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Evolutionary biology

Unravelling the determinants of insular body size shifts

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The island rule, a pattern of size shifts on islands, is an oft-cited but little understood phenomenon of evolutionary biology. Here, we explore the evolutionary mechanisms behind the rule in 184 mammal species, testing climatic, ecological and phylogenetic hypotheses in a robust quantitative framework. Our findings confirm the importance of species' ecological traits in determining both the strength and the direction of body size changes on islands. Although the island rule pattern appears relatively weak overall, we find strongest support for models incorporating trait, climatic and geographical factors in a phylogenetic context, lending support to the idea that the island rule is a complex phenomenon driven by interacting intrinsic and extrinsic mechanisms. Overall, we find that different clades may be evolutionarily predisposed to dwarfism or gigantism, but the magnitude of size changes depends more on adaptation to the novel island environment.

1. Introduction

Upon colonizing islands, populations of mammals often encounter new selective forces, leading to considerable shifts in body size. This phenomenon occurs with such frequency that Van Valen [1] deemed the pattern a 'rule of ecology'. The actual pattern is a complex, graded trend in which small mammals evolve larger size and vice versa [2,3]. However, this generalization may be an oversimplification of a weak overall pattern [3] where exceptions abound [4]. For example, insular size shifts appear to be concentrated in a few key clades [5], and the magnitude of size shifts within a single species can vary among islands [6].

Multiple individual processes have been posited to explain insular size shifts. These hypotheses range from species-level traits such as original body size [3] and diet [7] to biotic interactions such as relaxed predation and competition [8,9] and island-specific traits such as island area [10], isolation, productivity [11] and climate [12]. While each of these factors has some explanatory power, recent work suggests that the persistence and magnitude of insular size shifts reflect a combination of these extrinsic and intrinsic factors [13,14].

Although insights have been gained by recent analyses [13–15], questions still remain. For example, it is unclear why the presence and strength of the island rule pattern vary across clades and islands. In addition, the relative importance of various posited explanatory variables has not been explicitly quantified in the same study. Some key explanatory variables (e.g. differences in productivity, niche breadth and climate between islands and the mainland) remain unexamined. Analyses combining multiple explanatory variables are rare and often limited to specific clades [13] and sets of islands [14]. Phylogenetic analyses, which have the potential to elucidate underlying evolutionary constraints, are also rare (but see references [5,13,15]). Here, we assemble a dataset, including key climatic, geographical and biological data for 721 islands and 184 mammal species along with their insular size shifts. Our work goes beyond previous studies to incorporate characteristics of each species' mainland niche as well as island-specific factors in an explicit phylogenetic context. We specifically test

Table 1. Results from specific hypothesis models and global models (with and without phylogeny). AIC_c values are given for the best model for each hypothesis (1), plus the full model (2). Variables listed in bold reflect those with strong effects (95% CIs do not overlap zero), those in italics were included among the models with strong support ($\Delta AIC_c \leq 2$) and those in plain text were not present in any models where $\Delta AIC_c \leq 2$. K is the number of parameters in the model and r^2 is the coefficient of determination. For models including phylogeny, λ is listed to reflect the degree of phylogenetic signal in the model.

model	variables	K	AIC_c	r^2
habitat	1. mean annual temp, min npp, std elevation	6	-117.220	0.084
	2. <i>std annual temp, mean annual precip, std annual precip, max elevation, mean elevation, max npp, mean npp, std npp, median elevation, std annual precip</i>	16	-99.617	0.088
productivity	1. min npp, max npp	5	-81.820	0.035
	2. <i>mean npp, median npp, std npp, npp ratio</i>	9	-75.300	0.037
isolation	1. island area, distance to continent	5	-64.790	0.011
	2. <i>distance to islands, islands within 100 km</i>	7	-61.500	0.002
mainland	1. area of range, max npp, annual mean temp	6	-97.100	0.058
	2. <i>range lat midpoint, annual mean precip, min npp, std npp, pet mean</i>	11	-90.923	0.063
species traits	1. log mass, trophic, lifestyle class (full model)	14	-124.273	0.113
mainland : island	1. precip. ratio, npp ratio	5	-63.330	0.010
	2. <i>temp ratio, area ratio</i>	7	-59.506	0.010
global	1. fact1, fact2, fact5, log mass, trophic	14	-136.300	0.128
	2. <i>fact3, fact4, lifestyle class</i>	19	-132.004	0.135
global + phyl	1. fact2, fact5 ($\lambda = 0.370$)	6	-192.500	0.175
	2. <i>fact1, fact3, fact4, log mass, lifestyle class, trophic</i> ($\lambda = 0.312$)	20	-177.107	0.190
null	intercept-only	2	-62.365	
abs (1-size ratio)	1. <i>fact3, log mass, trophic, lifestyle class</i>	15	-1268.780	0.080
	2. <i>fact1, fact2, fact4, fact5</i>	19	-1262.237	0.082
global + phyl	1. <i>fact2, fact5</i> ($\lambda = 0.116$)	6	-1363.770	0.172
	2. <i>fact1, fact3, fact4, log mass, lifestyle class, trophic</i> ($\lambda = 0.079$)	20	-1267.778	0.055
null	intercept-only	2	-1235.609	

and compare multiple models pertaining to six general hypotheses in a phylogenetic framework to explain both the direction and magnitude of insular size changes.

2. Material and methods

Body size data for island and adjacent mainland mammal populations were taken from Meiri *et al.* [4]. We used the normalized size ratio (NSR), i.e. the ratio of the average body size of the island population to the mainland population, as the dependent variable in our models. Values greater than one indicate a shift towards larger sizes, less than one smaller sizes, on the island. We also examined the absolute size ratio (ASR), i.e. the absolute value of one minus the size ratio, as the dependent variable to test whether the magnitude of the size shift was predicted by different variables. We chose the non-NSR for ASR calculations to preserve the magnitude of the measured shift, but correlations between NSR and non-NSRs are high (0.86). For each mammal population, we gathered 10 biological variables, 20 island geographical and environmental variables and 10 mainland geographical and environmental variables. Details of the dataset and variables can be found in the electronic supplementary material and the dataset is available on Dryad at <http://dx.doi.org/10.5061/dryad.1b736>.

We first constructed and tested models pertaining to six general hypotheses (area and isolation), species traits (e.g. trophic level, lifestyle class), island climate, island productivity, mainland

climate (as a proxy for niche breadth of species) and climatic differences (between the island and mainland) presented previously in the literature to explain the island rule (table 1).

Second, we constructed a complete, global model incorporating all hypotheses. Variance inflation factors (VIFs) computed for predictors suggested serious issues of multicollinearity (VIFs > 10 for 11 variables; VIF > 5 are considered evidence of problematic multicollinearity); therefore, we used factor analysis to reduce continuous predictors to orthogonal factors (see the electronic supplementary material): factor 1 represents climatic variables of the island and mainland, i.e. the climatic niche of the species; factor 2, the topographic complexity and area of the island; factor 3, island productivity; factor 4, island precipitation; and factor 5, range of productivity across a species' mainland range.

Models were analysed using generalized least-squares (GLS) regression in R, and global models were compared with and without phylogenetic information using phylogenetic GLS (PGLS) [16]. For all models, we also used a weighting function to account for the heterogeneity in variance of NSR and ASR with several environmental variables (see the electronic supplementary material). For PGLS models, we estimated Pagel's lambda to adjust the phylogenetic correction according to the degree of phylogenetic signal in the model (see the electronic supplementary material) based on the mammalian supertree [17]. The tree was pruned to the species in our analysis, with polytomies at species tips to account for species with populations inhabiting more than one island.

We used Akaike's information criterion corrected (AIC_c) for small-sample sizes to evaluate the strength of support for the

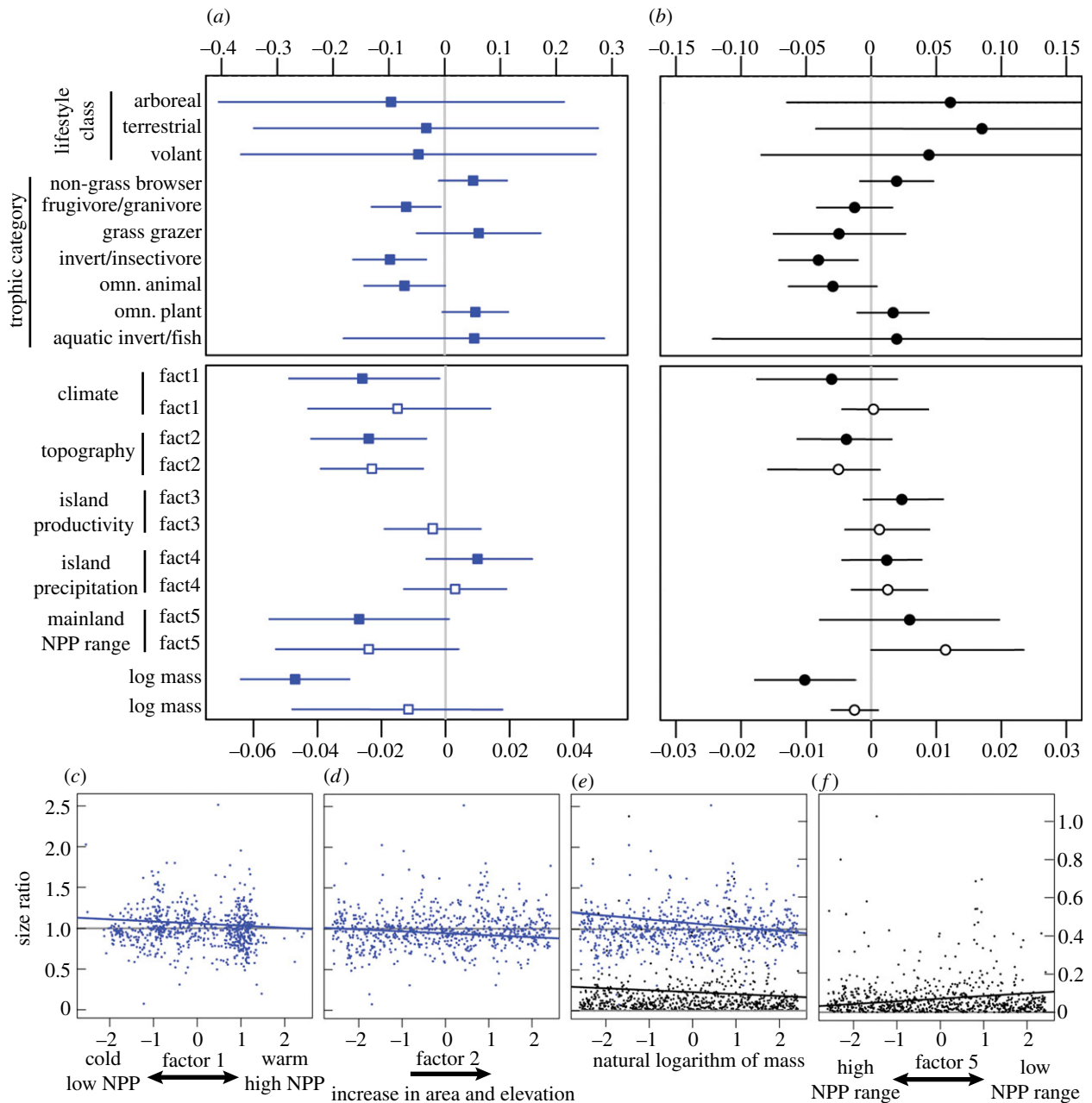


Figure 1. Model-averaged effect sizes for parameters included in strongly supported models ($\Delta AIC_c \leq 2$) explaining normalized (a) and absolute (b) size ratios. Open and closed symbols reflect estimates from models with and without phylogeny respectively. (c–f) Phylogenetically uncorrected data, plus trend lines for continuous variables with strong effects on the normalized size ratio (blue) and absolute size ratio (black). Horizontal grey lines at 1.0 (c–e) and zero (e–f) reflect no change in size between insular and closest mainland population. (f) Factor 5 trendline is for illustrative purposes only, as the final average model controlled for phylogeny.

various models. We ranked models based on AIC_c scores (ΔAIC_c). All models with $\Delta AIC_c \leq 2$ were considered to have strong support and were assigned Akaike weights (w_i) to calculate model-averaged parameter estimates and unconditional 95% confidence intervals (95% CIs). We concluded that there was little evidence for the effect of a predictor variable on size change when the 95% CIs overlapped zero.

3. Results and discussion

Among models testing specific island rule hypotheses, NSR was best explained by a species traits model, including body size, trophic level and lifestyle class, all of which are often phylogenetically structured (table 1). The island habitat hypothesis and the mainland climate hypothesis also had strong support. All other specific island rule hypotheses performed poorly, with an intercept-only model

yielding more support (table 1). Overall, models with the least support reflected hypotheses pertaining to isolation and differences between the mainland and island climates.

Global models predicting NSR that incorporated multiple hypotheses received much stronger support relative to single-hypothesis models (table 1). This included a mixture of species traits and climatic variables, some of which were phylogenetically linked. The evidence ratio favouring the global model over the best-supported single-hypothesis model was greater than 47 (ratio of w_i for the global model compared with w_i for the species-trait model). Thus, our findings, along with those of prior studies [13,14], suggest that the pattern of size shifts on islands reflects multiple processes.

In general, the island rule pattern appears relatively weak. None of the models accounts for more than 18.6 per cent of the variance in island size shifts (see electronic supplementary material, table S1). In part, this may reflect factors not

captured in our analysis, such as competition and predation, which are difficult to quantify. However, the island rule pattern is still worth considering, as even weak selection gradients can produce substantial evolutionary consequences over long time spans [18].

Several factors do emerge as consistent predictors of NSR (figure 1). Average mass of the mainland population appears across all phylogenetically uncorrected models, such that larger mammals get smaller on islands and vice versa. Trophic level, as previously proposed [2,8], emerges in most models. However, the trophic effect, while significant, is rarely consistent and appears in just a few trophic groups. Island topographic heterogeneity (factor 2) also leads to shifts towards smaller sizes, whereas less heterogeneity produces a slight trend towards larger sizes or no shift at all, a finding potentially attributable to niche availability [14]. Climatic niche (factor 1) also appears to be important (figure 1). On average, cooler and less productive islands produce shifts towards larger sizes, whereas warmer and more productive islands produce shifts towards smaller sizes. This could reflect an adaptation to colder environments, *sensu* Bergmann's rule, because large animals lose less heat relative to mass [19]. These patterns may also reflect increased competition and predation if warmer islands harbour more species. Alternatively, many mainland climatic variables also load positively with factor 1, and the adaptation of species to their mainland climates would be expected to control the magnitude and direction of size shifts on the island.

With regard to ASR, the average mass of the mainland population and trophic level emerged in the basic model without accounting for phylogeny. With phylogenetic correction, factor 5, range of mainland productivity, affects the magnitude of the size shift, although the 95% CI approaches, but does not overlap, zero (figure 1). To restate, those species that experience a greater range of productivity on the mainland, or climatic variables producing these gradients (such as precipitation and temperature) are less likely to exhibit dramatic size shifts on islands. This pattern could result because species with broader climatic niches possess greater phenotypic plasticity and are able to adjust to novel island environments. Indeed, for successful invasion of species into novel environments, phenotypic plasticity is often key [20]. Alternatively, the island is less likely to represent a novel climatic environment for species with a broad niche.

In either case, the evolutionary pressure to change in size would be minimal. Although variation in productivity has been proposed to account for insular size shifts [11], our results quantitatively demonstrate its importance for the first time.

Consistent with prior work [21], explicitly accounting for phylogenetic relatedness improved fits considerably (table 1 and figure 1). The effects of trophic level and mass are lost when accounting for phylogenetic relatedness. Likewise, factor 1, the climatic niche, is also not significant when phylogeny is included. These results are unsurprising as mass, trophic level and climatic niche are all phylogenetically structured [22–24]. In contrast to previous studies [5] however, we find a weaker phylogenetic signal for ASR (magnitude of size shifts; electronic supplementary material), suggesting that the strength of size shifts is less clade-specific than is the directionality. Different clades may be evolutionarily predisposed to dwarfism or gigantism, but the magnitude of size changes depends more on adaptation to the local environment [21].

Over the past four decades, the island rule puzzle has generated wide interest and many competing hypotheses. A mammal species, colonizing an island for the first time, may encounter a completely novel environment, which can select for rapid changes in body size and other traits. However, as our results demonstrate, selection pressures on insular body size are often weak and phylogenetically and ecologically context-dependent. Our findings, which incorporate a broad set of characteristics from each species' mainland niche as well as island-specific factors, suggest that the direction of size shifts is primarily tied to the evolutionary history of species, i.e. body size, trophic level and climatic niche. The exception is island elevational heterogeneity that may correlate with niche availability on the island. The magnitude, as opposed to direction, of the size change is less dependent on phylogenetically structured traits and is primarily influenced by a species' climatic niche breadth in its mainland range. Thus, we find that the island rule is a macroevolutionary pattern emerging from each species' suite of intrinsic traits and niche breadth interacting with the unique constraints of island life.

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