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ORIGINAL ARTICLE

Of mice and mammoths: evaluations of causal explanations for body size evolution in insular mammals

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ABSTRACT

Aim We investigated the hypothesis that the insular body size of mammals results from selective forces whose influence varies with characteristics of the focal islands and the focal species, and with interactions among species (ecological displacement and release).

Location Islands world-wide.

Methods We assembled data on the geographic characteristics (area, isolation, maximum elevation, latitude) and climate (annual averages and seasonality of temperature and precipitation) of islands, and on the ecological and morphological characteristics of focal species (number of mammalian competitors and predators, diet, body size of mainland reference populations) that were most relevant to our hypothesis (385 insular populations from 98 species of extant, non-volant mammals across 248 islands). We used regression tree analyses to examine the hypothesized contextual importance of these factors in explaining variation in the insular body size of mammals.

Results The results of regression tree analyses were consistent with predictions based on hypotheses of ecological release (more pronounced changes in body size on islands lacking mammalian competitors or predators), immigrant selection (more pronounced gigantism in small species inhabiting more isolated islands), thermoregulation and endurance during periods of climatic or environmental stress (more pronounced gigantism of small mammals on islands of higher latitudes or on those with colder and more seasonal climates), and resource subsidies (larger body size for mammals that utilize aquatic prey). The results, however, were not consistent with a prediction based on resource limitation and island area; that is, the insular body size of large mammals was not positively correlated with island area.

Main conclusions These results support the hypothesis that the body size evolution of insular mammals is influenced by a combination of selective forces whose relative importance and nature of influence are contextual. While there may exist a theoretical optimal body size for mammals in general, the optimum for a particular insular population varies in a predictable manner with characteristics of the islands and the species, and with interactions among species. This study did, however, produce some unanticipated results that merit further study – patterns associated with Bergmann's rule are amplified on islands, and the body size of small mammals appears to peak at intermediate and not maximum values of latitude and island isolation.

Keywords

Area, body size, climate, evolution, island rule, islands, isolation, latitude, mammals, regression trees.

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INTRODUCTION

Among the most spectacular phenomena in nature are the evolutionary anomalies of island life – herbaceous plants that are elsewhere small becoming woody and reaching the stature of trees, many species of insects and birds losing the power of flight, and evolutionary marvels among mammals that include proboscideans dwarfing to the size of ponies, and shrew-like insectivores reaching the size of small dogs (see Lomolino *et al.*, 2010). These seemingly incredible bouts of body size evolution in insular mammals constitute bookends of a pattern that seemed so general that Van Valen (1973) labelled it the island rule, and is now described as a graded trend from gigantism in small species to dwarfism in large species of mammals (Heaney, 1978; Lomolino, 1985, 2005). The pattern is referred to as 'graded' because the degree of body size change decreases as we move from considering species of extreme, ancestral (mainland) size, which change most dramatically, to those of intermediate ancestral size, which change more subtly or not at all (Fig. 1). Because the body size of extant mammals on isolated islands converges on a relatively narrow range of intermediate sizes (from *c.* 100 to 500 g), this size range is sometimes hypothesized to be optimal for mammals, although the particular optimum is predicted to vary with the bauplan and trophic strategy of the species considered (e.g. quadrupedal ruminant herbivore or volant insectivore; Maurer *et al.*, 1992; Lomolino, 2005).

Beside their intrinsic and sometimes compelling attraction, insular anomalies such as those associated with the island rule offer perhaps unrivalled insights into the fundamental forces driving biodiversity in general; in this case, those influencing body size evolution in mainland as well as in insular communities. Thus, research on the body size of insular mammals has explored not only the generality and variants of the pattern, but also causal explanations for body size evolution in general. Whether or not there exist optimal sizes for particular bauplans and trophic strategies, ecological interactions are likely to play a central role in body size evolution – possibly driving diversification in the body size of lineages on the mainland over evolutionary time (consistent with Cope's rule; Alroy, 1998; Kingsolver & Pfennig, 2004; MacFadden, 2005; Hone *et al.*, 2008), and rapid reversals in this trend in ecologically simple systems such as islands (see Millien, 2006). That is, the fundamental distinction of insular biotas may not be their isolation or limited area *per se*, but the resultant depauperate and disharmonic nature of their communities, in particular their paucity of non-volant mammals, whose dispersal abilities typically are more limited than those of birds. If this hypothesis is correct, the body size evolution of mammals of isolated islands should be influenced both by ecological character displacement (from conspecifics and from other resident vertebrates, namely birds and reptiles, which tend to be small) and by character release (from mammalian competitors and predators) (see Simberloff *et al.*, 2000; Grant & Grant, 2006; Meiri *et al.*, 2011).

This ecological hypothesis for body size evolution on islands provides some useful predictions for investigating the causality of the island rule, and for identifying forces influencing body size evolution in general. In particular, rather than predicting just the graded trend and body size convergence, this hypothesis predicts that the direction and magnitude of body size evolution, and the underlying selection forces should be contextual, that is, dependent on the size and trophic strategies of both the focal species and those species with which they

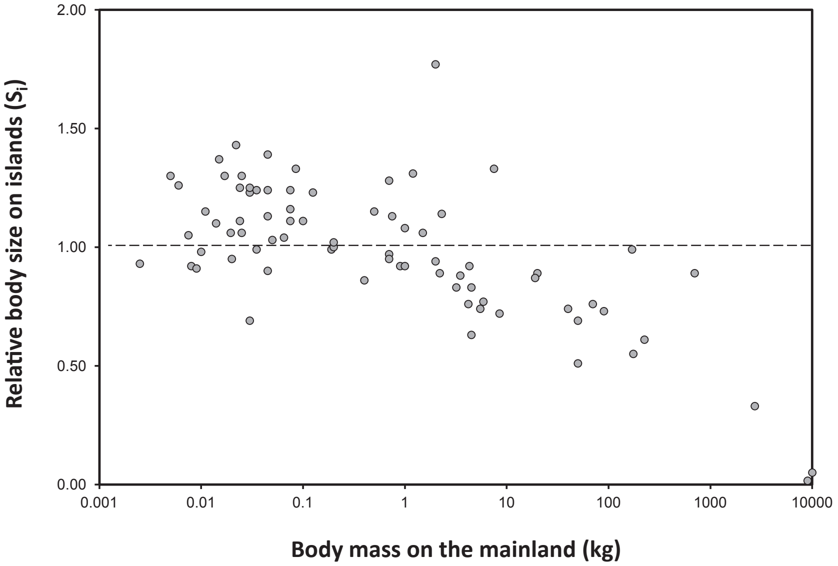

Figure 1 The island rule describes a graded trend of insular body size from gigantism in mice and other small mammals to dwarfism in elephants, mammoths and other large mammals. Each symbol represents the average insular body size for populations of a particular species. S_i is the mass of the insular population divided by that of its closest mainland population; the *x*-axis shows the body mass of mainland reference populations, in $\log_{10}$ scale (modified from Lomolino, 1985).

interact [see, e.g. Palombo's (2009) review of fossil mammals of the Mediterranean islands, which indicates that intra-guild competition was a major driver of body size evolution in these species].

Alternative, but possibly complementary, hypotheses for the insular evolution of body size also generate predictions that are contextual in nature. The immigrant selection–thrifty genotype hypothesis (Neel, 1962; Lomolino, 1984, 1985, 1989; Bindon & Baker, 1997) asserts that, because larger individuals should have greater physiological endurance and dispersal capacities, more isolated islands should be colonized by a subset of source populations biased in favour of the larger individuals and larger species. The resultant prediction is that the body size of insular populations of a particular species should increase with island isolation. Immigrant selection should be most influential in smaller species (those most likely to be limited by dispersal distances), but may also influence body size evolution in larger mammals if they inhabit very remote islands (e.g. humans of Polynesia). Similarly, the resource-limitation hypothesis also generates a contextual prediction. Because resource requirements tend to increase with body size, the limited area and total productivity of islands, as well as the supra-normal densities exhibited by many insular populations, should select for smaller individuals, but this selection should be most intense for larger species (those whose resource requirements are more likely to approach the carrying capacities of insular environments). A corollary prediction of the resource-limitation hypothesis is that the degree of dwarfism and gigantism exhibited by a particular species should be influenced by their diet and habitat (smaller sizes in terrestrial carnivores than in herbivores; larger sizes in species such as mink, otter and bears that feed on aquatic prey, which are more abundant in marine and insular systems than in continental ones).

Similarly, because climate influences both resource requirements and primary productivity, body size evolution should also be influenced by climatic conditions on both islands and mainland systems. Bergmann's rule (Bergmann, 1847) is perhaps the most familiar of ecogeographic rules, stating that the body size of many mammals and other vertebrates increases with latitude. Explanations for patterns consistent with Bergmann's rule include those based on thermoregulation, physiological endurance during winter conditions, and ecological interactions. Briefly, larger mammals have more insulation (lower conductance) and greater energy stores relative to the energy needs for thermoregulation and survival under winter, or otherwise inclement, conditions (Calder, 1974; McNab, 2002). Therefore, larger mammals should have

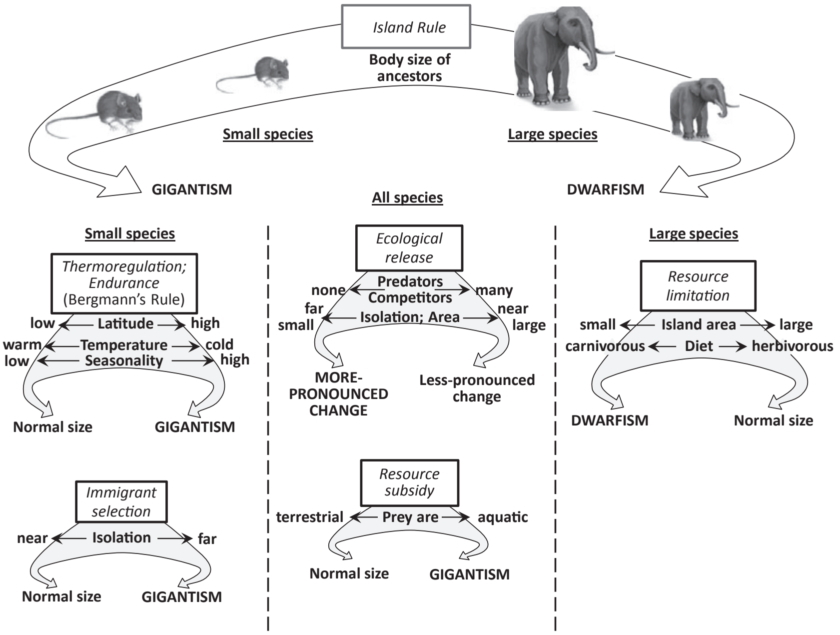

Figure 2 Conceptual model illustrating the contextual nature of selective forces hypothesized to influence the body size evolution of insular mammals. These selective forces are proposed to be contextual because their relative importance and the nature of their effects on body size (promoting gigantism or dwarfism) vary in a predictable manner with characteristics of the species – in particular, the body size of their mainland ancestors. Here we have illustrated the causal nature of body size variation as dichotomous splits, so that the form of these predictions is consistent with the statistical approach we utilize to assess the empirical patterns of body size variation among islands and species, namely regression tree analysis. Selective forces hypothesized to influence the evolution of insular body size are enclosed in rectangles; variables associated with these selective forces are listed below in the branching symbols; and predicted effects (gigantism, dwarfism, normal size, more-pronounced change, and less-pronounced change in body size) of particular states or levels of those variables are indicated below the arrows. (Image of deer mouse courtesy of US Center for Disease Control; images of elephant courtesy of Sinauer Associates.)

an advantage in regions with colder and more seasonal climates. In an alternative, ecological explanation for latitudinal gradients in body size, McNab (1971) reasoned that larger mammals can also exploit a broader range of foods (larger granivores can process large as well as small seeds; larger predators can take large as well as small prey), but smaller size may be an adaptation to avoid competition by feeding more efficiently on smaller prey in species-rich systems. Because species diversity declines with latitude, gradients of increasing body size may represent ecological character release in high-latitude environments, with small species increasing in size in systems lacking their larger competitors. Again, we expect this pattern to be contextual; that is, based on McNab's reasoning, latitudinal gradients in body size consistent with Bergmann's rule should be most prevalent in smaller species, namely those most likely to be the smaller members of a guild of competing mammals.

Our purpose here is to investigate the causality of body size evolution on islands by testing predictions consistent with the above hypotheses, namely that the optimal body size of insular populations of mammals should vary in a predictable manner with characteristics of the focal islands and focal species, and with ecological interactions among species (ecological release and displacement within disharmonic biotas). The predictions illustrated in Fig. 2 emphasize the contextual nature of selective forces influencing body size; that is, that the importance of these forces and their effects on insular populations depend on the body size of the ancestral populations.

MATERIALS AND METHODS

Database of body size evolution in extant mammals

The data are an update of those developed by the senior author in his earlier analyses of body size evolution in extant, insular mammals, which can be found in Lomolino (1985, 2005). The sources for these data are reported in those papers and are available on the resources website of the International Biogeography Society (http://biogeography.org/html/Resources/databases.html). In addition to the data from the original version of this database, we have added the environmental (predictor) variables described below. This expanded database, which now includes information on the body size of 385 insular populations (98 species) and 15 predictor variables describing geographic, ecological and climatic conditions of the species or the 248 focal islands, will be made available on the International Biogeography Society website for database resources (above).

Description of variables

We calculated the response variable as the mass of the focal, insular population divided by that of its apparent mainland relative, the latter based on geographic proximity and taxonomic designation. Measurements given in linear dimensions were first cubed to express relative insular body size (S_i) in mass equivalence. For simplicity of discussion, we use the terms 'gigantism' and 'dwarfism' to refer to insular populations with S_i values greater or less than 1.0, respectively.

Predictor variables included the body mass of mainland relatives (which serves to set the contextual nature of other variables) and variables most closely associated with alternative hypotheses for body size evolution in mammals. Island area was taken from databases of islands of the world, including the UN Island database (http://islands.unep.ch/Iindex.htm; accessed 15 July 2010) and the Atlas of Canadian Sea Islands (http://atlas.nrcan.gc.ca/site/english/learningresources/facts/islands.html; accessed 15 July 2010), and from source papers (those used in Lomolino, 1985, 2005) reporting body size of the focal, insular population, when island area was given. Island isolation was measured using Google Earth's distance tool to calculate the straight-line distance to the nearest mainland area with the reference mainland population. We acknowledge that other, more complex, measures of isolation could have been considered, but we chose this one for its simplicity and comparability, and because other measures require a more intimate knowledge of the particular focal species, archipelago and regional conditions (e.g. swimming ability, the ability to travel by rafting or crossing ice during winter, prevailing winds and ocean currents). We calculated the maximum elevation using Google Earth's 3-D terrain function.

Climatic conditions were calculated using DIVA-GIS 7.30 (Hijmans *et al.*, 2001), which includes the 19 WORLDCLIM bioclimatic variables (for a description of these variables see Hijmans *et al.*, 2005; http://www.worldclim.org/). Of the 19 climatic variables available, we selected the five that we deemed most closely associated with climate-based explanations for Bergmann's rule: mean annual temperature, annual precipitation, isothermality (an inverse measure of variability in temperature), and seasonality of temperature and precipitation (see Smith *et al.*, 1995; Yom-Tov & Yom-Tov, 2004, 2005; Millien *et al.*, 2006). Our analyses assume that the recording period for these bioclimatic variables (1950–2000), while post-dating the actual time period of body size evolution in the focal, insular populations, is characteristic of or at least strongly correlated with climatic conditions during that period.

We used two variables to describe the trophic characteristics of these species, namely whether they depended primarily on terrestrial or aquatic prey, and whether they were herbivores, carnivores, insectivores or omnivores (based on descriptions of diets provided by the University of Michigan's Animal Diversity Web, http://animaldiversity.ummz.umich.edu/site/index.html; accessed 15 June 2010). Variables describing ecological conditions of the focal insular communities included the species richness (number of species) of the mammalian predators or competitors most likely to interact directly with the focal insular population. Although body size evolution may also be influenced by ecological interactions with non-mammalian predators and competitors (e.g. raptors and avian competitors), the high dispersal abilities of these species relative to non-volant mammals suggest that ecological pressures from these taxa are less variable and, therefore, less likely to account for inferred evolutionary changes in body size of the focal, mammalian populations. We also assume here that, although the focal species may have interacted with a diverse assemblage of mammals and other vertebrates through diffuse competition, its body size evolution was most strongly influenced by direct (two-species) interactions. The numbers of mammalian predators and competitors of the focal species were estimated by first developing a list of all other mammals co-occurring on the focal island, and then consulting general references on the diet and habitats of those species to determine which ones were likely to be significant predators or competitors of the focal insular population. Sources we consulted to develop the list of co-occurring predators and competitors included the original sources for body size measurements of the focal species (see Lomolino, 1985, 2005; and the databases available at the International Biogeography Society Resources website), the database on insular Carnivora developed by Meiri (2005), and general works on regional mammals (for mammals of North America, Wilson & Ruff, 1999; British Isles, Arnold, 1984; Harris & Yalden, 2008; north-eastern United States, Werner, 1956; Lomolino, 1983; Adler & Wilson, 1985; British Columbia, Nagorsen, 2005; Mediterranean Sea, Sarà, 1998; M. Sarà, Universita di Palermo, Italy, pers. comm. 2009; Indonesia, Meijaard, 2003; Sea of Cortes, Case *et al.*, 2002, B. R. Riddle, University of Nevada, Las Vegas, NV, USA, pers. comm. 2009). We also included species of exotic mammals as potential competitors and predators. Because exotics are, by definition, more recent and therefore less likely to have influenced the body size evolution of the focal mammal than native mammals, the potential influence of exotic mammalian competitors was analysed separately from that of native competitors and predators.

Statistical analyses

We used regression tree analysis (RTA) to investigate the factors influencing the body size evolution of extant insular mammals. RTA is a recursive, binary machine-learning method that has some key advantages over traditional regression methods. As summarized in Olden *et al.* (2008), these include that RTA is nonparametric and distribution-free and thus does not require transformations. RTA is capable of handling categorical, interval and continuous variables, is able to deal efficiently with missing variables and with high dimensionality, and is not affected by outliers. It is, however, capable of providing readily interpretable descriptions of the relationships between predictor and response variables even when complex, contextual relationships exist (i.e. when the relationships between these variables varies among subgroups of the data – in this case, larger versus small mammals). In contrast, traditional linear methods can only uncover relationships that are globally significant (i.e. consistent across the entire data set). As Davidson *et al.* (2009) also point out, one especially important advantage of machine-learning methods in ecological and evolutionary applications is that they do not assume data independence, thus alleviating the need for phylogenetic controls of such data (see also Westoby *et al.*, 1995; Melo *et al.*, 2009).

The principal product of RTA is a recursively branching tree that describes the direct, interactive and contextual relationships between the response variable (here S_i) and a subset of the predictor variables (geographic, ecological and climatic variables). The first split, or branch, is determined by first sorting the entire data set by the values of each predictor variable and then determining which of those variables is best at splitting the data into two subgroups that are most homogeneous with respect to values of the response variable. The process is then repeated for each of the subsequent branches of subgroups until a stopping rule is satisfied (either by reaching an *a priori* limit to the minimal number of observations in terminal branches, a maximum number of terminal nodes, or an allowable error or heterogeneity in the subgroups). To prevent over-fitting, these 'maximal trees' are then pruned (using cross-validation of learning and test data sets; see Bell, 1999) until an optimal tree is selected. Here, we consider the best tree as that having the smallest relative error rate for predicting test data based on models (trees) developed from independent training data (see Olden *et al.*, 2008).

In addition to producing trees with splits based on the primary variables, RTA also investigates the importance, or potential contribution, of all other variables included in the analysis over all branches of the best tree, even if those variables were not used in the tree. This avoids the possibility that the influence of other variables will be masked and not show up in regression trees simply because they are correlated with the primary variable (i.e. those actually used in the best tree). Here, importance values are standardized and expressed as a percentage of the value for the variable with the highest importance measure.

We used the CART (classification and regression tree analysis) module of Salford Systems' Predictive Mining Suite (California Statistical Software, Inc., San Diego, CA; see Breiman *et al.*, 1984; Steinberg & Colla, 1997; Steinberg & Golovnya, 2006) to run the RTA of body size patterns in extant insular mammals. We ran four separate analyses of these data – two for all extant mammals, and two for just the rodents considered separately. For each of these species groups, we ran two RTAs for two sets of predictor variables – one in which latitude was used instead of climatic variables, and the other with climatic variables but not latitude. We used Salford's CART default settings, which included using the least square regression methods for splitting trees and a minimal parent node size of 10.

RESULTS

The median insular body size (S_i) for extant mammals analysed here was 1.06, indicating a modest tendency for gigantism in insular, non-volant mammals, in general (i.e. the insular body mass was 6% greater than the body mass of the reference population on the mainland). This was expected, given that most of the focal populations were rodents, which tend towards gigantism on islands. Species of extant mammals included those whose mainland relatives ranged in size from 2.5 g (white-toothed pygmy shrew, *Suncus etruscus*) to 700 kg (brown bear, *Ursus arctos*). Most of these species were herbivores that feed on terrestrial resources (see Appendix S1 in Supporting Information). Of the 248 islands included in this study, just over half were off the coasts of north-western North America. Islands ranged from tropical to arctic and from desert to rain forest environments (absolute latitude ranged from 0.5° to 80.6°, mean annual temperature from −16.0 to 28.3 °C, and annual precipitation from 36 to 3566 mm).

Regression trees

Relative errors of the best trees (i.e. their abilities to predict test data based on models generated from training data) ranged from 0.62 for all extant mammals to 0.80 (*R*-squared values, which describe the abilities of the models to explain training data, ranged from 0.54 to 0.41). For analyses with all extant mammals, trees within one standard error of the prediction accuracy of the best tree did not introduce any novel, primary variables ('primary variables' are those that formed the splits in the most accurate tree). For the rodents, one tree within one standard deviation of the best tree for analyses using climatic variables included maximum elevation as an additional splitting, predictor variable, and one tree for analyses using latitude instead of climatic variables included the body mass of reference populations as an additional predictor.

The structures of all four trees were generally consistent with the predictions depicted in Fig. 2. Each of the four regression trees generated in these analyses revealed the generality of the island rule pattern *sensu stricto*, and the contextual nature of the predictor variables. That is, the body mass of reference, mainland populations was the primary branch in all but one of these trees (Fig. 3). This variable achieved the highest importance value overall (Appendix S1), and the influence of geographic, ecological and climatic variables differed for large versus small mammals.

The structures of the two trees for analyses with all extant mammals were similar to each other, indicating that the degree of gigantism in small species was more pronounced for populations inhabiting islands that had smaller areas and were more isolated. Body size differences between insular and mainland populations were also more pronounced for mammals inhabiting islands that lacked native mammalian competitors (the influence of exotic competitors and predators was negligible in comparison to that of native mammals; see Tables S2–S5 in Appendix S1). Body size increased for both small and large mammals that were more dependent on aquatic prey. Note, however, that the degree of gigantism in small mammals peaked on the moderately isolated (> 17.1 but < 44.4 km) islands, rather than on the most isolated ones (Fig. 4). As predicted, body size evolution did not appear to be influenced by island isolation for large mammals. Importance values for all variables analysed, and analyses of surrogates for primary predictors used in the actual trees (Appendix S1) indicated that the body size evolution of insular mammals was also more pronounced for populations inhabiting low-lying islands (presumably those of limited habitat diversity) that lacked mammalian predators and competitors.

Contrary to one of the predictions of the resource-limitation hypothesis, neither of the analyses (with latitude or with climatic variables substituted for latitude) for all extant mammals detected an influence of island area on the degree of dwarfism of large mammals, and importance values indicated that the influence of island area was stronger for small than for large mammals (see Appendix S1). The body size evolution of large mammals, however, was strongly influenced by their dependence on terrestrial versus aquatic prey.

The structures of the trees for all extant mammals, combined, were also consistent with predictions based on Bergmann's rule. The degree of gigantism of insular small mammals on small islands increased with latitude from the tropics through the subtropics, but then appeared to peak at around 50° latitude (Fig. 4). Importance values for all predictor variables (see Appendix S1) also indicated that the degree of gigantism exhibited by small mammals was also associated with climate, being most pronounced in regions that are cold and highly seasonal (low isothermality and high seasonality of temperature). As predicted, the body size evolution of large mammals on islands did not appear to be strongly influenced by latitude or by climatic conditions (note the relatively low importance values for these variables in larger versus small mammals; Appendix S1).

For both of these trees, the most extreme cases of dwarfism (median $S_i = 0.74$) occurred for insular populations of large (> 2692 g) mammals restricted to terrestrial prey. The most extreme cases of gigantism (median $S_i = 1.77$) occurred for insular populations of small mammals that inhabited large islands and used aquatic prey; however, this latter result reflects the influence of just two insular populations. Those cases aside, the most extreme case of gigantism (median $S_i = 1.65$) for the tree using latitude as a surrogate for climate was for small mammals on relatively small (< 64.5 km^2) and remote (> 17.1 km) islands within temperate latitudes, and lacking mammalian competitors. When climatic variables were substituted for latitude, the most extreme cases of gigantism (median $S_i = 1.63$) occurred for very small mammals (< 282 g) inhabiting small (< 64.5 km^2), isolated (> 16.1 km) islands that lacked competitors and occurred in all but the wettest regions (annual precipitation < 2.94 m).

Regression tree analyses of data for insular rodents taken separately yielded qualitatively similar results, although these trees included fewer variables and branches, which is not surprising given that the sample size was more limited (239 vs. 385 insular populations). Importance values were relatively high for what we view as the contextual variable, body mass of the reference (mainland) population, consistent with the island rule *sensu stricto* (Fig. 3c). However, island area had a

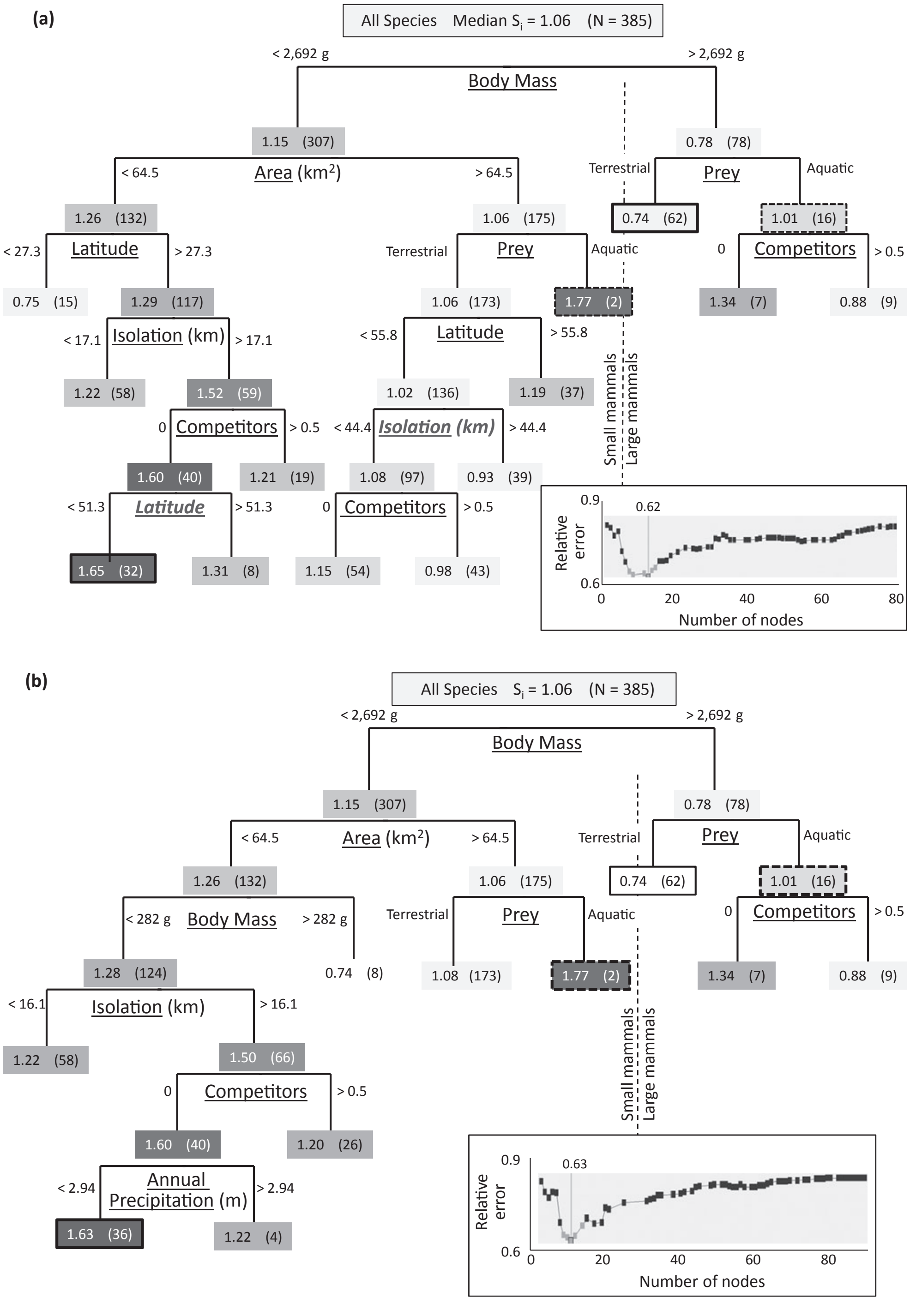

Figure 3 Regression trees generated from analyses of (a) all non-volant mammals studied and including all predictor variables except for climatic variables; (b) all non-volant mammals studied, and all predictor variables except that climatic variables were used instead of latitude; (c) rodents and including all predictor variables except for climatic variables; (d) rodents and all predictor variables except that climatic variables were used instead of latitude. Variables used for each split are underlined, and the critical values for each split are indicated to the left and right of each branch. Numbers in shaded boxes are the median insular body size (S_i), with the number of insular populations included in this split reported in parentheses, and the degree of shading of these boxes varying in proportion to the level of S_i (darker shading for higher values, i.e. more pronounced levels of gigantism). Boxes with solid, bold outlines denote the most extreme gigantism or dwarfism; those with dashed outlines denote populations of species that utilize aquatic prey; and variables with bold, grey italic letters identify those whose effects were partially inconsistent with our predictions, in that body size appeared to peak at intermediate levels of these variables (latitude and isolation; see Fig. 4). Graphs in the insets illustrate relative errors of predictive models as a function of tree complexity (number of terminal nodes). The vertical grey line in these graphs marks the best tree (that with the minimum relative error in predicting test data based on training data), and grey boxes denote alternative trees whose relative errors were within one standard deviation of that of the best tree.

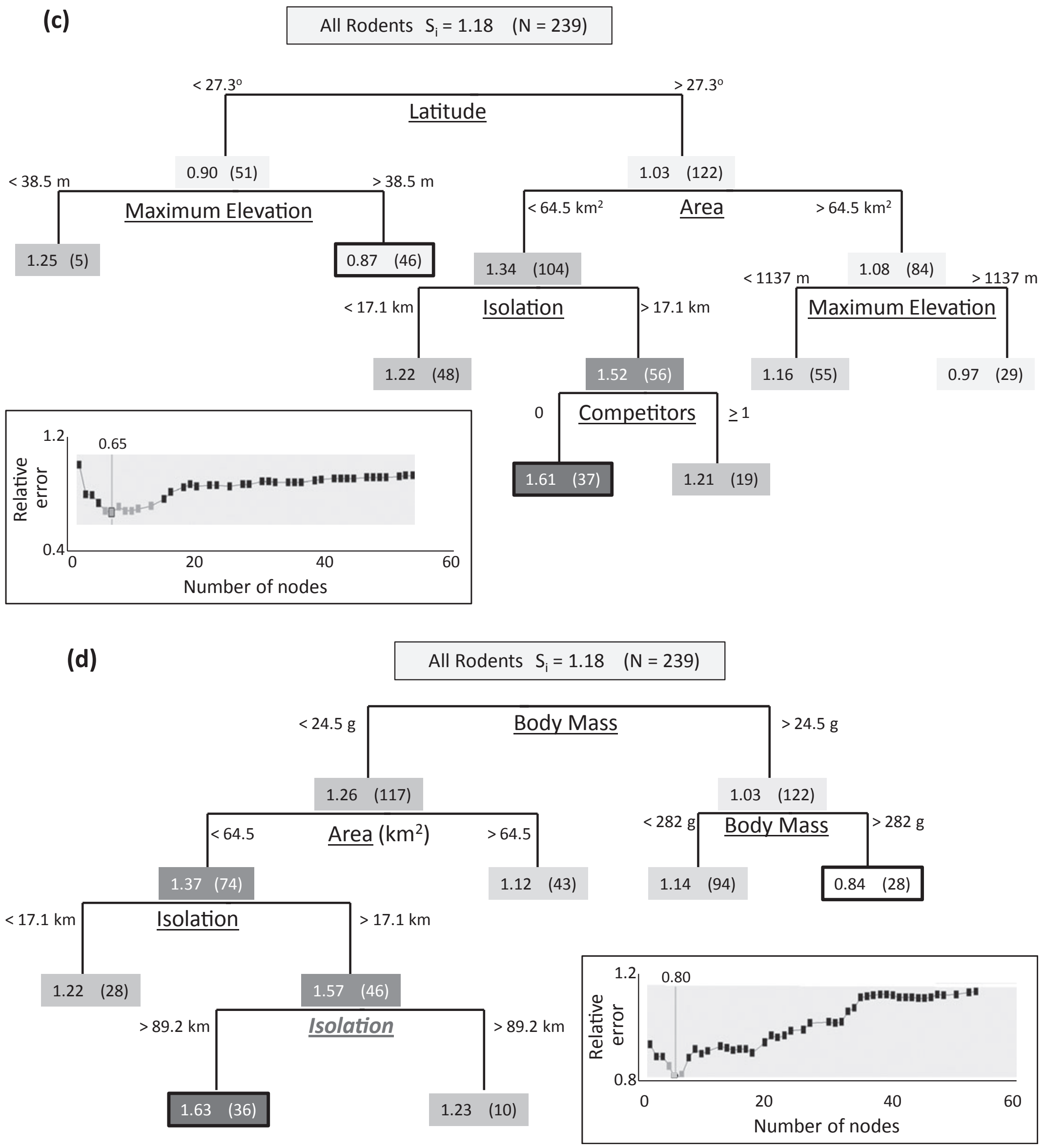

Figure 3 Continued

somewhat higher importance value than body mass in one of the two analyses for insular rodents (see Appendix S1). As we observed in the above trees for all mammals combined, we failed to detect results consistent with the area *per se* form of the resource-limitation hypothesis in large rodents (body size of insular populations of rodents was actually *larger* on smaller islands; Fig. 3c,d). On the other hand, both regression trees for rodents yielded results consistent with predictions of hypotheses based on ecological release, immigrant selection and climatic drivers of the latitudinal pattern associated with Bergmann's rule (Fig. 3c,d; see Appendix S1). Gigantism in rodents was most pronounced for those inhabiting islands that were extra-tropical (> 27.3° latitude), small, remote and lacking competitors (Fig. 3c), and for smaller species (those < 24.5 g) occurring on small islands of intermediate isolation (between 17.1 and 89.2 km isolation; Fig. 3d).

DISCUSSION

Given the fundamental importance of body size in influencing many physiological and ecological characteristics of mammals, it is not surprising that insular body size evolution appears to be associated with a variety of environmental factors, and that the influence of these factors is contextual, that is, varying with the body size of the ancestor of the focal species (Fig. 3). Of the hypotheses that we were able to investigate, only the area *per se* version of the resource-limitation hypothesis failed to garner strong support. From this we infer that the evolution of extant species of large mammals is more strongly influenced by the types and diversity of resources available and by the presence of competitors and predators (mammalian and otherwise) than by any ability of these species to perceive or be directly affected by the total space available.

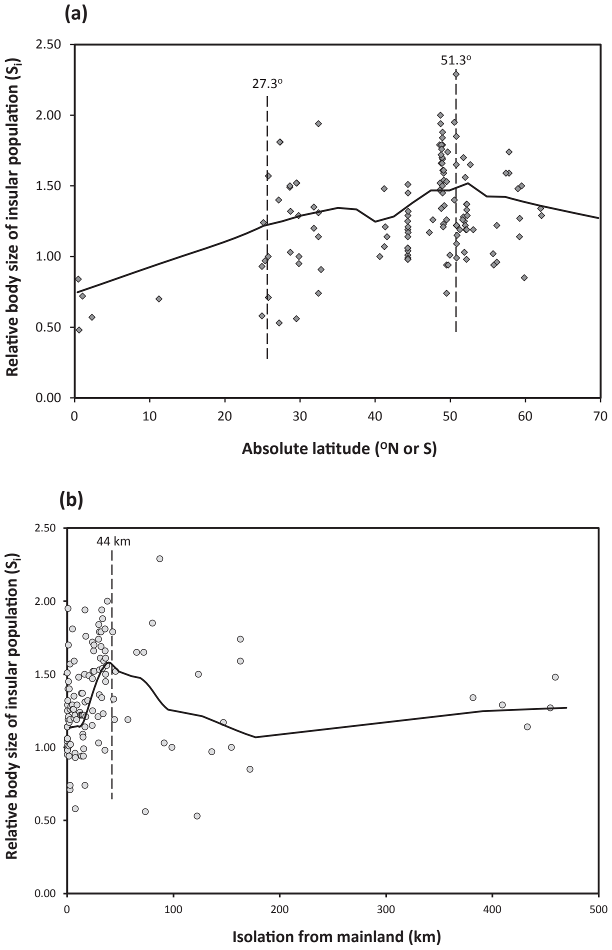

Figure 4 Insular body size (S_i = mass of the insular population divided by that of its closest mainland population) tends to increase with (a) latitude (consistent with patterns associated with Bergmann's rule) and with (b) isolation (consistent with predictions of the immigrant selection hypothesis), but in both cases S_i appears to decline or level-off at the highest levels of these variables (i.e. apparently peaking at roughly 50° latitude and 40 km isolation). Black trend lines are from LOESS regressions with smoothing parameter alpha = 0.5; see Fig. 3(a,b). Data illustrated here are those for small (< 282 g) mammals on small (< 64.5 km^2) islands.

As we noted earlier, the body size evolution of small mammals was strongly influenced by island area, but this was in a direction counter to the area *per se* prediction of the resource-limitation hypothesis [see Yom-Tov *et al.* (1999) for a similar, inverse relationship between island size and the body size of *Rattus exulans* on the Hawaiian, Solomon and New Zealand's offshore islands]. We interpret area here as a surrogate for the diversity of habitats and of predators and competitors, all of which should be lower and result in the ecological release of small mammals on small islands (note, however, that a limited number of studies of particular species of mammals have reported positive correlations between insular body size and island area – see table 3 in Lomolino, 2005; and for evidence from the fossil record, see Palombo, 2009). That large mammals with aquatic prey (namely brown bears) exhibited little if any dwarfism on islands is consistent with the resource-subsidy hypothesis (Fig. 2). Consistent with this inference, Hilderbrand *et al.* (1999) found that the body mass of female brown bears (*Ursus arctos*) was strongly correlated with the availability of marine prey (i.e. salmon), and Meiri *et al.* (2007) reported that the body size of this species was inversely correlated with distance to the nearest salmon spawning area.

These analyses also yielded results that were at least partially at odds with the predictions tested here, but were quite valuable in identifying areas for future study. Two of these apparent anomalies involve predictors of body size evolution in small mammals. The degree of gigantism in these species, although initially increasing with isolation and latitude, appeared to peak on islands located within intermediate ranges of these variables (*c.* 40 km isolation and 50° latitude; Fig. 4). We offer the following speculative explanations, again acknowledging the need for further study. First, as hypothesized in the Introduction, the effects of immigrant selection (gigantism) should be most pronounced in smaller mammals. Extending this to the species and community levels, this implies that the most isolated islands are less likely to include smaller species (those exhibiting more pronounced bouts of gigantism – waif or rafting species are obvious exceptions). Increasing isolation will lead to increasing gigantism in small mammals until a particular point at which they simply become less likely to get established, thus yielding a mid-isolation peak in gigantism.

The apparent mid-latitudinal peak in body size was also surprising, but perhaps just as interesting and potentially informative. Geist (1987) reported a similar pattern, with the body size of North American deer (*Alces*, *Rangifer* and *Odocoileus*, combined) and the grey wolf (*Canis lupus*) peaking between 50° and 70° latitude. We can offer an explanation for our results, again speculative, but analogous to that for the body size–isolation trend discussed above. The latitudinal gradient in climatic conditions is likely to select not only for larger individuals of small mammals, but also for larger species at high temperate to boreal latitudes. Because gigantism is likely to be less pronounced in larger species, the degree of gigantism exhibited by insular mammals should decline over the higher latitudes. Alternatively, climatic conditions on islands of supra-temperate latitudes may put a premium on being small enough to exploit subnivean and subterranean environments in order to escape the extremely harsh conditions above the surface, again reducing the trend towards gigantism through the higher latitudes.

In retrospect, perhaps the most surprising feature of the observed latitudinal pattern of insular body size is that we observed any such pattern at all. Remember that our measure of insular body size (S_i) was expressed relative to a measure of body size of mainland populations at approximately the same latitude. Thus, a latitudinal gradient in this variable (essentially, the degree of gigantism in small mammals) implies that the forces contributing to gigantism of small mammals are

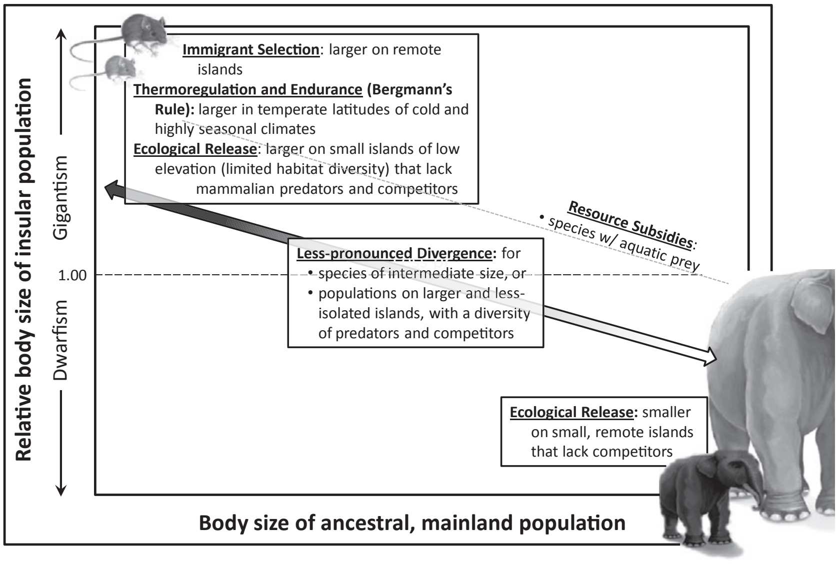

Figure 5 Summary of patterns and principal processes influencing body size evolution, based on the results of regression tree analysis of body size variation among extant, insular mammals. (Image of deer mouse courtesy of US Center for Disease Control; modified images of elephant courtesy of Sinauer Associates.)

intensified on insular versus continental systems. While climatic conditions may favour a larger body size for small mammals that occur at higher latitudes (mainland or islands), immigrant selection and ecological release from competitors and predators on small, isolated and ecologically simple (low-elevation) insular ecosystems may intensify this trend. This latitudinal gradient in insular body size of small mammals is probably not the result of differences between continental and insular (maritime) climates. Although it is generally true that insular climates tend to be more moderate, and our results did indicate that body size varied with climatic conditions, moderate climates should favour reduced rather than intensified gigantism in these mammals (see the explanation of Bergmann's rule in the Introduction).

One final note on the concept of an optimal size and the ecology of body size evolution: if we were to imagine an unrealistic world in which organisms were not influenced (competed with or preyed upon) by each other, then the optimal size would be microscopic – just large enough to replicate DNA rapidly and with minimal energy. However, interactions among conspecifics and among species are intrinsic and fundamental to natural selection. The optimal size of individuals within a population depends on the size and habits of all others in its community. In species-rich mainland biotas, these ecological interactions are among the principal drivers of diversification in body size and of all other traits that it influences. On species-poor islands, ecological release often reverses this trend. However, the evolutionary marvels of island life are also the products of ecological displacement from the limited and highly unbalanced (disharmonic) assemblages of other island residents.

Thus, while the body size evolution of extant insular mammals typically proceeds towards convergence on an intermediate body size, other taxa may exhibit more directional trends in body size and stature. New Zealand's extinct moas may be the classic case in point. While New Zealand lacks native non-volant mammals, character displacement from the rich native avifauna of New Zealand (including large predators as well as many small avian competitors) may have driven the evolution of ancestral moas towards increasingly larger body size and towards convergence on niches more similar to those of the absent ungulates than to those of birds. Evolutionary trends in plants of isolated archipelagos may have also been strongly influenced by both ecological displacement (from a diversity of rapidly colonizing herbaceous plants) and ecological release (as a result of the generally more limited dispersal capacities of the tree species that typically dominated forested ecosystems on the mainland). The result is the frequent evolution of woodiness and tree-stature in insular populations derived from herbaceous lineages of plants, but rarely the reverse trend (Darwin, 1859, p. 392; Carlquist, 1974; Bohle *et al.*, 1996; Grant, 2001; Whittaker & Fernández-Palacios, 2007; but see Lloyd, 1981 for putative cases of 'dwarfism', or evolution of more prostrate growth, in selected plants of New Zealand).

CONCLUSIONS

This research represents a significant advance over previous studies in that here we have been able to directly explore factors contributing to scatter about the general island-rule trend (Fig. 1) and to test predictions associated with alternative or complementary hypotheses for body size evolution in general. The results support the conceptual model illustrated in Fig. 2, and the fundamental assumption that body size evolution is influenced by a combination of forces whose relative importance is contextual, varying in a predictable manner with the body size of the focal ancestral species. Within this contextual framework, however, insular body size is also strongly influenced by characteristics of the focal islands, including the nature of their ecological communities, their geographic isolation, and climate (Fig. 5). The results also support the resource-subsidy hypothesis, with species capable of exploiting aquatic prey exhibiting a large body size in comparison to species with more terrestrial diets (this effect was amplified on islands lacking mammalian competitors).

Finally, while the list of hypotheses and predictions we analysed is not exhaustive, it does include what we believe to be the most significant ones discussed in the literature to date (see summaries in Whittaker & Fernández-Palacios, 2007; Lomolino *et al.*, 2010). More importantly, our assessment of these hypotheses provides compelling evidence for an overarching hypothesis of evolution of insular body size in mammals – there may indeed exist a theoretical optimum size for mammals in general (as hypothesized by Maurer *et al.*, 1992), but the optimum for particular insular populations varies in a predictable manner, both with the characteristics of the species (their bauplan and trophic strategies) and with the characteristics of insular environments. Maurer *et al.* (1992) estimated the optimal body size for mammals by noting where the trend line for the function in Fig. 1 intercepts the line where $S_i = 1.00$ (roughly between 0.1 and 0.5 kg). Trend lines, however, vary substantially among functional and taxonomic groups of mammals, yielding inferred optimal body sizes ranging from *c.* 0.3 kg in extant rodents and 6.9 kg in extant ungulates, to well over 10 kg in ungulates and proboscideans that inhabited Mediterranean islands during the Pliocene and Pleistocene (Lomolino, 2005; see also fig. 14.26c in Lomolino *et al.*, 2010).

We find the latter results for very large but extinct mammals intriguing, albeit preliminary and worthy of further study. Accordingly, we are currently expanding the current database on the body size of insular mammals to include extinct species that inhabited palaeo-islands across the globe, which will enable analyses with a much broader range of predictor variables, including ancestral (mainland) body sizes ranging up to 10,000 kg (versus the maximum of 700 kg in the current study of extant mammals). Furthermore, although our current analysis of extant mammals included some impressive bouts of gigantism and dwarfism (the most extreme cases in the current study included insular populations with $S_i = 2.29$ and 0.39 for *Peromyscus keeni* and *Nasua narica*, respectively), these may pale in comparison to results from the insular fossil record, which will have involved much more extended periods of isolation, changes in island size and isolation over time, an absence of anthropogenic impacts, and a broader range of species (shrews to proboscideans).

In summary, the utility of the island rule is not that it describes a pattern of exceptional generality, but that the graded trend and now explicable scatter about the trend provide invaluable insights into the forces influencing the evolution of one of life's most fundamental traits – body size.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Additional tables (Tables S1–S5) and figure (Figure S1) describing the islands studied and the predictions and results of regression tree analyses.

BIOSKETCH

Mark V. Lomolino is a professor of biology, and founding member and past president of the International Biogeography Society (http://www.biogeography.org). His research and teaching focus on the biogeography, community ecology, evolution and conservation of animals inhabiting islands or island-like ecosystems.

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