07.12.2017

Professor Brian McGill,

Editor in Chief

Global Ecology and Biogeography

Dear Prof. McGill,

We attach a revised version of our manuscript **'Inconsistent patterns of body size evolution in co-occurring island reptiles'** (Ref. GEB-2017-0100; title modified according to referee's suggestion). The manuscript was reviewed by a new anonymous referee and the Editor, Dr. Ana Santos, added her own comments. We were happy to see the supportive review and thanks the editor and the referee for their important suggestions. We followed most of these and revised the manuscript accordingly. Below please find a point by point description of how we dealt with each comment. We hope you will find our manuscript is now at level and ready for publication in *Global Ecology and Biogeography*.

Sincerely,

Yuval Itescu on behalf of all authors

EDITOR'S COMMENTS TO AUTHORS
Editor: Santos, Ana
Comments to the Author:

First, I want to apologize for the delay in the editorial process. Sometimes it takes longer that we would like to, as it happened with your manuscript.

Your manuscript was evaluated by a referee that was not involved in the first round of reviews. I share his view of your paper, and I think it has improved greatly since your previous submission. This new reviewer suggests that you use and AIC based model selection. I think this is a good suggestion and it would strengthen your results, but I will leave it up to you to decide if you should include these analyses in the manuscript. What I strongly advise you to do is to follow his suggestion of highlighting more your general conclusions that the island rule is not universal.

We thank the editor for her supporting comments. As we specify below, we included AICc scores in a new appendix and highlighted in the abstract and in the concluding paragraph of the discussion that our results contrast the generality theory of size evolution on islands.

Dr. Ana Santos, Editor

REVIEWER COMMENTS TO AUTHORS

Referee: 1

Comments to the Author

.

Referee: 2

Comments to the Author

This is a nice work. I didn’t get to review the first round, but this version seems robust an straightforward, so to me it was a good decision to eliminate the additional analyses on the species with more data. I’ve got two significant comments, and a few small ones.

To me the lack of general predictive power of your predictors over all species is the most important result, so I’m really glad you chose to put this in front and make a paper about the lack of general “island rules”. By highlighting that responses differ among species rather than trying to explain each species separately based on correlations you make a great job, so I’m 100% in line with the importance of the paper and its timeliness. That is why I think you should highlight it a bit more, tweaking the text to put such heterogeneity in front, e.g. in the title, where I use “Heterogeneous” or “Non coherent” rather than “Divergent”. Similarly, in the abstract the main conclusions need to start a straightforward sentence saying something like “There are no universal drivers of body size evolution on Aegean reptiles.” And also that “this rejects/contradicts former theory”. Some of this rewording is needed also in the discussion, although very little. In particular, you need to stress that you are rejecting former theory in the last paragraph, as part of your take-home message.

Thanks for this suggestion. We changed the text according to it.

To me the main problem remaining in the text is model selection. Although I would agree with you in that your selection of models based on R2 scores provides sound insights on the lack of general drivers, so the conclusions will stand out, I found the reasoning not to use AIC scores a bit unconvincing. Since I'm not a biostatistician I could certainly live with it, but after reading your response to Diniz-Filho I wonder whether you used AIC in the correct way, for it penalizes the amount of variables in the model. And AICc scores are particularly suited for datasets with low sample size, as some of yours are. Here, the pick would be to compare models according to their Akaike weight; that is, the probability that a particular model is the most informative. I'm sure you'll have models with, say, 20 or 30% probability competing as the best model for several species. Anyway, I think you shouldn't abandon the information approach so quickly, and provide AICc results in the supplement, although perhaps not the raw results, which I concur, would be confusing.

As we stated in the text (and in the reply to referees in the previous round of revision), we are not comfortable with relying on AIC (or even AICc) scores to determine which model is the most informative, and Mac Nally et al.'s recent paper (Journal of Applied Ecology, 2017, "Model selection using information criteria, but is the 'best' model any good?" http://onlinelibrary.wiley.com/doi/10.1111/1365-2664.13060/abstract) clearly and compellingly explains why: first, the model with the lowest AIC may simply be the best of a group of non-informative models (like the best of infectious diseases - you still do not want it), and second, the penalty AIC applies to adding additional parameters (2) is too modest. We now cite this paper in the text. We also added a paragraph of discussion regarding this point as we think our results serve as a good example for why to prefer p-value based model selection over information criteria based model selection for studies such as ours. Nevertheless, we accept the referee's suggestion to let the readers get our impression themselves, and now present AICc scores of the best models (ΔAICc ≤ 2) for each species in a new supplementary file.

To me the most compelling of your results, and actually the real reason why a frequentist approach is sound here, is your meta-analysis. So why not doing something similar based on AIC weights? AIC scores are not comparable among models based on different datasets, but AIC weights are if the same parameters are tested, so why not just summing all AIC weights per predictor across all species? Here the total weight of a predictor for a species it would be the sum of the AICw of all models where it is present. Given that all models are tested for AICw, the closer to 1, the more informative a variable is. And across all species, the closer to 16, the closer it is to be a general predictor, informative regardless of the species. I think I can hear you saying "but we have showed that with the meta-analysis", but I can also hear other readers saying "but they use R2s! Surely there would be general patterns if they had used AICs". So I still find quite useful to show that results are consistent across analytical paradigms. What this approach certainly does not provide is a pick on the homogeneity signs of the relationships, it just tells you about how often it is informative. But your work will be more trustworthy if it includes similar results from a different approach.

We thank the referee for this suggestion but think that using AIC weights to show what we have shown in the meta-analysis is somewhat confusing, especially since, as the referee rightly mentions, it provides no information about the direction of the effect of the predictor. Therefore, although we do show the AICc based models in Appendix 5, we prefer not to include the AIC weights analysis.

Besides that I have little to say. I really think that the decision of leaving out the more detailed analyses on a few species is sound. The current work is clear and straightforward, and stands out as a valuable contribution for GEB in my opinion, and these other analyses can be published elsewhere.

Some minor comments follow:
Abstract. In the methods you don't tell which kind of analyses you use.

Now added.

In line 52 I'd substitute "We analyse" for "We use linear models and meta-analyses to determine which predictors are more informative, analysing the data for all reptiles…"

Sentence rephrased.

Line74. To be certain, here you refer to MacArthur & Wilson's Equilibrium Theory of Island Biogeography (ETIB). Currently island biogeography theory (ibt) includes many other topics, such as, e.g., that habitat heterogeneity within the island also increases species richness, to mention one you may be familiar with, or that increasing isolation and area determine a radiation zone where cladogenesis starts to be more important than anagenesis. No need to cite these latter theories, just rephrase and mention ETIB rather than just ibt.

We actually want to emphasize only the depauperate nature of islands, rather than point to any (often contentious) mechanism, so we added a citation for Darlington (1957) and retain just the citation for the 1963 paper of MacArthur and Wilson, rather than the more inclusive 1967 book

L242-243. Please show these results (as supplementary material), and rephrase this sentence (it is grammatically incorrect)

We now realized that the sentence as we originally phrased it may be a bit misleading: differences between males and females in their response to single predictors do exist in some of the study species, but our general conclusion, that different factors affect body size in different species, is maintained even if we test only females or only males. Since we want to avoid any confusion by our readers, and since the inter-sexual differences in body size evolution are not the focus of this study (but perhaps an interesting study question in its own right), but rather the interspecific differences, we omitted the sentence from the text.

L366. I'd start this paragraph with "Strikingly" or similar, to highlight your most important result (see my first comment).

We thank the referee for this suggestion, but we think that specifically here it is not appropriate to use “strikingly” or other such strong wording, as we are not the first that failed supporting Heaney’s prediction.

L483-486. Rephrase this sentence, it is fragmentary and difficult to read. I probably can make out for 2 or 3 separate sentences.

Done.

Figures 2 and 3. Please put variable names in the Y axes, so the reader does not have to jump continuously to the caption to understand the figure.

The names of the variables on the Y axes are now clearly marked in figures 2 & 3.

Research paper

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

Yuval Itescu[1] (yuvitescu@gmail.com), Rachel Schwarz[1] (rachelschwarz13@gmail.com), Colin Donihue[2] (colin_donihue@fas.harvard.edu) , Alex Slavenko[1] (slavenko@mail.tau.ac.il), Stephanos A. Roussos[3,4] (stephanos.roussos@unt.edu), Kostas Sagonas[5] (k.sagonas@qmul.ac.uk), Efstratios D. Valakos[6] (evalakos@biol.uoa.gr), Johannes Foufopoulos[7] (jfoufop@umich.edu), Panayiotis Pafilis[6] (ppafil@biol.uoa.gr), Shai Meiri[1] (uncshai@post.tau.ac.il)

[1] *School of Zoology, Tel Aviv University, Tel Aviv 6997801, Israel*

[2] *Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA*

[3] *Department of Biological Sciences, University of North Texas, Denton, TX 76203, USA*

[4] *Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, USA*

[5] *School of Biological and Chemical Sciences, Queen Mary University of London, London E1 4NS, UK*

[6] *Department of Biology, National and Kapodistrian University of Athens, Athens 157-84, Greece*

[7] *School of Natural Resources and Environment, University of Michigan, Ann Arbor, Ann Arbor, MI 48109, USA*

Key words: body size, competition, island area, isolation, lizards, predation, snakes.

Short running title: Body size evolution in insular reptiles

Corresponding Author: Yuval Itescu, Department of Zoology, Tel Aviv University, Tel Aviv 6997801, Israel; phone: +972 640 9811, fax: +972 640 9403; yuvitescu@gmail.com

Number of words in the abstract: 300

Number of words in the main text: 5515

Number of references: 73

ABSTRACT

Aim Animal body sizes are often remarkably variable across islands, but despite much research we still poorly understand both patterns and 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, what the common patterns are, and whether co-occurring species respond similarly to insular conditions.

Location Aegean Sea islands.

Time period 1984-2016.

Major taxa studied Reptiles.

Methods We combined field work, 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 directly assess the effects of island area, isolation (both spatial and temporal), predation and inter-specific 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 single species.

Results Body size varies with different predictors across the species we studied, and patterns differ within families and between lizards and snakes. While each predictor influenced body size in at least one species, 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, 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 over-simplify patterns and processes of reptile body-size evolution on islands. Instead, species' autecology and island particularities interact to drive the course of size evolution.

INTRODUCTION

Identifying 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 (Van Valen, 1973; Lomolino, 2005; Köhler et al., 2008). The most debated pattern is the “island rule”, suggesting insular animals tend to evolve a medium body size (Van Valen, 1973; Lomolino, 2005; Faubry & Svenning, 2016 cf. Meiri, 2007; Itescu et al., 2014; Leisler & Winkler, 2015Insular 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; Melton, 1982; Lomolino, 2005). 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).

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 while large species become smaller on such islands. Other studies, however, found minor support for such relationships in mammals (Meiri et al., 2005, 2006), snakes (Boback, 2003), and lizards (Meiri, 2007). Heaney (1978) predicted the body size of small mammals decreases while that of large mammals increases with increasing area (see also Melton, 1982; Marquet & Taper, 1998). 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 island distance from the nearest mainland (e.g., Anderson & Handley, 2002, Meik et al., 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 (Heaney, 1978; Arnold, 1979). Anderson & 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 later possibly showing a stronger effect in small species.

Reptiles are well-known for their extreme-sized insular forms: giant tortoises and Komodo dragons on one hand, and the world's smallest lizards (*Sphaerodactylus* geckos and *Brookesia* chameleons; Hedges & Thomas, 2001; Glaw et al., 2012) and snakes (Caribbean *Tetracheilostoma* threadsnakes; Hedges, 2008) on the other. Whether reptile body sizes tend to grow or diminish on islands compared to the mainland seems to be a clade-specific characteristic (see e.g., Case, 1978; Boback & Guyer, 2003; Meiri, 2007, 2008). How island area and isolation affect reptile body size evolution is unclear. Previous studies provided inconsistent results (cf. Soulé, 1966; Hasegawa & Moriguchi, 1989; Boback, 2003; Meiri, 2007; Meik et al., 2010; Donihue et al., 2016). 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 et al., 2007). Relaxed interspecific competition allows niche shifts and promotes size changes (Soulé, 1966; Schoener, 1970; Case, 1978; Hasegawa, 2003; but see Dunham et al., 1978). Ecological release (both from predators and interspecific competitors) is also thought to promote higher population densities, and consequently stronger intraspecific competition and aggressiveness (Pafilis et al., 2009; Donihue et al., 2016), which in turn favors large sizes, although smaller size is expected where early maturity is advantageous (Melton, 1982; Palkovacs, 2003).

To date, insular reptile body size evolution studies either contrasted mainland and island species or populations (e.g., Case, 1978; Boback & Guyer, 2003; Meiri, 2007; Itescu et al., 2014), or examined the effects of some predictors across populations of a single species (e.g., Soulé, 1966; Meik et al., 2010) or genus (Dunham et al., 1978). It remains unclear which island characteristics primarily drive body size evolution, what the common patterns are, and whether co-occurring species respond similarly 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, primary productivity, etc., but remain relatively uniform among such co-occurring species (Meiri et al., 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 et al., 2016), making this system ideal to study size evolution on islands. We aimed to test several hypotheses: 1. Small species increase in size while large species become smaller as islands decrease in area, increase in isolation (in time and space), and harbor fewer predators and competitors for the focal species (Heaney, 1978; Lomolino, 2005); 2. 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 while the effect of predation is not size-dependent (Heaney, 1978); 4. Body size patterns on islands are consistent across taxa (Lomolino, 2005; Köhler et al., 2008).

METHODS

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 et al., 2005). Consequently, faunal composition and resource availability vary greatly across islands. Fifty reptile species inhabit Aegean Sea islands, with the gecko *Mediodactylus kotschyi* and the lacertid *Podarcis erhardii* being most common, inhabiting even very small islets (Valakos et al., 2008).

Data collection

We measured specimens in the field during spring and summer periodically over 33 years (1984-2016). We further 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 Appendix 1 for a list). We recorded sex and body size for 9951 adult individuals of eight lizard and eight snake species originating from 273 islands (Table 1, Appendix 2). 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 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=0.23; *M. kotschyi*: field=43.35 mm, museum=43.68 mm, n=25, t=-1.05, p=0.30). We therefore pooled museum, literature and field data in all further analyzes.

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 may 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 maximum depth between a focal island and the last landmass to which it was connected with regional-specific charts of sea-level change since the LGM (see Foufopoulos & Ives, 1999; Foufopoulos et al., 2011). Maximum depths were drawn from fine resolution bathymetric maps of the Hellenic Navy Hydrographic Service (www.hnhs.gr/geoindex/). Estimations were calculated to a one year resolution, and we did not round values although we acknowledge and do not presume our method can accurately estimate isolation time at such a fine resolution. Temporal isolation of islands isolated earlier than the LGM were assembled from the literature (Appendix 3). 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 (Appendix 4). Birds were excluded since 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 excluding 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 et al., 2017). The correlation coefficient (r) was 0.90 ($p<0.01$). We therefore feel confident to exclude bird counts from our database. We could not quantify potential predatory arthropods (e.g., spiders, scorpions, centipedes) since reports on either predation on reptiles by arthropods, and island specific faunal list 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.

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 and hence, maximize variation in the predictor variables. To avoid size biases due to sexual size dimorphism, we calculated population mean body size by averaging male and female means. Only for *Ablepharus kitaibelii* we used a mean of all individuals regardless of sex since 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 log-transformed body mass of each species. We expected to find a positive relationship where Heaney's prediction holds, since it asserts small species would show negative body size-predictor slopes, medium-sized species would have slopes equal to zero, and large species 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 while predation is equally important across all size classes, we regressed the absolute value of the correlation coefficients against log-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 since it is comparable across taxa, eliminating biases driven by body shape, and therefore is more suitable for inter-specific comparisons than body length (Feldman & Meiri, 2013; Feldman et al., 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 log10-transformed body size (against tested predictors) for all species, to standardize the r values we analyzed. 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 ($\alpha<0.05$), using both linear and quadratic terms. We avoided using the Akaike information criteria for model selection (AIC or AICc scores) because the models with the lowest scores often had predictors which were poorly associated with size (i.e. had p values >0.05 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 et al., 2017). Thus, the much maligned p-value approach proved more conservative. Nevertheless, we present the AICc-based best models for each species in Appendix 5 to highlight that our general conclusions are robust for using different model-selection approaches.

We avoided over-parameterization by limiting models to include a maximum of three data points (i.e., islands) per tested predictor. We discarded predictors which were highly co-linear with others (variance inflation factor ≥ 5) in the same model. To meet the assumptions of parametric tests we log10-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 analyzed correlation coefficients (r) as the dependent variable we used the r values from regressions of log10-transformed body size (against tested predictors) for all species to standardize the analyzed values.

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 15 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 (Fig. 1; see full univariate model statistics in Appendix 6). Following 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 island area was the most frequently significant predictor. For snakes, 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, Fig. 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=0.06±0.07, p=0.40. R^2=0.05) and interspecific competition (slope=0.08±0.06, p=0.23. R^2=0.10) for body size variation is not size-dependent (Fig. 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 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).

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 likely 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, while large species tend to become smaller as geographic 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 (Melton, 1982; Filin & Ziv, 2004; Lomolino, 2005). However, when the effects of area and isolation on reptile body size are directly tested, results are often inconsistent. For snakes, Hasegawa & Moriguchi (1989) found a negative 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 *Telescopus 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 geographic isolation whereas we found a negative 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 (Soulè, 1966; Dunham et al., 1978; Losos et al., 2004; Meiri, 2007, 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 (Van Valen, 1973; Lomolino, 2005). 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 supports his prediction that the importance of predation for size variation on island is not size-biased.

Surprisingly, we only found few, weak effects of biotic interactions. As 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 body size of most of our study species (less 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\predators. Therefore, we suspect that despite its common use as a predation pressure index in the literature (e.g., Pérez-Mellado et al., 1997; Cooper et al., 2004), predator richness poorly reflects predation intensity (Meiri et al., 2005; Itescu et al., 2017). Similarly, 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 this 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 under conditions of stronger intra-specific 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 et al., 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 (Schwaner, 1985; Shine, 1987; Hasegawa & Moriguchi, 1989; Hasegawa, 2003; Boback, 2003; Meiri, 2007, 2008).

Furthermore, resource limitation may drive cannibalism in insular reptiles, consequently selecting for larger body sizes (Pafilis et al., 2009).

While body size variation on islands is commonly examined under a framework of adaptations, 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 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 may 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., due 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 (King, 1989; Hasegawa & Mori, 2008). Founder effects may also have a role in shaping body size patterns, especially in small, remote and young islands (Kolbe et al., 2012). Thus body size variation is not necessarily or solely adaptive, and novel approaches (Diniz-Filho & Raia, 2017) may allow better 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. In contrast, 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), in 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. Likely, 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 different isolation indices affect one group more strongly than the other. However, we speculate that either 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, while 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 robustly examine this aspect. 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 co-exist, and that we can correctly identify all important competitors and predators). Since we consistently kept these assumptions regarding all species and islands, we are confident they have not biased our results. Perhaps the most important drawback, and most challenging to face, is small sample sizes. With almost 10,000 adult reptiles examined we still came quite 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 properly analyzed. 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 only had data from few individuals. We acknowledge the possibility that low statistical power may have affected our results in some cases. Yet, the general patterns and inconsistencies we found across species are apparent even across the few best-sampled species, thus we have confidence 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 robustly draw valid conclusions 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 *Natrix natrix* and *Eirenis modestus*. Using AICc, we could only show 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 to those in Appendix 5). 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 $p < 0.05$). Often, however, the models with the lowest AICc contained more predictors – including predictors that the p-value based method rejected as uninformative (Appendix 5). We think that, if anything, $p = 0.05$ is not conservative enough (e.g., Johnson, 2013; Benjamin et al., 2017). Using a model selection method that is even more liberal would have made us infer that many variables, that have the most tenuous relationship with animal size evolution on islands, are actually important. We thus use p values not because of any theoretical views about its merit, but because we prefer to err on the side of caution.

The results of this 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 island is probably species- and island-specific, and generalizations over-simplify 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.

ACKNOWLEDGMENTS

We thank Aviv Bejerano, Stav Brown, Nir Einav, Tamar Freud, Alison Gainsbury, Efrat Golan, Eden Goshen, Anat Hartmann, Simon Jamison, Lama Khoury, Menachem Kurzits, Shani Levinkind, Amir Lewin, Erez Maza, Michael Mosses, Gaya Savion, Eylon Sharoni, Achiad Sviri, Oliver Tallowin, Karin Tamar, Alexandros Vezyrakis and Keren-Or Werheimer for all their help with field work. We deeply appreciate the assistance of Michael Franzen, and Frank Glaw (Zoologische Staatssammlung München), Dennis Rödder, Ursula Butt, and Wolfgang Böhme (Zoologische Forschungsmuseum Alexander Koenig, Bonn), Petros Lymberakis and Manolis Papadimitrakis (Natural History Museum Crete), while working in the collections they manage. We thank the editor Dr. Ana Santos, the reviewer Dr. J.A.F.

Diniz-Filho, and two anonymous reviewers for providing insightful and constructive reviews, that greatly contributed to improve earlier versions of this paper. All work was conducted with permission from the Greek Ministry of Environment, Energy, and Climate Change (Permit 20305/824). The study was funded by an Israel Science Foundation (ISF) grant #1005/12. The authors have no conflict of interests to declare.

SUPPORTING INFORMATION

Appendix 1. Reference list for literature containing body size data.

Appendix 2. Data used for analyses.

Appendix 3. Literature sources for isolation time of islands isolated before LGM.

Appendix 4. A list of potential predator species included in our analyses.

Appendix 5. Best models for each species based on AICc scores.

Appendix 6. Full statistics of single-predictor linear and curvilinear models.

DATA ACCESSIBILITY

All the data analyzed in this study is available in Appendix 2.

BIOSKETCH

Yuval Itescu is a PhD candidate interested in the biogeographic patterns and the processes driving the evolution of morphological and life history trait variation of animals in general and insular animals specifically. He is also fascinated by the implications of the insular environment on the ecology of insular fauna.

REFERENCES

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

Anderson, R.P. & Handley, C.O. (2002) Dwarfism in insular sloths: biogeography, selection, and evolutionary rate. *Evolution*, **56**, 1045-1058.

Arnold, E.N. (1979) Indian Ocean giant tortoises: their systematics and island adaptations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **286**, 127-145.

Arnold, T.W. (2010) Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management*, **74**, 1175-1178.

Aubret, F. (2012) Body-size evolution on islands: are adult size variations in tiger snakes a nonadaptive consequence of selection on birth size? *The American Naturalist*, **179**, 756-767.

Aubret, F. (2015) Island colonisation and the evolutionary rates of body size in insular neonate snakes. *Heredity*, **115**, 349-356.

Benjamin, D.J., Berger, J.O., Johannesson, M., Nosek, B.A., Wagenmakers, E.-J., Berk, R., Bollen, K.A., Brembs, B., Brown, L., Camerer, C., Cesarini, D., Chambers, C.D., Clyde, M., Cook, T.D., De Boeck, P., Dienes, Z., Dreber, A., Easwaran, K., Efferson, C., Fehr, E., Fidler, F., Field, A.P., Forster, M., George, E.I., Gonzalez, R., Goodman, S., Green, E., Green, D.P., Greenwald, A., Hadfield, J.D., Hedges, L.V., Held, L., Ho, T.H., Hoijtink, H., Hruschka, D.J., Imai, K., Imbens, G., Ioannidis, J.P.A., Jeon, M., Jones, J.H., Kirchler, M., Laibson, D., List, J., Little, R., Lupia, A., Machery, E., Maxwell, S.E., McCarthy, M., Moore, D., Morgan, S.L., Munafó, M., Nakagawa, S., Nyhan, B., Parker, T.H., Pericchi, L., Perugini, M., Rouder, J., Rousseau, J., Savalei, V., Schönbrodt, F.D., Sellke, T., Sinclair, B., Tingley, D., Van Zandt, T., Vazire, S., Watts, D.J., Winship, C., Wolpert, R.L., Xie, Y., Young, C., Zinman, J. & Johnson, V.E. (2017) Redefine statistical significance. *Nature Human Behaviour*, DOI:10.1038/s41562-017-0189-z.

Boback, S.M. (2003) Body size evolution in snakes: evidence from island populations. *Copeia*, **2003**, 81-94.

Boback, S.M. & Guyer, C. (2003) Empirical evidence for an optimal body size in snakes. *Evolution*, **57**, 345-451.

Calsbeek, R. & Cox, R.M. (2010) Experimentally assessing the relative importance of predation and competition as agents of selection. *Nature*, **465**, 613-616.

Calsbeek, R. & Cox, R.M. (2011) Calsbeek & Cox reply. *Nature*, **475**, E3-E3.

Case, T.J. (1976) Body size differences between populations of the chuckwalla, *Sauromalus obesus*. *Ecology*, **57**, 313-323.

Case, T.J. (1978) A general explanation for insular body size trends in terrestrial vertebrates. *Ecology*, **59**, 1-18.

Case, T.J. & Schwaner, T.D. (1993) Island/mainland body size differences in Australian varanid lizards. *Oecologia*, **94**, 102-109.

Cooper, W.E., Pérez-Mellado, V. & Vitt, L.J. (2004) Ease and effectiveness of costly autotomy vary with predation intensity among lizard populations. *Journal of Zoology*, **262**, 243-255.

Darlington, P.J. (1957) *Zoogeography: the geographical distribution of animals*. John Wiley & Sons, New York.

Diniz-Filho, J.A.F. & Raia, P. (2017) Island Rule, quantitative genetics and brain–body size evolution in *Homo floresiensis*. *Proceedings of the Royal Society B: Biological Sciences*, **284**, 20171065.

Donihue, C.M., Brock, K.M., Foufopoulos, J. & Herrel, A. (2016) Feed or fight: testing the impact of food availability and intraspecific aggression on the functional ecology of an island lizard. *Functional Ecology*, **30**, 566-575.

Dunham, A.E., Tinkle, D.W. & Gibbons, J.W. (1978) Body Size in Island Lizards: A Cautionary Tale. *Ecology*, **59**, 1230-1238.

Faurby, S. & Svenning, J.-C. (2016) Resurrection of the Island Rule: Human-Driven Extinctions Have Obscured a Basic Evolutionary Pattern. *The American Naturalist*, **187**, 812-820.

Feldman, A. & Meiri, S. (2013) Length–mass allometry in snakes. *Biological Journal of the Linnean Society*, **108**, 161-172.

Feldman, A., Sabath, N., Pyron, R.A., Mayrose, I. & Meiri, S. (2016) Body sizes and diversification rates of lizards, snakes, amphisbaenians and the tuatara. *Global Ecology and Biogeography*, **25**, 187-197.

Fielding, J., Turland, N.J. & Mathew, B. (2005) *Flowers of Crete*, Royal Botanic Gardens, Kew, London, Surrey, UK.

Filin, I. & Ziv, Y. (2004) New theory of insular evolution: unifying the loss of dispersability and body-mass change. *Evolutionary Ecology Research*, **6**, 115-124.

Forsman, A. (1991) Variation in sexual size dimorphism and maximum body size among adder populations: effects of prey size. *The Journal of Animal Ecology*, **60**, 253-267.

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

Foufopoulos, J., Kilpatrick, A.M. & Ives, A.R. (2011) Climate change and elevated extinction rates of reptiles from Mediterranean islands. *The American Naturalist*, **177**, 119-129.

Glaw, F., Köhler, J., Townsend, T.M. & Vences, M. (2012) Rivaling the world's smallest reptiles: discovery of miniaturized and microendemic new species of leaf chameleons (*Brookesia*) from northern Madagascar. *Plos One*, **7**, e31314.

Hasegawa, M. (2003) Ecological diversification of insular terrestrial reptiles: a review of the studies on the lizard and snakes of the Izu Islands. *Global Environmental Research*, **7**, 59-68.

Hasegawa, M. & Mori, A. (2008) Does a gigantic insular snake grow faster or live longer to be gigantic? Evidence from a long-term field study. *South American Journal of Herpetology*, **3**, 145-154.

Hasegawa, M. & Moriguchi, H. (1989) Geographic variation in food habits, body size and life history traits of the snakes on the Izu Islands. *Current Herpetology in East*

Asia (ed. by M. Matui, T. Hikida and R.C. Goris), pp. 414-432. The Herpetological Society of Japan.

Heaney, L.R. (1978) Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. *Evolution*, **32**, 29-44.

Heaney, L.R. (2000) Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. *Global Ecology and Biogeography*, **9**, 59-74.

Hedges, S.B. (2008) At the lower size limit in snakes: two new species of threadsnakes (Squamata: Leptotyphlopidae: *Leptotyphlops*) from the Lesser Antilles. *Zootaxa*, **1841**, 1-30.

Hedges, S.B. & Thomas, R. (2001) At the lower size limit in amniote vertebrates: a new diminutive lizard from the West Indies. *Caribbean journal of Science*, **37**, 168-173.

Itescu, Y. (2017) *Evolution on islands: testing the extent and consistency of the effects of island characteristics*. Ph.D. thesis, Tel Aviv University, Israel.

Itescu, Y., Karraker, N.E., Raia, P., Pritchard, P.C.H. & Meiri, S. (2014) Is the island rule general? Turtles disagree. *Global Ecology and Biogeography*, **23**, 689-700.

Itescu, Y., Schwarz, R., Meiri, S. & Pafilis, P. (2017) Intra-specific competition, not predation, drives lizard tail loss on islands. *Journal of Animal Ecology*, **86**, 66-74.

Itescu, Y., Schwarz, R., Moses, M., Pafilis, P. & Meiri, S. (2016) Record sizes for the Turkish house gecko, *Hemidactylus turcicus*, from Aegean islands, Greece. *The Herpetological Bulletin*, **138**, 24-26.

Johnson, V.E. (2013) Revised standards for statistical evidence. *Proceedings of the National Academy of Sciences*, **110**, 19313-19317.

Keehn, J.E., Nieto, N.C., Tracy, C.R., Gienger, C.M. & Feldman, C.R. (2013) Evolution on a desert island: body size divergence between the reptiles of Nevada's Anaho Island and the mainland around Pyramid Lake. *Journal of Zoology*, **291**, 269-278.

King, R.B. (1989) Body size variation among island and mainland snake populations. *Herpetologica*, **45**, 84-88.

Köhler, M., Moyà-Solà, S. & Wrangham, R.W. (2008) Island rules cannot be broken. *Trends in Ecology & Evolution*, **23**, 6-7.

Kolbe, J.J., Leal, M., Schoener, T.W., Spiller, D.A. & Losos, J.B. (2012) Founder effects persist despite adaptive differentiation: a field experiment with lizards. *Science*, **335**, 1086-1089.

Laliberté, E. (2011) *Metacor: Meta-analysis of correlation coefficients. R package.* http://CRAN.R-project.org/package=metacor

Leisler, B. & Winkler, H. (2015) Evolution of island warblers: beyond bills and masses. *Journal of Avian Biology*, **46**, 236-244.

Lomolino, M.V. (2005) Body size evolution in insular vertebrates: generality of the island rule. *Journal of Biogeography*, **32**, 1683-1699.

Losos, J.B. & Pringle, R.M. (2011) Competition, predation and natural selection in island lizards. *Nature*, **475**, E1-E2.

Losos, J.B., Schoener, T.W. & Spiller, D.A. (2004) Predator-induced behaviour shifts and natural selection in field-experimental lizard populations. *Nature*, **432**, 505-508.

Lymberakis, P. & Poulakakis, N. (2010) Three continents claiming an archipelago: the evolution of Aegean's herpetofaunal diversity. *Diversity*, **2**, 233-255.

MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373-387.

Mac Nally, R., Duncan, R.P., Thomson, J.R. & Yen, J.D.L. (2017) Model selection using information criteria, but is the 'best' model any good? *Journal of Applied Ecology*, DOI: 10.1111/1365-2664.13060.

Madsen, T. & Shine, R. (1993) Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. *Evolution*, **47**, 321-325.

Marquet, P.A. & Taper, M.L. (1998) On size and area: patterns of mammalian body size extremes across landmasses. *Evolutionary Ecology*, **12**, 127-139.

Meik, J.M., Lawing, A.M. & Pires-daSilva, A. (2010) Body size evolution in insular speckled rattlesnakes (Viperidae: *Crotalus mitchellii*). *Plos One*, **5**, e9524.

Meik, J.M., Schaack, S., Ingrasci, M.J., Lawing, A.M., Setser, K., Mociño-Deloya, E. & Flores-Villela, O. (2012) Notes on activity, body size variation, and diet in insular speckled rattlesnakes from the western Sea of Cortés, Mexico. *Herpetological Review*, **43**, 556-560.

Meiri, S. (2007) Size evolution in island lizards. *Global Ecology and Biogeography*, **16**, 702-708.

Meiri, S. (2008) Evolution and ecology of lizard body sizes. *Global Ecology and Biogeography*, **17**, 724-734.

Meiri, S., Dayan, T. & Simberloff, D. (2005) Area, isolation and body size evolution in insular carnivores. *Ecology Letters*, **8**, 1211-1217.

Meiri, S., Kadison, A.E., Novosolov, M., Pafilis, P., Foufopoulos, J., Itescu, Y., Raia, P. & Pincheira-Donoso, D. (2014) The number of competitor species is unlinked to sexual dimorphism. *Journal of Animal Ecology*, **83**, 1302-1312.

Meiri, S., Meijaard, E., Wich, S.A., Groves, C.P. & Helgen, K.M. (2008) Mammals of Borneo–small size on a large island. *Journal of Biogeography*, **35**, 1087-1094.

Melton, R.H. (1982) Body size and island *Peromyscus*: a pattern and a hypothesis. *Evolutionary theory*, **6**, 113-126.

Pafilis, P., Meiri, S., Foufopoulos, J. & Valakos, E. (2009) Intraspecific competition and high food availability are associated with insular gigantism in a lizard. *Naturwissenschaften*, **96**, 1107-1113.

Palkovacs, E.P. (2003) Explaining adaptive shifts in body size on islands: a life history approach. *Oikos*, **103**, 37-44.

Pérez-Mellado, V., Corti, C. & Lo Cascioa, P. (1997) Tail autotomy and extinction in Mediterranean lizards. A preliminary study of continental and insular populations. *Journal of Zoology*, **243**, 533-541.

Schoener, T.W. (1970) Size patterns in West Indian *Anolis* lizards. II. Correlations with the sizes of particular sympatric species-displacement and convergence. *The American Naturalist*, **104**, 155-174.

Schwaner, T.D. (1985) Population structure of black tiger snakes, *Notechis ater niger*, on offshore islands of South Australia. *Biology of Australasian frogs and reptiles* (ed. by G. Grigg, R. Shine and H. Ehmann), pp. 35-46. Royal Zoological Society of New South Wales.

Shine, R. (1987) Ecological comparisons of island and mainland populations of Australian tigersnakes (*Notechis*: Elapidae). *Herpetologica*, **43**, 233-240.

Soulé, M. (1966) Trends in the insular radiation of a lizard. *The American Naturalist*, **100**, 47-64.

Valakos, E.D., Pafilis, P., Sotiropoulos, K., Lymberakis, P., Maragou, P. & Foufopoulos, J. (2008) *The amphibians and reptiles of Greece*. Edition Chimaira, Frankfurt am Main.

Van Valen, L. (1973) Pattern and the balance of nature. *Evolutionary theory*, **1**, 31-49.

Vervust, B., Grbac, I. & Van Damme, R. (2007) Differences in morphology, performance and behaviour between recently diverged populations of *Podarcis sicula* mirror differences in predation pressure. *Oikos*, **116**, 1343-1352.

Vincent, S.E., Brandley, M.C., Kuriyama, T., Mori, A., Herrel, A. & Hasegawa, M. (2009) Insular gigantism and dwarfism in a snake, adaptive response or spandrel to selection on gape size. *Nature Precedings*, http://precedings.nature.com/documents/3360/version/1.

Appendices containing references for data sources

Appendix 1 - Reference list for literature containing body size data

Appendix 3 - Literature sources for isolation time of islands isolated before the LGM**.**

Appendix 4. A list of potential predator species included in our analyses (with references for sources indicating their potential as reptile predators).

Table 1. Summary of data and the effects of each predictor on each species. (+) marks a positive correlation; (-) a negative correlation; (∪) a positive quadratic relationship; (∩) a negative quadratic relationship; (NS) non-significant correlation; Full statistics of all models (with sample sizes) are given in Table 2. Population mean size range refers to SVL in lizards and total length in snakes.

Group	Family	Species	Islands	Individuals	Population mean size range (mm)	Species mean body mass (g)	Area	Distance from the mainland	Distance from closest larger island	Time since isolation	Predators	Competitors
Lizards	Gekkonidae	*Hemidactylus turcicus*	27	270	42.04 – 59.89	3.3	+	NS	NS	NS	NS	NS
		Mediodactylus kotschyi	86	2071	33.52 – 49.88	2.8	-	NS	NS	NS	NS	∩
	Lacertidae	*Podarcis erhardii*	118	5323	52.87 – 75.23	6.0	-	-	+	NS	NS	NS
		Podarcis gaigeae	14	641	57.37 – 77.67	8.4	NS	-	+	-	NS	NS
		Podarcis milensis	8	116	53.65 – 67.09	4.1	-	NS	NS	+	NS	NS
		Lacerta trilineata	16	231	107.33 – 141.85	69.9	-	+	NS	NS	NS	NS
		Ophisops elegans	14	143	40.10 – 48.53	2.0	+	NS	NS	NS	-	NS
	Scincidae	*Ablepharus kitaibelii*	24	180	35.66 – 44.84	1.4	NS	+	NS	NS	NS	NS
Snakes	Boidae	*Eryx jaculus*	8	48	269.79 – 516.33	52.5	NS	-	NS	NS	-	NS
	Colubridae	*Dolichophis caspius*	11	72	1085.40 – 1886.00	625.2	NS	NS	NS	NS	-	+
		Eirenis modestus	8	33	386.00 – 543.00	19.8	NS	NS	NS	NS	NS	NS
		Elaphe quatuorlineata	11	70	1036.20 – 1525.61	846.9	NS	-	NS	NS	NS	NS
		Natrix natrix	11	55	566.25 – 910.00	91.6	NS	NS	NS	NS	NS	NS
		Telescopus fallax	12	56	477.43 – 903.33	44.9	∩	NS	NS	NS	NS	NS
	Viperidae	*Vipera ammodytes*	15	152	281.33 – 592.25	28.1	NS	-	NS	NS	NS	NS
		Vipera xanthina	8	51	490.78 – 1493.33	276.0	NS	NS	NS	∪	NS	NS

Table 2. Best models by species. n is island sample size. Body size was log10-transformed in species marked with (*).

Group	Family	Species	n	Predictor	Slope	SE	Intercept	SE	P	Adjusted R^2
Lizards	Gekkonidae	*Hemidactylus turcicus*	27	log area	1.91	0.59	46.37	1.01	<0.01	0.26
		Mediodactylus kotschyi	86	log area	-0.86	0.44	39.64	0.88	0.05	0.10
				competitor richness	2.81	0.81			<0.01	
				competitor richness (^2)	-0.38	0.12			<0.01	
	Lacertidae	*Podarcis erhardii**	118	log area	(-)<0.01	<0.01	1.80	<0.01	0.02	0.07
				distance from the mainland	(-)<0.01	<0.01			0.01	
				log distance from closest larger landmass	0.01	<0.01			0.04	
		*Podarcis gaigeae**	14	distance from the mainland	(-)<0.01	<0.01	2.53	0.19	<0.01	0.51
				log distance from closest larger landmass	0.07	0.02			0.01	
				log time since isolation	-0.08	0.02			<0.01	
		Podarcis milensis	8	log area	-2.23	0.74	48.63	3.80	0.03	0.75
				log time since isolation	2.06	0.68			0.03	
		Lacerta trilineata	16	log area	-7.28	3.01	136.02	7.45	0.03	0.43
				distance from the mainland	0.14	0.05			0.01	
		Ophisops elegans	14	log area	3.06	1.00	41.61	1.28	0.01	0.36
				predator richness	-0.67	0.28			0.04	
	Scincidae	*Ablepharus kitaibelii*	24	distance from the mainland	0.03	0.01	39.13	0.73	<0.01	0.30
Snakes	Boidae	*Eryx jaculus*	8	distance from the mainland	-5.77	0.55	1302.57	89.63	<0.01	0.94
				predator richness	-26.20	3.56			<0.01	
	Colubridae	*Dolichophis caspius*	11	predator richness	-326.08	88.43	2751.25	391.42	0.01	0.58
				competitor richness	447.95	116.38			<0.01	
		Eirenis modestus	8	none	-	-	-	-	-	-
		Elaphe quatuorlineata	11	distance from the mainland	-2.79	0.48	1482.29	37.59	<0.01	0.77
		*Natrix natrix**	11	none	-	-	-	-	-	-
		*Telescopus fallax**	12	log area	0.55	0.21	2.04	0.26	0.03	0.43
				(log area)^2	-0.09	0.04			0.04	
	Viperidae	*Vipera*	15	distance from the mainland	(-)<0.01	<0.01	2.74	0.04	<0.01	0.63

Group	Family	Species	n	Predictor	Slope	SE	Intercept	SE	P	Adjusted R^2
		*ammodytes**								
		*Vipera xanthina**	8	log time since isolation (log time since isolation)^2	-6.94 0.71	1.86 0.19	19.42	4.39	0.01 0.01	0.65

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 (g). Significant results are highlighted in bold.

Predictors	**Slope**	**SE**	**Intercept**	**SE**	**P**	**R^2**
Log area	0.14	0.13	-0.11	0.21	0.32	0.07
Distance from the mainland	**-0.30**	**0.12**	**0.22**	**0.20**	**0.03**	**0.29**
Log Distance from closest larger island	**-0.20**	**0.08**	**0.33**	**0.13**	**0.03**	**0.30**
Log Time since isolation	**-0.30**	**0.09**	**0.36**	**0.15**	**0.01**	**0.42**
Predator richness	0.20	0.11	-0.18	0.19	0.11	0.17
Competitor richness	0.13	0.11	-0.04	0.18	0.27	0.08

Table 4. Meta-analysis results for all reptiles, only lizards and only snakes. P values are for H_0: r=0. Significant results are highlighted in bold.

Predictors	**All reptiles**			**Lizards**			**Snakes**		
	Mean r	**Range (r)**	**P**	**Mean r**	**Range (r)**	**P**	**Mean r**	**Range (r)**	**P**
Log area (km^2)	0.108	-0.106 – 0.313	0.16	-0.082	-0.326 – 0.173	0.27	**0.410**	**0.146 – 0.620**	**<0.01**
Distance from the mainland (km)	-0.201	-0.433 – 0.055	0.06	0.130	-0.129 – 0.372	0.16	**-0.581**	**-0.777 – -0.281**	**<0.01**
Log distance from closest larger island (km)	0.068	-0.070 – 0.204	0.17	**0.152**	**-0.028 – 0.323**	**0.05**	-0.124	-0.361 – 0.128	0.17
Log time since isolation (years)	-0.042	-0.224 – 0.142	0.33	0.077	-0.134 – 0.282	0.24	**-0.263**	**-0.536 – 0.058**	**0.05**
Predator richness	0.096	-0.098 – 0.284	0.16	-0.088	-0.278 – 0.108	0.19	**0.443**	**0.182 – 0.645**	**<0.01**
Competitor richness	0.147	-0.035 – 0.320	0.06	0.003	-0.190 – 0.196	0.49	**0.423**	**0.179 – 0.618**	**<0.01**

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: SVL for species a, b, e, f, g, h; Log SVL for species c, d; Total length for species i, j, k, l; Log total length for species m, n, o, p. Full trend lines indicate a significant relationship ($p<0.05$).

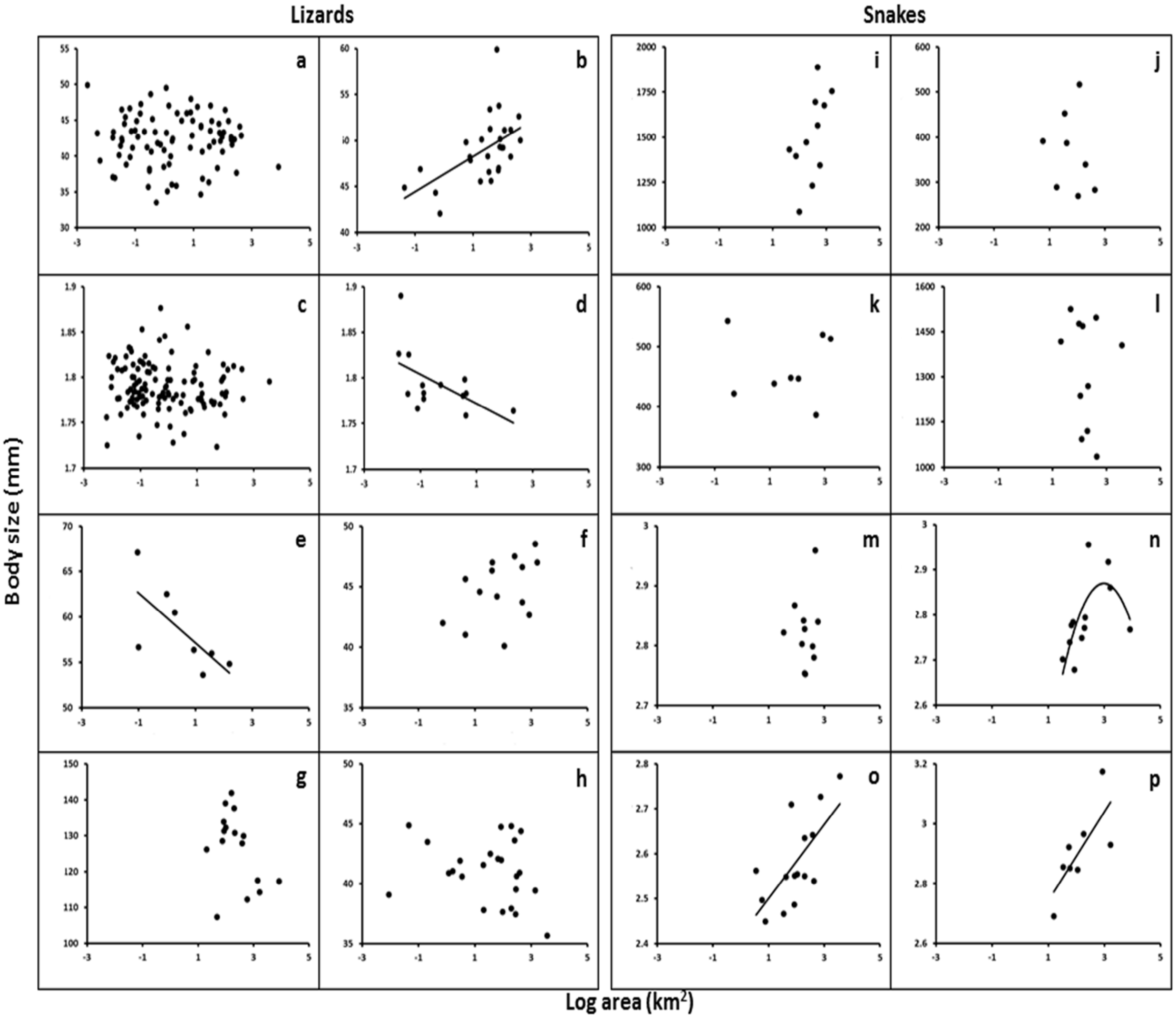


Figure 2. The relationship between the correlation coefficient (r) of body length (mm; SVL for lizards, total length for snakes, see text) against each predictor variable and the log mean body mass (g) of each species. Panels show: **a** – log island area (km^2); **b** – distance from the mainland (km); **c** – log distance from the closest larger island (km); **d** - log time since isolation (years); **e** – predator richness; **f** – competitor richness. n=16 species in all cases. Trend lines are shown only if they are statistically significant.

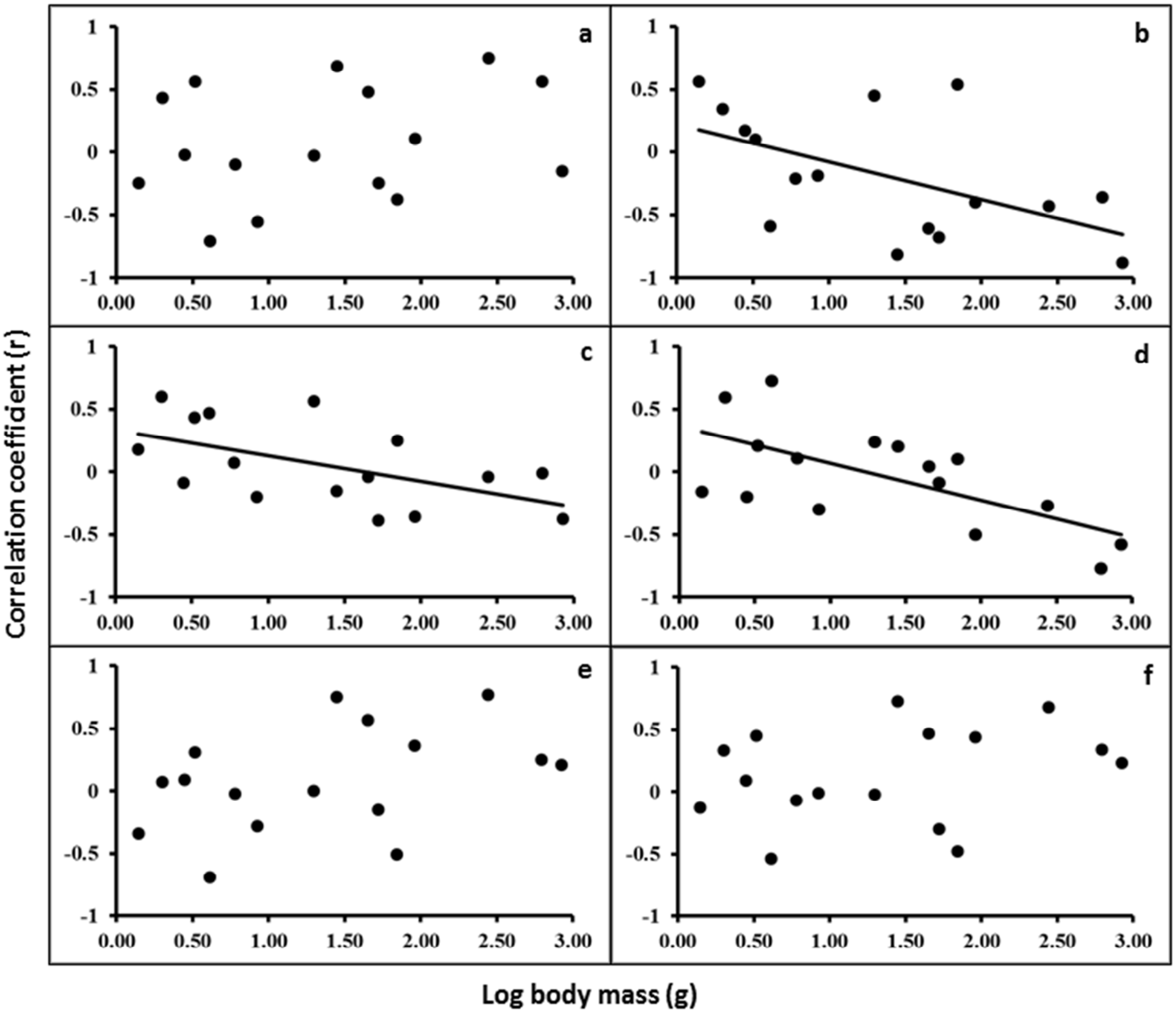
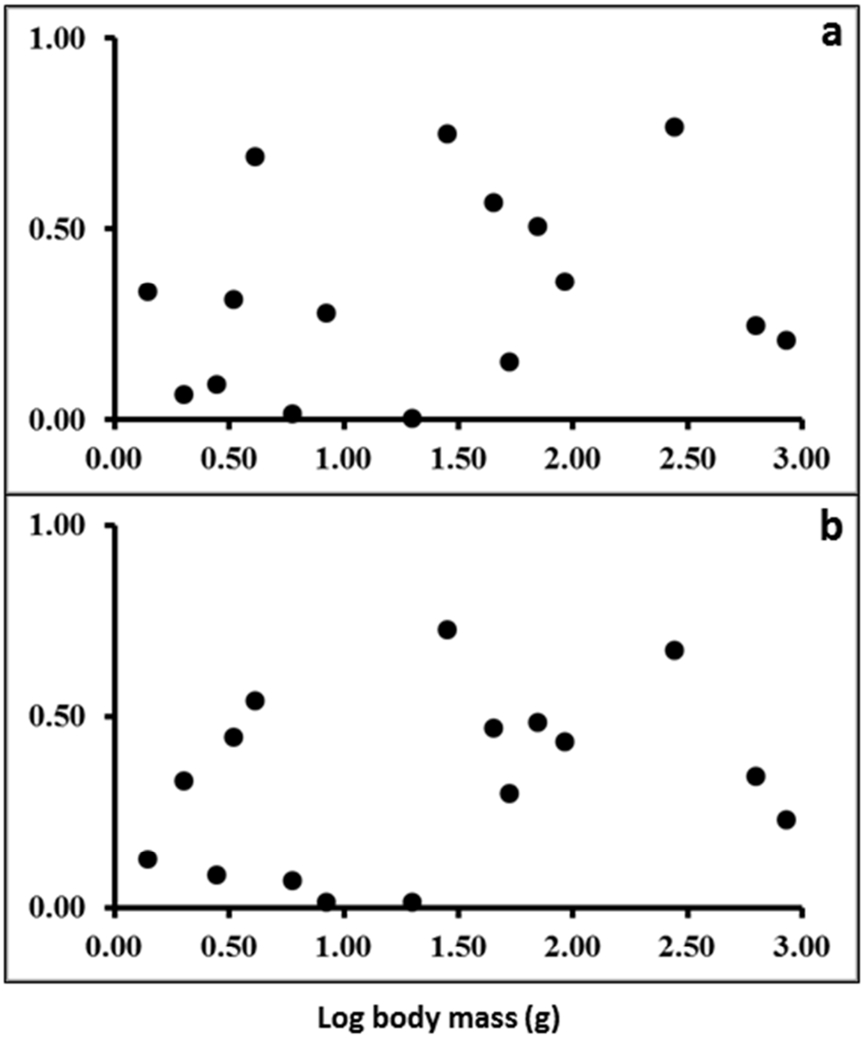


Figure 3. The relationship between the absolute value of the correlation coefficient (r) of body length (mm; SVL for lizards, total length for snakes, see text) against predator richness (**a**) and competitor richness (**b**) and the log mean body mass (g) of each species.



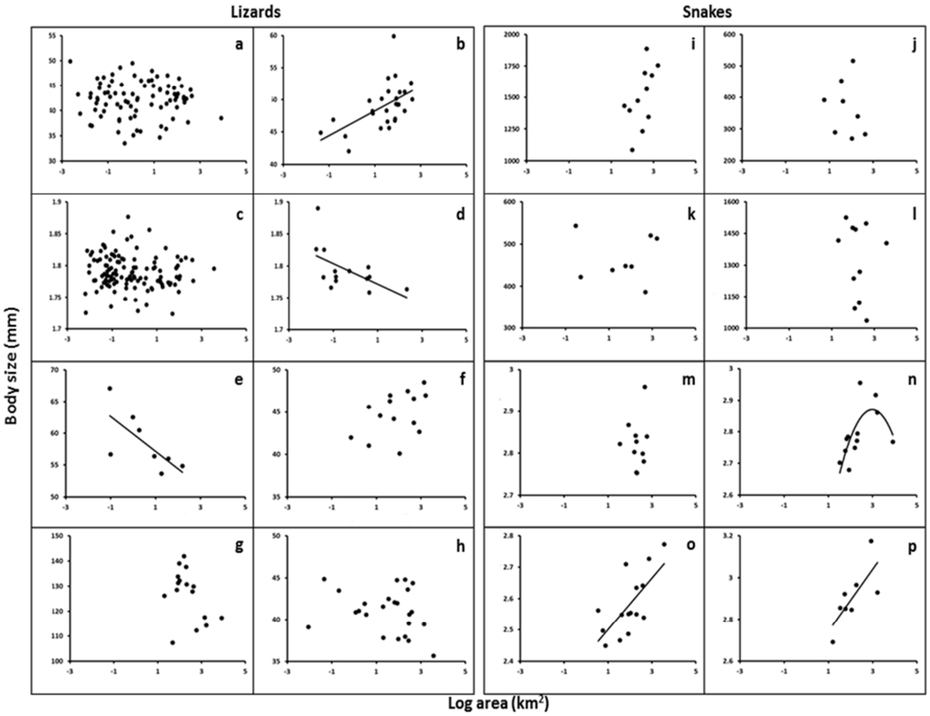


Figure 1. Body size as a function of island area: a – Mediodactylus kotschyi; b – Hemidactylus turcicus; c – Podarcis erhardii; d – Podarcis gaigeae; e – Podarcis milensis; f – Ophisops elegans; g – Lacerta trilineata; h – Ablepharus kitaibelii; i –Dolichophis caspius; j – Eryx jaculus; k – Eirenis modestus; l – Elaphe quatuorlineata; m – Natrix natrix; n – Telescopus fallax; o – Vipera ammodytes; p – Vipera xanthina. Body size index is: SVL for species a, b, e, f, g, h; Log SVL for species c, d; Total length for species i, j, k, l; Log total length for species m, n, o, p. Full trend lines indicate a significant relationship ($p<0.05$).

81x60mm (300 x 300 DPI)

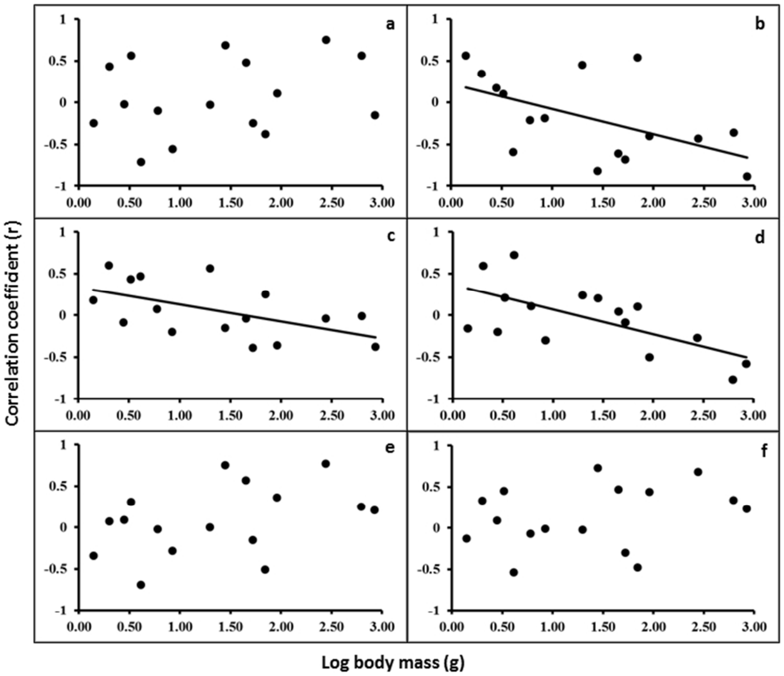


Figure 2. The relationship between the correlation coefficient (r) of body length (mm; SVL for lizards, total length for snakes, see text) against each predictor variable and the log mean body mass (g) of each species. Panels show: a – log island area (km2); b – distance from the mainland (km); c – log distance from the closest larger island (km); d - log time since isolation (years); e – predator richness; f – competitor richness. n=16 species in all cases. Trend lines are shown only if they are statistically significant.

81x60mm (300 x 300 DPI)

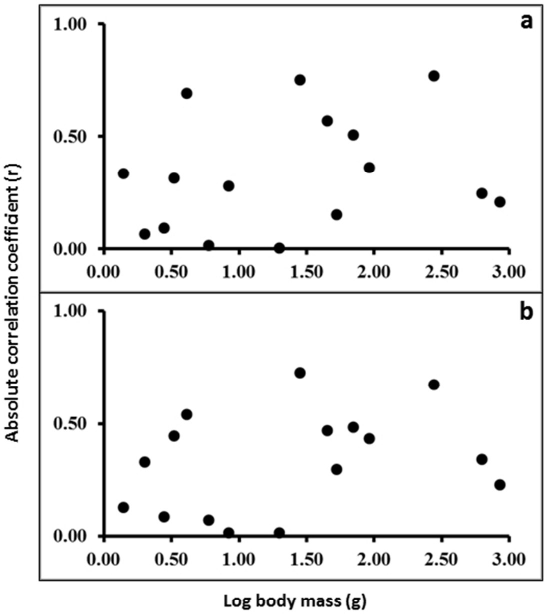


Figure 3. The relationship between the absolute value of the correlation coefficient (r) of body length (mm; SVL for lizards, total length for snakes, see text) against predator richness (a) and competitor richness (b) and the log mean body mass (g) of each species.

81x60mm (300 x 300 DPI)