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SYNTHESIS

Of mice and mammoths: generality and antiquity of the island rule

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ABSTRACT

Aim We assessed the generality of the island rule in a database comprising 1593 populations of insular mammals (439 species, including 63 species of fossil mammals), and tested whether observed patterns differed among taxonomic and functional groups.

Location Islands world-wide.

Methods We measured museum specimens (fossil mammals) and reviewed the literature to compile a database of insular animal body size (S_i = mean mass of individuals from an insular population divided by that of individuals from an ancestral or mainland population, M). We used linear regressions to investigate the relationship between S_i and M, and ANCOVA to compare trends among taxonomic and functional groups.

Results S_i was significantly and negatively related to the mass of the ancestral or mainland population across all mammals and within all orders of extant mammals analysed, and across palaeo-insular (considered separately) mammals as well. Insular body size was significantly smaller for bats and insectivores than for the other orders studied here, but significantly larger for mammals that utilized aquatic prey than for those restricted to terrestrial prey.

Main conclusions The island rule appears to be a pervasive pattern, exhibited by mammals from a broad range of orders, functional groups and time periods. There remains, however, much scatter about the general trend; this residual variation may be highly informative as it appears consistent with differences among species, islands and environmental characteristics hypothesized to influence body size evolution in general. The more pronounced gigantism and dwarfism of palaeo-insular mammals, in particular, is consistent with a hypothesis that emphasizes the importance of ecological interactions (time in isolation from mammalian predators and competitors was 0.1 to > 1.0 Myr for palaeo-insular mammals, but < 0.01 Myr for extant populations of insular mammals). While ecological displacement may be a major force driving diversification in body size in high-diversity biotas, ecological release in species-poor biotas often results in the convergence of insular mammals on the size of intermediate but absent species.

Keywords
Body size, dwarfism, evolution, fossils, gigantism, island rule, islands, mammals.

INTRODUCTION

The island rule describes a graded trend in insular populations of vertebrates from gigantism in small species to dwarfism in large species (Fig. 1). The generality of this pattern has been evaluated for a variety of vertebrates and for a limited selection of invertebrates as well (Lomolino, 1985, 2005; McClain *et al.*, 2006). The pattern has also been inferred, albeit to a much more limited degree, for several species of palaeo-insular mammals (e.g. see Vaufrey, 1929; Sondaar,

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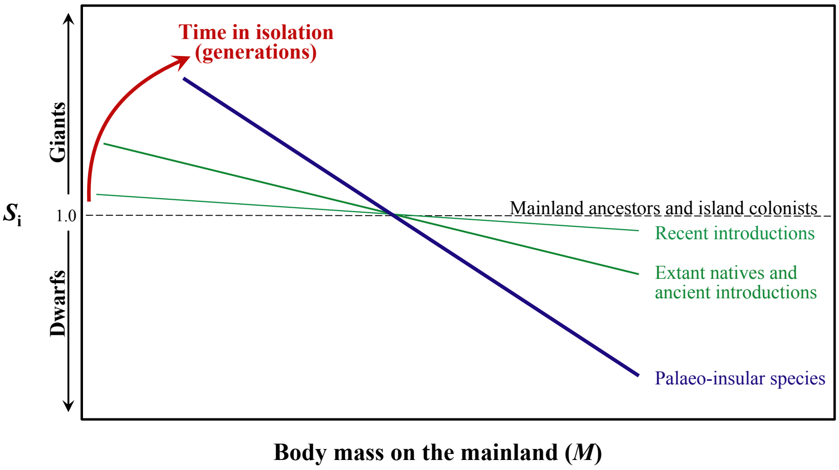

Figure 1 A conceptual model for the development of insular body size trends (the island rule) over time. The island rule describes a graded trend from gigantism in small mammals to dwarfism in large mammals. Because the body size evolution of insular mammals should develop with time in isolation, the slope of the line describing the relationship between the relative body size of insular mammals (S_i) and the mass of mainland or ancestral forms (M) should decrease (become steeper) with age of insular populations (S_i = mass of insular population/M).

1977; Azzaroli, 1982; Malatesta, 1985; Roth, 1992; Raia *et al.*, 2003; Palombo, 2004, 2007, 2009; Millien, 2006; Raia & Meiri, 2006; Bromham & Cardillo, 2007; de Vos *et al.*, 2007; van der Geer *et al.*, 2010). Indeed, two of the most spectacular cases of body size evolution in any mammal are those of the extinct elephant (*Palaeoloxodon falconeri*) from Spinagallo Cave (Siracusa, Sicily; middle Pleistocene), which dwarfed to < 5% of the size (body mass) of its mainland ancestor (*Palaeoloxodon antiquus*), and the giant erinaceomorph insectivore (*Deinogalerix koenigswaldi*) of the Gargano, a palaeo-island of southern Italy (late Miocene), which reached over 100 times the size of its ancestor (see Appendix S1 in the Supporting Information). A rigorous assessment of the island rule for palaeo-insular mammals, equivalent to those conducted for extant mammals, is lacking. This is understandable given the challenges of working with the fossil record, where the body mass of a majority of the insular species or that of their mainland ancestors has until now been unknown or poorly defined (Damuth & MacFadden, 1990). With sufficient information now available, it is possible to address these shortfalls and to assess the applicability of the island rule to a broad diversity of palaeo-insular mammals and to integrate the results obtained here with those available for extant mammals.

Even for extant species of mammals, however, there remains some debate regarding both the generality and, in particular, the causality of the island rule pattern (Roth, 2001; Palkovacs, 2003; Meiri *et al.*, 2004a,b, 2008; Durst & Roth, 2012; Lomolino *et al.*, 2012). At least some of this debate derives from the appreciable scatter about the trend, where the independent variable (body mass of individuals of the mainland or ancestral form, M) typically explains < 30% of the variation in insular body size (S_i = mean mass of individuals from an insular population divided by M). This variation about the general trend, however, is both expected and highly informative, as it provides key insights into the factors influencing body size evolution in general. That is, while there may be a theoretical, optimal body size that small and large species may converge on in low-diversity systems (where the trend intersects the horizontal dashed line in Fig. 1), the optimal size for any particular insular population (extant or fossil) should vary, albeit in a predictable manner, with characteristics of the island, species, and interactions among resident, insular species (see Lomolino, 1984, 2005; Fooden & Albrecht, 1993; Lomolino *et al.*, 2012).

The results of the regression tree analyses that we conducted in an earlier paper published in this journal (Lomolino *et al.*, 2012) are generally consistent with this ecological hypothesis of body size evolution. Body size divergence was more pronounced for populations that inhabited islands lacking mammalian competitors and predators (i.e. where ecological release should be more prevalent); gigantism was more pronounced in populations of small mammals that inhabited the more isolated islands (consistent with the prediction that immigration capacity is greater for larger mammals) and islands at higher latitudes and with colder and more seasonal climates (consistent with patterns associated with Bergmann's rule); and the insular body size of both small and large mammals tended to be greater for species that feed on aquatic prey (consistent with the ecological subsidies of marine productivity; see relevant discussion in Lomolino *et al.*, 2012). Our results, however, failed to support the contention that body size in large mammals should increase with island area, and did yield two unanticipated results: latitudinal trends of body size in small mammals were amplified on islands, and the body size of populations of small mammals appeared to peak not at the highest but at intermediate ranges of latitude and island isolation.

Our purpose here is to conduct the most comprehensive assessment to date of the island rule pattern *sensu stricto* (i.e. the predicted, negative relationship between S_i and M) in mammals, by substantially expanding the database we used earlier (Lomolino *et al.*, 2012). Our extensive literature review along with our ongoing taxonomic revisions and direct measurements of museum specimens of palaeo-insular mammals have resulted in a database that now includes information on the insular body sizes of 1593 populations of terrestrial mammals from 18 orders (Artiodactyla, Carnivora, Chiroptera, Dasyuromorphia, Dermoptera, Didelphimorphia, Diprotodontia, 'Insectivora' – Insectivora and Erinaceomorpha, Lagomorpha, Monotremata, Peramelemorphia, Pholidota, Pilosa, Primates, Proboscidea, Rodentia, Scandentia) and 439 species (including 63 species from the fossil record). Specifically, we will test whether the slope of the island rule pattern is significantly less than zero, and then test whether the pattern differs among the principal groups comprising our database; that is, among mammalian orders (which differ in dispersal capacity, resource requirements, and other characteristics that should influence body size evolution), and for native versus introduced populations, populations that utilize aquatic versus those restricted to terrestrial prey, and extant versus fossil mammals.

Finally, the latter group – palaeo-insular mammals of the late Miocene to early Holocene epochs – offers a potentially invaluable opportunity to investigate body size evolution over a broad span of time (time in isolation was 0.1 to > 1.0 Myr for palaeo-insular mammals, but < 0.01 Myr for extant populations of insular mammals), and range in body size (including multiple species of small, as well as very large, palaeo-insular mammals – in particular, hippos and proboscideans). Accordingly, we utilize the fossil record to assess the antiquity of the island rule pattern and to test whether body size evolution was more pronounced in palaeo-insular mammals, given their much more extended period of time for divergence, than in extant species (Fig. 1).

MATERIALS AND METHODS

Data collection and calculations of S_i

Our extensive database is available as Appendix S2, and includes S_i values (mean mass of individuals from an insular population divided by that of individuals from an ancestral or mainland population, M), body mass of mainland or ancestral forms, island identity, and references for body size measurements for each of the insular populations used in this study. Estimations of S_i values were restricted to comparisons of adults and, when available, comparisons among individuals of the same gender. When body size measurements reported in the literature were expressed in linear dimensions (e.g. greatest skull length or body length), we calculated the ratio of the cubed linear dimensions so that all S_i values are expressed as mass equivalents.

The process of estimating relative body sizes (S_i values) for palaeo-insular mammals is more challenging than that for extant mammals as it requires geographical reconstructions of ancient islands and mainland sources of their populations, along with accurate assessments of taxonomic relationships among fossil mammals. Ancestral populations were chosen based on the revision of the best available studies of taxonomy and phylogeny in the literature, combined with data on dispersal routes during the geological period corresponding to the most parsimonious time window of dispersal to the palaeo-island. The calculation of S_i values (in mass equivalents) for fossil species requires allometric formulae that are specific to the species, the skeletal measurements (of teeth, skulls or limb bones), and the nature of body size change (e.g. insular dwarfism or gigantism) in the focal taxon (see Damuth & MacFadden, 1990, for an extensive discussion on alternative allometric regressions and related problems). In total, we used 19 different regressions provided in 12 papers (see the Supporting Information for an extensive description of methods, measurements taken and specimens used). For Proboscidea, we used regressions based on limb bone lengths, as palaeo-insular proboscideans tend to have different proportions from living elephants (Herridge, 2010). For Artiodactyla, we mainly used articular and shaft dimensions of limb elements, as the allometric scaling of limb bones tends to change during dwarfism (Köhler & Moyà-Solà, 2004; van der Geer *et al.*, 2010). For rodents, insectivores and lagomorphs, we used regressions based on dental elements and, wherever possible, on postcranial measurements as well (see Table 1 and Supporting Information).

The origin of extant insular populations – as native or introduced – was determined by consulting the introduced species databases compiled by D. F. Sax, the Global Invasive Species Database (http://www.issg.org/database/), and species accounts on the Animal Diversity Web (http://animaldiversity.ummz.umich.edu/accounts/Mammalia/). Information on the type of prey utilized, namely aquatic or terrestrial, was determined by consulting the original publication (source for body size measurements) and species descriptions provided by the Animal Diversity Web.

The heterogeneous nature of this database – derived from reports from hundreds of researchers, utilizing a variety of measures of body size, and from a wide variety of islands and time periods – is likely to produce considerable measurement error and unexplained variation. Such variation is likely to reduce the power of tests for the predicted pattern rather than to bias the results in favour of detecting such a pattern (i.e. such error is highly unlikely to produce a bias that would both inflate S_i values for small mammals and underestimate S_i values for large mammals).

Statistical analyses

We used linear regressions to investigate the relationship between S_i and M, using the ordinary least squares methods in this model 1 regression, where the value of M for each population was assumed fixed and assigned to that of the species based on values reported in the literature and on our own estimates (see Appendix S1). In addition to using the semi-log regression model [S_i as a function of $\log(M)$], which is the approach utilized in most earlier studies of the island rule pattern, we also used a log–log model, which in retrospect seems more appropriate given that the semi-log model can generate predicted S_i values below 0 (i.e. a negative body size) when very large mammals are considered. We first conducted preliminary regressions of all data for populations of extant terrestrial mammals within orders to identify and remove those points that were identified as having undue influence on the results (i.e. we deleted observations if

Table 1 Variation in insular body size (S_i as a proportion of ancestral body mass) among palaeo-insular mammals (see Supporting Information).

Order	Insular species	Ancestor	Log$_{10}$ (ancestral body mass) (g)	S_i	Palaeo-island†
Artiodactyla	*Bubalus cebuensis*	*B. bubalis*	5.9777	0.17	Cebu
Artiodactyla	*Cervus elaphus siciliae*	*C. elaphus*	5.3522	0.45	Sicily
Artiodactyla	*Cervus elaphus*	*C. elaphus*	5.3522	0.27	Malta
Artiodactyla	*Dama carburangelensis*	*D. dama tiberina*	4.9294	0.65	Sicily
Artiodactyla	*Duboisia santeng*	*Boselaphus tragocamelus*	5.2553	0.27	Java
Artiodactyla	*Hippopotamus creutzburgi*	*H. antiquus*	6.5022	0.13	Crete
Artiodactyla	*Hippopotamus lemerlei*	*H. amphibius*	6.1746	0.25	Madagascar
Artiodactyla	*Hippopotamus madagascariensis*	*H. amphibius*	6.1746	0.26	Madagascar
Artiodactyla	*Hippopotamus melitensis*	*H. amphibius*	6.1746	0.60	Malta
Artiodactyla	*Hippopotamus minor*	*H. antiquus*	6.5022	0.04	Cyprus
Artiodactyla	*Hippopotamus pentlandi*	*H. amphibius*	6.1746	0.74	Sicily
Artiodactyla	*Megaloceros cazioti*	*M. verticornis*	5.7612	0.13	Corsica–Sardinia
Artiodactyla	*Myotragus balearicus*	*Aragoral mudejar*	5.1523	0.18	Majorca–Minorca
Artiodactyla	*Sus sondaari*	*S. arvernensis*	4.7993	0.64	Sardinia
Proboscidea	*Mammuthus creticus*	*M. meridionalis*	6.9278	0.04	Crete
Proboscidea	*Mammuthus exilis*	*M. columbi*	6.8919	0.17	Santa Rosa
Proboscidea	*Mammuthus lamarmorai*	*M. meridionalis*	6.9278	0.08	Sardinia
Proboscidea	*Mammuthus primigenius*	*M. primigenius*	6.7390	0.47	Wrangel
Proboscidea	*Palaeoloxodon ‘cypriotes’*	*P. antiquus*	6.9018	0.07	Cyprus
Proboscidea	*Palaeoloxodon ‘mnaidriensis’*	*P. antiquus*	6.9018	0.17	Sicily
Proboscidea	*Palaeoloxodon creutzburgi*	*P. antiquus*	6.9018	0.38	Crete
Proboscidea	*Palaeoloxodon falconeri*	*P. antiquus*	6.9018	0.02	Sicily
Proboscidea	*Palaeoloxodon tiliensis*	*P. antiquus*	6.9018	0.09	Tilos
Proboscidea	*Stegodon florensis*	*S. ganesa*	6.5658	0.47	Flores
Proboscidea	*Stegodon sompoensis*	*S. ganesa*	6.5658	0.20	South Sulawesi
Proboscidea	*Stegodon trigonocephalus*	*S. ganesa*	6.5658	0.75	Java
Rodentia	*Agathaeromys praeuniversitatis**	*A. donovani*	1.8921	0.29	Bonaire
Rodentia	*Hattomys gargantua**	*H. beetsi*	2.2466	4.96	Gargano
Rodentia	*Hypnomys morpheus*	*Eliomys quercinus*	1.8692	3.09	Majorca–Minorca
Rodentia	*Kritimys catreus*	*K.* aff. *K. kiridus*	2.2046	3.24	Crete
Rodentia	*Leithia cartei*	*Eliomys quercinus*	1.8692	3.00	Sicily
Rodentia	*Leithia melitensis*	*Eliomys quercinus*	1.8692	13.53	Sicily
Rodentia	*Microtus (Terricola)* ex gr. *M. savii*	*M. (T.) savii*	2.0065	1.26	Sicily
Rodentia	*Microtus (Tyrrhenicola) henseli*	*M. ruffoi*	2.1064	1.78	Corsica–Sardinia
Rodentia	*Mikrotia magna**	smallest *Mikrotia* (Biancone 1)	1.6254	9.48	Gargano
Rodentia	*Mikrotia* middle-sized lineage*	smallest *Mikrotia* (Biancone 1)	1.6254	3.32	Gargano
Rodentia	*Mikrotia* small-sized lineage*	smallest *Mikrotia* (Biancone 1)	1.6254	1.06	Gargano
Rodentia	*Mus minotaurus*	*M. musculus*	1.2222	3.23	Crete
Rodentia	*Rhagamys orthodon*	*Rhagapodemus ballesioi*	1.5336	2.63	Corsica–Sardinia
Insectivora	*Crocidura esuae*	*C. russula*	1.0476	1.07	Sicily
Insectivora	*Talpa tyrrhenica*	*Talpa minor*	2.0492	1.16	Sardinia
Insectivora (aquatic)	*‘Asoriculus’ henseli*	*Asoriculus gibberodon*	0.9675	3.05	Corsica–Sardinia
Insectivora (aquatic)	*Deinogalerix brevirostris*	*Parasorex socialis*	1.6737	140.50	Gargano
Insectivora (aquatic)	*Deinogalerix koenigswaldi*	*Parasorex socialis*	1.6737	207.31	Gargano
Insectivora (aquatic)	*Nesiotites hidalgo*	*Asoriculus gibberodon*	0.9675	4.51	Majorca–Minorca
Lagomorpha	*Gymnesicolagus gelaberti*	*Prolagus crusafonti*	2.1797	35.83	Majorca
Lagomorpha	*Hypolagus peregrinus*	*H. gromovi*	3.7149	0.65	Sicily (northern palaeo-island)
Lagomorpha	*Nuralagus rex*	*Alilepus turolensis*	3.0792	10.00	Minorca
Lagomorpha	*Prolagus imperialis*	*P. oeningensis*	1.9257	7.01	Gargano
Lagomorpha	*Prolagus sardus*	*P. michauxi*	2.2951	2.27	Corsica–Sardinia
Carnivora	*Cynotherium sardous*	*Xenocyon lycaonoides*	4.4246	0.49	Corsica–Sardinia
Carnivora	*Enhydrictis galictoides*	*Pannonictis nesti*	3.7235	0.85	Corsica–Sardinia
Carnivora	*Mececyon trinilensis*	*Xenocyon lycaonoides*	4.4246	0.39	Java
Carnivora	*Mustelercta arzilla*	*Pannonictis nesti*	3.7235	0.98	Sicily

Table 1 Continued

Order	Insular species	Ancestor	Log_{10} (ancestral body mass) (g)	S_i	Palaeo-island†
Carnivora	*Oriensictis nipponica*	*O. melina*	3.8609	1.00	Kyushu
Carnivora (aquatic prey)	*Algarolutra majori*	*Lutra simplicidens*	3.8041	0.89	Sardinia
Carnivora (aquatic prey)	*Cyrnolutra castiglionis*	*Lutra simplicidens*	3.8041	1.20	Corsica
Carnivora (aquatic prey)	*Lutra trinacriae*	*L. simplicidens*	3.8041	1.11	Sicily
Carnivora (aquatic prey)	*Lutrogale cretensis*	*L. perspicillata*	4.0821	1.17	Crete
Carnivora (aquatic prey)	*Megalenhydris barbaricina*	*Lutra simplicidens*	3.8041	2.79	Sardinia
Carnivora (aquatic prey)	*Pannonictis* sp.	*P. nesti*	3.7235	1.51	Sardinia
Carnivora (aquatic prey)	*Sardolutra ichnusae*	*Lutra simplicidens*	3.8041	1.05	Sardinia
Primates	*Macaca majori*	*M. florentina*	4.0700	0.66	Sardinia

*Calculation of S_i based on comparison to this early chronospecies on this island.

†Owing to the dynamics of sea level and the seafloor through the Miocene to Holocene epochs the palaeo-islands listed here include areas that are currently peninsulas (Gargano, Italy), regions of current islands (northern palaeo-island of Sicily; south Sulawesi), or separate islands that were previously joined (Corsica–Sardinia; Majorca–Minorca).

the Cook's *D*-statistic exceeded 0.05 and the observations exceeded the 95% confidence limits of regression trends). The resulting 15 records of undue influence were excluded, leaving 1530 insular populations included in all subsequent analyses of extant mammals. We used *t*-tests to test the prediction that the slopes of the relationship between S_i and M differed between native and non-native populations of extant mammals, and between populations of extant and palaeo-insular mammals, where t = (difference in slopes)/$(s_1^2 + s_2^2)^{0.5}$, and s_1 and s_2 are the standard errors of the slopes being compared.

We chose not to use phylogenetic adjusted regressions here because, while they can be highly informative in the proper applications, either they are infeasible for fossil mammals with uncertain phylogenetic relationships, or they may introduce Narcissus effects (*sensu* Colwell & Winkler, 1984) by filtering out the influence of variables of interest that are correlated with phylogeny (e.g. body size of the mainland, ancestral species), or they can be inappropriate and less accurate than ordinary least squares regressions even when independent variables have a strong phylogenetic signal (Revell, 2010) or when the rate of anagenetic variation exceeds that of cladogenesis (see Ricklefs & Starck, 1996; Björklund, 1997; Losos, 2003, 2011; McNab, 2003; Carvalho *et al.*, 2006; Sibly *et al.*, 2012). This is almost certainly the case in studies of the island rule where the dependent variable (S_i) is actually a contrast itself between a pair of populations (insular versus mainland, or derived versus ancestral populations). The degree to which S_i values differ from 1.0 (i.e. where insular populations exhibit gigantism or dwarfism) reflects relatively rapid, anagenetic changes in body size within lineages, and the level of evolutionary divergence and independence among populations. We did, however, also use regression tree analysis (RTA) as a means of verifying that our results were not the spurious outcome of non-independence among replicates (populations). RTA is a recursive, machine-learning method that is nonparametric and distribution-free, does not require data transformations or assumptions of data independence and, therefore, alleviates any need for phylogenetic controls of such data (see Westoby *et al.*, 1995; Olden *et al.*, 2008; Davidson *et al.*, 2009; Melo *et al.*, 2009; Durst & Roth, 2012; Lomolino *et al.*, 2012). The results of RTA of the current database (summarized in Table S17 & Fig. S1 in Appendix S1) are consistent with those of linear regressions conducted here, with results of classification tree analyses conducted by Durst & Roth (2012) in rodents, and with our earlier application of RTA to investigate the causality of the island rule in terrestrial mammals, albeit in that case (Lomolino *et al.*, 2012) with a more limited data set (the current database includes over four times as many insular populations).

We used analysis of covariance (ANCOVA) to compare island rule trends among the taxonomic and functional groups in our database: among orders of extant mammals; extant natives versus those introduced onto islands; mammals with aquatic versus those with terrestrial prey; and extant versus palaeo-insular mammals. ANCOVA can be set to assume identical slopes, but tests for the statistical significance of differences in intercepts of trends among groups. Statistical analyses were conducted using XLSTAT (version 2012; Addinsoft, New York, USA).

RESULTS

Generality of the pattern in extant mammals

Linear regression results (Table 2) indicated that the island rule pattern (negative relationship between S_i and M) was significant across populations of all extant mammals combined (n = 1530 populations), and across populations within all of the orders where sample sizes were adequate (n > 20 insular populations) for these analyses. The pattern was also highly significant across all extant mammals when S_i values were averaged to the species level (n = 376 species; Table 2).

Table 2 Results of linear regression analysis of the relationship between relative insular body size (S_i) and mass of the ancestral or reference population on the mainland (M).

Taxonomic or functional group	n (populations or species)	Slope (P slope $\geq$ 0.0)	r^2
Regression model: $S_i = b_0 + b_1(\text{Log}_{10}(M))$			
Extant insular mammals			
All populations	1530	−0.082 (< 0.0001)	0.128
Populations with terrestrial prey	1425	−0.098 (< 0.0001)	0.168
Populations with aquatic prey	105	−0.073 (0.002)	0.077
Populations of natives with terrestrial prey	1263	−0.100 (< 0.0001)	0.178
Populations of introduced mammals with terrestrial prey	162	−0.080 (< 0.0001)	0.116
Populations of mammals with terrestrial prey within			
Artiodactyla	61	−0.222 (< 0.0001)	0.367
Carnivora	324	−0.049 (0.0002)	0.038
Chiroptera	158	−0.133 (< 0.0001)	0.164
Insectivora	115	−0.102 (< 0.0001)	0.196
Lagomorpha	25	−0.367 (0.0075)	0.231
Marsupials	40	−0.101 (0.0166)	0.114
Primates	123	−0.089 (0.0234)	0.032
Primates, excluding *Macaca fascicularis* (where n = 73)	50	−0.098 (0.0226)	0.081
Rodentia	500	−0.182 (< 0.0001)	0.132
Scandentia	59	−0.168 (0.0345)	0.195
Populations of carnivores with aquatic prey	96	−0.039 (0.0555)	0.027
Species (populations averaged to species level)			
All species of mammals	376	−0.085 (< 0.0001)	0.158
Species of mammals with terrestrial prey	357	−0.091 (< 0.0001)	0.195
Palaeo-insular mammals			
All species	63	−4.183 (0.015)	0.074
Species with terrestrial prey	52	−1.065 (0.0014)	0.165
Excluding one record of undue influence (*Gymesicolagus gelaberti*; Cook's D statistic = 0.84)	51	−0.747 (< 0.0001)	0.317
Regression model: $\text{Log}_{10}(S_i) = b_0 + b_1(\text{Log}_{10}(M))$			
Extant species with terrestrial prey	357	−0.053 (< 0.0001)	0.201
Palaeo-insular species with terrestrial prey	52	−0.264 (< 0.0001)	0.646

ANCOVA conducted at the species level indicated that the intercepts of these trends did differ among some orders, with insular bats and insectivores exhibiting significantly lower S_i values (–0.20 and –0.18, respectively) in comparison with other mammals (after correcting for mass of the species on the mainland; Table 3, Fig. 2). Although slopes of the relationship between S_i and M were also significantly < 0.0 for populations of terrestrial natives and for those of introduced mammals, taken separately (n = 1263 and 162 populations, respectively), intercepts of the regressions for these two groups differed significantly, with introduced populations tending to exhibit somewhat (+ 0.071) higher S_i values (Table 3, Fig. 3). Contrary to one of the predictions illustrated in Fig. 1, the slope of the island rule pattern was only slightly (+ 0.02) and not significantly shallower (more positive) for introduced populations than that for native populations of mammals ($t = 1.08$, $P > 0.25$, d.f. = 1421).

As observed in previous studies (Lomolino, 1985, 2005), insular body sizes were higher for mammals utilizing aquatic prey (e.g. fish, aquatic invertebrates and carcasses of marine mammals) than for those restricted to feeding on terrestrial plants or animals. This difference among mammals with alternative prey was significant over all populations of mammals (S_i values 0.22 higher for mammals with aquatic prey than for those with terrestrial prey; Fig. 4a), and for members of the order Carnivora, taken separately (S_i values 0.18 higher for carnivores that utilized aquatic prey than for those restricted to terrestrial prey; ANCOVA; Table 3, Fig. 4b). Although the numbers of aquatic populations within other mammalian orders were insufficient to justify statistical comparisons, all four of the Artiodactyla utilizing aquatic prey (four populations of *Sus barbatus*), all three of the aquatic-feeding insectivores (one population of *Sorex palustris* and two of *Echinosorex gymnura*), and the only aquatic-feeding rodent included in this study (*Oryzomys couesi*) exhibited relatively high S_i values (i.e. higher than that predicted based on the regression line for mammals with terrestrial prey – solid line in Fig. 4a). The only monotreme included in this study,

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Table 3 Results of analysis of covariance (ANCOVA) of the island rule pattern among various taxonomic and functional groups of extant, insular mammals.

Among species within taxonomic groups	Slope	(*P* slope not < 0.0)	*n*	r^2
Seven orders with ≥ 19 species	–0.130	< 0.0001	327	0.305
	Intercept	(*P* intercept = generalized intercept)		
Artiodactyla	1.317	0.953	19	
Carnivora	1.337	0.712	57	
Chiroptera	1.126	< 0.0001	66	
Insectivora	1.145	< 0.001	29	
Marsupials	1.364	0.416	21	
Primates	1.354	0.495	38	
Rodents	1.321	–*	97	
Between populations of mammals with terrestrial prey that were native and those that were introduced onto the focal islands				
	Slope	(*P* slope not < 0.0)		
	–0.098	< 0.0001	1425	0.177
	Intercept	(*P* intercept = generalized intercept)		
Introduced populations	1.302	< 0.001	162	
Native populations	1.231	–*	1263	
Between mammal populations utilizing aquatic prey and those restricted to terrestrial prey				
	Slope	(*P* slope not < 0.0)		
	–0.096	< 0.0001	1530	0.167
	Intercept	(*P* intercept = generalized intercept)		
Aquatic prey	1.453	< 0.0001	105	
Terrestrial prey	1.236	–*	1425	
Between populations of carnivores utilizing aquatic prey and those restricted to terrestrial prey				
	Slope	(*P* slope not < 0.0)		
	–0.047	< 0.0001	420	0.132
	Intercept	(*P* intercept = generalized intercept)		
Aquatic prey	1.248	< 0.0001	96	
Terrestrial prey	1.068	–*	324	

**P*-value not reported because this comparison is redundant with above.

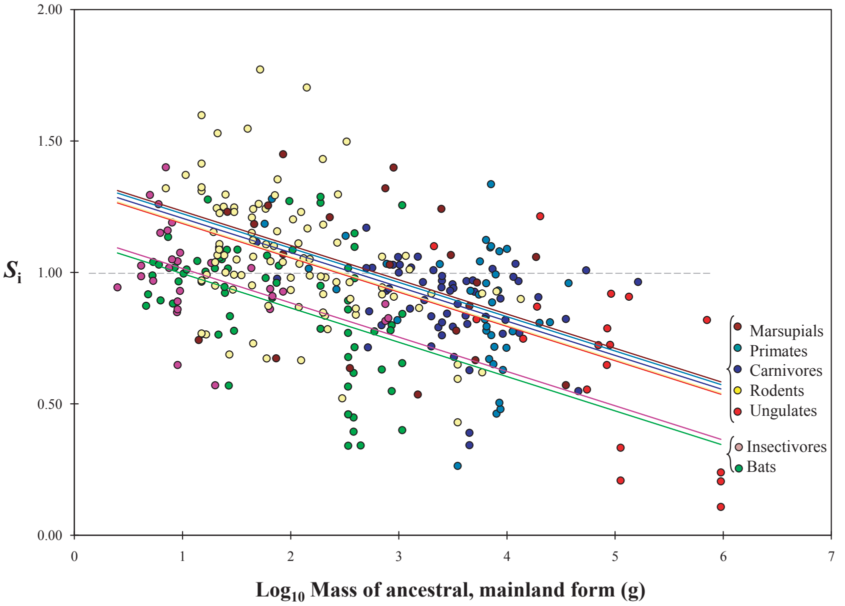

Figure 2 Differences in the island rule pattern among the seven orders of extant mammals with at least 19 species (each observation represents the average for populations of that species). The intercept of this relationship was significantly lower for bats and for insectivores than for the other orders considered here (based on ANCOVA; *n* = 327; see Table 3).

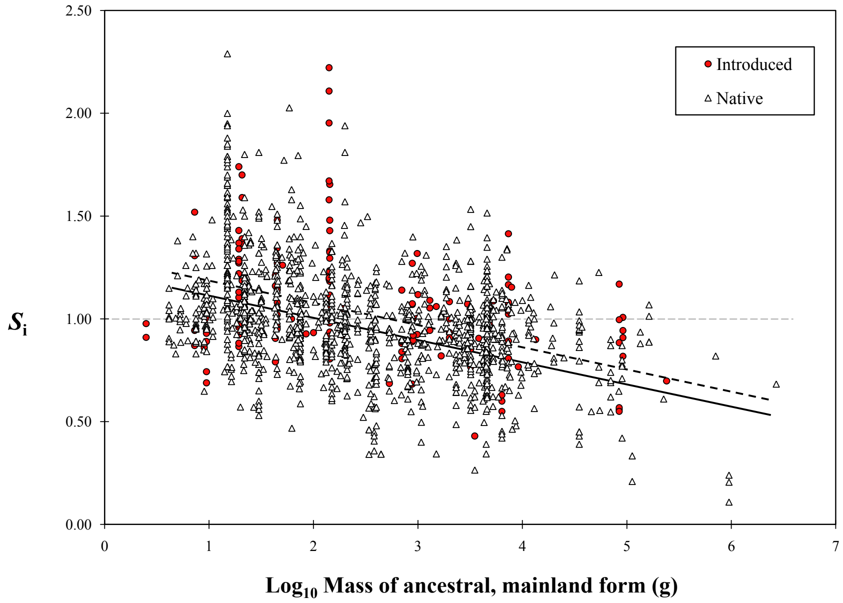

Figure 3 Trends in insular body size of native and introduced mammals. The intercept of the island rule pattern was slightly, albeit significantly, higher for introduced versus native populations of extant mammals (populations with terrestrial prey; based on ANCOVA; $n = 1425$; see Table 3).

namely the duck-billed platypus (*Ornithorhynchus anatinus*), which feeds on aquatic invertebrates, also exhibited an insular body size that exceeded the trend for mammals with terrestrial prey (observed $S_i = 1.27$ versus a predicted value of 0.89 for mammals of the same mass but restricted to terrestrial prey; see Fig. 4a; see also Price *et al.*, 2012).

Antiquity of the pattern

As predicted, palaeo-insular mammals exhibited a much broader range in insular body size than extant mammals (Table 1, Fig. 5). This includes the extreme cases of gigantism exhibited by two erinaceomorph insectivores (*Deinogalerix* spp., exceeding 100 times the mass of their mainland ancestors), two lagomorphs, namely *Nuralagus rex* and *Gymnesicolagus gelaberti*, and one rodent, *Leithia melitenis* (at least 10 times the mass of their ancestors). The degree of dwarfism exhibited by palaeo-insular mammals was just as extreme, with two proboscideans, *Mammuthus creticus* and *Palaeoloxodon falconeri*, and a hippo, *Hippopotamus minor* (= *Phanourios minor*), dwarfing to less than 5% of the mass of their mainland ancestors (Fig. 6).

Body size variation among palaeo-insular mammals was consistent with the island rule, exhibiting a highly significant, negative relationship between S_i and M (see Tables 1 & 2, Fig. 5). There was also some indication, albeit limited, that the insular body size of fossil mammals is influenced by type of prey, with species that utilized aquatic prey exhibiting relatively high S_i values in comparison to those predicted for palaeo-insular mammals with terrestrial prey (solid, black line in Fig. 5). Also as predicted, the slope of the island rule relationship was significantly steeper (more negative) for palaeo-insular species than for species of extant mammals (Table 2, Fig. 5; t (difference between slopes) = 7.47, $P < 0.0001$, d.f. = 405).

DISCUSSION

This analysis of body size evolution in insular mammals (extant as well as fossil), the most comprehensive to date, reveals that the island rule is indeed a pervasive pattern, exhibited across all mammals and across each of the nine orders of extant mammals with sufficient sample sizes, as well as across the 63 species of palaeo-insular mammals studied here. As we anticipated, there remained much variation about island rule trends (r^2 values ranging from < 0.03 to 0.65), but this is to be expected given that the current study did not control for variation in characteristics of species and islands known to influence the evolution of body size of insular mammals. Our earlier paper (Lomolino *et al.*, 2012) on causal explanations for the body size evolution of insular mammals employed regression tree analyses (a recursive, binary machine-learning method), which not only provided an alternative means of confirming the island rule pattern, but also revealed the contextual nature of factors influencing body size evolution – indicating that while co-occurring competitors and predators influenced the body size variation of both small and large mammals, climatic conditions, latitude, and island area and isolation influenced evolution of small (those < 2692 g), but not large, mammals. While our primary focus here was on pattern and not process, our results did indicate that future studies of causality of body size evolution in insular mammals should include not only physiographic, climatic and ecological characteristics of the islands, but also the age (time in isolation) of the insular populations.

For extant mammals, the similarity in island rule patterns for native and non-native populations (Fig. 3) may, at least in part, derive from the inclusion of both recent and ancient introductions (some > 1000 BP) in our analysis, but this also suggests that body size divergence on islands may proceed

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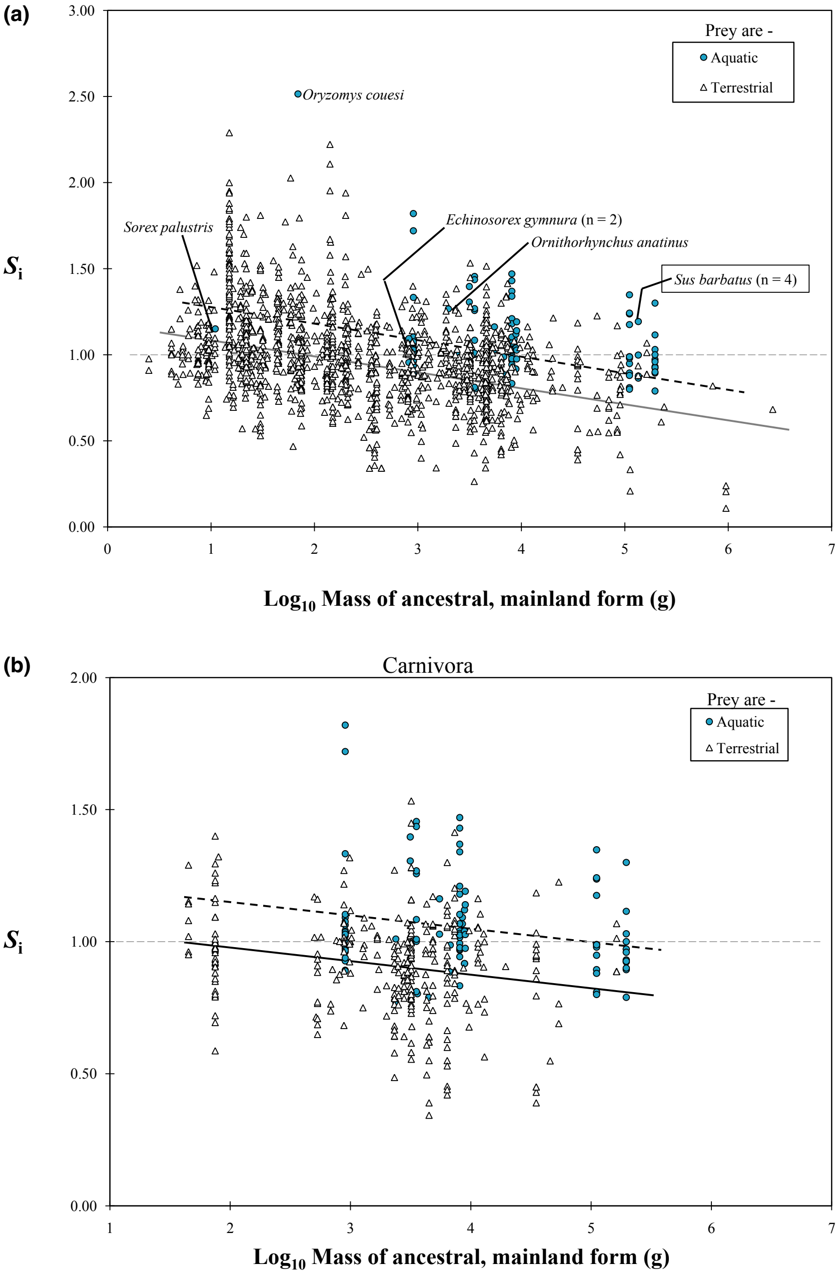

Figure 4 Differences in insular body size of mammals with aquatic prey in comparison to those with terrestrial prey. Populations of mammals utilizing aquatic prey tend to exhibit higher insular body sizes than those restricted to terrestrial prey, probably reflecting the high subsidy of marine productivity for insular populations. This difference in intercepts of the regression lines was consistent across all extant mammals (a, with labels for populations of selected species of mammals with aquatic prey, see main text) as well as for carnivores considered separately (b) (based on ANCOVA; n = 1530; see Table 3).

very rapidly following colonization (whether natural or human-assisted). Lister (1989, 1996) hypothesized that body size evolution in insular mammals may take place in two stages: an initial stage of very rapid change (that lasts for a few thousand years) followed by a second stage of slower, but ultimately much more pronounced, change (for reports on relatively rapid changes in body size in the initial stages of island evolution see Pergams & Ashley, 1999, 2001; Yom-Tov *et al.*, 1999; Schmidt & Jensen, 2003; Millien & Damuth, 2004; Millien, 2006). The great majority of the extant populations studied here are of mid- to late Holocene origin, derived from populations that established following the last glacial recession and subsequent dynamics in climate, sea level, habitats and faunal assemblages (the latter often including the arrival of human populations and associated disturbances). Thus, we infer that the patterns we observe for extant populations are characteristic of those for the initial stages of body size change, while the substantially more pronounced changes in body size of palaeo-insular mammals may correspond to Lister's hypothesized second stage of insular divergence in body size. We acknowledge that this inference requires more rigorous analyses, and more information on ages of insular populations than is currently available, at least for the majority of populations studied here.

Recent analyses by Evans *et al.* (2012), however, do provide a means of calibrating the rates of mammal evolution, with body size increases of threefold requiring some

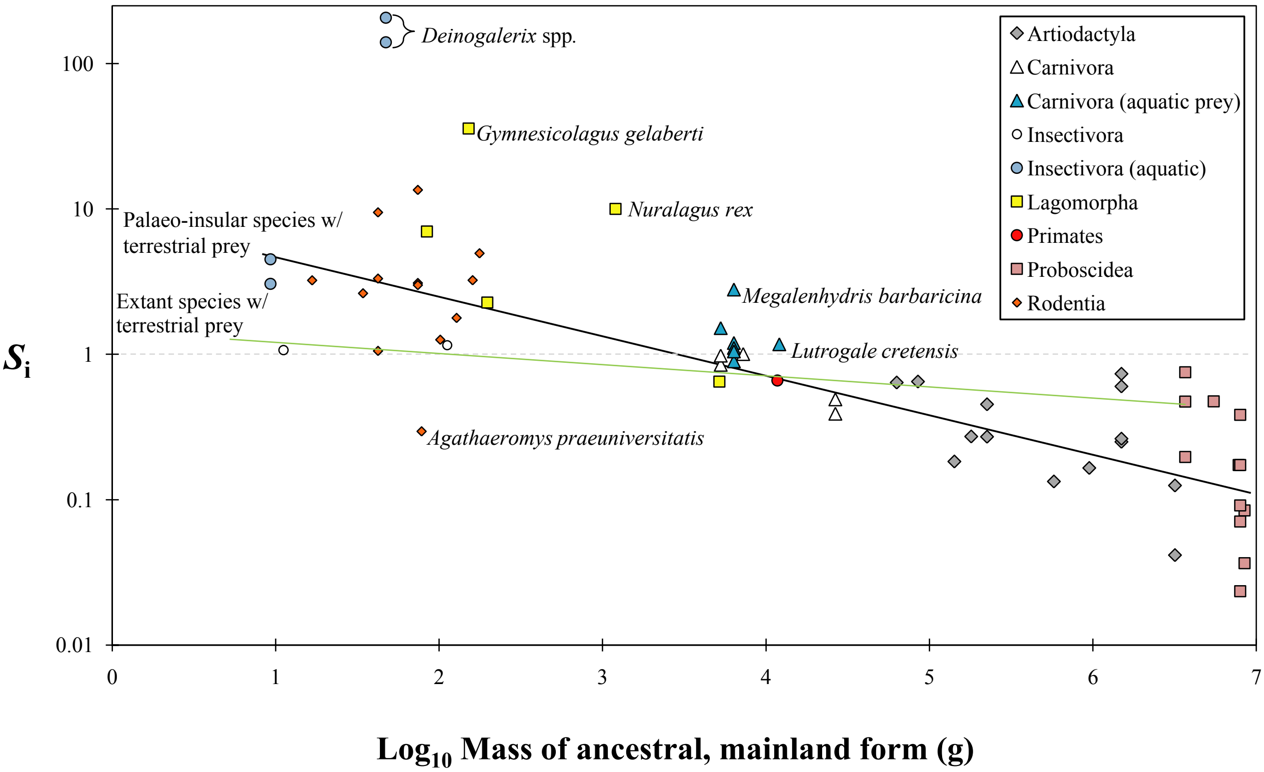

Figure 5 Differences in insular body size trends of palaeo-insular (black trend line, labelled symbols) and extant insular mammals (green trend line). The body size variation among species of palaeo-insular mammals (here in double-logarithmic scale) is consistent with the island rule, but the slope of the relationship between insular body size and mass of the ancestral, mainland species is significantly steeper (more negative) for palaeo-insular species (solid, black line; $n = 52$) than for extant species of mammals (solid, green line; $n = 357$) (see Fig. 1, Tables 1 & 2).

16,000 generations (as little as 4000 years for small mammals undergoing gigantism), whereas insular dwarfism of the same degree (a threefold decline) may require roughly 1000 generations (*c.* 25,000 years in elephants and other very large species, given their long generation times). On the other hand, the 10- to 100-fold changes in body size such as we observed for palaeo-insular mammals would require from 300,000 to 1.1×10^6 generations for extreme gigantism of small mammals, and 8000 to 0.12×10^6 generations for extreme dwarfism of very large mammals (Evans *et al.*, 2012). Our results accord well with these estimates, with S_i ranging from 0.11 to 2.52 for extant mammals (ages, i.e. time in isolation, < 0.01 Myr), while ranging from 0.02 to over 200 for palaeo-insular mammals (ages ranging from 0.1 to > 1.0 Myr). It is noteworthy that the estimated time in isolation for the most extreme cases of insular gigantism reported here for palaeo-insular mammals exceeded 1 Myr, while that for the most extreme cases of dwarfism (*Mammuthus creticus*, *M. lamarmorai*, *Palaeoloxodon falconeri* and *P. tiliensis*) ranged from 0.01 to 1 Myr (Table 1, Figs 5 & 6).

One alternative, but complementary, explanation for the more pronounced changes in body size of many palaeo-insular mammals is that they result not just from their long residence times on the islands, but also from the fact that their residence pre-dates the arrival of humans. This hypothesis, proposed by Sondaar (1987, 1991), assumes that such marvels of evolution in splendid isolation (i.e. the extreme giants and dwarfs) could not have evolved and coexisted with humans because they are particularly susceptible to the direct actions of humans on insular species, as well as to the indirect effects of habitat alteration and introduced species (commensals that become predators or competitors, or transmit disease).

This explanation for the more extreme body size evolution of palaeo-insular mammals is also consistent with an ecological hypothesis for the island rule (Lomolino *et al.*, 2012; see also Losos & Ricklefs, 2009), which predicts that it is not the age of insular populations per se, but their time in ecological isolation from mammalian predators and competitors (including humans and their commensals) that should most strongly influence body size evolution on islands. In short, ecological displacement on the mainland and in other large and ecologically diverse systems (e.g. Madagascar and the larger islands of the Philippines) drives diversification in body size, while release in ecologically simple, insular communities (in particular those lacking humans and other ecologically dominant mammals) results in convergence on the size of intermediate but absent species. The ultimate result is that,

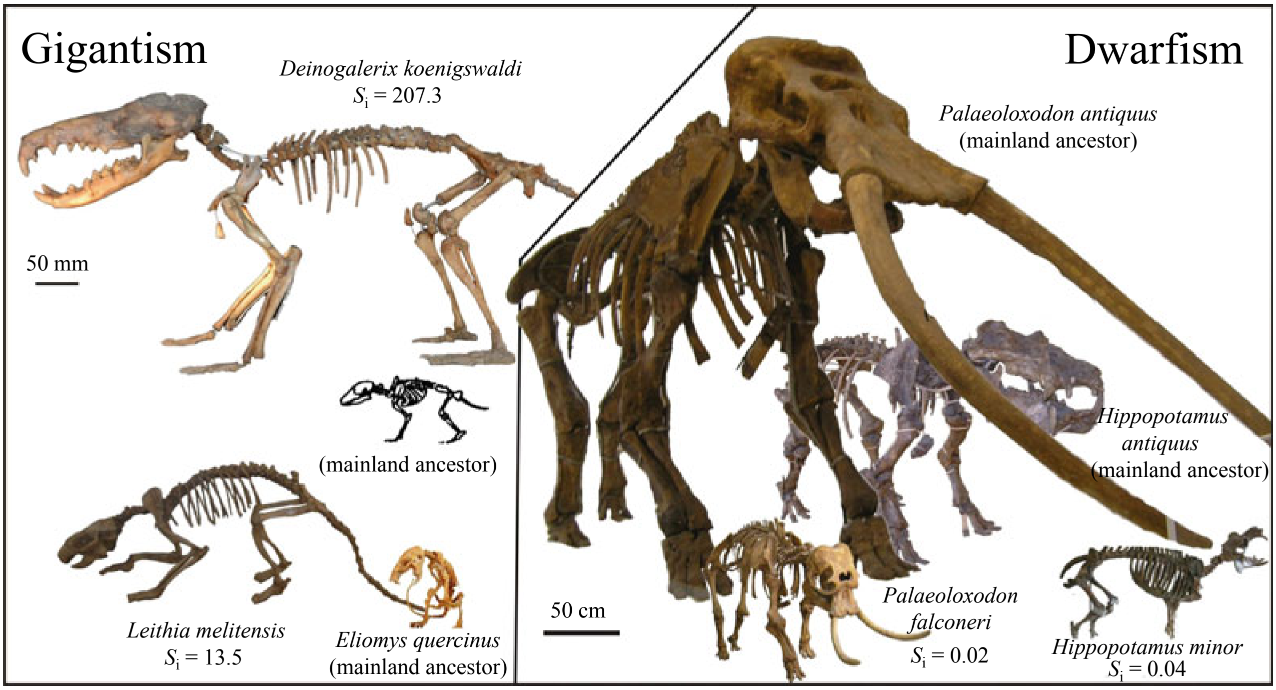

Figure 6 Some of the most remarkable cases of body size evolution in insular mammals. Of the 1593 insular populations studied here, by far the most remarkable cases of body size evolution were observed in palaeo-insular mammals, including the extreme gigantism of erinaceomorph insectivores (e.g. *Deinogalerix koenigswaldi*), rodents (e.g. *Leithia melitensis*) and lagomorphs, and the extreme dwarfism of ungulates (e.g. *Hippopotamus minor*) and proboscideans (e.g. *Palaeoloxodon falconeri*) (S_i = mass of insular form divided by that of its ancestral or mainland form; see Fig. 5, Table 1). Photos and drawings by G. Lyras, based on the following mounted skeletons: *Palaeoloxodon antiquus* (MPUR), *Hippopotamus antiquus* (IGF), *Deinogalerix koeningswaldi* (RGM Naturalis), *Eliomys quercinus* (MGG), *Leithia melitensis* (MGG), *Palaeoloxodon falconeri* (Senckenberg Naturmuseum, Frankfurt am Main), *Hippopotamus minor* (AMPG); see Appendix S1 for institutional abbreviations.

whether native or introduced, flying or non-volant, aquatic or terrestrial, recent or ancient, small species tend to increase and large species tend to decrease in size on ecologically simple (species-poor) islands.

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SUPPORTING INFORMATION

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

Appendix S1 Additional tables, references and related information describing the methods, sources and data used for analyses of body size variation among palaeo-insular mammals (Tables S1–S16) and extant mammals (Tables S17, Fig. S1).

Appendix S2 Database for mammal body size evolution in extant mammals and sources for the data).

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.

Author contributions: D.F.S., M.R.P. and M.V.L. developed the initial design for this research; M.V.L. developed the database for extant insular mammals, conducted the analyses and wrote this paper with the assistance of all authors; A.A.E.G, G.A.L, M.R.P. and R.R. developed the database for palaeo-insular mammals and the Supporting Information; and G.A.L. composed Fig. 6.

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