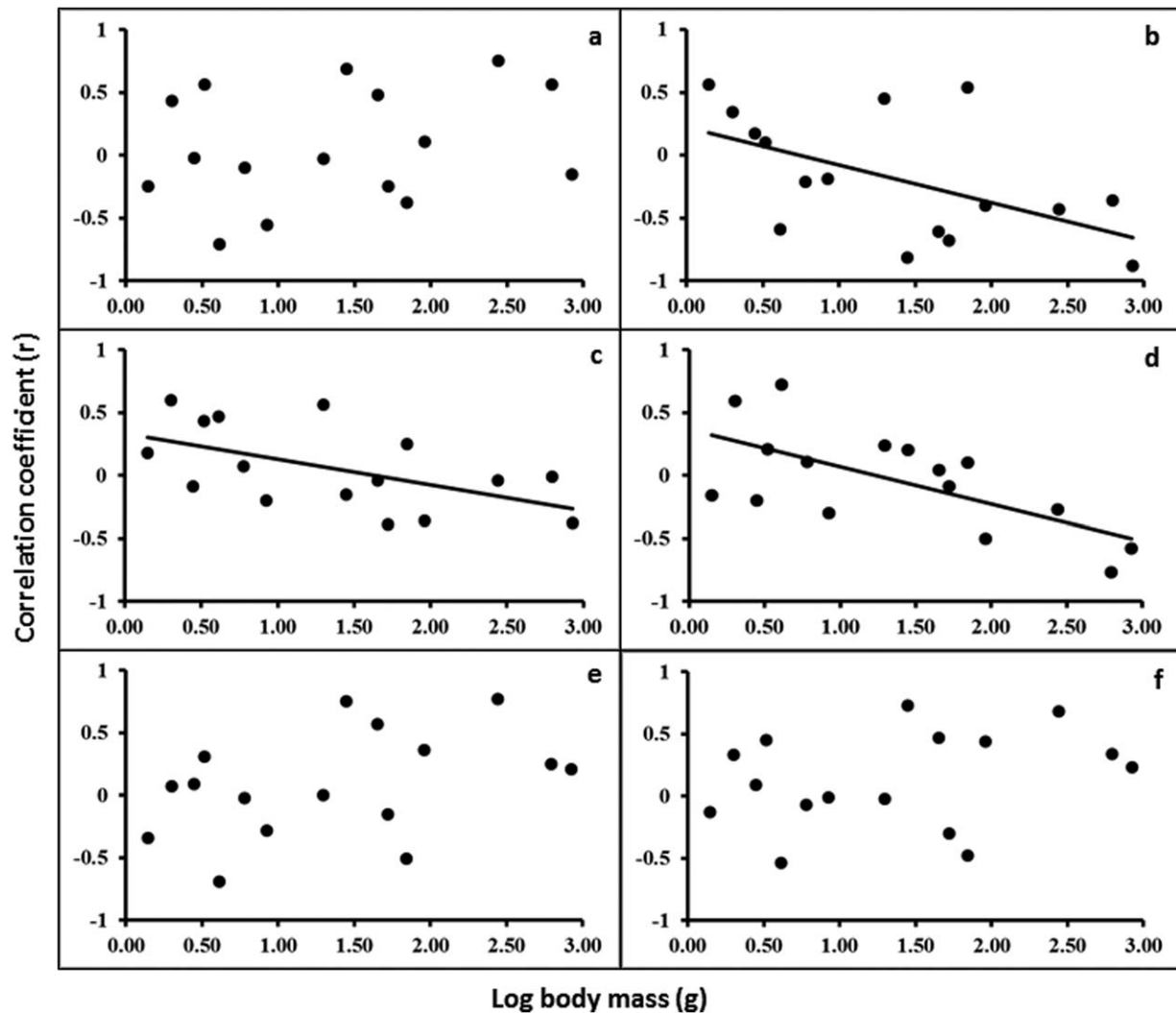


FIGURE 2 The relationship between the correlation coefficient (r) of body length (in millimetres; snout–vent length for lizards and total length for snakes; see main text) against each predictor variable and the log mean body mass (in grams) of each species. Panels show: (a) log island area (in square kilometres); (b) distance from the mainland (in kilometres); (c) log distance from the closest larger island (in kilometres); (d) log time since isolation (in years); (e) predator richness; and (f) competitor richness. $n = 16$ species in all cases. Trend lines are shown only if they are statistically significant

relationship. The frequent inclusion of island area in the best models of lizards (for seven out of eight species) is somewhat surprising, considering results of previous studies (Dunham et al., 1978; Losos, Schoener, & Spiller, 2004; Meiri, 2007; Soulé, 1966; but see Donihue et al., 2016). However, the fact that the direction of the relationship changes across species points to no general trend.

We cannot support most of Heaney's (1978) predictions in the case of reptiles. It is clear that none of the island characteristics we examined drives reptile body size patterns in the predicted way. Moreover, isolation, regardless of the index tested, shows the opposite patterns. These results highlight a role of island isolation in driving reptile body size evolution (Lomolino, 2005; Van Valen, 1973). Island area, however, in contrast to theory (Heaney, 1978; Lomolino, 2005), has no overall effect on patterns of reptile body size variation on islands, at least in the Aegean Sea archipelago. Our results also refute Heaney's (1978) prediction that interspecific competition influences small species

more strongly than large species, but support his prediction that the importance of predation for size variation on island is not size biased.

Surprisingly, we found only a few, weak effects of biotic interactions. Given that others have used island area and isolation as proxies for biotic effects and found significant associations with body size (Lomolino, 2005), we expected that testing the effect of the biotic interactions directly would result in stronger patterns. This, however, proved false. Predator and competitor richness did not affect the body size of most of our study species (fewer than a quarter of the species had these factors included in their best model). For snakes, but not for lizards or for reptiles in general (i.e., as a group), the meta-analysis showed a tendency towards larger sizes where predator and competitor richness is greater. We think the weak effect of competitor and predator richness implies that maybe many, possibly inefficient, competitors and predators do not necessarily impose a stronger selection pressure than one or two dominant competitors or predators.

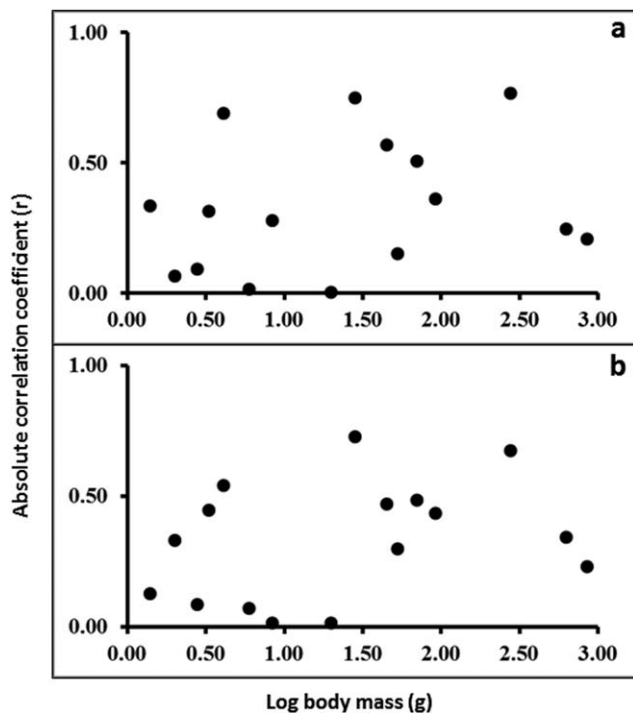


FIGURE 3 The relationship between the absolute value of the correlation coefficient (r) of body length (in millimetres; SVL for lizards, total length for snakes, see text) against (a) predator richness and (b) competitor richness and the log mean body mass (in grams) of each species

Therefore, we suspect that despite its common use as a predation pressure index in the literature (e.g., Cooper, Prez-Mellado, & Vitt, 2004; Pérez-Mellado, Corti, & Lo Cascio, 1997), predator richness poorly reflects predation intensity (Itescu et al., 2017; Meiri et al., 2005). Likewise, competitor richness may be a weak index of competition intensity (Meiri et al., 2014). Another possibility is that significant evolutionary changes are apparent only on predator-free, rather than predator-poor, islands.

Two important factors that we did not test in the present study but are often thought to shape body size evolution on islands are intraspecific competition and resource limitation (Case, 1978; Melton, 1982). For example, gigantism on islands has been explained by the need to evolve a large size in conditions of stronger intraspecific

competition, where predation pressure is low (Pafilis et al., 2009). Territoriality, which involves defending resources against conspecifics and characterizes some of our study species, is also thought to be associated with larger sizes on islands (Case, 1978; Keehn, Nieto, Tracy, Gienger, & Feldman, 2013; but see Case & Schwaner, 1993). Richer resources, in terms of prey size, prey diversity and prey availability, are usually associated in reptiles with increased body sizes on islands as well, especially for snakes (Boback, 2003; Hasegawa, 2003; Hasegawa & Moriguchi, 1989; Meiri, 2007, 2008; Schwaner, 1985; Shine, 1987). Furthermore, resource limitation may drive cannibalism in insular reptiles, consequently selecting for larger body sizes (Pafilis et al., 2009).

Body size variation on islands is commonly examined under a framework of adaptations, but one cannot rule out alternative possibilities, such as habitat-driven plastic phenotypic responses (in contrast to adaptive genetic response) or founder effects. These possibilities seem especially relevant in our study system, considering the minor effect that commonly suggested selection agents have on reptile body size patterns. For example, individual growth rates can vary as a result of genetic changes (i.e., adaptation) or plastic changes (e.g., more food permits faster growth). There are indications that plastic growth rate variability across insular populations resulting from variation in resource availability might produce non-adaptive body size differences (Case, 1976; Forsman, 1991; Madsen & Shine, 1993). Additionally, where predators are rare, foraging and basking times may increase, thereby allowing enhanced growth. Of course, direct selection on growth rates rather than on body size per se (e.g., owing to ontogenetic differences in food limitation, competition intensity or size-biased predation pressure) may also drive population-level body size variation (Aubret, 2012). Vincent et al. (2009) proposed that body size variation in snakes is no more than an evolutionary spandrel, with gape size being the true trait under selection. Another alternative non-adaptive explanation for body size variation across populations is that where adult mortality rates are low (e.g., where predation is low) larger adult sizes are attained because individuals survive longer, and reptiles grow throughout their lives (Hasegawa & Mori, 2008; King, 1989). Founder effects may also have a role in shaping body size patterns, especially in small, remote and young islands (Kolbe, Leal, Schoener, Spiller, & Losos, 2012). Thus, body size variation is not necessarily or solely adaptive, and new approaches (Diniz-Filho & Raia, 2017) might allow better

TABLE 4 Meta-analysis results for all reptiles, only lizards and only snakes

Predictors	All reptiles			Lizards			Snakes		
	Mean r	Range (r)	p -value	Mean r	Range (r)	p -value	Mean r	Range (r)	p -value
Log area (km ²)	.108	-.106 to .313	.16	-.082	-.326 to .173	.27	.410	.146 to .620	< .01
Distance from the mainland (km)	-.201	-.433 to .055	.06	.130	-.129 to .372	.16	-.581	-.777 to -.281	< .01
Log distance from closest larger island (km)	.068	-.070 to .204	.17	.152	-.028 to .323	.05	-.124	-.361 to .128	.17
Log time since isolation (years)	-.042	-.224 to .142	.33	.077	-.134 to .282	.24	-.263	-.536 to .058	.05
Predator richness	.096	-.098 to .284	.16	-.088	-.278 to .108	.19	.443	.182 to .645	< .01
Competitor richness	.147	-.035 to .320	.06	.003	-.190 to .196	.49	.423	.179 to .618	< .01

Note. p -values are for H_0 : mean correlation coefficient (r) = 0. Significant results are highlighted in bold.

discrimination between adaptive and non-adaptive patterns in the near future.

An interesting and important pattern that emerged from our results is that lizards and snakes, at the sub-order level, differ markedly in how their sizes respond to the factors we studied. In fact, we found they show an exactly opposite picture to each other. Lizard body size shows no general response to island conditions, except for a weak tendency to decline with distance from the closest larger island. On the contrary, snake body size responds to most factors apart from distance from the closest larger island. It tends to increase with island area, competitor richness and predator richness, and to decline with distance from the mainland and with time since isolation. Generally, the patterns found for snakes follow the common predictions regarding insular evolution in large species (Heaney, 1978). Interestingly, however, those of lizards do not follow the patterns predicted for small species (Heaney, 1978), for the most part. The patterns we found for each of the two groups separately suggest that the overall effect of isolation on reptile body size is somewhat complex. It is likely that the negative trend in the cases of the distance from the mainland and time since isolation are driven by the tendency of snakes (i.e., generally larger species) towards dwarfism as these factors increase. In contrast, the negative trend for the distance from the closest larger island is probably driven by the tendency of lizards (i.e., generally smaller species) to grow larger on more remote islands. At this point, we cannot discern the reasons why different isolation indices affect one group more strongly than the other. However, we speculate either that the effect of isolation reflects another factor or combination of factors that affect lizards and snakes differently (e.g., the absence of rats on remote islands, which offer quality food for snakes, but possibly prey upon lizards and their eggs), or that the variation of one group is adaptive, whereas that of the other is led by strong founder effect signals or is non-adaptive. Inconsistent patterns of lizard and snake body size evolution on islands have been shown before (e.g., the island rule, cf. Boback & Guyer, 2003 for snakes and Meiri, 2007 for lizards).

Conducting a comparative study of such a wide scope as this one will always create logistic and methodological challenges, and several caveats should be noted. The role of shared ancestral condition in shaping body size variation on islands needs to be addressed by comparing phylogenetic and non-phylogenetic models. However, the population-level phylogenies currently available for the studied species did not allow us to examine this aspect robustly. Therefore, we highlight the importance of island-level molecular studies, which will generally facilitate further investigation of evolutionary patterns. The nature of some of our predictors (e.g., competitor richness, predator richness) necessitates some general assumptions (e.g., that a predator species preys upon its prey species wherever they coexist, and that we can correctly identify all important competitors and predators). Given that we consistently kept these assumptions regarding all species and islands, we are confident that they have not biased our results. Perhaps the most important drawback, and the most challenging to face, is small sample sizes. With almost 10,000 adult reptiles examined, we still came rather short in samples for some populations and for certain species. Several species (e.g., *Macrovipera schweizeri*, *Blanus strauchi*, *Podarcis*

levendis) simply occur on too few islands to be analysed properly. For the rest, an inherent trade-off exists between the numbers of sampled islands and sampled individuals per island. Our main unit of analysis was the population, and therefore, we aimed to maximize the number of islands for each species (thus also maximizing the variance in predictor values). This, however, may come at the expense of accurately assessing population-level mean body sizes, because for some islands we had data from only a few individuals. We acknowledge the possibility that low statistical power might have affected our results in some cases. Nonetheless, the general patterns and inconsistencies we found across species are apparent even across the few best-sampled species. Thus we have confidence that our conclusions are valid. Moreover, the number of species we examined and the number of insular populations we sampled within each of these species are both of unprecedented scope, at least for reptiles. We think this enables us to draw valid conclusions robustly from our results.

Our results provide a compelling example for the statistical issue of which model-selection approach to prefer. The best AIC (or AICc) models are often poor overall, and thus relying on AIC scores alone can be problematic for biological inference. For example, using p -values we infer that none of the predictors we tested explains the variation in body size of *N. natrix* and *E. modestus*. Using AICc, we could show only that there are multiple predictors that are equally good (i.e., equally bad in these cases). In many cases, the AICc method simply proves far less conservative than the p -value-based one (cf. models in Table 2 with those in Supporting Information Appendix S5). In no case did the model, or undistinguishable group of models, with the lowest AICc contain fewer predictors than the best model with only significant predictors (at $p < .05$). Often, however, the models with the lowest AICc contained more predictors, including predictors that the p -value-based method rejected as uninformative (Supporting Information Appendix S5). We think that, if anything, $p = .05$ is not conservative enough (e.g., Benjamin et al., 2017; Johnson, 2013). Using a model-selection method that is even more liberal would have made us infer that many variables, which have the most tenuous relationship with animal size evolution on islands, are, in fact, important. We thus use p -values not because of any theoretical views about their merit, but because we prefer to err on the side of caution.

The results of the present study indicate that, to a large extent, different species respond idiosyncratically to the insular environment. Thus, reptile body size variation seems to be affected more by species identity than by island conditions, at least in this study system. This contradicts the theory asserting that evolutionary patterns of body size on islands are general across different taxa. The fact that none of the predictors we tested consistently affected a majority of the species, and that the best models differed greatly across species, highlights the importance of testing several potential driving mechanisms simultaneously, as we did, to prevent unjustified generalizations from being reached. We thus conclude that body size evolution on islands is probably species and island specific, and that generalizations oversimplify the complex patterns and processes of size evolution. This study elucidates the need for a major re-thinking of the insular evolution paradigm, away from island characteristics as monotonous predictors of

animal trait evolution, and into the need to quantify relevant ecological effects for different study systems.

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DATA ACCESSIBILITY

All the data analysed in this study are available in Supporting Information Appendix S2.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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